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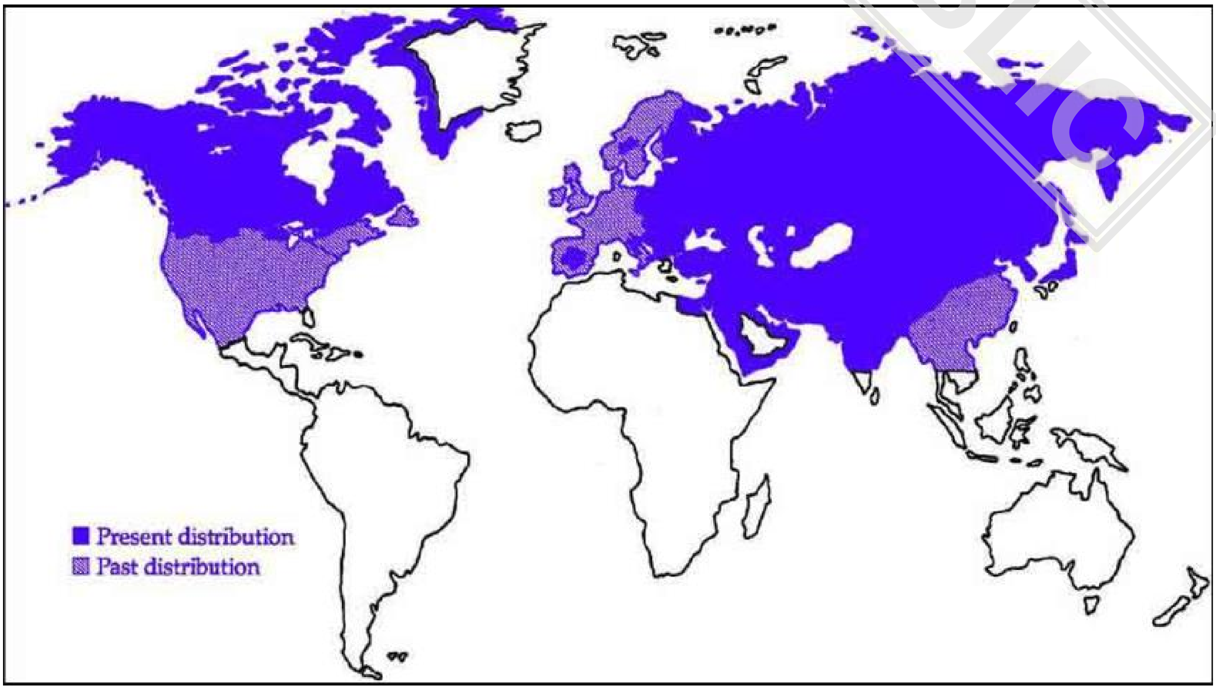
INFORMATION

From: To:	General Secretariat of the Council Working Party on the Environment
N° prev. doc.:	ST 15686/25
Subject:	Request submitted by Gesellschaft zur Schutz der Wölfe e.V for internal review under Article 10 of Regulation (EC) 1367/2006 on the Directive (EU) 2025/1237 of the European Parliament and of the Council, of 17 June 2025, amending Council Directive 92/43/EEC as regards the protection status of wolves – Annexes 11-19

Delegations will find attached Annexes 11-19 to the request on the above-mentioned subject, as received from Gesellschaft zur Schutz der Wölfe e.V [Society for the Protection of Wolves e.V.].

Anlage A.11

aus Caniglia 2008, Non-invasive genetics and wolf (Canis lupus) population size estimation in the Northern Italian Apennines



Do recolonising wolves trigger non-consumptive effects in European ecosystems? A review of evidence

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WILDLIFE BIOLOGY

Review

Do recolonising wolves trigger non-consumptive effects in European ecosystems? A review of evidence

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Predators can affect ecosystems through non-consumptive effects (NCE) on their prey, which can lead to cascading effects on the vegetation. In mammalian communities, such cascading effects on whole ecosystems have mainly been demonstrated in protected areas, but the extent to which such effects may occur in more human-dominated landscapes remains disputable. With the recolonisation of wolves *Canis lupus* in Europe, understanding the potential for such cascading processes becomes crucial for understanding the ecological consequences of wolf recovery and making appropriate management recommendations. Here, we investigate the evidence for non-consumptive effects of wolves on their wild ungulate prey and cascading effects on the vegetation in European landscapes. We reviewed empirical studies reporting wild ungulate responses to wolves involving spatio-temporal behaviour at large and fine spatial scales, activity patterns, vigilance, grouping, physiological effects, and effects on the vegetation. We reveal that non-consumptive effects of wolves in Europe have been studied in few regions and with focus on regions with low human impact, are highly context-dependent, and might often be overruled by human-related factors. Hence, we highlight the need for a description of human influence in NCE studies. We discuss challenges in NCE research and the potential for advances in future research on NCE of wolves in a human-dominated landscape. We emphasise the need for wildlife management to restore ecosystem complexity and processes, to allow non-consumptive predator effects to occur.

Keywords: behavioural responses (to predation), human-dominated landscape, non-consumptive effects, risk effects/predation risk, trophic cascades, ungulate prey, wolf *Canis lupus*

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Introduction

Large mammalian herbivores are crucial in structuring terrestrial ecosystems (Gordon et al. 2004, Schmitz 2008). They affect vegetation structure by foraging and trampling (Kuijper et al. 2010, Hempson et al. 2015, Churski et al. 2017), by influencing nutrient cycling (Murray et al. 2013), and seed dispersal (Iravani et al. 2011, Jaroszewicz et al. 2013). In this way, herbivores can influence vegetation across multiple spatial scales, from local to landscape levels (Woodward et al. 2004, Moncrieff et al. 2016), resulting in cascading impacts on numerous species and processes (Ripple et al. 2014).

Herbivore communities themselves are influenced by bottom–up effects (e.g. food availability) and top–down effects (i.e. predation). Thus, by affecting prey communities, predators can exert indirect effects on the vegetation. Different mechanisms can induce these ecological effects of large carnivores on their prey. Historically, studies on predator–prey interactions mainly focused on consumptive effects, where predators affect population densities by killing their prey (Messier 1991, Ripple and Beschta 2012). In addition to such 'lethal' or 'consumptive' effects on the population dynamics of prey, the presence of predators can also induce antipredator responses in behaviour or physiology (Lima and Dill 1990, Boonstra et al. 1998, Creel et al. 2005). Such behavioural or physiological changes in response to predator presence are referred to as 'non-consumptive effects' (hereafter NCE).The importance of NCE of predators has often been documented in invertebrates, especially in aquatic systems, where NCE can be much stronger than consumptive effects (Preisser et al. 2005). In terrestrial vertebrate communities the interest in NCE and potential trophic cascades has increased in the past decades (Say-Sallaz et al. 2019) with the recovery of large carnivores (Chapron et al. 2014, Ripple et al. 2014).

Large carnivores have the potential to create trophic cascades (Ripple et al. 2014). However, the extent and relative contribution of NCE compared to direct lethal effects is still debated (Creel and Christianson 2008, White et al. 2008, Kauffman et al. 2010, Marshall et al. 2013, Middleton et al. 2013, Peterson et al. 2014). The main body of literature on NCE in terrestrial vertebrates originates from large protected areas (Kuijper et al. 2016). Case studies from Yellowstone National Park (USA) showed how prey species changed their behaviour when predation risk was modified by the reintroduction of wolves *Canis lupus* (Fortin et al. 2005, Creel and Christianson 2008, Kauffman et al. 2010). In response to returning predators, prey animals have been shown to change vigilance, grouping behaviour, space use, or habitat selection (Fortin et al. 2005, Winnie and Creel 2007, Thaker et al. 2011, Clinchy et al. 2013). Such changes in prey behaviour were documented to affect the ecosystem through modified feeding pressure on certain plant communities (Fortin et al. 2005) or nutrient cycling (Roux et al. 2018). Similar effects caused by the return of an apex predator have been reported in the Serengeti National Park, where the lion *Panthera leo* was reintroduced (Skinner and Hunter 1998) or in the Yosemite National Park after the recolonisation of the cougar *Puma concolor* (Ripple and Beschta 2008). However, surprisingly little is known about NCE in human-dominated landscapes, which we here define as a landscape that is substantially shaped by humans and is extensively used for a variety of human activities, including hunting, agriculture, forestry, urbanization, and industrial purposes. Compared to national parks or wilderness areas, human-dominated landscapes are characterized by the presence of human-made structures resulting in high degrees of fragmentation. In such landscapes, human impact can still vary strongly with, for example, human population density, infrastructure, habitat modifications, and the level of human disturbance (recreational activity, hunting, or forestry). In Europe (especially central Europe), the landscape is mostly human-dominated and a low-conflict coexistence between large carnivores and humans can be challenging. Cascading effects through large carnivores are often reported as important ecosystem services provided by top predators. Most NCE, however, were reported in large national parks and we need to better understand how large carnivores can affect the ecosystem in such human-dominated landscapes.

One of the most conflict-prone large carnivore species is the Eurasian wolf. The Eurasian wolf *C. l. lupus* was extirpated in the early 1900s in most European countries, but has recently recolonized large parts of its original range (Chapron et al. 2014). In many parts of Europe, wolves are returning to landscapes that are densely populated by humans and where human impact influences animal populations, behaviour, and trophic interactions (Fig. 1, Chapron et al. 2014). These landscapes present a mosaic of various types of human land use and very dense linear infrastructures. Forests, an important habitat of wolves, have been strongly modified through a substantial network of forest roads (Bojarska et al. 2021), forestry activities, or are affected by hunting practices and recreational activities.

A key question is whether, under these conditions, wolves can still create ecological impacts as documented in large national parks. Kuijper et al. (2016) reviewed how anthropogenic effects on large carnivore density or behaviour can alter their ecological function, and how human-induced changes in prey species and the landscape limit the impact of large carnivores. They concluded that the potential for density-mediated trophic cascades (mainly caused by consumptive effects) is restricted to areas where carnivores reach ecologically functional densities or where even low carnivore densities can impact prey densities, i.e. in rather unproductive areas (Kuijper et al. 2016). NCE, however, might have a higher potential for cascading through trophic levels than direct effects, since predators have been documented to affect prey behaviour even at low densities (Laundré et al. 2001). Say-Sallaz (2019) reviewed the empirical literature on NCE from large carnivore–ungulate systems worldwide and revealed a bias of studies on NCE from protected areas and with a focus on anti-predator behavioural responses. Here, we specifically focus on the NCE of wolves in Europe, including their indirect effects on the vegetation. This allows us to investigate the wolf–prey–vegetation interactions more specifically and synthesise ecosystem effects of wolves documented in Europe.

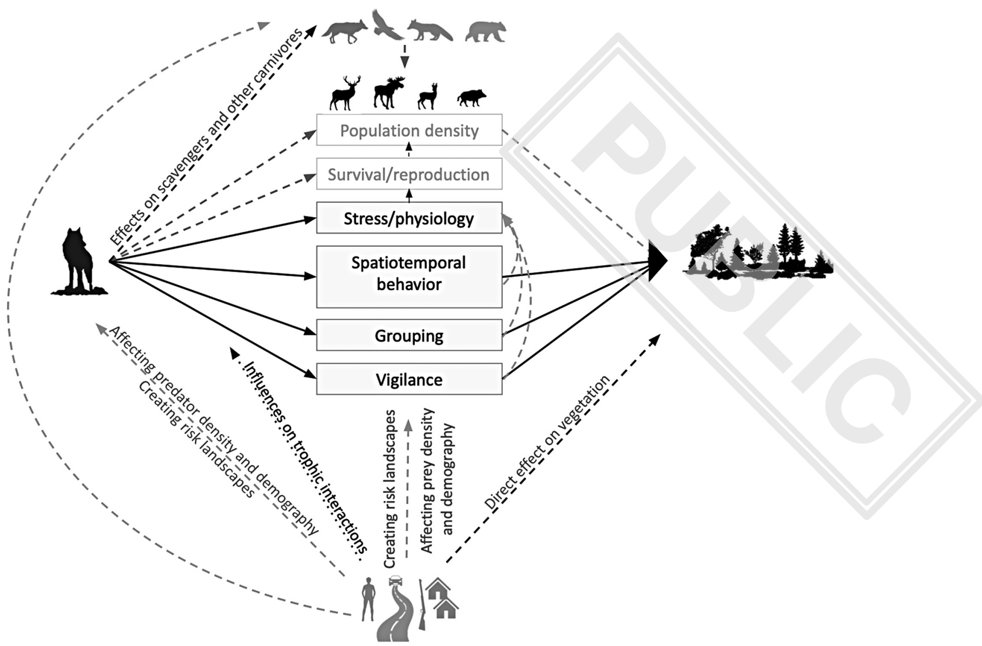

Figure 1. Simplified conceptual framework of predator effects on prey and on the vegetation. Solid lines indicate the non-consumptive effects (NCE) we considered in this study, whereas dashed lines indicate effects that were not considered in our review. Human effects on wolves or ungulate species were only considered if found as explaining variables in papers focusing on NCE of wolves on ungulate prey.

Literature search

We performed a systematic search in Web of Science that included keywords related to 'non-consumptive effects' (among others as e.g. 'risk effect*'), '*C. lupus*', 'ungulate prey', and 'Europe' (or any European country) connected with the Boolean connector AND (see Supporting information for a detailed list of searched keywords). We identified 234 studies (as of 26 September 2023). After an initial screening of title and abstracts, we selected 34 studies that were conducted at least partially in Europe and explicitly investigated NCE of wolf on large prey (> 15 kg, Ripple et al. 2014) and were published in peer reviewed journals in English. Thus, we excluded studies focusing on direct, consumptive impacts, as well as papers analysing theoretical or published data (Supporting information). To the 34 remaining studies, we added studies found in other literature databases (Google Scholar and BioOne, n = 4) and studies that were referred to in other studies (n = 3). Thus, we ended up with a total number of 41 relevant studies (Supporting information).

We classified NCE of wolves on their ungulate prey into the following categories (Table 1, Fig. 1): 1) landscape-scale spatial behaviour, 2) fine-scale spatial behaviour, 3) activity patterns, 4) vigilance behaviour, 5) grouping behaviour, 6) physiological effects, and 7) effects on the vegetation. We extracted the country where the study was performed, the prey species, and the method used to study prey behaviour. To describe the predation risk, we categorised the measure of wolf presence as follows (Moll et al. 2017 for more details): presence–absence, probabilistic occurrence, probabilistic kill occurrence, or experimental cues. We did not include direct human effects on prey species in the search terms, but assessed whether the studies on NCE included measures of anthropogenic effects (e.g. the distance to settlements, hunting, or general human activity). Given the small number of studies in each category and a diverse set of methods, a quantitative analysis was unfortunately not possible. Consequently, we summarize and discuss the findings of the studies investigating NCE of wolves in Europe qualitatively.

Where and how is our knowledge generated?

Spatial distribution and focal prey species of studies

A large number of the studies we found were performed in Białowieża Primaeval Forest in Poland (13/41, 31.7%) and Sweden (11/41, 26.8%) (Fig. 2). Thus, most of the studies were performed either in a relatively large, undisturbed system, where wolves were never completely extinct (Białowieża Primaeval Forest), or in managed forest systems with relatively low human densities (Sweden).

Since some studies looked at multiple categories of NCEs, multiple species or included different regions, we treated each investigated combination of effect, species, and region as a single observation in further analyses. If, for example, a study included data from temporal activity as well as vigilance behaviour of two different prey species, this study resulted in four observations. Thus, the 41 studies resulted in 89 observations. The most studied species was red deer *Cervus elaphus* with 23 observations in 14 studies, followed by roe deer *Capreolus capreolus* with 17 observations in 13 studies, moose *Alces alces* with 15 observations in 12 studies, and wild boar

Table 1. Overview of non-consumptive effects in Europe for each effect category. Note that one study can have multiple observations of different categories.

Category	n	Current knowledge in Europe	Current challenges	Suggestions for future studies
2.1.1 Large-scale	15 studies 25 observations	Factors related to human activity overrule predator effects. Effects at the large spatial scale have mainly been found in national parks where human impact is reduced	Studies often focus on spatial overlap of wolves and their prey. This does not allow any conclusions about causality	Exploit the potential of telemetry data for analysing prey species behaviour. Compare prey habitat preferences between areas with and without wolves. More consideration of temporal patterns
2.1.2 Fine-scale	7 studies 14 observations	Most studies report fine-scale effects of wolves on prey (decreased visitation rate or duration). One study found no effect on visitation rate/duration, but reported increased vigilance	All studies on fine-scale responses have been performed in national parks. Human effects or context-dependence thus have not been investigated	Study human-dominated landscapes outside national parks. Camera trap studies should report visitation rates/ duration and vigilance, as different strategies could be applied by prey animals
2.1.3 Temporal	6 studies 11 observations	Generally high temporal overlap between wolf and prey activity patterns (Rossa et al. 2021, Esttore et al. 2023)	Studies report temporal overlap but lack comparison with reference areas without predator presence (except Mori et al. 2020). No experimental studies	Combine studies using experimental predator cues with analyses of activity patterns. Find reference areas to study prey activity patterns when predators are absent
2.2.1 Vigilance	7 studies 9 observations	Large-scale together with small-scale risk factors can create fine-scale risk patches where vigilance is increased (and/or fine-scale spatial avoidance; section 2.1.2. above). Anthropogenic effects can overrule the effects of natural predators	Most studies have been performed in one region (Białowieża Forest) and in a protected environment (national parks)	Unveil the conditions under which NCE of wolves occur (i.e. small-scale risk factors). Different levels of human activity as well as temporal factors deserve further exploration
2.2.2 Grouping	4 studies 5 observations	Different species and sexes show different responses in grouping behaviour. Predator presence might be less important than e.g. other environmental or human-related factors	Few studies were found. Many potential alternative predictors can be responsible for effects (e.g. competition, food quality, habitat structure)	Investigate wolf effects on grouping behaviour in relation to the potential for cascading effects. Consider intraspecific differences in responses
2.3 Physiological effects	6 studies 9 observations	Wolves can affect stress levels or parasite prevalence in prey, but species differ in their responses and anthropogenic factors might be more important than wolf presence	Causality is not clear, e.g. reduced growth rates can be caused by stress but also by changes in habitat selection. Wolf presence and human presence are negatively correlated so both could be the cause of observed effects	Design experimental studies to disentangle human- and wolf-related effects
3.4 Cascading	12 studies 16 observations	Wolf presence and small-scale risk factors can result in patches with reduced browsing pressure and increased tree regeneration. These effects are most pronounced in undisturbed areas	Most research has been performed in national parks, mostly Białowieża Forest, or in Scandinavia. Hard to disentangle consumptive and non-consumptive effects	Explore interactions of wolf presence and anthropogenic factors. Evaluate the economic consequences of changes in browsing patterns. Study vegetation types other than forests. Sapling survival might be more ecologically relevant than browsing damage

Sus scrofa with 12 observations in nine studies. In Europe, the most widely distributed and most abundant prey species for wolves are red deer, roe deer, and wild boar (Okarma 1995, Zlatanova et al. 2014). Thus, most studies on NCE of wolves at the European level have been performed on the most abundant prey species, except for an overrepresentation of moose (at the European scale).

Methodologies and predation risk assessment

The reviewed studies include a variety of measurements for predation risk, such as presence–absence of wolves in space (Bonnot et al. 2018, van Ginkel et al. 2019a) or time (Grignolio et al. 2019), predicted occurrence (based on habitat use, Bubnicki et al. 2019) or gradients in intensity of use by

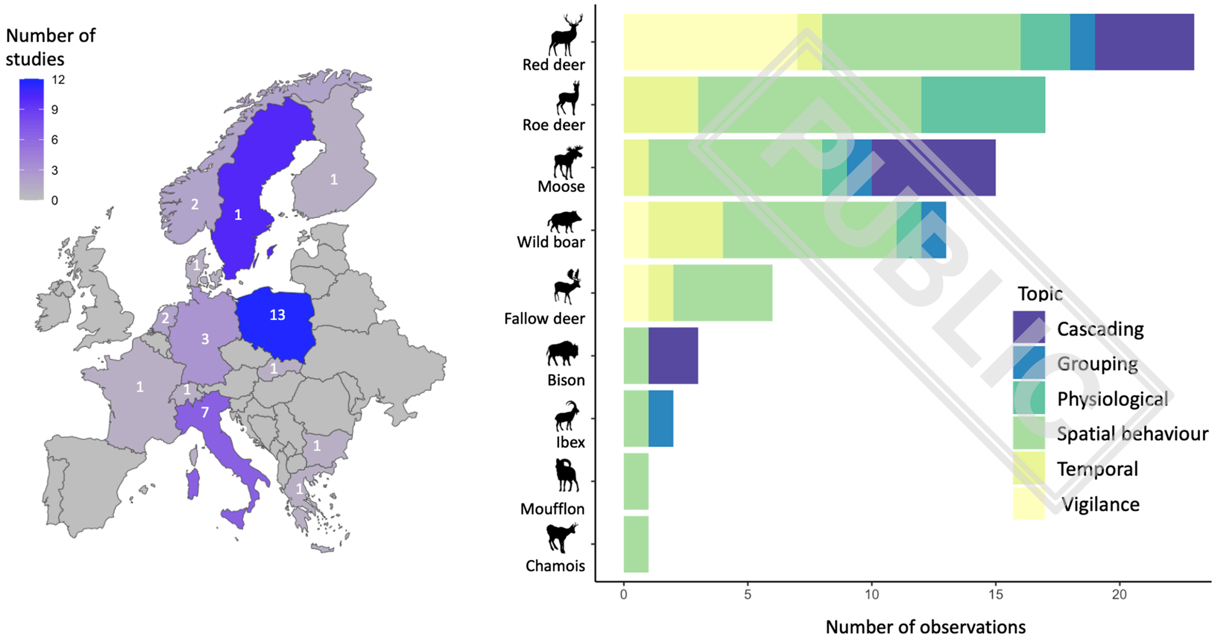

Figure 2. Number of studies on non-consumptive effects of wolves per country in Europe (left, n = 41) and number of observations (each investigated combination of effect, species and region in a study) per species and category (right, n = 89). The observations were classified according to the prey species in focus.

wolves, e.g. core areas of wolf territories versus peripheral areas (Kuijper et al. 2013). Other studies used experimental cues to simulate predation risk (Kuijper et al. 2014). Also, for prey responses, different measurements have been used. Especially for spatial behaviour, a variety of methods and different predictors have been employed, ranging from simply assessing spatial overlap of wolves and their prey based on indirect signs (Popova et al. 2018) to predicting spatial distributions based on modelled camera trap data (Bubnicki et al. 2019).

GPS information was only used in a few studies to investigate prey behaviour in response to predator presence (Eriksen et al. 2009, 2011, Nicholson et al. 2014), even though GPS tracking is probably the most common method for investigating wolf spatial behaviour. To study the fine-scale response of prey to wolf presence, camera traps and indirect signs of presence (mainly pellet counts) have been used more widely. Altogether, we document high methodological variation in the measurement of wolf predation risk as well as prey responses (Supporting information). This lack of standardisation hinders quantitative analyses and complicates drawing general conclusions from the studies (Moll et al. 2017, Prugh et al. 2019).

Assessment of human effects

Human activities might influence behaviourally mediated effects created by wolves (Kuijper et al. 2016) and, therefore, assessing the degree of human influence is important. However, studies included in this review often lack a thorough description of the type and strength of anthropogenic effects or human disturbance. Almost half of the studies (46.3%) and more than half of the observations (56.1%) were performed in protected areas where hunting, forestry, and agricultural land use were at least partially restricted. However, the degree of human activities varies strongly between national parks (van Beeck Calkoen et al. 2020). To what extent these activities are restricted is not reported in most of the studies.

Studies on habitat selection of prey species often include variables related to the intensity of human land use (e.g. forest exploitation, hunting Theuerkauf and Rouys 2008). These studies, however, mostly do not consider any interactions between anthropogenic effects and effects of wolf presence on prey behaviour. Thus, most studies do not consider whether wolf-prey interactions change in regions with high versus low human activity (Proudman et al. 2020).

Which non-consumptive effects by wolves are documented in Europe?

Spatio-temporal responses

Most studies reported only temporal or spatial results or reported them separately, which is also why we report the results in different sections, although temporal responses should not be considered isolated from spatial patterns (discussion, Kohl et al. 2018). Spatial responses to predation risk can occur at different spatial scales: at the large scale, prey might react to general presence of predators, while at a smaller scale they might avoid small-scale risk factors, such as escape impediments.

Large-scale spatial responses

Habitat selection based on wolf habitat use / suitability

At large spatial scales (large-scale habitat use and home range selection), studies generally found that human influence, vegetation structure, and prey-related variables, such as sex and reproductive status, are more important for explaining habitat selection by large ungulates than the presence of wolves (Theuerkauf and Rouys 2008, Nicholson et al. 2014). An exception is the study of Bubnicki et al. (2019), which showed that patterns of landscape use by red deer were predominantly determined by patterns in wolf space use in the Białowieża Forest. Which environmental variables are important varies between ungulate species (Theuerkauf and Rouys 2008, Bubnicki et al. 2019). Theuerkauf and Rouys (2008) did not find evidence for a general impact of wolf presence on large-scale ungulate distribution. They concluded that anthropogenic impacts affect local intensity of use by prey stronger than predation risk by wolves. Red deer seemed to prefer areas selected by wolves. It is, however, not clear whether this is due to a lack of avoidance by prey or by the attraction of wolves to areas with high prey densities (Roder et al. 2020). In the same area, Bubnicki et al. (2019), on the other hand, found lower red deer presence and relative densities in areas with high wolf use. The intensity of wolf use did not influence relative densities of other prey species (Bubnicki et al. 2019).

In the Italian Apennines, where wild boar is the main prey of wolves, crop damage was negatively correlated with wolf habitat suitability, suggesting that wild boars avoid the most suitable wolf habitat, leading to a redistribution of crop damage in the landscape (Davoli et al. 2022).

Spatial overlap

A study in the Ligurian Alps found high spatial overlap between the wolf and its main prey (roe deer and wild boar), indicating low spatial avoidance at a large landscape scale (Torretta et al. 2016). The authors document lower spatial overlap of wolves with fallow deer and chamois, which are less preyed upon by wolves, and deduce that wolves select areas of high use by their main prey. Also, no evidence for spatial avoidance of fallow deer and wolves was found in a study conducted in an Italian national park (Esattore et al. 2022). However, they found evidence for other NCE (sections below). The opposite results were found in a study conducted in a national park in southern Italy, which found low spatial overlap of wolves with their main wild prey (wild boar), which might indicate that prey avoids areas of high predation risk (Mori et al. 2020).

Popova et al. (2018) compared the selection of different habitat types between the wolf and its main prey (roe deer and wild boar). They found selection of different habitat types between wolf and roe deer and concluded that the prey avoids the predator (Popova et al. 2018). Such differences in habitat selection can, however, arise through different mechanisms including bottom-up effects, and therefore cannot be directly attributed to predation risk alone.

Habitat selection before and after wolf recolonization

Comparing habitat selection of moose before and after wolf establishment showed some effects of wolf presence: moose reduced their use of bogs after wolf recolonisation, but there was no change in the use of open or closed habitat in general (Sand et al. 2021). Thus, there are indications that the presence of wolves affects the space use of moose but, in general, studies report a lack of behavioural adjustments in response to predator presence in Scandinavia (Sand et al. 2006, Eriksen et al. 2009).

Mouflons *Ovis aries* reduced the distance to refuge areas and used patches with higher values in elevation, slope, and ruggedness since wolves recolonized the study area in the western Italian Alps (Tizzani et al. 2022). Similarly, after wolf recolonisation in Gran Paradiso National Park (Italy), male ibex started to spend less time in forage-rich, flat areas and selected more rocky slopes, which provided a refuge (Grignolio et al. 2019). However, they continued to use areas where wolves could move easily, while feeding in smaller groups. Hence, continuing to utilise higher-quality but riskier feeding sites despite the presence of predators might be compensated for by a reduction in group size (section 'Grouping behaviour').

The mixed evidence for effects of wolf presence on large-scale habitat selection by ungulates in Europe might be related to the fact that the daily home range of ungulates is much smaller than the daily home range of wolves. Thus, prey might avoid encounters with predators by high mobility within their home ranges, which might not be detected by purely spatial analyses of habitat selection. (Pusenius et al. 2020) found that moose in Finland increased their movement speed (distance between two consecutive GPS relocations/ time) when predation risk was higher, but no such effect was found in moose in Scandinavia (Wikenros et al. 2016). This indicates that higher mobility may be an anti-predator mechanism not yet developed by moose in Scandinavia, where compared to Finland wolves have returned only recently (Sand et al. 2006).

Migration

We have only found one study investigating migratory behaviour of deer in the Carpathians, which showed that avoiding high winter predation risk might be a driver of downhill migration in red deer (Smolko et al. 2018). However, this study did not demonstrate behavioural shifts in direct response to predator presence by comparing areas or time periods with and without wolves.

In general, we have found inconsistent evidence for effects of wolves on large-scale habitat selection of their prey in Europe. Reported effects were mainly found in protected areas. Thus, anthropogenic factors and bottom-up effects seem to influence habitat selection of large ungulates more strongly than wolf presence.

Fine-scale responses

In cultural landscapes, the home range and habitat selection of ungulates might be constrained by human influences, and spatial responses to predator presence might be more evident at fine spatial scales. When predators are present, ungulates may adjust their behaviour near landscape elements that increase perceived predation risk, such as escape impediments or dense vegetation that reduces visibility (Kuijper et al. 2013 2015, van Ginkel et al. 2019a).

Observational studies of responses to fine-scale landscape structures
Kuijper et al. (2015) studied the effect of large pieces of deadwood (hereafter, tree logs) on ungulate behaviour in Białowieża Forest (Poland) and found that red deer avoided such tree logs more inside than outside of wolf core areas (Kuijper et al. 2015). This avoidance led to reduced browsing pressure around the logs and increased chances for tree recruitment (Kuijper et al. 2013, van Ginkel et al. 2019a, Section 'Cascading effects on vegetation').

Responses to experimental cues
van Beek Calkoen et al. (2021) showed that at sites with predator cues (scat and urine), visitation duration (but not visitation rate) by red deer was reduced. This again indicates that deer might increase mobility to avoid predation risk (van Beeck Calkoen et al. 2021). Another study on free-ranging deer in Białowieża, however, found no evidence for decreased visitation rate or duration on sites with wolf scent (scat) but only observed higher vigilance (Kuijper et al. 2014). Accordingly, van Ginkel et al. (2019a) found no effect of the presence of wolf urine on the visitation rate/duration of red deer, both in areas with and without resident wolves (van Ginkel et al. 2019a). These studies, however, also studied other responses than visitation rate/duration, such as vigilance behaviour. Given that there are multiple strategies to avoid predation risk, the responses should not be analysed independently, as –depending on the context – different strategies might be applied (Kuijper et al. 2014).

Strong context-dependence became also evident in a study on prey responses to wolf sound playbacks. While cervids did not lower visitation rates, wild boar showed lower visitation rates with wolf sounds than with sheep sounds, but only in broadleaved forest and over a short time period (Weterings et al. 2022). Also, in Sweden the trapping rate of ungulates (roe deer and fallow deer) and the damage to crops was lower when playback sounds of dogs, wolves, and humans were played (Widén et al. 2022). However, there was no comparison with a control sound.

Temporal avoidance

We found eight studies considering temporal avoidance. In the Pollino National Park in southern Italy, the activity overlap of ungulates and wolves was generally high and, for the main prey, the wild boar, even higher in areas of high wolf occurrence (Mori et al. 2020). In the Maremma National Park in central Italy, however, fallow deer (the main prey of wolves in the region) had lower temporal overlap with wolves at sites where wolf activity was high (Rossa et al. 2021). This effect was, however, only visible in winter and not in summer (Rossa et al. 2021). Both studies were performed in protected areas but showed opposite results for different prey species. Mori et al. (2020) explain their results with wolves trying to maximise activity overlap with their prey, whereas Rossa et al. (2021) argued that fallow deer avoided time periods of high wolf activity. A factor that might affect different temporal overlap could be the different recolonisation history of wolves in both Italian national parks. While wolves have never been extinct in the Pollino National Park, the Maremma National Park was recently recolonised by wolves (Ferretti et al. 2019), which could present another factor affecting the potential for NCE.

In a study in the Italian western Alps, seasonal differences in temporal overlap between wolves and their main prey (roe deer and wild boar) were documented. The activity overlap increased during the non-denning season of wolves compared to the denning season. This increase was significant for roe deer, indicating that roe deer changed their activity patterns to avoid wolves during the wolf denning season (Torretta et al. 2016). However, shifts in the wolves' space use or other factors could have influenced this effect.

In Moldavia and Greece high temporal overlap of wolves and roe deer was found; however, roe deer activity peaked when wolf activity decreased (Popova et al. 2018, Petridou et al. 2023). In a study looking at activity synchronisation between wolves and moose in Norway, moose activity peaked at dusk, whereas the wolves' activity peaked at dawn (Eriksen et al. 2011). Also a study on fallow deer in an Italian national park found different activity patterns of wolves and fallow deer, with fallow deer being mainly active during daylight, whereas wolves were mainly nocturnal (Esattore et al. 2023). However, simply looking at activity overlap cannot inform about the underlying mechanisms and cannot be solely used to conclude about temporal avoidance or to assess the NCE of wolves on their prey.

Other behavioural adaptations

Vigilance

Vigilance behaviour presents a potential trade-off between foraging and risk avoidance. Especially when animals stop foraging to engage in vigilance (Blanchard and Fritz 2007), they spend less time with energy intake. This might affect individual survival and thus population dynamics, but also reduce biomass removal by herbivores and thus affect vegetation growth. Thus, increased vigilance of prey has the potential to induce trophic cascades.

We found seven studies investigating vigilance behaviour in response to wolf cues. Fallow deer in an Italian national park showed more often and longer vigilance behaviour at sites with higher wolf activity (Esattore et al. 2023). Also, red deer in the Polish Białowieża Forest increased their vigilance close to risky places (i.e. tree logs representing small-scale escape impediments). However, this effect was only visible in core areas of wolf territories (Kuijper et al. 2015).

Predator cues, such as the presence of wolf scats, also led to increased vigilance levels in red deer but not in wild boar in Białowieża (Kuijper et al. 2014). In contrast to these results, a study testing the vigilance behaviour in response to wolf urine in wolf-free areas in National Park Veluwezoom in the Netherlands, and in areas with wolf presence in the Białowieża National Park, did not find any effect of wolf urine on the vigilance behaviour of red deer (van Ginkel et al. 2019b). The authors argue that the lack of response might be a result of the quality of wolf urine. Also in other experimental studies, wolf scent had no effect on vigilance behaviour (van Beeck Calkoen et al. 2021, van Ginkel et al. 2021). However, the visitation duration and browsing intensity in plots with wolf scent was reduced, indicating that deer might increase mobility to avoid predation risk (section 'Spatiotemporal responses').

The above-mentioned studies documenting effects of wolf presence on deer vigilance were all performed in national parks or enclosures. When comparing protected and non-protected areas in Białowieża, deer showed higher levels of vigilance during the hunting season and at diurnal hours in non-protected areas (Proudman et al. 2020). In contrast, in protected areas, red deer were more vigilant at night, possibly related to higher wolf activity in areas where human disturbances are strongly restricted. These results indicate that wolves' impacts on red deer vigilance behaviour seem to be superimposed by anthropogenic effects in areas with high human disturbance and hunting.

Grouping behaviour

We found four studies investigating grouping behaviour of ungulates in response to wolf predation risk. Red deer and male moose tended to form larger groups in the presence of wolves (Jędrzejewski et al. 1992, Månsson et al. 2017), while group size of male ibex decreased (Grignolio et al. 2019). Moose grouping behaviour generally seemed to be little affected by predator presence, which aligns with results from other studies (Nicholson et al. 2014, Wikenros et al. 2016). Male ibex changed their behaviour in response to wolf recolonisation within a relatively short period of time. However, female ibex and moose with calves did not change their grouping behaviour in response to predation risk (Månsson et al. 2017, Grignolio et al. 2019). This leads to the assumption that their behaviour is either determined by other factors, such as forage quality, or – in the case of moose – that they have lost their antipredator behaviour in the absence of predators. Also, an experimental study in the Netherlands, where prey was naïve to wolves, found no effect of wolf acoustic playbacks on group sizes of wild boar or cervid species (Weterings et al. 2022).

Other factors such as population density, snow depth, and hunting were important predictors of grouping behaviour (Dzięciołowski 1979, Månsson et al. 2017, Grignolio et al. 2019), indicating that grouping in wild ungulates is influenced by a complex set of factors (Creel et al. 2014).

Physiological effects and parasite prevalence

We found six studies related to physiological effects and one study related to parasite prevalence in response to wolf presence. In the French Alps, roe deer fawn body mass was consistently lower in wolf core areas compared to peripheral areas (Randon et al. 2020). The mechanisms of such a difference in body mass in response to wolf presence are unclear. They could be related to increased stress, but also to changes in habitat selection or higher vigilance levels. However, the effect size was relatively small (~ 1 kg) compared to effects of, for example, population density (> 3 kg, Douhard et al. 2013), and the variation was correlated with variation in roe deer abundance in both areas. Thus, this effect had likely been caused by an unmeasured factor (Randon et al. 2020).

In roe deer populations in Poland, Zbyryt et al. (2017) found lower and less variable faecal glucocorticoid metabolite (FGM) concentration in areas with high predator presence (wolf and Eurasian lynx *Lynx lynx*) compared to areas with low predator presence. However, human-related factors had more substantial effects on the stress level of ungulates than effects of predators (Zbyryt et al. 2017). In eastern Poland, roe deer expressed elevated stress levels in areas with wolves present, but the effect of wind farms on stress levels seemed to be more important than the effect of predators (Klich et al. 2020). In contrast, moose in Sweden reacted more strongly to predator presence than to human-related factors: hair cortisol levels decreased with the distance to wolf territories, whereas anthropogenic effects did not affect hair cortisol levels (Spong et al. 2020). In contrast, the blood cortisol level of roe deer captured in wooden box traps was 30% higher in areas with wolves and lynx present compared to a predator-free and human-dominated landscape (Bonnot et al. 2018). These findings are based on blood cortisol, which reflects how roe deer reacted to acute stressors, indicating that differences are rather due to handling than to a general stress level.

Parasite prevalence

Predator presence might also influence parasite prevalence in ungulates. They can lead to healthier ungulate populations, as reduced population size might hinder parasite spread, and infected and old individuals might be removed from the population (Packer et al. 2003). In contrast, the life cycle of some parasites depends on two specific hosts, with ungulates as the intermediate host (e.g. *Sarcocystis* sp.). Infected ungulates might become more vulnerable prey for carnivores, which then serve as the definitive host. Thus, the presence of wolves might be linked to parasite infections in ungulates as they add to the guild of definite hosts. Higher probabilities of *Sarcocystis* sp. infection were found for red deer in areas with wolves present, but not for roe deer or wild boar (Lesniak et al. 2018). For other diseases, however, predation can reduce the prevalence of infection without leading to a reduction in prey population density, because disease-induced mortality can compensate for predation mortality (Tanner et al. 2019).

Cascading effects on vegetation

In central Europe, cascading effects of wolves on lower trophic levels have only been studied extensively in the Polish Białowieża Forest. Studies measuring indirect effects of wolves on the vegetation found that, inside wolf core areas, browsing intensity was reduced near structures that might impede escape or hinder visibility (i.e. coarse woody debris or fallen tree logs (Kuijper et al. 2013, van Ginkel et al. 2019a), resulting in a higher percentage of trees growing out of reach of browsing ungulates. The effect of fine-scale habitat structures was much more robust in high-risk areas for prey inside of wolf territories than in low-risk areas outside of wolf core areas (Kuijper et al. 2013, van Ginkel et al. 2019a). These studies were performed in the most undisturbed parts of the Białowieża Forest, i.e. in the national park that excludes hunting and forestry activities. A recent experimental study outside the Białowieża National Park, in an adjacent area where hunting and forestry occur, illustrated that visual obstructions (similar to tree logs) strongly reduced deer browsing pressure and led to increased tree growth (van Ginkel et al. 2021), indicating that similar risk effects can also occur in a more human-disturbed environment.

Also at the landscape scale, changes in patterns of space use by red deer caused by wolf presence led to a measurable reduction of browsing intensity and changes in the relative recruitment of different tree species inside and outside the Białowieża National Park (Bubnicki et al. 2019). Consequently, tree species that were most vulnerable to deer browsing had a higher chance of recruitment in places with frequent wolf presence (Bubnicki et al. 2019) or, at a smaller scale, in places hindering deer browsing due to (visual) impediments (van Ginkel et al. 2021).

Wolf presence can also affect forage selection, potentially leading to shifts in the plant community. Red deer foraged more on broadleaved tree species and less on forbs in high-risk than in low-risk areas (Churski et al. 2021). This effect, however, was only present in the national park and not in the managed forest.

In an area more recently recolonized by wolves in Switzerland, a pilot study on the local tree regeneration showed that ungulate densities, as indicated by local ungulate harvest, and the percentage of saplings with browsed leader shoot, decreased in the wolves' summer core zone (Kupferschmid 2017). Due to the pilot character of the study, data were lacking to evaluate if this might have been related to indirect effects of wolf presence, i.e. shifts in ungulates' spatio-temporal, social, or foraging behaviour, or other potential factors such as changes in hunting effort. An experimental study on captive red deer in the Bavarian Forest, Germany, did not document a shift in selectivity for certain tree species in proximity to simulated wolf cues. However, visitation duration and browsing intensity decreased in the presence of wolf scent, which might impact plant growth rates and thus affect forest ecosystems in the long term (van Beeck Calkoen et al. 2021).

Results from moose, the main prey of wolves in Sweden, show a different pattern than observed in red deer in other parts of Europe. The probability of moose browsing was higher inside wolf territories compared to outside of wolf territories (Gicquel et al. 2020, Ausilio et al. 2021), which seems related to higher moose abundance inside wolf territories (Ausilio et al. 2021). Also, van Beeck Calkoen et al. (2018) found higher browsing damage in high-wolf–utilisation areas. The authors related their findings to a confounding effect, as these areas were characterised by lower productivity (because of higher elevation) that led to reduced tree density and height, which are associated with an increase in moose browsing intensity (van Beeck Calkoen et al. 2018). They also related their finding to anthropogenic effects, as high-wolf–utilisation areas are characterised by a lower human influence index and situated at higher elevations than low-wolf–utilisation areas. Thus, human activities could push wolves into less productive parts of the landscape with lower overall tree densities and higher moose browsing levels (caused by bottom–up processes). These findings illustrate that simply comparing areas with and without wolves might lead to erroneous conclusions when no other (human-related) confounding factors are considered.

Not only human settlements, but also roads present key features of anthropogenic impacts. Inside wolf territories, however, browsing of rowan *Sorbus aucuparia*, the tree species most preferred by moose, decreased close to secondary roads, while increasing close to secondary roads outside wolf territories (Loosen et al. 2021). The roadsides thus appear to be perceived as riskier by moose in the presence of predators.

Discussion

Complexity and context-dependence of non-consumptive effects

We found inconsistent evidence for NCE of wolves on their large ungulate prey in Europe, highlighting the context-dependence of NCE. There is evidence that, under certain conditions, wolves can affect patterns of space use and behaviour of their prey, which in turn can affect the vegetation (Kuijper et al. 2013, 2015, Bubnicki et al. 2019, van Ginkel et al. 2019a). Less intense use of risky feeding areas has the potential to create a fine-scale mosaic of patches with lower grazing/browsing pressure and thus promote a more heterogeneous landscape (sections 'Fine-scale responses' and 'cascading effects'). These effects have been found mainly at a small spatial scale (landscape-scale patterns in Bubnicki et al. 2019) and in relatively undisturbed systems (i.e. no hunting/forestry), suggesting that NCE are easily overruled by human-related factors. Thus, humans can influence and alter predator–prey relationships, limiting the potential ecological role of predators (Ciucci et al. 2020). Most evidence for NCE in Europe comes from the Białowieża Forest, and there are indications that NCE can lead to measurable cascading effects. However, outside of non-disturbed areas, anthropogenic effects might quickly overrule these effects of natural predators.

In addition to anthropogenic impacts, further factors lead to context-dependence of NCE. Species – or even sexes, age classes, or individuals in different states – might vary in their sensitivity to risk effects from either human or non-human predators. While red deer, roe deer, and fallow deer showed changes in their behaviour in response to predator presence under certain conditions, other species such as wild boar or moose seemed less sensitive to predator presence (Fig. 3). Moose and wild boar might have higher changes of surviving an encounter with wolves, so there might be less selective pressure to avoid such encounters. For smaller prey, mortality after an encounter might be much higher and, thus, they might have been selected to have increased avoidance behaviour. Different species (or even individuals) might adopt different strategies, and some might specialise in avoidance of risky places while others specialise in early detection (e.g. through vigilance or grouping) or other defence mechanisms (Makin et al. 2017, Gaynor et al. 2019).

Quantifying the risk landscape and human influences

To document effects of predation risk on prey behaviour, we need to quantify the risk landscape. The presented studies used different methods to measure predation risk by wolves, but it is questionable if these measures are equivalent to the landscape of fear perceived by the prey (Moll et al. 2017, Prugh et al. 2019). For example, habitat suitability of predators is often used to predict predation risk, but might not be a good predictor for the landscape of fear. Thus, there might be a mismatch between what we measure and what is perceived by prey.

Not only quantifying the risk landscape, but also quantifying human impact is challenging. Human impact can vary with, for example, human density, infrastructure, the level of hunting, forestry, and recreational activity and each of those variants of human impact might affect wildlife differently. Many studies included here did not estimate human impact in the study region, thus making comparing different studies considerably challenging.

The majority of European studies investigating wolves' effects on herbivore behaviour were conducted in national parks, where human impact is assumed to be weaker than in non-protected areas. However, European national parks are subject to relatively high human impact (especially compared to the large national parks in North America), and truly undisturbed areas are rare (van Beeck Calkoen et al. 2020). In human-dominated landscapes, the effects of humans on wildlife behaviour can exceed those of natural predators (Theuerkauf and Rouys 2008, Ciuti et al. 2012) and human risk factors can interact with predator-induced risk factors (Proffitt et al. 2009, Rogala et al. 2011, Kuijper et al. 2015). Human activities can directly affect the behaviour and spatial distribution of ungulates (Benhaiem et al. 2008, Rogala et al. 2011) or indirectly by affecting predator distribution (Theuerkauf et al. 2003, Theuerkauf and Rouys 2008, Rogala et al. 2011). Thus, we must be very careful when interpreting study results on NCE of wolves in the presence of anthropogenic effects without the recognition of potential indirect effects of human–carnivore–prey interactions. It is challenging to interpret the effects of predators isolated from anthropogenic effects, since they generally coexist in Europe. Thus, there is a need for studies in more human-dominated landscapes, which allow us to study the interacting effects of humans and natural predators.

Additionally, the correlation of human activity with wolf presence makes it very difficult to disentangle wolf-induced effects and human-induced effects, emphasizing the need to consider indirect effects of humans on carnivore behaviour. While the presence of wolves may not have a significant impact on forest vegetation in human-dominated areas, it can have effects in undisturbed forest systems.

Spatial scales and constraints

Most studies we found here indicate that risk factors for ungulate prey act at different spatial scales – impediments acting as a risk factor at a fine scale and carnivore distribution

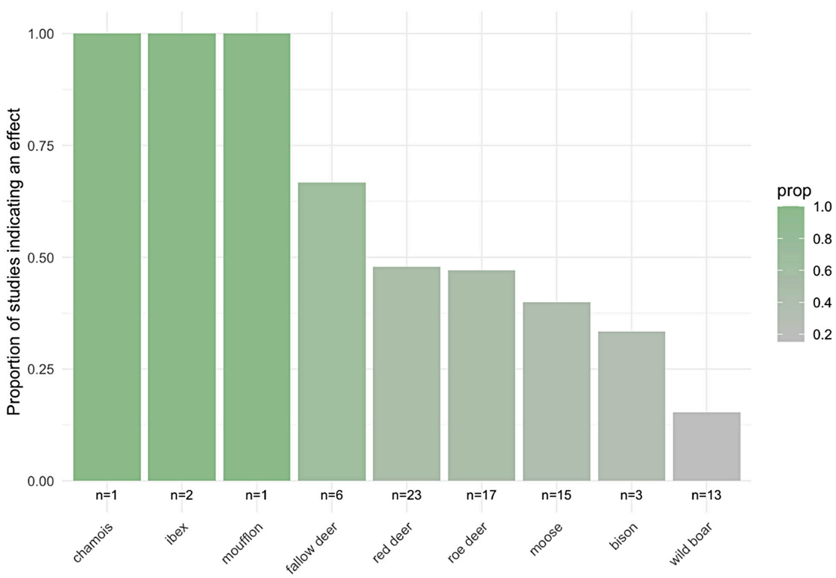

Figure 3. Proportion of observations indicating non-consumptive effects (NCE) and number of observations per prey species.

shaping the perceived risk at the landscape scale. Most importantly, these factors interact and shape the functional role of large carnivores in ecosystem processes. We thus would expect NCE to mainly appear in response to small-scale risk factors when combined with the presence of wolves at larger scales. In many cases, large-scale habitat selection of ungulates seems to be strongly affected by anthropogenic factors, such as hunting or forest exploitation, whereas predation risk by wolves seems to have relatively minor effects. To understand how large carnivores indirectly affect the vegetation in ecosystems, it is crucial to consider interactive effects between fine- and landscape-scale risk factors, as we might see effects only under certain conditions (Wirsing et al. 2021).

In addition, spatial constraints (e.g. through anthropogenic structures) might prevent the occurrence of large-scale changes, so that even though prey might perceive predation risk from returning predators, it may not be able to react to it (Gaynor et al. 2019). Prey species in the human-dominated landscape of Europe live in a complex environment with multiple (human and non-human) predators and competitors, and further anthropogenic stressors (Lone et al. 2014). Thus, an important question is how much potential the prey has left to adapt their habitat selection to a new risk factor such as the wolf. In Europe, for example, suitable wildlife habitat areas are often small and homogenised due to intense forestry. Large herbivores are mainly present in forest-dominated landscapes, while most of the open landscape is used for agricultural production. Anthropogenic factors thus limit the potential for large-scale behavioural changes, as a heterogeneous landscape of fear (i.e. including low-risk regions) is crucial for NCE to be detectable (Cromsigt et al. 2013). Within the constraints on large-scale space use, prey might avoid predation by high mobility or a more heterogeneous habitat use. Such subtle changes can be hard to detect with the methods used in most studies. But also increased mobility or more heterogeneous habitat use could have consequences for browsing and grazing pressure, seed dispersal, nutrient fluxes, and transmission of parasites or diseases (Winnie et al. 2006), and lead to cascading effects at the larger scale. This has, however, not been directly demonstrated in Europe yet, although there are hints towards higher prey mobility (Pusenius et al. 2020, van Beeck Calkoen et al. 2021) and large-scale effects on browsing patterns in the presence of wolves (Bubnicki et al. 2019). Generally, in human-dominated landscapes, prey species might prioritise adaptation to the risk landscape imposed by humans, which could weaken responses to other risk landscapes (e.g. from large carnivores).

Studies investigating temporal and spatial overlap generally found mixed results (Fig. 4, Popova et al. 2018, Mori et al. 2020; except for Esattore et al. 2023). In general, we need to be careful with the interpretation of causal relationships of spatial and temporal overlap, especially if there are no data from reference areas/time periods. Additionally, activity patterns of herbivores are already strongly adapted to the presence of humans, and there might be few opportunities left for avoiding the activity periods of carnivores. How complex and dynamic NCE can turn out to be is illustrated by the fact that herbivores might even increase their space use close to human settlements to reduce wolf predation risk (Kuijper et al. 2015, Proudman et al. 2020), while temporarily avoiding humans during the day.

Limitations and methodological challenges

Unfortunately, we were not able to quantitatively analyse factors leading to the documentation of NCE. We only found a limited number of studies per section/species. Even more challenging was that different studies within a section applied different methods, complicating a quantitative analysis. Ideally, we would have been able to test indications of human disturbance on the documentation of NCE. This was, however, not possible, as for most of the studies we were not able to extract information on human activities. Even a comparison of studies within national parks with studies outside of national parks is debatable, as human disturbance has multiple dimensions (hunting, forestry, recreational activities), which can strongly vary in national parks (van Beeck Calkoen et al. 2020).

Another factor hampering quantitative analysis is the multidimensionality of prey response. Prey can use different strategies for dealing with increased predation risk. In this review, we presented the results on different NCE in separate sections (similar to most of the papers reported). However, NCE in one section cannot be separated from effects in another section. For example, spatial and temporal avoidance cannot be isolated from each other or other behavioural adaptations (i.e. grouping or vigilance). All these effects can interact, and one mechanism can compensate for another (Torretta et al. 2016, Grignolio et al. 2019). For example, risky places can be used at safe times, indicating that the landscape of fear is dynamic over time (Kohl et al. 2018). Additionally, NCE might be dependent on the season. For example, in winter, prey might have to accept higher predation risk as they cannot afford to trade lower predation risk with lower energy intake. Furthermore, there are multiple strategies to solve the same dilemma. Some individuals/populations/species might apply alternative strategies and, while some prey might increase their vigilance while using risky places, others might rather avoid such places while keeping their vigilance behaviour constant. Given that there might be individual variation in these strategies, effects can stay undetected depending on the scale we are looking at.

Studies investigating temporal avoidance mostly measured temporal overlap. Even though there are indications for temporal avoidance of wolves by prey, it is challenging to show causal relationships from activity overlap data, and we advocate interpreting these results carefully when no reference area is available or when no comparative data exist from times when wolves were not present in the study area. Furthermore, it needs to be clarified whether prey are adapting their activity patterns to avoid predation, or wolves are adapting their activity to increase hunting success, or both. Additionally, the potential for adaptations in activity patterns might be overruled by human influence, which is known to

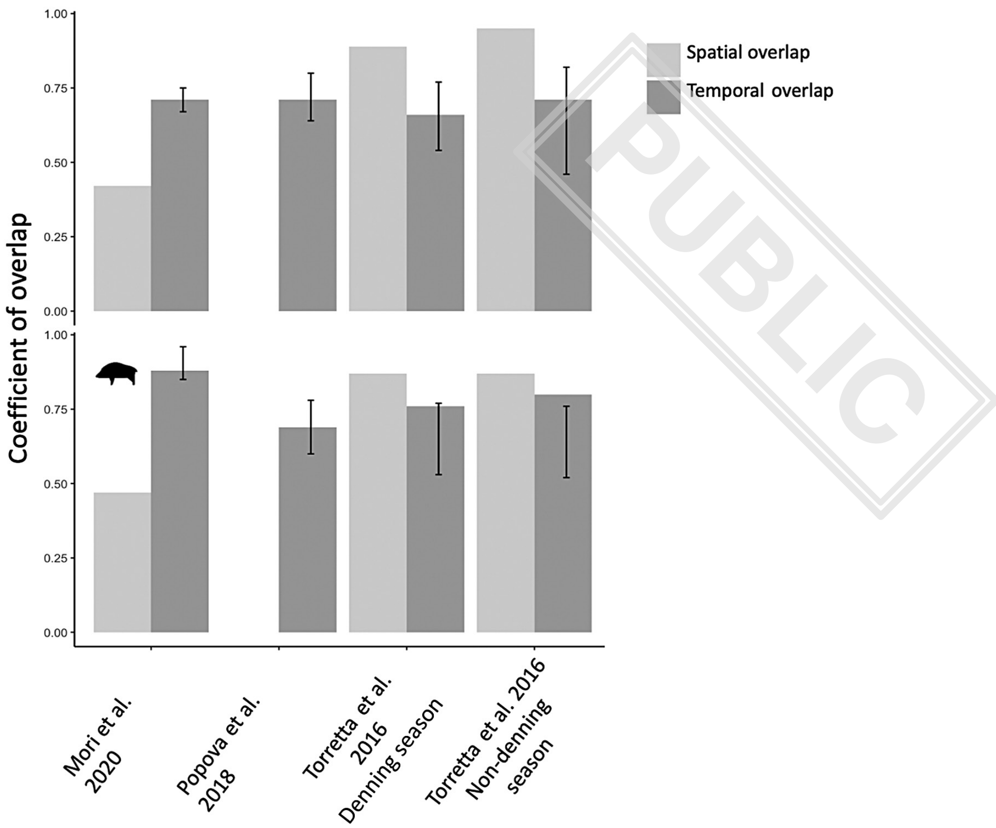

Figure 4. Spatial and temporal overlap coefficients with wolves provided by the respective studies for roe deer (upper panel) and wild boar (lower panel). Error bars show standard errors for temporal overlap (as reported in the studies), but no measure of uncertainty is provided for spatial overlap; in Torretta et al. 2016 the uncertainty measures were not clearly reported and are thus not provided here. The studies provided two different estimates for spatial overlap (UDOI in Torretta et al. 2016, Pika index in Mori et al. 2020), but both are bound between 0 and 1, with 1 indicating high overlap and 0 low spatial overlap. Popova et al. (2018) did not provide an estimate of spatial overlap.

be an important driver of temporal activity patterns in ungulates and carnivores (Stankowich 2008, van Doormaal et al. 2015). Moreover, temporal avoidance might reduce spatial effects, as prey might use risky places at safe times (Kohl et al. 2018). Thus, temporal responses should not be considered isolated from spatial patterns.

Effects of predators on the vegetation have so far only been studied in forest systems (except for Davoli et al. 2022) and the extent of cascading effects in vegetation types other than forests, such as shrub or open grassland, remains unclear. Such open areas in Europe are typically occupied by humans, and low-disturbance open areas are much rarer than undisturbed forested areas, so that the potential for observing cascading effects of wolves in vegetation types other than forest seems limited.

We are aware that there might be a publication bias and that more results that find NCE might be published compared to studies that found no effect. Further, we have missed grey literature and literature that was not published in English. We found some reports investigating NCE in Germany and Switzerland (Gärtner and Noack 2009, Nitze 2012, Kupferschmid et al. 2018a, b), but excluded them from the systematic review as they were not published in English, and we are not able to include grey literature in other languages.

Future research and methodological advancements

Future research on NCE in Europe should try to quantify human impact in the studies to allow for a synthesis from multiple regions with varying predator presence as well as varying human impact on different levels (tourism, forestry, hunting). Further, different strategies to lower predation risk should be considered in the same study, and factors should not be looked at in isolation. Considering vigilance and grouping behaviour, as well as spatial and temporal dynamics, together and not separately in future studies would allow a more integrated understanding of wolf NCE, in line with the landscape of fear as a dynamic concept (Palmer et al. 2022).

Not only large herbivores, but also other trophic levels such as scavengers, can be affected by apex predators through competition (Wikenros et al. 2010, 2017, Krofel et al. 2017), facilitation (Selva and Fortuna 2007, van Dijk et al. 2008, Wikenros et al. 2013, Focardi et al. 2017, Rossa et al. 2021), or hybridisation (Moura et al. 2014). Such effects in turn can have indirect effects on the herbivore community. In this review, however, we have not considered effects of wolves on scavengers, mesopredator, or other apex predators, or potential combined effects of several apex predators in more complex food webs, because the majority of studies only considered one predator species. In future studies, however, we need to account for multiple predators when investigating ungulate responses to predation risk (Moll et al. 2017). Moreover, we have not taken into account the complexity of the prey guild, which might influence the potential for behaviourally mediated effects since, in ecosystems with high complexity, redundancy effects might mask trophic cascades through compensation by other species (Fahimipour et al. 2017). In addition, cascading effects through non-ungulate prey should be explored. In particular, beavers are commonly preyed upon by wolves where the species overlap and can have strong effects on the ecosystem (Gable et al. 2018).

Advances in technology will allow for higher-resolution data collection. We have documented very few studies using GPS telemetry for the assessment of space use of wolves and their prey. This technology can provide essential insights by providing data for the whole home range of the collared individuals, but is limited to the collared individuals. Thus, combining multiple approaches, e.g. GPS-telemetry and camera traps, can be very powerful. However, with new possibilities for data collection and the combination of multiple approaches, it will become increasingly essential to have common standards that allow for comparing different studies and synthesising the knowledge generated in different regions and under different environmental conditions (Moll et al. 2017, Prugh et al. 2019).

Conclusions and implications

Our review shows that wolves recolonizing Europe rarely led to critical changes in the ecosystems (Table 1), so that exaggerating or romanticising their role in ecosystem functioning does not seem appropriate (Mech 2012). However, in addition to changing the population dynamics and/or the behaviour of prey, wolves might have other effects on the ecosystem, such as controlling the spread of infectious diseases in prey populations (Packer et al. 2003) or providing carcasses for the scavenger community (Wikenros et al. 2013). Here we documented a strong context-dependence of NCE on prey behaviour and stronger effects in areas with relatively low human impact. In Europe, such areas are extremely rare as, in more than two thirds of the national parks, wildlife is regulated and less than 30% of the national parks have a non-intervention zone of at least 75% of the area (van Beeck Calkoen et al. 2020).

If we aim to restore the complexity of ecosystems and ecosystem processes, we should think about creating more landscapes with a lower human impact and therefore a higher potential for these carnivore-induced impacts to occur. In the human-dominated landscape of Europe, this is, however, currently not the most realistic scenario. Regarding a land-sharing view, we need more knowledge on the effects of carnivores on the ecosystem with a focus on the influence of human activities on predator–prey relationships and resulting cascading effects.

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Author contributions

Nina Gerber: Conceptualization (lead); Writing – original draft (lead); Data collection (equal); Writing – review sections (lead); Writing – general sections (lead); Interpretation and structural editing (equal). **Friederike Riesch**: Conceptualization (equal); Writing – original draft (lead); Data collection (equal); Writing – review sections (lead); Writing – general sections (equal); Interpretation and structural editing (lead). **Katarzyna Bojarska**: Interpretation and structural editing (lead). **Maria Zetsche**: Conceptualization (supporting); Writing – original draft (supporting); Data collection (equal); Writing – review sections (equal). **Nina-K. Rohwer**: Writing – original draft (supporting); Data collection (equal); Writing – review sections (supporting). **Johannes Signer**: Conceptualization (supporting); Interpretation and structural editing (equal). **Johannes Isselstein**: Conceptualization (supporting); Interpretation and structural editing (equal). **Sven Herzog**: Conceptualization (supporting); Interpretation and structural editing (equal). **Henryk Okarma**: Conceptualization (supporting); Interpretation and structural editing (equal). **Dries P. J. Kuijper**: Conceptualization (supporting); Interpretation and structural editing (equal). **Niko Balkenhol**: Conceptualization (lead); Writing – original draft (supporting); Writing – general sections (supporting); Interpretation and structural editing (lead).

Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Ausilio, G., Sand, H., Månsson, J., Mathisen, K. M. and Wikenros, C. 2021. Ecological effects of wolves in anthropogenic landscapes: the potential for trophic cascades is context-dependent. – Front. Ecol. Evol. 8: 481.

van Beeck Calkoen, S. T. S., Kuijper, D. P. J., Sand, H., Singh, N. J., Wieren, S. E. van and Cromsigt, J. P. G. M. 2018. Does wolf presence reduce moose browsing intensity in young forest plantations? – Ecography 41: 1776–1787.

van Beeck Calkoen, S. T. S. et al. 2020. Ungulate management in European national parks: why a more integrated European policy is needed. – J. Environ. Manage. 260: 110068.
van Beeck Calkoen, S. T. S., Kreikenbohm, R., Kuijper, D. P. J. and Heurich, M. 2021. Olfactory cues of large carnivores modify red deer behavior and browsing intensity. – Behav. Ecol. 32: 982–992.
Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. J. M., Morellet, N. and Verheyden, H. 2008. Hunting increases vigilance levels in roe deer and modifies feeding site selection. – Anim. Behav. 76: 611–618.
Blanchard, P. and Fritz, H. 2007. Induced or routine vigilance while foraging. – Oikos 116: 1603–1608.
Bojarska, K., Maugeri, L., Kuehn, R., Król, W., Theuerkauf, J., Okarma, H. and Gula, R. 2021. Wolves under cover: the importance of human-related factors in resting site selection in a commercial forest. – For. Ecol. Manage. 497: 119511.
Bonnot, N. C., Bergvall, U. A., Jarnemo, A. and Kjellander, P. 2018. Who's afraid of the big bad wolf? Variation in the stress response among personalities and populations in a large wild herbivore. – Oecologia 188: 85–95.
Boonstra, R., Hik, D., Singleton, G. R. and Tinnikov, A. 1998. The impact of predator-induced stress on the snowshoe hare cycle. – Ecol. Monogr. 68: 371–394.
Bubnicki, J. W., Churski, M., Schmidt, K., Diserens, T. A. and Kuijper, D. P. J. 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. – eLife 8: e44937.
Chapron, G. et al. 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. – Science 346: 1517–1519.
Churski, M., Bubnicki, J. W., Jędrzejewska, B., Kuijper, D. P. J. and Cromsigt, J. P. G. M. 2017. Brown world forests: increased ungulate browsing keeps temperate trees in recruitment bottlenecks in resource hotspots. – New Phytol. 214: 158–168.
Churski, M., Spitzer, R., Coissac, E., Taberlet, P., Lescinskaite, J., van Ginkel, H. A. L., Kuijper, D. P. J. and Cromsigt, J. P. G. M. 2021. How do forest management and wolf space-use affect diet composition of the wolf's main prey, the red deer versus a non-prey species, the European bison? – For. Ecol. Manage. 479: 118620.
Ciucci, P., Mancinelli, S., Boitani, L., Gallo, O. and Grottoli, L. 2020. Anthropogenic food subsidies hinder the ecological role of wolves: insights for conservation of apex predators in human-modified landscapes. – Global Ecol. Conserv. 21: e00841.
Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A. and Boyce, M. S. 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. – PLoS One 7: e50611.
Clinchy, M., Sheriff, M. J. and Zanette, L. Y. 2013. Predator-induced stress and the ecology of fear. – Funct. Ecol. 27: 56–65.
Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. – Trends Ecol. Evol. 23: 194–201.
Creel, S., Winnie, J., Maxwell, B., Hamlin, K. and Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. – Ecology 86: 3387–3397.
Creel, S., Schuette, P. and Christianson, D. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. – Behav. Ecol. 25: 773–784.
Cromsigt, J. P. G. M., Kuijper, D. P. J., Adam, M., Beschta, R. L., Churski, M., Eycott, A., Kerley, G. I. H., Mysterud, A., Schmidt, K. and West, K. 2013. Hunting for fear: innovating management of human–wildlife conflicts. – J. Appl. Ecol. 50: 544–549.
Davoli, M., Ghoddousi, A., Sabatini, F. M., Fabbri, E., Caniglia, R. und Kuemmerle, T. 2022. Changing patterns of conflict between humans, carnivores and crop-raiding prey as large carnivores recolonize human-dominated landscapes. – Biol. Conserv. 269: 109553.
van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H. and Landa, A. 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. – J. Anim. Ecol. 77: 1183–1190.
van Doormaal, N., Ohashi, H., Koike, S. and Kaji, K. 2015. Influence of human activities on the activity patterns of Japanese sika deer (*Cervus nippon*) and wild boar (*Sus scrofa*) in central Japan. – Eur. J. Wildl. Res. 61: 517–527.
Douhard, M., Gaillard, J. M., Delorme, D., Capron, G., Duncan, P., Klein, F. and Bonenfant, C. 2013. Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. – Ecology 94: 1805–1814.
Dzięciołowski, R. 1979. Structure and spatial organization of deer populations. – Acta Theriol. 24: 3–21.
Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H. P., Arnemo, J. M., Gundersen, H., Milner, J. M., Liberg, O., Linnell, J., Pedersen, H. C., Sand, H., Solberg, E. J. and Storaas, T. 2009. Encounter frequencies between GPS-collared wolves (*Canis lupus*) and moose (*Alces alces*) in a Scandinavian wolf territory. – Ecol. Res. 24: 547.
Eriksen, A., Wabakken, P., Zimmermann, B., Andreassen, H. P., Arnemo, J. M., Gundersen, H., Liberg, O., Linnell, J., Milner, J. M., Pedersen, H. C., Sand, H., Solberg, E. J. and Storaas, T. 2011. Activity patterns of predator and prey: a simultaneous study of GPS-collared wolves and moose. – Anim. Behav. 81: 423–431.
Esattore, B., Rossi, A. C., Bazzoni, F., Riggio, C. and Oliveira, R. 2022. Same place, different time, head up: multiple antipredator responses to a recolonizing apex predator. – Curr. Zool. 26: zoac083.
Esattore, B., Rossi, A. C., Bazzoni, F., Riggio, C., Oliveira, R., Leggiero, I. and Ferretti, F. 2023. Same place, different time, head up: multiple antipredator responses to a recolonizing apex predator. – Curr. Zool. 69: 703–717.
Fahimipour, A. K., Anderson, K. E. and Williams, R. J. 2017. Compensation masks trophic cascades in complex food webs. – Theor. Ecol. 10: 245–253.
Ferretti, F., Lovari, S., Mancino, V., Burrini, L. and Rossa, M. 2019. Food habits of wolves and selection of wild ungulates in a prey-rich Mediterranean coastal area. – Mamm. Biol. 99: 119–127.
Focardi, S., Materassi, M., Innocenti, G. and Berzi, D. 2017. Kleptoparasitism and scavenging can stabilize ecosystem dynamics. – Am. Nat. 190: 398–409.
Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. and Mao, J. S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. – Ecology 86: 1320–1330.
Gable, T. D., Windels, S. K., Romanski, M. C. and Rosell, F. 2018. The forgotten prey of an iconic predator: a review of interactions between grey wolves *Canis lupus* and beavers *Castor* spp. – Mam. Rev. 48: 123–138.
Gärtner, S. and Noack, R. 2009. Populationsentwicklung und Schälschäden des Rothirsches in den nordostsächsischen Wolfsgebieten. – Artenschutzreport 23: 27–32.

Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. and Brashares, J. S. 2019. Landscapes of fear: spatial patterns of risk perception and response. – Trends Ecol. Evol. 34: 355–368.
Gicquel, M., Sand, H., Månsson, J., Wallgren, M. and Wikenros, C. 2020. Does recolonization of wolves affect moose browsing damage on young Scots pine? – For. Ecol. Manage. 473: 118298.
van Ginkel, H. A. L., Kuijper, D. P. J., Schotanus, J. and Smit, C. 2019a. Wolves and tree logs: landscape-scale and fine-scale risk factors interactively influence tree regeneration. – Ecosystems 22: 202–212.
van Ginkel, H. A. L., Smit, C. and Kuijper, D. P. J. 2019b. Behavioral response of naïve and non-naïve deer to wolf urine. – PLoS One 14: e0223248.
van Ginkel, H. A. L., Churski, M., Kuijper, D. P. J. and Smit, C. 2021. Impediments affect deer foraging decisions and sapling performance. – For. Ecol. Manage. 482: 118838.
Gordon, I. J., Hester, A. J. and Festa-Bianchet, M. 2004. Review: the management of wild large herbivores to meet economic, conservation and environmental objectives. – J. Appl. Ecol. 41: 1021–1031.
Grignolio, S., Brivio, F., Sica, N. and Apollonio, M. 2019. Sexual differences in the behavioural response to a variation in predation risk. – Ethology 125: 603–612.
Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smit, I. P. J. and Vickers, K. J. 2015. Ecology of grazing lawns in Africa. – Biol. Rev. 90: 979–994.
Iravani, M., Schütz, M., Edwards, P. J., Risch, A. C., Scheidegger, C. and Wagner, H. H. 2011. Seed dispersal in red deer (*Cervus elaphus* L.) dung and its potential importance for vegetation dynamics in subalpine grasslands. – Basic Appl. Ecol. 12: 505–515.
Jaroszewicz, B., Pirożnikow, E. and Sondej, I. 2013. Endozoochory by the guild of ungulates in Europe's primeval forest. – For. Ecol. Manage. 305: 21–28.
Jędrzejewski, W., Jędrzejewska, B., Okarma, H. and Ruprecht, A. L. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Bialowieża National Park, Poland. – Oecologia 90: 27–36.
Kauffman, M. J., Brodie, J. F. and Jules, E. S. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. – Ecology 91: 2742–2755.
Klich, D., Łopucki, R., Ścibior, A., Gołębiowska, D. and Wojciechowska, M. 2020. Roe deer stress response to a wind farms: methodological and practical implications. – Ecol. Indic. 117: 106658.
Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., White, P. J., Smith, D. W. and MacNulty, D. R. 2018. Diel predator activity drives a dynamic landscape of fear. – Ecol. Monogr. 88: 638–652.
Krofel, M., Giannatos, G., Ćirovič, D., Stoyanov, S. and Newsome, T. M. 2017. Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution? – Hystrix Ital. J. Mammal. 28: 9–15.
Kuijper, D. P. J., Cromsigt, J. P. G. M., Jędrzejewska, B., Miścicki, S., Churski, M., Jędrzejewski, W. and Kweczlich, I. 2010. Bottom-up versus top-down control of tree regeneration in the Białowieża Primeval Forest, Poland. – J. Ecol. 98: 888–899.
Kuijper, D. P. J., de Kleine, C., Churski, M., van Hooft, P., Bubnicki, J. and Jędrzejewska, B. 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. – Ecography 36: 1263–1275.
Kuijper, D. P. J., Verwijmeren, M., Churski, M., Zbyryt, A., Schmidt, K., Jędrzejewska, B. and Smit, C. 2014. What cues do ungulates use to assess predation risk in dense temperate forests? – PLoS One 9: e84607.
Kuijper, D. P. J., Bubnicki, J. W., Churski, M., Mols, B. and van Hooft, P. 2015. Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. – Behav. Ecol. 26: 1558–1568.
Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K. and Cromsigt, J. P. G. M. 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. – Proc. R. Soc. B 283: 20161625.
Kupferschmid, A. 2017. Local trophic cascading impact of wolves on tree regeneration in summer and winter areas of ungulates. – In: Bauch, K. (ed.), 6th symposium for research in protected areas. Salzburger Nationalparkfonds, pp. 353–356.
Kupferschmid, A., Beeli, F. and Thormann, J.-J. 2018a. Effekte des ersten Schweizerischen Wolfsrudels in der Neuzeit auf die lokale Baumverjüngung. – Ökojagd Mag. Ökologischen Jagdverbandes 22: 14–18.
Kupferschmid, A., Beeli, F. and Thormann, J.-J. 2018b. Effekte des Wolfrudels am Calanda auf die lokale Waldverjüngung. – Bünder Wald 71: 37–44.
Laundré, J. W., Hernández, L. and Altendorf, K. B. 2001. Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. – Can. J. Zool. 79: 1401–1409.
Lesniak, I., Heckmann, I., Franz, M., Greenwood, A. D., Heitlinger, E., Hofer, H. and Krone, O. 2018. Recolonizing gray wolves increase parasite infection risk in their prey. – Ecol. Evol. 8: 2160–2170.
Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.
Lone, K., Loe, L. E., Gobakken, T., Linnell, J. D. C., Odden, J., Remmen, J. and Mysterud, A. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. – Oikos 123: 641–651.
Loosen, A. E., Devineau, O., Zimmermann, B., Cromsigt, J. P. G. M., Pfeffer, S. E., Skarpe, C. and Mathisen, K. M. 2021. Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia. – Ecosphere 12: e03358.
Makin, D. F., Chamaillé-Jammes, S. and Shrader, A. M. 2017. Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. – Anim. Behav. 127: 225–231.
Månsson, J., Prima, M. C., Nicholson, K. L., Wikenros, C. and Sand, H. 2017. Group or ungroup – moose behavioural response to recolonization of wolves. – Front. Zool. 14: 10.
Marshall, K. N., Hobbs, N. T. and Cooper, D. J. 2013. Stream hydrology limits recovery of riparian ecosystems after wolf reintroduction. – Proc. R. Soc. B 280: 20122977.
Mech, L. D. 2012. Is science in danger of sanctifying the wolf? – Biol. Conserv. 150: 143–149.
Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. – J. Anim. Ecol. 60: 377–393.
Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Jimenez, M. D., Cook, R. C., Cook, J. G., Albeke, S. E., Sawyer, H. and White, P. J. 2013. Linking anti-predator behaviour to prey

demography reveals limited risk effects of an actively hunting large carnivore. – Ecol. Lett. 16: 1023–1030.
Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., Hayward, M. W., Millspaugh, J. J. and Montgomery, R. A. 2017. The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. – J. Anim. Ecol. 86: 749–765.
Moncrieff, G. R., Bond, W. J. and Higgins, S. I. 2016. Revising the biome concept for understanding and predicting global change impacts. – J. Biogeogr. 43: 863–873.
Mori, E., Bagnato, S., Serroni, P., Sangiuliano, A., Rotondaro, F., Marchianò, V., Cascini, V., Poerio, L. and Ferretti, F. 2020. Spatiotemporal mechanisms of coexistence in an European mammal community in a protected area of southern Italy. – J. Zool. 310: 232–245.
Moura, A. E., Tsingarska, E., Dąbrowski, M. J., Czarnomska, S. D., Jędrzejewska, B. and Pilot, M. 2014. Unregulated hunting and genetic recovery from a severe population decline: the cautionary case of Bulgarian wolves. – Conserv. Genet. 15: 405–417.
Murray, B. D., Webster, C. R. and Bump, J.K. 2013. Broadening the ecological context of ungulate–ecosystem interactions: the importance of space, seasonality, and nitrogen. Ecology 94: 1317–1326.
Nicholson, K. L., Milleret, C., Månsson, J. and Sand, H. 2014. Testing the risk of predation hypothesis: the influence of recolonizing wolves on habitat use by moose. – Oecologia 176: 69–80.
Nitze, M. 2012. Schalenwildforschung im Wolfsgebiet der Oberlausitz-Projektzeitraum 2007–2010. – Forschungsbericht der Forstzoologie/AG Wildforschung, TU Dresden.
Okarma, H. 1995. The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. – Acta Theriol. 40: 335–386.
Packer, C., Holt, R. D., Hudson, P. J., Lafferty, K. D. and Dobson, A. P. 2003. Keeping the herds healthy and alert: implications of predator control for infectious disease. – Ecol. Lett. 6: 797–802.
Palmer, M. S., Gaynor, K. M., Becker, J. A., Abraham, J. O., Mumma, M. A. and Pringle, R. M. 2022. Dynamic landscapes of fear: understanding spatiotemporal risk. – Trends Ecol. Evol. 37: 911–925.
Peterson, R. O., Vucetich, J. A., Bump, J. M. and Smith, D. W. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. – Annu. Rev. Ecol. Evol. Syst. 45: 1–22.
Petridou, M., Benson, J. F., Gimenez, O. and Kati, V. 2023. Spatiotemporal patterns of wolves, and sympatric predators and prey relative to human disturbance in northwestern Greece. – Diversity 15: 184.
Popova, E., Zlatanova, D., Dolapchiev, N., Stojanov, A., Doykin, N. and Peteov, P. 2018. In: Zagorchev, L. (ed.) The grey wolf and its prey – insights from camera trapping in Osogovo Mtn in Bulgaria and Macedonia. – Ann.Sofia Univ. 'St. Kliment Ohridski', pp. 266–277.
Preisser, E. L., Bolnick, D. I. and Benard, M. F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. – Ecology 86: 501–509.
Proffitt, K. M., Grigg, J. L., Hamlin, K. L. and Garrott, R. A. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. – J. Wildl. Manage. 73: 345–356.
Proudman, N. J., Churski, M., Bubnicki, J. W., Nilsson, J.-Å., Kuijper, D. P. J., Proudman, N. J., Churski, M., Bubnicki, J. W., Nilsson, J.-Å. and Kuijper, D. P. J. 2020. Red deer allocate vigilance differently in response to spatio-temporal patterns of risk from human hunters and wolves. – Wildl. Res. 48: 163–174.
Prugh, L. R., Sivy, K. J., Mahoney, P. J., Ganz, T. R., Ditmer, M. A., van de Kerk, M., Gilbert, S. L. and Montgomery, R. A. 2019. Designing studies of predation risk for improved inference in carnivore–ungulate systems. – Biol. Conserv. 232: 194–207.
Pusenius, J., Kukko, T., Melin, M., Laaksonen, S. and Kojola, I. 2020. Wolf predation risk and moose movement in eastern Finland. – Wildl. Biol. 2020: 1–9.
Randon, M., Bonenfant, C., Michallet, J., Chevrier, T., Toïgo, C., Gaillard, J.-M. and Valeix, M. 2020. Population responses of roe deer to the recolonization of the French Vercors by wolves. – Popul. Ecol. 62: 244–257.
Ripple, W. J. and Beschta, R. L. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. – Biol. Conserv. 141: 1249–1256.
Ripple, W. J. and Beschta, R. L. 2012. Large predators limit herbivore densities in northern forest ecosystems. – Eur. J. Wildl. Res. 58: 733–742.
Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D. and Wirsing, A. J. 2014. Status and ecological effects of the world's largest carnivores. – Science 343: 1241484.
Roder, S., Biollaz, F., Mettaz, S., Zimmermann, F., Manz, R., Kéry, M., Vignali, S., Fumagalli, L., Arlettaz, R. and Braunisch, V. 2020. Deer density drives habitat use of establishing wolves in the western European Alps. – J. Appl. Ecol. 57: 995–1008.
Rogala, J. K., Hebblewhite, M., Whittington, J., White, C. A., Coleshill, J. and Musiani, M. 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. – Ecol. Soc. 16: 16.
Rossa, M., Lovari, S. and Ferretti, F. 2021. Spatiotemporal patterns of wolf, mesocarnivores and prey in a Mediterranean area. – Behav. Ecol. Sociobiol. 75: 32.
Roux, E. le, Kerley, G. I. H. and Cromsigt, J. P. G. M. 2018. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. – Curr. Biol. 28: 2493–2499.e3.
Sand, H., Wikenros, C., Wabakken, P. and Liberg, O. 2006. Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? – Proc. R. Soc. B 273: 1421–1427.
Sand, H., Jamieson, M., Andrén, H., Wikenros, C., Cromsigt, J. and Månsson, J. 2021. Behavioral effects of wolf presence on moose habitat selection: testing the landscape of fear hypothesis in an anthropogenic landscape. – Oecologia 197: 101–116.
Say-Sallaz, E., Chamaillé-Jammes, S., Fritz, H. and Valeix, M. 2019. Non-consumptive effects of predation in large terrestrial mammals: mapping our knowledge and revealing the tip of the iceberg. – Biol. Conserv. 235: 36–52.
Schmitz, O. J. 2008. Herbivory from individuals to ecosystems. – Annu. Rev. Ecol. Evol. Syst. 39: 133–152.
Selva, N. and Fortuna, M. A. 2007. The nested structure of a scavenger community. – Proc. R. Soc. B 1613: 1101–1108.
Skinner, J. D. and Hunter, L. T. B. 1998. Vigilance behaviour in African ungulates: the role of predation pressure. – Behaviour 135: 195–211.
Smolko, P., Veselovská, A. and Kropil, R. 2018. Seasonal dynamics of forage for red deer in temperate forests: importance of the

habitat properties, stand development stage and overstorey dynamics. – Wildl. Biol. 2018: 1–10.
Spong, G., Gould, N. P., Sahlén, E., Cromsigt, J. P. G. M., Kindberg, J. and DePerno, C. S. 2020. Large-scale spatial variation of chronic stress signals in moose. – PLoS One 15: e0225990.
Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. – Biol. Conserv. 141: 2159–2173.
Tanner, E., White, A., Acevedo, P., Balseiro, A., Marcos, J. and Gortázar, C. 2019. Wolves contribute to disease control in a multi-host system. – Sci. Rep. 9: 7940.
Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M. and Slotow, R. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. – Ecology 92: 398–407.
Theuerkauf, J. and Rouys, S. 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża forest, Poland. – For. Ecol. Manage. 256: 1325–1332.
Theuerkauf, J., Jędrzejewski, W., Schmidt, K. and Gula, R. 2003. Spatiotemporal segregation of wolves from humans in the Bialowieza forest (Poland). – J. Wildl. Manage. 67: 706–716.
Tizzani, P., Bessone, M., Rossi, L. and Meneguz, P. G. 2022. Does predation risk affect spatial use in an introduced ungulate species? The case of a Mediterranean mouflon alpine colony. – Eur. J. Wildl. Res. 68: 66.
Torretta, E., Serafini, M., Imbert, C., Milanesi, P. and Meriggi, A. 2016. Wolves and wild ungulates in the Ligurian Alps (western Italy): prey selection and spatial-temporal interactions. – Mammalia 81: 537–551.
Weterings, M. J. A., Meister, N., Fey, K., Jansen, P. A., van Langevelde, F. and Kuipers, H. J. 2022. Context-dependent responses of naïve ungulates to wolf-sound playback in a human-dominated landscape. – Anim. Behav. 185: 9–20.
White, P. J., Garrott, R. A., Cherry, S., Watson, F. G. R., Gower, C. N., Becker, M. S. and Meredith, E. 2008. Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. Chapter 21. – In: Garrott, R. A., White, P. J. and Watson, F. G. R. (eds), Terrestrial ecology. Elsevier, pp. 451–476.
Widén, A., Clinchy, M., Felton, A. M., Hofmeester, T. R., Kuijper, D. P. J., Singh, N. J., Widemo, F., Zanette, L. Y. und Cromsigt, J. P. G. M. 2022. Playbacks of predator vocalizations reduce crop damage by ungulates. – Agric. Ecosyst. Environ. 328: 107853.
Wikenros, C., Liberg, O., Sand, H. and Andrén, H. 2010. Competition between recolonizing wolves and resident lynx in Sweden. – Can. J. Zool. 88: 271–279.
Wikenros, C., Sand, H., Ahlqvist, P. and Liberg, O. 2013. Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. – PLoS One 8: e77373.
Wikenros, C., Balogh, G., Sand, H., Nicholson, K. L. and Månsson, J. 2016. Mobility of moose–comparing the effects of wolf predation risk, reproductive status, and seasonality. – Ecol. Evol. 6: 8870–8880.
Wikenros, C., Aronsson, M., Liberg, O., Jarnemo, A., Hansson, J., Wallgren, M., Sand, H. and Bergström, R. 2017. Fear or food – abundance of red fox in relation to occurrence of lynx and wolf. – Sci. Rep. 7: 9059.
Winnie, J. and Creel, S. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. – Anim. Behav. 73: 215–225.
Winnie, J., Christianson, D., Creel, S. and Maxwell, B. 2006. Elk decision-making rules are simplified in the presence of wolves. – Behav. Ecol. Sociobiol. 61: 277–289.
Wirsing, A. J., Heithaus, M. R., Brown, J. S., Kotler, B. P. and Schmitz, O. J. 2021. The context dependence of non-consumptive predator effects. – Ecol. Lett. 24: 113–129.
Woodward, F. I., Lomas, M. R. and Kelly, C. K. 2004. Global climate and the distribution of plant biomes. – Philos. Trans. R. Soc. Lond. B 359: 1465–1476.
Zbyryt, A., Bubnicki, J. W., Kuijper, D. P. J., Dehnhard, M., Churski, M. and Schmidt, K. 2017. Do wild ungulates experience higher stress with humans than with large carnivores? – Behav. Ecol. 29: 19–30.
Zlatanova, D., Ahmed, A., Vlasseva, A. and Genov, P. 2014. Adaptive diet strategy of the wolf (*Canis lupus* L.) in Europe: a review. – Acta Zool. Bulg. 66: 439–452.

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Short communication

The strength of the Yellowstone trophic cascade after wolf reintroduction

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Trophic cascade strength

ABSTRACT

Trophic cascades, the indirect effects of predators propagating downward through food webs, play a critical role in shaping ecosystems. We evaluated the strength of a large carnivore-induced trophic cascade in northern Yellowstone National Park, focusing on riparian willows (*Salix* spp.) as primary producers. Using the $\log_{10}$ response ratio, a standardized indicator of trophic cascade strength, we quantified changes in willow crown volume following the 1995–96 reintroduction of gray wolves (*Canis lupus*), which completed the large carnivore guild. Reduced herbivory pressure from Rocky Mountain elk (*Cervus canadensis*) followed their reintroduction, leading to increased growth in willows. Crown volume, a proxy for above-ground biomass, was calculated using a predictive model based on willow height and was used to index primary producer response. Data from a 20-year study (2001–2020) revealed a relatively strong trophic cascade, with a ~1500 % increase in average willow crown volume and a $\log_{10}$ ratio of 1.21. This ratio surpassed 82 % of those reported in a global meta-analysis of trophic cascades. These results emphasize the importance of long-term monitoring to capture gradual and nonlinear ecosystem responses following predator reintroductions. They also underscore the substantial effect restored large carnivores can have on riparian vegetation and highlight the utility of crown volume as a metric for assessing trophic cascade strength.

1. Introduction

Trophic cascades are indirect effects of predators extending downward through food webs. These cascades can influence biodiversity, primary productivity, and nutrient cycling and are therefore key to understanding the structure and function of ecosystems (Estes et al., 2011). Impacts of these cascades are shaped by ecosystem type, productivity, environmental conditions, biological traits, and the plant response variables considered (Strong, 1992; Borer et al., 2005; Jia et al., 2018). Thus, determining the strength of a trophic cascade and whether a particular predator is influencing herbivores and plants in any given system requires measurement of plant traits that are reliably responsive to changing patterns of herbivory and comparable across ecosystems. Here, we use the $\log_{10}$

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response ratio to quantify the strength of a large carnivore trophic cascade in northern Yellowstone National Park, USA. The plant response $\log_{10}$ ratio is a widely-used, standardized indicator of trophic cascade strength that compares plant variables such as primary producer biomass in the presence or absence of predators, as mediated by herbivores (Shurin et al., 2002; Borer et al., 2005).

By the 1920s, gray wolves (*Canis lupus*) were locally extirpated and cougars (*Puma concolor*) were greatly reduced in Yellowstone National Park, leading to increased herbivory by Rocky Mountain elk (*Cervus canadensis*) on the park's northern elk winter range (Peterson et al., 2020). This increase in elk herbivory resulted in long-term suppression of palatable woody plants in riparian areas due to browsing, despite human hunting of elk along the park's northern boundary and a government elk culling program inside the park (Kay, 1990). Cougar numbers started increasing in the 1980s (Ripple et al., 2022), and the reintroduction of wolves in 1995 and 1996 completed the park's large carnivore guild, creating a natural experiment for evaluating the ecological effects of large predator restoration through a trophic cascade.

Researchers largely concur that the decline in woody plant communities in northern Yellowstone can be attributed primarily to the loss of wolves and the suppression of other large predators, which led to increased browsing by elk (Peterson et al., 2020). Similar results have also been found in Banff and Jasper National Parks following the loss of wolves (Hebblewhite et al., 2005; Beschta and Ripple, 2007a). The science appears relatively settled on the ecological effects of wolf extirpation, but questions remain in the Yellowstone ecosystem about the strength of the trophic cascade triggered by the restoration of wolves and other large carnivores. More broadly, there has been little work, worldwide, quantifying the strength of trophic cascades on plants after large carnivore restoration (Terborgh and Estes, 2010).

In northern Rocky Mountain locations, such as Yellowstone National Park, riparian areas normally occupy a small portion of the landscape. However, these areas are nevertheless important due to their high biodiversity and productivity. Here, our objectives were to 1) quantify the strength of trophic cascades in Yellowstone's northern range using the $\log_{10}$ ratio of change in riparian willows (*Salix sp*.) as primary producers, and 2) put this finding into context using a meta-analysis of other studies quantifying trophic cascade strength. Our purpose was to quantify trophic cascade strength only, not to characterize the stage of ecological restoration on the northern range.

2. Materials and methods

We used data from a 20-year study (2001–2020) of established willows growing on riparian floodplains and stream terraces in the park's northern range (Cooper and Hobbs, 2023; Hobbs et al., 2024). Willow height has typically been used in Yellowstone's riparian areas to help understand the ecosystem effects of large carnivore restoration following the reintroduction of wolves (Beschta and Ripple, 2016; Painter and Tercek, 2020; Hobbs et al., 2024). However, height may not be the most robust indicator of a trophic cascade's strength for willows because it does not fully capture the magnitude of the plants' overall growth or productivity. Willow crown volume encompasses the total three-dimensional space occupied by the willow's stems, branches and leaves, which correlates highly with above-ground willow biomass (Yao et al., 2021). Biomass is a popular variable for assessing the strength of a trophic cascade because it provides a measure of the amount of organic material available at the primary producer level (Shurin et al., 2002; Borer et al., 2005). See Fig. 1 as an example illustrating dramatic change in willow crown volume and biomass over time for several stream reaches in northern Yellowstone.

Recently, Kauffman and Cummings (2024) developed a model for predicting willow crown volume (m^3) from plant height using field data from various sites in northern Yellowstone National Park. Their dataset consists of 52 randomly selected willows exhibiting a wide range of heights and crown sizes, with heights ranging from 26 cm to 459 cm. They measured willow heights and horizontal crown dimensions and used these measurements to estimate crown volume, assuming a half-ellipsoid shape, and then fit a model to predict crown volume (m^3) from willow height (m). This model, which has $r^2 = 0.92$, estimates the natural log of willow volume (m^3) to be equal to [3.2511 × ln (height)] - 1.1763.

Based on the annual fall willow heights presented in Cooper and Hobbs (2023), we utilized the Kauffman and Cummings (2024) model to estimate the crown volume of each of their plants. We used these individual volume estimates to calculate the average crown volume by year along with the associated 95 % one-sample t-confidence intervals. We then calculated $\log_{10}$ ratios of average crown volume for each year relative to the first year, 2001, using the formula $\log_{10}\left(\frac{\overline{V_i}}{\overline{V_{2001}}}\right)$ where $\overline{V_i}$ and $\overline{V_{2001}}$ are the average volume in year *i* and year 2001 respectively. Similarly, we also calculated $\log_{10}$ ratios using the average height in each year. We considered northern range sites from the Cooper and Hobbs (2023) dataset where willows were fully accessible to ungulates (i.e., 4 control sites and 21 additional observational sites). Willows on their sites generally were consistent with the assumption of half-ellipsoid shape (Fig. 1), but this may not be the case in other areas where crown shape has been altered by intensive herbivory.

3. Results and discussion

Results indicated an average willow height of 92 cm in 2001, compared to 192 cm in 2020. This more than doubling of average willow height results in a $\log_{10}$ ratio of 0.32 from the beginning to the end of the study. Willow release from browsing actually began soon after wolf reintroduction in the late 1990s (Beschta and Ripple, 2007b; Beyer et al., 2007)—a few years before Cooper and Hobbs (2023) started collecting data in 2001. Thus, a $\log_{10}$ ratio of 0.32 for willow height may represent a conservative estimate of trophic cascade strength as some time had already passed since willows began growing taller (Painter and Tercek, 2020).

Based on the Cooper and Hobbs (2023) willow height data and the Kauffman and Cummings (2024) model, average willow crown

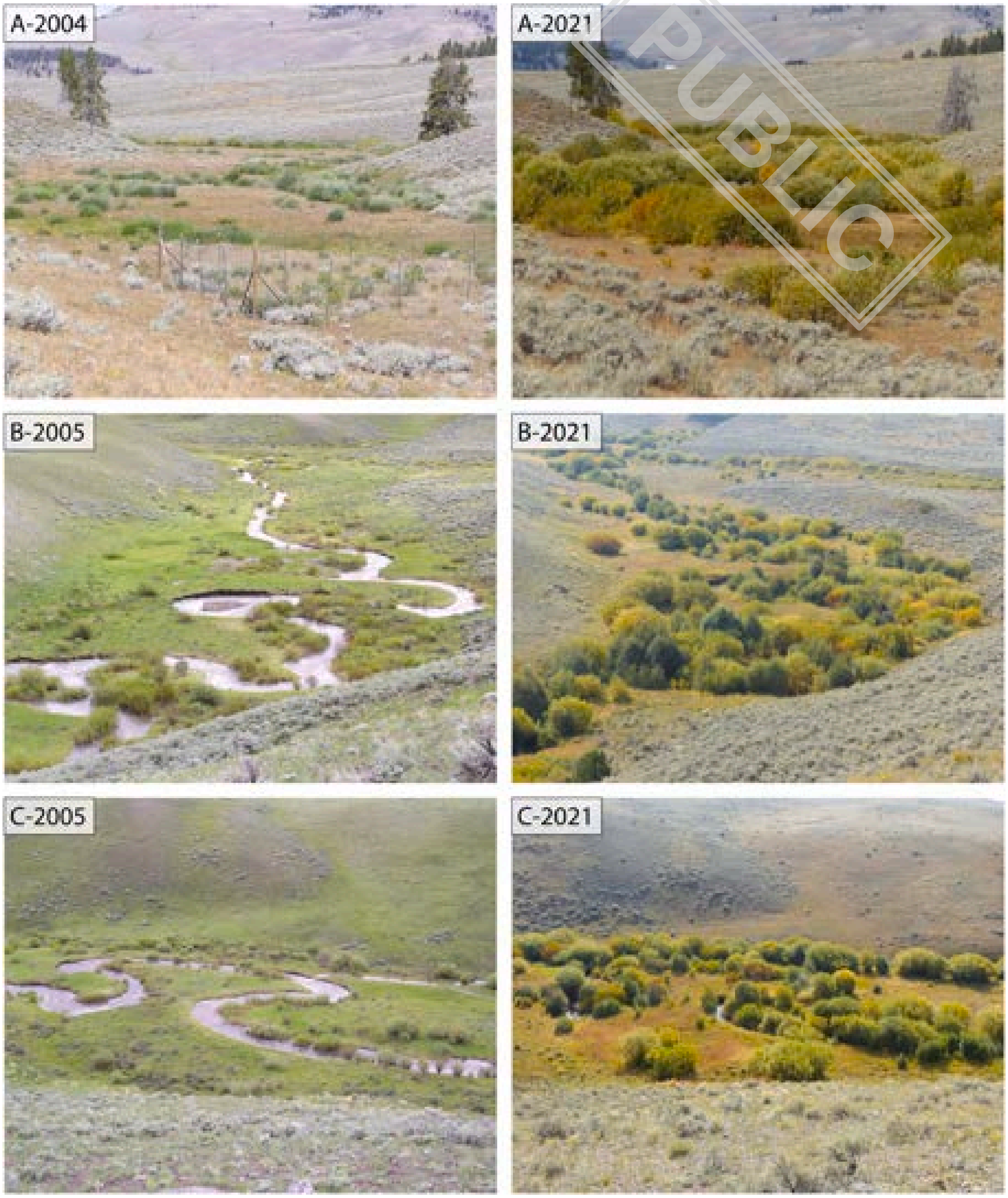

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Fig. 1. (A) Downstream view of the East Fork of Blacktail Deer Creek in August 2004 and September 2021, northern range of Yellowstone National Park, USA. Note the 2.4 m tall fenced ungulate exclosure near the bottom right of the 2004 photo with willows alongside sagebrush, which was part of a Cooper and Hobbs (2023) experimental site. In 2002, willow heights outside the newly constructed fence averaged 68 cm whereas willows inside the fence averaged 85 cm in height (25 % taller). In 2020, willow heights outside the fence averaged 165 cm while willows fully protected from ungulate herbivory inside the fence were 195 cm in height (18 % taller). The fence was constructed in 2001 and removed by the spring of 2021. The similarity, in this example, between inside and outside the exclosure in 2021 is consistent with the strong trophic cascade quantified in the full time-series dataset. (B) Upstream view of Blacktail Deer Creek in 2005 and 2021 and (C) an across channel view in 2005 and 2021 of another reach farther downstream. These chronosequence photographs should be considered examples only, but they do indicate that tall willows, with greatly increased crown volumes, had become relatively common along the valley bottom and floodplains of Blacktail Creek. Photo credits; R.L. Beschta, photo point location for (A) Lat.N 44°57'01" Long. W110°34'03" for (B) Lat. N44°57'58" Long. W110°35'30" and for (C) Lat. N44°57'58" Long. W110°35'28". See Figs. S1-S3 for high resolution versions of the photos.

volume increased approximately ~1500 % (0.3–4.8 m^3) from the start to the end of the 20-year willow study (Fig. 2A). This increase in crown volume indicates considerably more nesting habitat for birds, greater shading of streams, as well as other ecological benefits. Using willow crown volume as our basis, the plant $\log_{10}$ ratio from the start to the end of the dataset by Cooper and Hobbs (2023) was

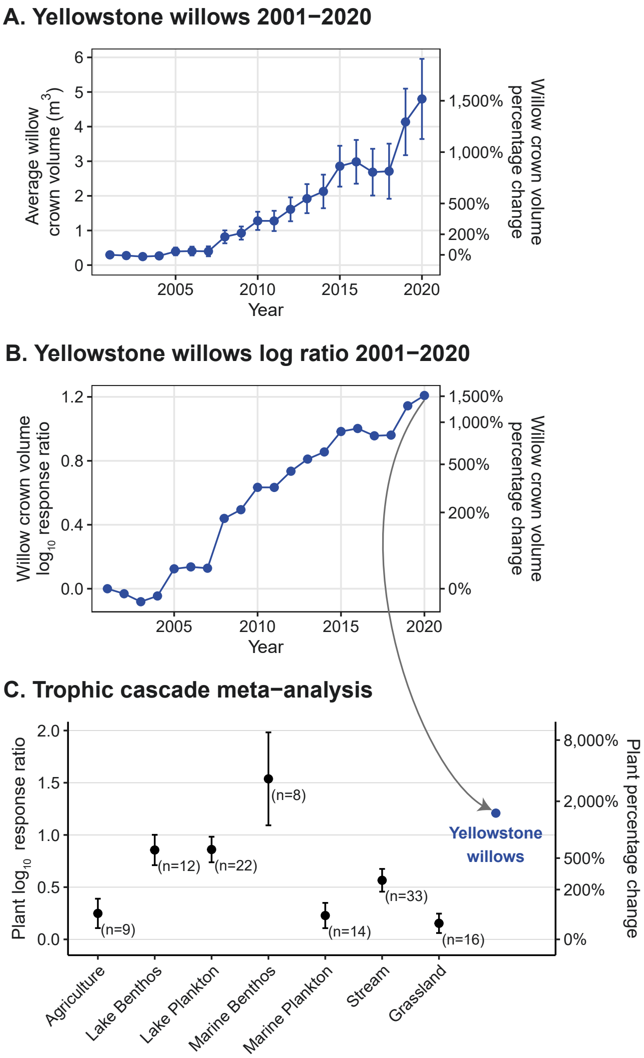

Fig. 2. The Yellowstone trophic cascade in context. Wolves were introduced into Yellowstone in 1995 and 1996. Between 2001 and 2020, estimated average willow crown volume in northern Yellowstone rose from approximately 0.30 m^3 to 4.80 m^3 (A; error bars indicate 95 % confidence intervals). This change corresponds to a $\log_{10}$ response ratio of 1.21 (B), which is substantially greater than the response ratios observed in many other studies (C). Willow crown volume was calculated using height data from Cooper and Hobbs (2023) and the crown volume model from Kauffman and Cummings (2024). Except for Yellowstone willows, average $\log_{10}$ ratios by system type were obtained from a trophic cascade meta-analysis of plant biomass studies (Borer et al., 2005); sample sizes are shown in parentheses; error bars represent one standard error of the mean (C).

1.21 (Fig. 2B). This value was greater than 93 (∼82 %) of the 114 unique plant $\log_{10}$ ratios reported in a meta-analysis by Borer et al. (2005) of trophic cascades that included a variety of freshwater, marine, and terrestrial systems around the world (Fig. 2C).

The crown volume $\log_{10}$ ratios generally increased year over year (Fig. 2B). Thus, considering the length of time since predator reintroduction can be essential when assessing trophic cascades' effects on plant communities. The return of predators may trigger immediate changes in ecosystem processes, such as decreased browsing due to influences on prey populations or behavior. However, their effect on plant community dynamics may unfold more gradually and non-linearly across a larger landscape (Newbold et al., 2020). Accordingly, early assessments may not capture the full impact of a restored predator, as plants with a long regeneration time often respond slowly to altered herbivore pressures and ecosystem dynamics. By contrast, long-term studies help to reveal trends in plant biomass, reflecting sustained predator-prey-plant interactions (Figs. 2A and 2B). Thus, accurately measuring trophic cascade effects on woody plants requires monitoring ecosystems over extended periods post-predator reintroduction. The magnification of the trophic cascade effects may continue through time, but at some point may become asymptotic or tempered as willows reach their maximum heights or other biotic or abiotic factors dampen the response.

Synthesis work has shown strong evidence of trophic cascades following wolf reintroduction in Yellowstone, including 24 studies that examined willows and other deciduous woody plants in riparian areas (Beschta and Ripple, 2016). All but two of these 24 studies reported increases in plant height, stem diameter, stem establishment, canopy cover, or recruitment. Over half of the studies assessed ungulate browsing, consistently finding that increased woody plant growth and cover followed reduced browsing pressure. Nearly half also investigated the influence of climatic and hydrologic variables on plant community changes and generally found that they were unlikely to have driven the observed changes to riparian plant communities. Thus, the trophic cascade in Yellowstone has been well documented and our goal here was to quantify the strength of the trophic cascade, which has not clearly been done to date.

The reintroduction of wolves into Yellowstone reveals how recovering ecosystems may diverge from their original states. For example, prior to the return of wolves, elk overbrowsing severely reduced riparian vegetation across the landscape and, in doing so, contributed to the loss of beavers (*Castor canadensis*), a keystone species essential for maintaining wetland habitats and stabilizing stream hydrology along some reaches. Subsequent increases in channel erosion caused significant downcutting of streams and lowering of water tables, thus inhibiting the recovery of riparian willows away from the streams. This situation represents an example of ecological hysteresis, where the system's trajectory of recovery does not exactly follow its path of degradation and highlights the emergence of alternative states, in which the ecosystem can attain an alternative configuration for an unknown length of time, despite the restoration of apex predators. As a result, the recovery trajectory is shaped by the interplay of trophic dynamics, altered abiotic conditions, and the long-term absence of keystone species like wolves and beavers, whereby recovering ecosystems may not yet have the full array of structural and functional attributes that were present historically (Peterson et al., 2020; Hobbs et al., 2024).

Though a before-after control-impact (BACI) experimental design would have allowed for the strongest inference, the data we used for this project are similar to most other trophic cascade studies that focus on the reintroduction of extirpated large predators into parts of their native range. This approach utilizes a "natural experiment," a form of observational study that examines the effects of naturally occurring events without deliberate manipulation. In this framework, temporal changes serve as the primary basis for comparison. This method is particularly useful with large landscapes and wide-ranging predators, especially within a national park setting where experimental manipulations are typically prohibited. Here, the first year of the time series (2001) represents the "before" data and since this measurement occurred several years after wolf reintroduction, any results should be viewed as conservative. Willow heights before the 1995–96 reintroduction of wolves were typically shorter than the "year 1" willow heights in 2001 (Singer et al., 1998; Barmore, 2003). In addition to yearly means of crown volume, we report the associated 95 % t-confidence intervals as a measure of variability to make these data more suitable for future meta-analysis on trophic cascades (see Table S1).

4. Conclusions

Because crown biomass and crown volume are highly correlated (Yao et al., 2021), we conclude that crown volume was a reasonable surrogate for assessing the strength of the trophic cascade in northern Yellowstone. Hence, as a proxy for the biomass of riparian willows, researchers investigating trophic cascades might consider methods to determine crown volume, rather than just using willow height. We also conclude that the large carnivore trophic cascade on Yellowstone willows was relatively strong as quantified by the $\log_{10}$ ratio of willow crown volume, compared to a variety of other published trophic cascade studies that used biomass as a response variable. Quantifying trophic cascade strength in Yellowstone's willow populations highlights not only the substantial impact of large carnivores on plants but also the importance of long-term monitoring to capture gradual ecological responses following predator reintroductions. This knowledge can inform future conservation efforts and adaptive management strategies, especially in ecosystems undergoing restoration, where accurate assessment of trophic cascade dynamics is essential for evaluating recovery progress and biodiversity outcomes.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03428.

Data availability

All data used in our analysis are available in the public repositories that we have cited.

References

Barmore, W.J., 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis, pp. 1962–1970. Yellowstone Center for Resources, Yellowstone National Park: Mammoth, WY.
Beschta, R.L., Ripple, W., 2007a. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Can. J. For. Res. 37, 1873–1885.
Beschta, R.L., Ripple, W.J., 2007b. Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. West. North Am. Nat. 67, 613–617.
Beschta, R.L., Ripple, W.J., 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. Biol. Conserv. 198, 93–103.
Beyer, H.L., Merrill, E.H., Varley, N., Boyce, M.S., 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecol. Appl. 17, 1563–1571.
Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2005. What determines the strength of a trophic cascade? Ecology 86, 528–537.
Cooper, D., Hobbs, N.T., 2023. Twenty years of Salix height in response to experimental manipulation of browsing and water table, northern range of Yellowstone National Park [Dataset]. http://doi.org/10.5061/dryad.sqv9s4n7n.
Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D. A., 2011. Trophic downgrading of planet earth. Science 333, 301–306.
Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144.
Hobbs, N.T., Johnston, D.B., Marshall, K.N., Wolf, E.C., Cooper, D.J., 2024. Does restoring apex predators to food webs restore ecosystems? Large carnivores in Yellowstone as a model system. Ecol. Monogr. 94, e1598.
Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., Luskin, M.S., 2018. Global signal of top-down control of terrestrial plant communities by herbivores. Proc. Natl. Acad. Sci. 115, 6237–6242.
Kauffman, J.B., Cummings, D., 2024. Predictive Equations for Determining Crown Area and Crown Volume of Recovering and Intact Willows Based upon Height at Yellowstone National Park. http://doi.org/10.6084/m9.figshare.27905172.v2.
Kay, C., 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm [PhD dissertation]. Utah State University: Logan, UT. USA.
Newbold, T., Tittensor, D.P., Harfoot, M.B., Scharlemann, J.P., Purves, D.W., 2020. Non-linear changes in modelled terrestrial ecosystems subjected to perturbations. Sci. Rep. 10, 14051.
Painter, L.E., Tercek, M.T., 2020. Tall willow thickets return to northern Yellowstone. Ecosphere 11, e03115.
Peterson, R., Beschta, R., Cooper, D., Hobbs, N., Johnston, D., Larsen, E., Marshall, K., Painter, L., Ripple, W., Rose, J., 2020. Indirect effects of carnivore restoration on vegetation. Yellowstone wolves: Science and discovery in the world's first national park 204–222.
Ripple, W.J., Beschta, R.L., Painter, L.E., 2022. The history of cougars in Yellowstone National Park. West. North Am. Nat. 82, 752–759.
Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecol. Lett. 5, 785–791.
Singer, F.J., Zeigenfuss, L.C., Cates, R.G., Barnett, D.T., 1998. Elk, multiple factors, and persistence of willows in national parks. Wildl. Soc. Bull. 26, 419–428.
Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73, 747.
Terborgh, J., Estes, D.J.A. (Eds.), 2010. Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature, first ed. Island Press.
Yao, X., Yang, G., Wu, B., Jiang, L., Wang, F., 2021. Biomass estimation models for six shrub species in Hunshandake Sandy Land in Inner Mongolia, Northern China. Forests 12.

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Corrigendum

Corrigendum to “The strength of the Yellowstone trophic cascade after wolf reintroduction” [Glob. Ecol. Conserv. 58 (2025) e03428]

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The authors regret that we had incorrectly assumed the log response ratios presented by Borer et al. (2005) were base10. We have since determined that they were actually calculated using the natural logarithm (ln). Consequently, here we have converted the Borer et al. (2005) results that we presented from natural log response ratios (mistakenly identified as base-10) to base-10 log response ratios.

Because of the logarithm base error, a portion of our original text in the second paragraph of section 3 needs to be corrected; “93 (~ 82 %)” should instead be “112 (~ 98 %).” Thus, the corrected paragraph is as follows:

> “Using willow crown volume as our basis, the plant $\log_{10}$ ratio from the start to the end of the dataset by Cooper and Hobbs (2023) was 1.21 (Fig. 2B). This value was greater than 112 (~98 %) of the 114 unique plant $\log_{10}$ ratios reported in a meta-analysis by Borer et al. (2005) of trophic cascades that included a variety of freshwater, marine, and terrestrial systems around the world (Fig. 2C).”

We have also provided an updated version of Fig. 2, where the Borer et al. (2005) average log response ratios (and standard errors) by system type shown in Fig. 2c have been adjusted from natural log to $\log_{10}$ values by dividing them by ln(10), which is approximately 2.30. This means these summary statistics were all 2.30 times smaller than what we originally reported, making the Yellowstone trophic cascade appear even stronger in context.

As noted in the original paper, average willow crown volume increased from 0.30 m^3 to 4.80 m^3, which corresponds to a roughly 16-fold (~ 1500 %) increase. This is equivalent to a log-10 response ratio of 1.21 and a natural log response ratio of 2.78.

The authors would like to apologise for any inconvenience caused.

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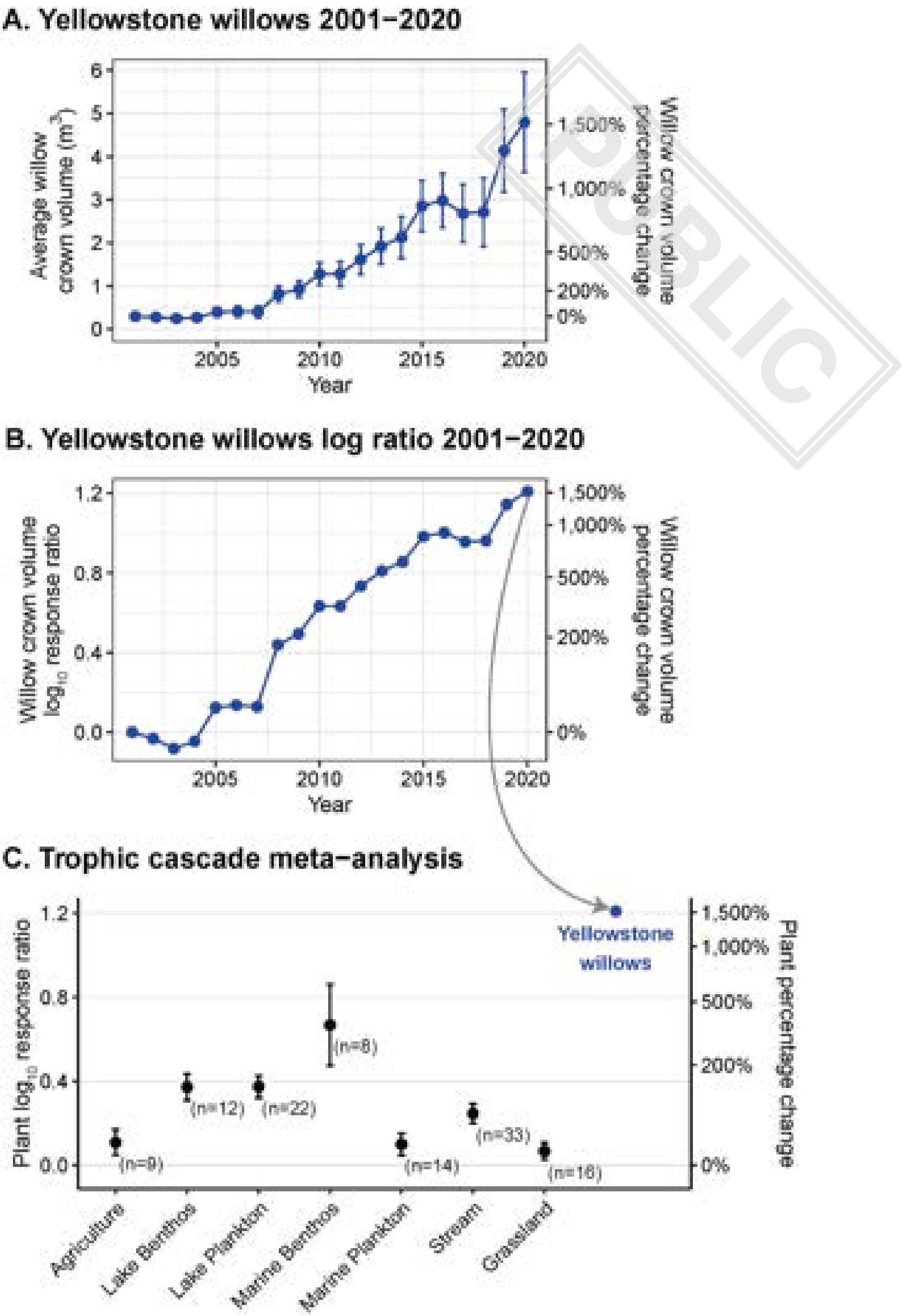

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References

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2005. What determines the strength of a trophic cascade? Ecology 86, 528–537.

Cooper, D., Hobbs, N.T., 2023. Twenty years of *Salix* height in response to experimental manipulation of browsing and water table, northern range of Yellowstone National Park [Dataset]. ⟨https://doi.org/10.5061/dryad.sqv9s4n7n⟩.

Kauffman, J.B., Cummings, D., 2024. Predictive Equations for Determining Crown Area and Crown Volume of Recovering and Intact Willows Based upon Height at Yellowstone National Park. ⟨https://doi.org/10.6084/m9.figshare.27905172.v2⟩.

European Commission

PUBLIC

THE SITUATION OF THE WOLF (*CANIS LUPUS*) IN THE EUROPEAN UNION

An In-depth Analysis

Written by the N2K GROUP EEIG
December 2023

THE N2K GROUP
European Economic Interest Group

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An In-depth Analysis

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TABLE OF CONTENTS

KEY FINDINGS

The following is a short summary of the key issues raised in each of the four chapters of the study.

1. Introduction

Having been extirpated from most of Europe during the 18th and 19th Centuries, wolves started to recover in the 1970s and are now present in most of the EU Member States. With the return of the wolf, comes also the return of conflicts with livestock.

Wolves in the EU are protected by the Bern Convention and the Habitats Directive, but the strict protection of wolves may be derogated under certain conditions to, *inter alia*, prevent serious damage to livestock or in the interests of public safety.

After the adoption of the European Parliament's non-legislative resolution on the protection of livestock farming and large carnivores in Europe in November 2022, the European Commission has committed itself to carrying out an in-depth analysis of available scientific and technical data on the wolf in the EU.

2. Conservation monitoring

Wolf monitoring – challenges and good practice examples

Wolf monitoring is challenging because of low population densities and elusive behaviour. Within the EU, estimates of wolf numbers and their precision vary greatly across different countries, making it difficult to obtain a clear overall picture and compare numbers.

Reliable data on population size and trends and other important variables is an essential requirement for objective, science-based decisions. This is emphasised in the European Parliament resolution which deplored the lack of harmonised wolf monitoring. A number of national monitoring methodologies are described further as they represent good practice.

Assessment of the conservation status of the wolf under the Habitats Directive

According to the latest conservation status assessment undertaken under Article 17 of the Habitats Directive, covering the reporting period 2013-2018, the wolf was reported to be present in 21 EU countries. Its overall EU population at that time was estimated at around 11,000- 17,000 (best value: 13,492 wolves).

Member States reported 39 regional conservation status assessments for that period. 21 showed an improving trend in conservation status, 14 showed a stable trend and only 1 (Croatia Mediterranean) showed a negative trend. Around half (18) were favourable (FV), while the other half (19) were unfavourable (with 16 unfavourable-inadequate (U1) and three unfavourable-bad (U2)), and two unknown (XX). Compared to the previous reporting period (2007-2012), FV assessments decreased slightly from 19 to 18. The conservation status of the wolf under the Habitats Directive is not uniform across the EU.

IUCN Red List European assessment

According to the wolf assessment carried out in 2018 by the International Union for Conservation of Nature (IUCN) Red List, six of the nine European wolf populations were considered as non-threatened. Three of these populations were considered as "Near Threatened" (Iberian, Italian Peninsula and

Karelian populations) and a further three were of "Least Concern" (the Dinaric-Balkan, the Carpathian and the Baltic populations). The remaining three were listed as "Vulnerable" (the Western- Central Alps, the Scandinavian and the Central Europe populations). Red List assessment of the wolf is not uniform at a pan-European level.

Updated information on wolf numbers in the European Union

In 2023, wolves have been detected across all EU Member States except Ireland, Cyprus and Malta, and there are breeding packs in 23 countries. In this analysis, about 20,300 wolves have been estimated in 2023 across the EU, a figure slightly higher than the 19,400 wolves estimated by Boitani et al. (2022) and significantly higher than the 11,193 wolves estimated in 2012. Overall, the number of wolves in the EU is increasing.

Threats and mortality

Deliberate and accidental killing by humans is the main cause of wolf mortality in Europe. The results of mortality assessments however depend on the study method used. In studies based on the collection of 'found-dead' wolves, mortality from legal hunting and culling and traffic prevails over other causes whereas, in radiotracking studies, poaching emerges as an important or the most important cause of mortality, sometimes also in countries where hunting/culling is allowed.

Wolf-dog hybridisation is also considered a conservation problem for the wolf in Europe. Although hybridisation between wolves and dogs has probably occurred throughout the history of the dog's domestication, genetic analysis demonstrates that both the dog and the wolf conserve a well-defined genetic identity. Sporadic hybridisation has been detected in all European wolf populations, but there is a higher percentage of hybrids in some Member States in southern Europe, mainly in Italy and Greece.

3. Role of the wolf in ecosystems and impacts on society

Role in ecosystems' functioning

The wolf plays an important role in the ecosystem. Although wolves in Europe cannot trigger the trophic cascades described in North American national parks, they can, in some circumstances, limit the rates of increase and densities of wild ungulates, and so reduce browsing, damage to agriculture and forestry, as well as ungulate–vehicle collisions and the incidence of diseases (e.g., tuberculosis, African swine fever) transmitted by wild ungulates to livestock.

In addition, wolves provide carrion for scavengers, may reduce densities of golden jackals and perform other forms of ecosystem services.

Predation on wild ungulates and implications for hunting

Wolves hunt wild ungulates and may sometimes compete with hunters for prey. However, wolves kill far fewer wild ungulates than hunters and select individuals with a lesser reproductive value. In certain conditions, wolves may regulate wild ungulate populations which may require an adjustment to existing harvest strategies.

Predation on farm and domestic animals

Predation of livestock has been the main cause of wolf persecution throughout history and is currently the main source of conflict between wolves and people.

Wolves kill annually at least 65,500 heads of livestock in the EU, 73% are sheep and goats, 19% cattle and 6% horses and donkeys. The highest damage to livestock is reported to occur in Spain, France and Italy (14,000-10,000 heads annually in each country). Sheep are mainly killed in France, cattle in Spain, horses in the mountains of southwestern Europe and semi-domestic reindeer in Finland and Sweden. Considering that there are about 60 million sheep in the EU, the level of sheep depredation by wolves represents an annual killing of 0.065%.

In general, damage to livestock has increased as the wolf population has grown. But, in some of the German federal states with the highest number of wolves, the frequency of wolf attacks on livestock has decreased significantly in recent years, which was associated to the use of adequate preventive measures.

On a large scale, the overall impact of wolves on livestock in the EU is very small, but at a local level, the pressure on rural communities can be high in certain areas.

Depredation levels are typically higher on free-ranging livestock and are lower in areas where wolves have never disappeared. Natural prey availability, landscape characteristics and protection measures also shape the incidence of damage to livestock.

Considerations about public safety

Although wolves can attack humans, no fatal wolf attacks on people have been recorded in Europe in the last 40 years. To reduce even more the already small risk that wolves pose to human safety, specific protocols have been developed to address the problem of bold and/or food-conditioned wolves.

4. Available measures to improve coexistence

Prevention measures to avoid livestock predation

The best way to reduce livestock losses due to wolf attacks is to apply effective and adapted measures to prevent wolf depredation. Much information has been published in recent years on the different methods available and their effectiveness in terms of livestock protection. Many of the publications come from EU funded LIFE Projects.

All emphasise the need to ensure that prevention measures are tailored to the specific circumstances of each exploitation and that expert advice in early phases is crucial.

Most of the prevention methods used in the EU have shown a high or moderate degree of effectiveness, but protecting free-ranging livestock remains very challenging.

Some EU countries, such as France and Germany, spend a significant amount of money for damage prevention. While the measures have not shown clear effectiveness in France, they appear to have reduced the extent of livestock damage in Germany.

Some measures can also be used to protect hunting dogs. The Natural Resources Institute of Finland has informed the public on radio-collared wolf positions, reducing the risks of attacks.

Compensatory measures

Damage caused by wolves to livestock is compensated in most of the EU countries, in general using the ex post facto system that requires the damage to be documented. In the European Union, around 18.7 million euros per year are paid in compensation for wolf damages. France pays the most money in terms of compensation (about 4.1 M euros in 2022). The most affluent MS and those where livestock is free-ranging tend to pay higher compensation per wolf and per year.

Opportunities for nature-based tourism and education

Wolf-related tourism can create income in rural areas and also lead to increased tolerance toward wolves at the local level. Tourism can also educate visitors about the ecology of wolves and how to coexist with them, raising awareness and promoting conservation efforts.

Wolf-related tourism should however be properly planned and regulated to prevent any negative impacts on wolves.

Information, advice, awareness raising

Numerous websites have been developed over the years by Member States, the European Commission, the Large Carnivore Initiative for Europe (LCIE) and NGOs to provide detailed information on wolf populations in the EU, raise awareness and offer advice for reducing human/animal conflicts.

Most LIFE projects on wolves also provide comprehensive information and advice on different types of prevention measures.

Dialogue with and involvement of stakeholders

Participation processes have proven useful to address divergences among stakeholders with contrasting opinions on wolves and their management. Since 2014, the European Commission has supported the establishment of the EU Platform on Coexistence between People and Large Carnivores involving representatives of different interest groups. Since 2018, thanks to a pilot project funded by the European Parliament, regional stakeholders' platforms have also been established in six Member States to improve the co-existence of large carnivores and humans.

Lethal control/culling of wolves

For those Member States where wolves are listed in Annex IV of the Habitats Directive, derogations can be used on a case-by-case basis, in line with the requirements of the Directive. The use of derogations is highly variable in the MS.

For instance, France (Annex IV), has introduced a maximum ceiling for all the targeted lethal removal authorizations of wolves. This has increased from 10% of the wolf population size in 2004 to 19-21% in 2021. Yet, the wolf population is still increasing.

In Sweden (Annex IV), wolves are culled by means of protective hunting (targeted lethal removal) and licenced hunting (non-targeted lethal removal). In the 2022-2023 winter season, 57 wolves were legally culled (14% of the population).

In Spain north of the river Duero, the wolf is listed in Annex V of the Habitats Directive (no derogations needed). Several methods of wolf hunting and control were used by the autonomous regions before the wolf was strictly protected in 2021. In Cantabria wolves were culled and hunted, in Castile and Leon they were hunted, in Asturias they were culled for the purpose of reducing livestock damage, and in Galicia wolves were considered as a game species,but managed *de facto* as a protected species.

Evidence in North America show that lethal control reduced damage to livestock only when it was intense enough to reduce wolf populations over large areas. In France, the research conducted to assess the effects of targeted culling on wolf depredations was inconclusive.

Protocol on Bold wolves

A bold wolf is a fearless wolf that repeatedly tolerates recognizable people within 30m or even actively approaches them. To reduce the risk posed by bold wolves, experts have published a protocol detailing how to act in different circumstances.

EU support for large carnivores under the Common Agricultural Policy (CAP)

EU funding mechanisms exist under the CAP to support livestock farmers who operate in areas where large carnivores are present. Of the 24 Member States with wolf populations, 10 Member States have included specific and targeted interventions for large carnivores under Pillar II in their CAP Strategic Plans. For three Member States, the interventions focus specifically on wolves. For the remainder, they cover also other large carnivores (bear, lynx, jackal).

A further five Member States have indirect sub-measures that could potentially help address the need to protect the grazing herd from predators even if this is not the objective of the measure.

Of the ten Member States with targeted interventions, six offer both Agri-Environment-Climate measures (AECMs) to compensate for livestock damage and investment schemes to protect livestock against predators. Four Member States offer just investment schemes to protect against predators.

1. INTRODUCTION

1.1 Environmental context

The wolf (*Canis lupus*) once occupied most of the Holarctic region in Eurasia and North America and is one of the terrestrial mammals with the largest natural range in the world. In Europe, the wolf is a native wildlife species and, as such, part of Europe's biodiversity and natural heritage. As with any wild species, it plays an ecological role in the ecosystems (see section 3.1) (Hoag et al. 2022). It was once present throughout the continent, including on the islands of Great Britain and Ireland, from where it was extirpated in the 17th and 18th centuries.

The wolf is an adaptable species, able to live in almost all habitats in the Holarctic region, from the High Arctic to the Arabian desert, as well as in many human-dominated landscapes in Europe and Asia. Wolves live in packs that usually contain five to ten individuals, formed by the breeding pair and its current offspring, along with some offspring from the previous year and sometimes also unrelated wolves.

In each pack, usually a single female gives birth once a year to 5 or 6 pups, whose survival in natural habitats depends on the availability of food *per capita*. Thanks to their reproductive capacity, wolves can withstand high mortality rates, and under the right conditions, wolf populations can recover fairly quickly. For example, the average rate of increase of wolves between 2000 and 2015 in Germany has been 36% per year (Reinhardt et al. 2019).

The territory of a wolf pack may extend over several hundred km^2, so the wolves usually live in very low densities, between 1 and 3 individuals / 100 km^2. Wolves can disperse over several dozen or hundreds of kilometres from their natal pack, even in European human-dominated landscapes, which enables them to recolonize regions and countries from where they had disappeared.

Although their diet can be varied, wolves are natural hunters of wild ungulates, such as red deer, roe deer, wild boar and moose, but they also have a tendency to attack unprotected livestock, especially sheep. This tendency has fuelled the animosity of agricultural societies, which has, in the past, led to the extermination of the wolf to reduce its impact on livestock.

As a result, many wolf populations disappeared, especially at the end of the 19th century and during much of the 20th century. In the 1960s and 1970s wolf populations reached their lowest levels in Europe. They almost completely disappeared from Finland, Scandinavia and central Europe and were confined to Eastern Europe and the southern European peninsulas, where a few small and fragmented populations survived close to extinction (Boitani 2003).

However, around 1970 the ecological and social changes that occurred in Europe allowed the recovery of the wolf and other large carnivores. The rural-urban migration led to natural reforestation and a dramatic increase of wild ungulates, thereby greatly improving habitat conditions for wolves. The combination of land abandonment, improvement of attitudes, legal protection and reduced human impacts on the landscape over the last decades of the 20th century has created the right conditions for a large-scale recovery of the wolf across Europe (Chapron et al. 2014).

Having been extirpated from large parts of the continent in the past, wolves are on the rebound and have resettled in parts of the EU, such as France and Germany and, more recently, even in densely populated countries like the Netherlands and Belgium.

1.2 Legal context

The conservation of the wolf in Europe is essentially governed by the Bern Convention[1] and the EU Habitats Directive[2]. The Bern Convention on the Conservation of European Wildlife and Natural Habitats came into force in 1982. The Bern Convention aims "*to conserve wild flora and fauna and their natural habitats, especially those species and habitats whose conservation requires the co-operation of several States*", giving particular emphasis to "endangered and vulnerable species", including wolves.

In particular, the Bern Convention requires its parties to take "appropriate and necessary legislative and administrative measures" to ensure the "protection" of Appendix III fauna and the "special protection" of Appendix II fauna. For species listed in Appendix II, the Convention requires the prohibition of, *inter alia*, the deliberate killing, capturing, and disturbing of individual animals belonging to listed taxa. Derogations are however possible under Art. 9 Bern Convention.

The wolf is listed as a specially protected species in Appendix II of the Convention. However, nine contracting parties of the European Union have submitted reservations on its legal status in their countries. Two of these countries (Lithuania and Spain) apply instead the more flexible protection regime of Appendix III to their wolf populations. The other seven states (Bulgaria, Czech Republic, Finland, Latvia, Poland, Slovakia and Slovenia), treat the wolf as not being listed on either of the Appendices of the Bern Convention (Trowborst and Fleurke 2019).

Adopted in 1992, the Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (the Habitats Directive) aims to promote the maintenance of biodiversity, taking account of economic, social, cultural and regional requirements. Together with the Birds Directive, it forms the cornerstone of Europe's nature conservation policy and establishes an EU wide ecological network of protected areas - called Natura 2000 - which should enable the natural habitat types and the species' habitats concerned to be maintained or, where appropriate, restored at a favourable conservation status in their natural range.

The overall objective of the Habitats Directive is to maintain or achieve a "favourable conservation status" for the species and natural habitat types listed in its annexes I, II, IV and V. The status of a species is deemed favourable when, *inter alia*, the species "is maintaining itself on a long-term basis as a viable component of its natural habitats" and "there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis."

For the majority of Member States, the wolf is listed in both Annex II of the Habitats Directive which requires Member States to designate core areas for the species under Natura 2000 and in Annex IV which requires its strict protection across its natural range both inside and outside protected areas.

Finland, Estonia, Greece (north of the 39th parallel), Latvia, Lithuania, and Spain (north of the Duero River) are not required to designate Natura 2000 sites for wolf (because of geographical exemptions given in Annex II for these countries). Moreover, for Bulgaria, Estonia, Latvia, Lithuania, Poland, Slovakia and parts of Greece (north of the 39th parallel), Finland (reindeer management area) and Spain (north of the Duero River) the wolf is listed in Annex V, which means that the wolf is not a strictly protected species in these Member States.

Some of Member States have also accorded a higher degree of protection for the wolf under national legislation, than that provided by the Directive. For example, in Poland, Greece (north of the 39th parallel), Spain (north of the Duero River) and Slovakia, wolf populations are strictly protected under national legislation despite being listed in Annex V of the Directive.

[1] coe.int/en/web/bern-convention

[2] The Habitats Directive (europa.eu)

Derogations are nevertheless possible under Article 16 in order to prevent serious damage (in particular to crops, livestock, forests, fisheries and water and other types of property) and in the interests of public health and public safety. Derogations are also possible for other imperative reasons of overriding public interest, including those of a social or economic nature, or in order to allow, under strict conditions, the taking or keeping of certain specimens of the species enjoying strict protection in limited numbers specified by the competent national authorities.

In other words, the existing rules on derogations make it possible to balance different interests against the conservation aims of the Directive. The Directive thus authorises Member States to take action to derogate from certain provisions in order to address the specific challenges they are currently facing in relation to the wolf population. In this context, Member States have at their disposal the appropriate means to address local conflicts and circumstances, in line with the principle of subsidiarity.

Member States make varying use of derogations. Some Member States have never or almost never used derogations to remove wolves (e.g., Portugal, Italy), some use derogations in a very limited way (e.g., Germany) while some others make use of derogations frequently or systematically (e.g., France, Sweden).

Considering the fragmented legal landscape and the transboundary nature of most wolf populations, transboundary cooperation at the population level has become a leading paradigm for large carnivore conservation both under the Bern Convention and the Habitats Directive (Linnell et al. 2008).

1.3 Political Context

In the 30 years since the Habitats Directive came into force, wolves in the EU have recovered significantly and are now occupying new Member States from where they had disappeared, such as France in the early 1990s, Germany in the early 2000s, and other countries of central and western Europe more recently. Some wolf populations that were endangered in 1992 have since then significantly increased (Chapron et al. 2014).

With the wolf‘s return, more frequent conflicts arise with livestock breeders mainly in areas where it was absent for decades. In such areas, the husbandry methods had adapted to a landscape devoid of large carnivores, leading to a decline in practices for managing and protecting grazing livestock in the presence of large predators. The recovery of wolf populations has led to a resumption of their predation on livestock.

On the other hand, the wolf also continues to enjoy strong public support, as demonstrated by the targeted data collection exercise launched by the European Commission in 2023[3]. Even if the aim of the exercise was not to collect opinions in favour or against the strict protection of the wolf in the EU, but to collect relevant data to feed into the comprehensive analysis of the wolf situation, over 70% of the respondents expressed their support for maintaining wolf protection status, compared to 29% in favour of reducing its protection status. An opinion poll conducted by Savanta on behalf of Eurogroup for Animals in six countries of the EU in 2020 also found that the majority of public believed that “wolves have a right to exist in the wild; belong to our natural environment and should be strictly [4]. Another more recent survey of residents in rural communities conducted by Savanta on behalf the same organisation in 10 EU countries reported “a significant 68% of those surveyed advocating to maintain the strict protection status of large carnivores”[5]

[3] Wolves in Europe (europa.eu)

[4] https://www.eurogroupforanimals.org/news/new-poll-shows-eu-citizens-stand-wolves

[5] https://www.eurogroupforanimals.org/files/eurogroupforanimals/2023-11/20231129_Survey%20Report%20Large%20carnivores.pdf

In 2022, Switzerland proposed downlisting the wolf from Appendix II (strictly protected species) to Appendix III (protected species) to the Bern Convention. The proposal was rejected by the parties of the Convention on 29 November 2022.

On 24 November 2022, the European Parliament adopted a non-legislative resolution on the protection of livestock farming and large carnivores in Europe[6]. The resolution reflects the different views of stakeholders about the wolf conflict.

It acknowledges the positive role played by EU biodiversity policy in the recovery of large carnivores. It stresses the importance of ensuring a balanced coexistence between humans, livestock and large carnivores, in particular in rural areas, and asks the Commission and the Member States to ensure long-term funding for both damage prevention and compensation.

It acknowledges that flexibilities exist under the current legal framework to manage trade-offs, while noting that these flexibilities should be explored further. The text emphasizes in particular that the rapid increase in the wolf population and in attacks on livestock makes it hard for national administrators to act effectively and decisively with the tools currently available to them, which causes detrimental impacts on livestock farming and rural communities.

It welcomes and supports the Swiss proposal to downgrade the protection status of wolves under the Bern Convention, pointing out that the conservation status of the wolf at pan-European level justifies a mitigation of its protection status. It asks the Commission to carry out additional studies and analyses, as well as an assessment of the effectiveness of damage mitigation measures tested or implemented under LIFE and other EU funding mechanisms. Finally, the resolution asks the Commission to develop an assessment procedure to enable the protection status of populations in particular regions to be amended as soon as the desired conservation status of species has been reached.

In its reply to the European Parliament's resolution, the European Commission[7] stated *inter alia* that in the course of 2023, the Commission would carry out an in-depth analysis of all available scientific and technical data, and all other relevant circumstances at hand, in order to assess whether further measures are needed, including for adapting the protection status of species of Community interest based on technical and scientific progress. This report constitutes the in-depth analysis that the Commission had undertaken to carry out.

[6] https://www.europarl.europa.eu/doceo/document/TA-9-2022-0423_EN.html

[7] https://environment.ec.europa.eu/news/follow-european-parliament-non-legislative-resolution-protection-livestock-farming-and-large-2023-06-06_en

2. CONSERVATION STATUS

2.1. Wolf monitoring – challenges and good practice examples

Monitoring wolf populations is challenging because of low population densities and elusive behaviour, but reliable data on population size and trends and other important variables, is an essential requirement for objective science-based decisions to be made on wolf management, especially at a time when public debate is highly polarized. This is emphasised in the European Parliament resolution which deplored the lack of harmonised wolf monitoring. It called on the Commission to ensure that Member States use appropriate monitoring methods for each of the different large carnivore species to allow for the compilation of high-quality, comparable and standardised data for an effective assessment of population levels.

In their report on wolf status in geographic Europe, Boitani et al. (2022) also highlighted that estimates of wolf numbers and their precision vary greatly across different countries, making it difficult to compare numbers. While most countries estimate the number of individuals, several countries estimate instead reproductive units (i.e., packs and pairs) and use conversion factors to translate it to numbers of individuals.

Boitani et al. (2022) considered that pack/pair numbers for monitoring purposes (i.e., keeping track of variation through time and space) but are less suited to meet the requirements of the current Red List system and other international systems for status assessment. "Pack to individual conversion factors are most frequently between 6 and 8 but may range from 4 (Belgium) to 10 (Sweden). The variation of conversion factors produces large variations in the estimates of wolf numbers and may be relevant when applying thresholds for conservation assessment." (Boitani et al. 2022).

The benefits of using the same wolf monitoring methods throughout the European Union has been pointed out many times, but this is not easy because wolf monitoring depends not only on ecological aspects (the size of the wolf population, the characteristics of the landscape, the availability of snow in winter, etc.) but also on operational and social aspects, such as the availability of economic and scientific resources, the availability of volunteers or workers to carry out field work, and the ability of institutions to coordinate the work.

Some EU countries, such as Sweden, France and Germany, carry out high-quality wolf monitoring and provide an open and efficient dissemination of the results. The three countries spend substantial economic and scientific resources and began monitoring when the first wolves appeared after their extinction. In addition, Sweden and the alpine zone of France have snow every winter, which facilitates wolf tracking and the collection of demographic and genetic data. We summarize below the characteristics of the permanent monitoring carried out in these countries as well as the monitoring at a population level of the Alpine wolf population carried out in seven European countries.

Wolf monitoring in Sweden

The Scandinavian wolf population is jointly monitored every year by Norwegian and Swedish authorities. The Swedish Environmental Protection Agency and the Norwegian Environment Agency have joint Scandinavian guidelines and instructions for monitoring of wolves. The County Administrative Boards in Sweden and the Norwegian Nature Inspectorate (SNO) together with Inland Norway University of Applied Sciences are responsible for collecting field data. They also confirm reports of tracks and other observations by the public, whose contributions are very important. Wolves are classified in different categories: family groups (three or more animals sharing a territory), territorial pairs, other stationary wolves, and vagrants. Also, number of reproductions is determined each year. This number is especially important as national management goals for the wolf population in both countries are expressed as number of reproducing units.

Three methods are used in combination. Snow-tracking is the basic method. At least 100 field workers are employed full time or part time to find and follow tracks of wolves during the monitoring season 1 October – 31 March. The second method is DNA-analysis, mainly based on wolf scats collected during tracking. DNA-analysis helps verify reproductions, identify newly established pairs, differentiate between neighbouring territories and identify new immigrants from the Finnish/Russian population. The third method is radio telemetry. 10-20 wolves are equipped with GPS-collars each year, this is used to determine the extent of their territories and to differentiate between neighbouring territories. All monitoring data are recorded in national databases and compiled each year in annual monitoring reports. The annual budget for large carnivore monitoring in the two countries combined in 2011 was approximately 5.8 million euro, of which approximately 1.5 million was spent on wolves (Liberg et al. 2012a; Wabakken et al. 2022).

A recent evaluation study concluded that the applied methods for wolf monitoring in Scandinavia worked well, suggesting that virtually all wolf packs, territorial pairs, and reproduction events were detected. Compared to the estimates of many other wildlife species, this yields an extremely low level of uncertainty regarding number and distribution of wolves. A major strength of the Scandinavian monitoring program is the combination of field observations from snow tracking and the collection of samples for DNA analyses. The identification of resident scent-marking individuals in territorial pairs and packs also provides important information about social status and reproduction, which allow for a better understanding of the drivers behind population dynamics and changes in genetic variation. Snow is an important factor for this kind of integrated methodological approach. Without snow, managers would have to rely solely on DNA analyses (Åkesson et al. 2022).

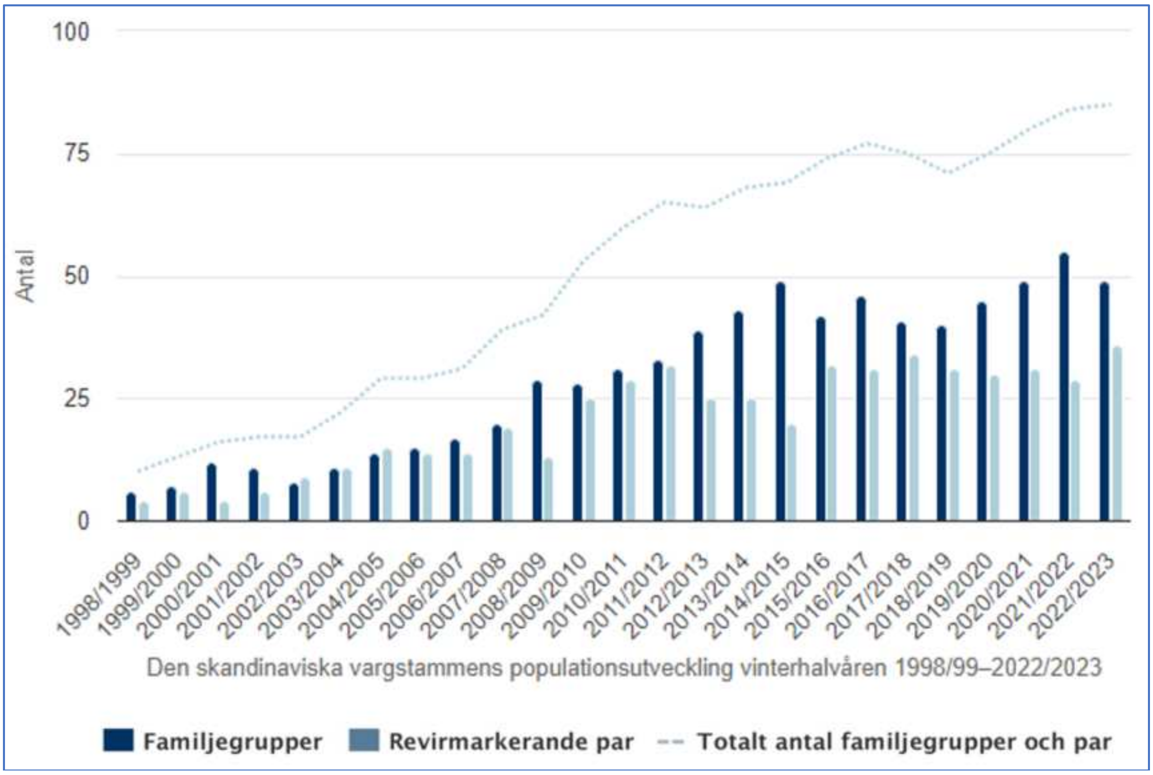

Fig. 2.1.1. Trend in territorial wolf units in Scandinavia (Sweden and Norway). Dark blue bars, packs; light blue, marking pairs. From [Varg, population Skandinavien (naturvardsverket.se)](naturvardsverket.se).

During winter 2022-2023, 49 packs of wolves were documented in Scandinavia (Sweden and Norway); 40 within Sweden, six across the Norwegian-Swedish border and three within Norway. 36 territorial pairs were confirmed: 29 within Sweden, three across the border and four within Norway. Multiplying the number of reproductions by 10, Scandinavian wolf numbers were estimated to 510 (95% CI = 403-663). The Swedish sub-population was estimated to 450 wolves (95% CI = 356-585), including half of the cross-boundary wolves. The calculations include both alive and dead wolves during the monitoring period. The method also allows for the detection of new Finnish-Russian immigrant wolves and an estimation of the inbreeding coefficient which is particularly important in this population with a severe inbreeding depression (Svensson et al. 2023).

Wolf monitoring in France

In France, monitoring is based on a national network of trained observers (n > 4000) distributed across the whole country. Members of the network collect data on signs of wolf presence (scat, visual observations, etc.) in their sampling area and report back to regional coordinators at the Office Français de la Biodiversité (OFB), the public agency responsible for monitoring the wolf population at the national scale. Data are individually checked against standardised technical criteria to check their reliability.

The data are then compiled and synthesised by the OFB in a single national database, and results are published regularly on a public website (https://www.loupfrance.fr/) following annual monitoring campaigns in both summer (new pack detection through elicited howling) and winter (population trend indexes and demographic parameter estimates using sign survey and non-invasive genetic capture-recapture estimates). The OFB also regularly provides training and workshops on wolf monitoring for new members of the network across the country.

Monitoring consists of two steps:

- First, a survey of signs of wolf presence at a large scale provides data from unknown individuals, thereby allowing the detection of new wolf occurrences, new pack formations, and the documentation of geographical trends. Reporting is done opportunistically over the whole area covered by the expert network. Validated data are mapped to monitor the change in wolf distribution over time on the 10 x 10 km EU reference grid.
- Second, when the wolf's presence is considered permanent, each territory is surveyed to estimate pack composition and population parameters (number of individuals, reproduction events, etc.). Surveys are carried out during both winter and summer. The winter survey is based on snow-tracking or on camera traps to monitor pack sizes and composition whereas, in summer, elicited howling protocols are implemented to confirm reproduction.

Finally, non-invasive molecular tracking has been conducted in France since 1995 to identify haplotypes, for genotyping and to monitor wolf-dog hybridization. This non-invasive monitoring is conducted by analysing the scats collected during the snow-tracking survey and then used to model population trends and demography using capture-recapture models (Duchamp et al. 2012; Duchamp & Simon 2022).

Thanks to this information there has been continuous information on the trend of permanent areas of wolf presence, number of breeding packs and estimated number of wolves in France since 1992. The wolf population is estimated at 1,104 individuals at the end of winter 2022-2023, and the 2021-2022 figure was revised upwards from 926 to 1,096 wolves by the OFB thanks to genetic analysis. In the summer of 2021, 145 Permanent Presence Zones including 128 packs and 17 non-packs were identified (Fig. 2.1.2). The wolf is still increasing and expanding in France[8].

[8] https://www.loupfrance.fr/suivi-du-loup/situation-du-loup-en-france/

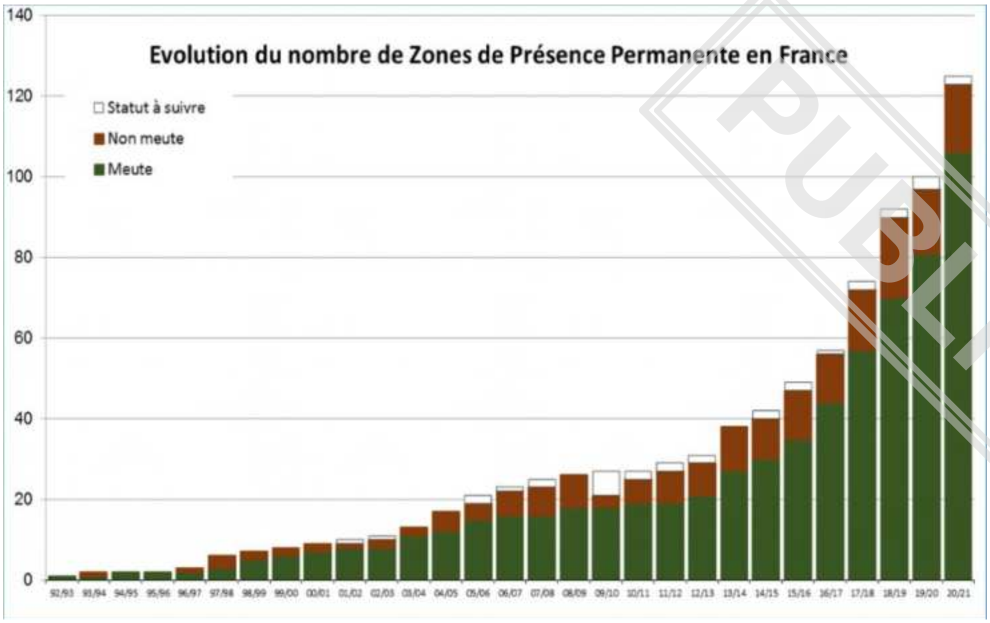

Fig. 2.1.2. Trend in Permanent Presence Zones of wolves in France (OFB). Green: pack; red: no pack; white: uncertain. From https://www.loupfrance.fr/suivi-du-loup/situation-du-loup-en-france/

Wolf monitoring in Germany

Following their extinction in the early 20th century, the first wolf pack was detected in Germany in 2000. Germany is a federal country consisting of 16 federal states (Länder) that are responsible for wolf monitoring. In order to make documentation and observations comparable across Germany, national monitoring standards for large carnivores were developed in 2009 and subsequently updated (Reinhardt et al. 2015).

Once a year, the national wolf monitoring meeting is coordinated by the Bundesamt für Naturschutz (BfN), the federal agency for nature conservation. Federal states present the data which are jointly evaluated and then compiled at a national level by the Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf (DBBW), the federal documentation and consultation centre on wolves[9] that publishes the results of the monitoring in annual reports and on the website. In 2015 the CEwolf scientific consortium was also founded to conduct standardized wolf genetic surveys in eight countries of Central Europe[10].

In Germany, the annual wolf monitoring aims to identify the area of occurrence (number of 10×10 km grid cells with confirmed wolf presence) and the population's size at a national level. Population size is calculated as an index which considers the number of confirmed packs and pairs (minimum count). The number of single territorial wolves (wolves that are resident in an area for at least 6 months, but as yet without a mate) is also provided. In addition, mature individuals confirmed within the wolf territories are counted. However, no attempt is made to get a robust estimate of the total number of wolves, as this would significantly increase the monitoring effort and associated costs. The number of packs and pairs is considered to be biologically more meaningful than the total number of individuals.
During summer, reproduction events are verified (mostly via camera traps) while the priority in winter is to collect genetic samples, if possible from the breeding (marking) individuals. The genetic analyses

[9] https://www.dbb-wolf.de
[10] https://www.senckenberg.de/en/institutes/senckenberg-research-institute-natural-history-museum-frankfurt/division-river-ecology-and-conservation/cewolf-consortium/

conducted by the Senckenberg Centre for wildlife genetics play an important role in the monitoring (Reinhardt 2022).

Between 1 May 2022 and 30 April 2023, 184 packs, 47 pairs and 22 territorial lone wolves were detected in Germany. The reproduction of 169 packs and the presence of 635 pups were confirmed. The territorial wolves occurred in 12 federal states and 21 packs crossed federal state borders[11].

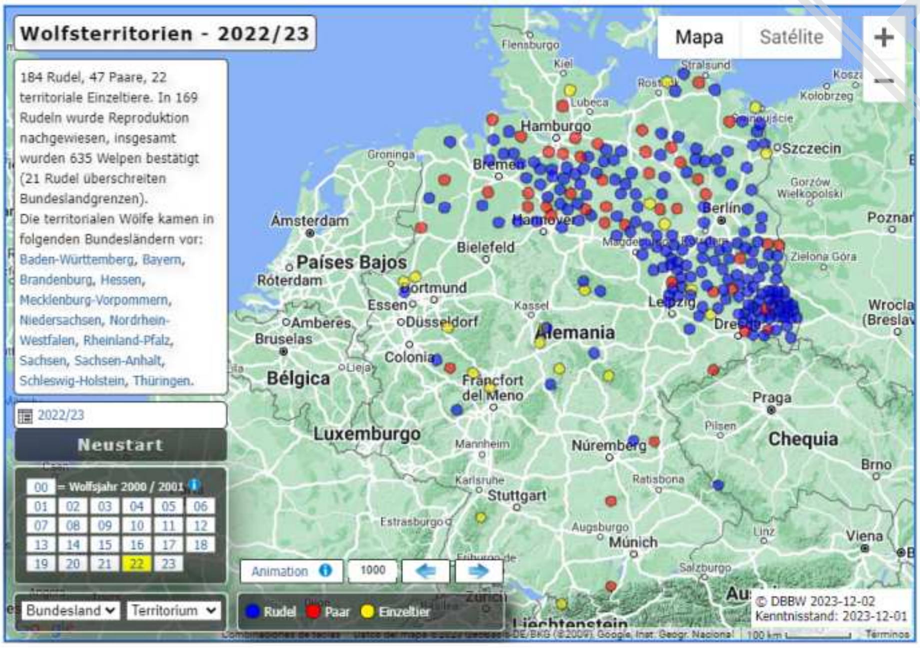

Fig. 2.1.3. DBBW website which shows the results of monitoring in Germany. Blue: pack; red: pair; yellow: lone wolf. From https://www.dbb-wolf.de/Wolfsvorkommen/territorien/karte-der-territorien

Wolf monitoring in Italy

In Italy, a first national wolf survey was carried out during 2020-2021 both in the Alps and in the Apennines. The survey method included transects along 85,000 km carried out by more than 3,000 field assistants in the 1000 10x10 km grids where wolf presence had been previously detected, and also involved the collection and genotyping of scats and the estimation of wolf numbers using spatially explicit capture-recapture models.

The information provided by snow-tracking and camera traps was also used. In the study period, wolves were present in 41,600 km^2 in the Alps and in 108,534 km^2 in the Apennine. In total, 3307 wolves were estimated (confidence interval 95%: 2945-3608) in both areas. The field monitoring required a huge logistical, technical and coordination effort, involving a large number of field assistants, institutions and associations from all over Italy. The creation of a national network of trained operators will be another important outcome of this project in the long term[12].

Monitoring at a population level: the Alpine wolf population

Wolf expansion in Europe is occurring over administrative boundaries and most wolf populations are shared by two or more countries (see section 2.3 on European wolf populations). The "Guidelines for

[11] dbb-wolf.de/wolf-occurrence/confirmed-territories/map-of-territorie
[12] Risultati — Italiano (isprambiente.gov.it

Population Level Management Plans for Large Carnivores in Europe" (Linnell et al. 2008), endorsed by the European Commission, emphasized the importance of monitoring wolves at the population level.

As already seen, this transboundary monitoring is carried out in the Scandinavian wolf population, between Sweden and Norway. Another notorious case of monitoring at a population level is that of the Alpine wolf population that began to form in the early 1990s with wolves that dispersed from the Apennines (Fabbri et al. 2007). This population currently covers seven countries (Italy, France, Austria, Switzerland, Slovenia, Liechtenstein and Germany), making the development of a joint and coordinated monitoring program particularly challenging (Marucco et al. 2023).

After founding the Wolf Alpine Group (WAG), researchers developed uniform criteria for the assessment and interpretation of field data collected in the frame of different national monitoring programs. This standardization allowed for data comparability across borders and the joint evaluation of distribution and consistency at the population level. The WAG documented the increase in the number of wolf reproductive units (packs and pairs) over 21 years, from 1 in 1993–1994 up to 243 units (206 packs and 37 pairs) in 2020–2021, and examined the pattern of expansion over the Alps. This long-term and large-scale approach is a successful example of transboundary monitoring of a large carnivore population that, despite administrative fragmentation, provides robust indexes of population size and distribution that are relevant for wolf conservation and management at the transnational Alpine scale (Marucco et al. 2023).

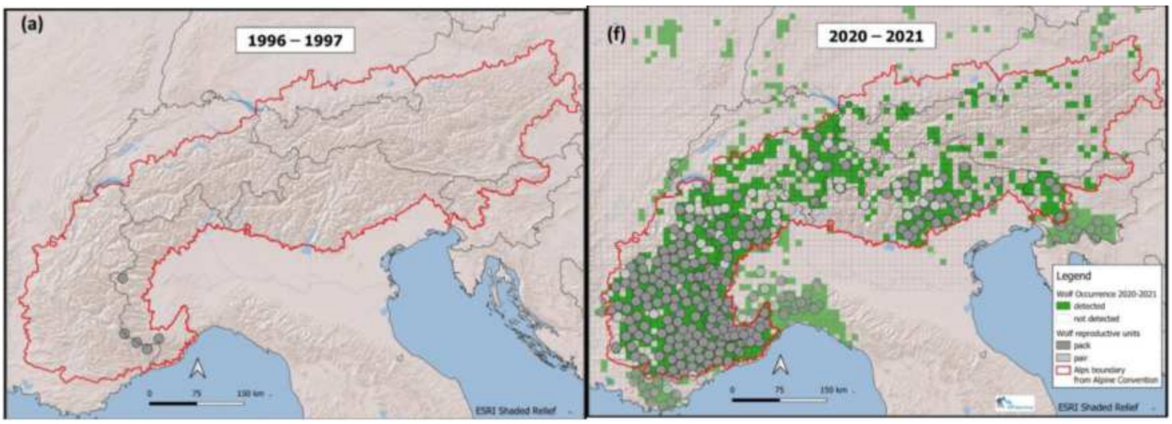

Fig. 2.1.4. Increase and expansion of the Alpine wolf population from 1996-1997 to 2020-2021. From Marucco et al. (2023).

2.2. Conservation status assessments according to Article 17 of the Habitats Directive

Under Article 17 of the Habitats Directive, each Member State is obliged to report every six years to the European Commission on the conservation status of the natural habitats and species listed in the Annexes that are present in their country. The European Environment Agency then pools the data together and makes an assessment of the conservation status per EU biogeographic region in order to see how well they are faring within each of the EU's nine biogeographical regions.

At the EU biogeographical level, the most recent 'Article 17' reports covering the period 2013-2018 conclude that the wolf is present in seven biogeographical regions of the European Union (Pannonian, Continental, Alpine, Atlantic, Mediterranean, Black Sea and Boreal)[13]. However, it only has a favourable conservation status in the Alpine region[14]. In the other six, the wolf has an unfavourable-

[13] https://nature-art17.eionet.europa.eu/article17/species/summary/?period=5&group=Mammals&subject=Canis+lupus&region=

[14] The Alpine biogeographical region includes the Alps, the Apennines, the Pyrenees, the Scandes and the Carpathians

inadequate conservation status, meaning that, even if the species is no longer threatened in the foreseeable future, further efforts are required for it to reach a favourable conservation status across the region. In the previous assessment (2007-2012), the wolf was in favourable conservation status in two of the seven biogeographical regions, the Alpine and the Atlantic.

To recall, according to the Habitats Directive, the status of a species is deemed favourable when, *inter alia*, the species "is maintaining itself on a long-term basis as a viable component of its natural habitats" and "there is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis."

For species, the four components that define a conservation status assessment are range, population, habitat and future prospects. All four elements need to be favourable (or three favourable and one unknown) for the species to be considered to have reached a favourable conservation status. The latest Article 17 provides the following information on each of the components as regards the wolf:

- *Range.* Wolves extend over an area of 1,706,690 km^2 in the EU. The largest area is found in the Boreal biogeographic region (44.5% of the wolf range), followed by the Continental (23.8%) and the Mediterranean (15.7%). The range is increasing in 6 of the 7 regions and stable in the remaining (Black Sea). The status of the range is favourable in three regions (Alpine, Black Sea and Boreal) and unfavourable –inadequate in the remaining four regions.
- *Population Status.* In 2013-2018 there were around **11,000-17,000 wolves in the EU (best value: 13,492** wolves), of which 28.5% were in the Continental region, 27.8% in the Alpine and 23.7% in the Mediterranean. The population trend is increasing in four regions (Pannonian, Continental, Mediterranean and Boreal), stable in two (Alpine and Black Sea) and unknown in the Atlantic. The population status is favourable in one region (Alpine) and unfavourable –inadequate in the remaining six. In accordance with the art. 17 reporting guidelines, the short-term trends assessed by MS refer to a period of about 12 years/two reporting cycles (Table 2.2.1).
- *Habitat:* The habitat is improving in two regions (Alpine and Mediterranean) and stable in the rest. The status of the habitat is favourable in six regions and unfavourable –inadequate only in the Mediterranean region.
- *Future prospects:* The future prospects are favourable for the Alpine and Boreal regions, unfavourable –inadequate for the remaining four regions and unknown for the Atlantic region.

MEMBER STATES	Number of wolves	Trend
Austria	29-36	+
Belgium	4-6	Not reported
Bulgaria	800-1200	=
Croatia	172-194	+
Czech Republic	5-80	+
Estonia	180-260	+
Finland	168-193	=
France	387-477	+
Germany	152-166	+
Greece	907-1134	+
Hungary	40-60	+
Italy	1363-2765	+
Latvia	1126-1187	+
Lithuania	136-200	=

Luxembourg	1-2	+
Poland	1190-2582	+
Portugal	118	=
Romania	2500-3000	=
Slovakia	302-610	=
Slovenia	72-78	+
Spain	1234-2390	uncertain
Sweden	310-430	+

Table 2.2.1. Number of wolves and trend in EU Member States according to the last Art. 17 reporting (2013-2018). + increasing; = stable.

In the reporting 2013-2018, 21 countries reported 39 national biogeographic assessments, of which 18 were favourable (FV), 16 unfavourable-inadequate (U1), three unfavourable-bad (U2), and two unknown (XX). The previous reporting (2012-2017) included 33 regional assessments. Although wolves have shown an overall positive population trend since 2017, the wolf assessments with a favourable conservation status decreased slightly from 19 (2007 – 2012) to 18 (2013 – 2018). At the same time, the number of wolf assessments with an unfavourable conservation status (U1 + U2) increased from 13 to 19.

At the Member State level, in the period 2013-2018 the wolf had not yet achieved a favourable conservation status in most countries. Only five (Romania, Lithuania, Latvia, Estonia and Italy) have reported the wolf as being in favourable conservation status in all their biogeographical regions where the species occurs.

2.3. IUCN red list assessment at population level and Member State level

The Large Carnivore Initiative for Europe (LCIE) categorized the wolf into 10 populations based on a combination of distribution and social, ecological and political factors (Boitani et al. 2015; Boitani 2018): North-Western Iberian, Sierra Morena, Alpine, Italian Peninsula, Carpathian, Dinaric-Balkan, Baltic, Karelian, Scandinavian and Central European Lowlands.

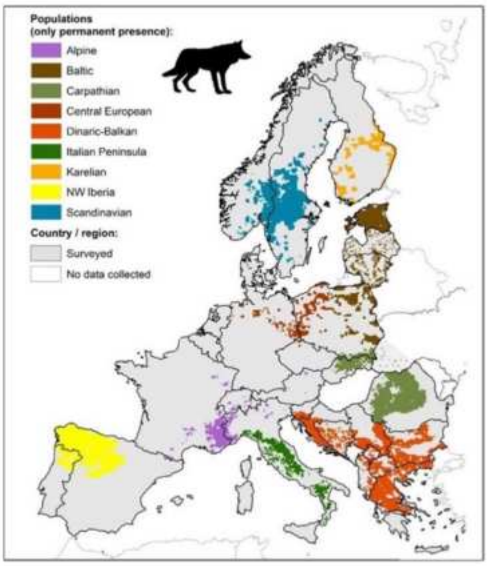

Fig. 2.3.1. Wolf populations in Europe in 2015 (from Boitani et al. 2022). The map does not show yet the wolf areas recently established in the Netherlands, Belgium and other countries of central Europe.

All populations are the results of natural dynamics as no wolf reintroduction has ever been carried out in Europe. The Sierra Morena (southern Spain) population has been declared (virtually) extinct in 2014, although it was probably already extinct when it was first established, between 2012 and 2015.

European Red List assessment of the wolf

The International Union for Conservation of Nature (IUCN)'s Red List of Threatened Species has become the world's most comprehensive information source on the global conservation status of animal, fungi and plant species. The assessment considers qualitative data on the geographic range, the population size (the main information used for wolves) and trend for the classification of species or populations. Threatened populations can be in three categories: Critically endangered (CR): extremely high risk of extinction in the wild; Endangered (E): very high risk of extinction; or Vulnerable (VU): high risk of extinction. The non-threatened categories are Near Threatened (NT) (not threatened but close to qualifying for or likely to qualify for a threatened category in the near future) or Least Concern (LC): widespread and abundant taxa.

The conservation status of species can be assessed on a global scale, considering their entire distribution area, or on a regional scale. The smaller the scale at which a population is assessed, the more likely it is to be listed as threatened, since it has fewer individuals and a smaller range. Sometimes, the wolf assessment on a national (especially in small countries) or local scale becomes meaningless.

The conservation status of the wolf (*Canis lupus*) has been assessed by the IUCN at the global level, at the European level and also at the level of each European population. At a global scale, the wolf is listed as Least Concern (Boitani et al. 2018). The global population is stable and estimated to be in the order of 200-250 thousand individuals. In geographic Europe, the wolf is also listed as Least Concern (Boitani 2018). The overall European wolf population can be viewed as a large metapopulation with several distinct fragments, although dispersal could theoretically connect almost all fragments, and connections are being re-established in many areas. Following the bottleneck of the 1960s and 1970s, the European wolf population is generally increasing in number and expanding its distribution range.

However, some European populations are still small and not all have more than 1,000 mature individuals (the thresholds below which a population would be listed as "Vulnerable" under the Red List criterion D.1). The number of wolves in geographic Europe (excluding Russia) was likely to exceed 17,000 in 2018.

The conservation status of each European population has been assessed by Boitani (2018). Of the nine currently existing European populations, six were considered as non-threatened and the three remaining were listed as Vulnerable (the Western- Central Alps, the Scandinavian and the Central Europe populations), all of them under the criteria D.1, i.e., "population size estimated to number fewer than 1000 mature individuals"[15]. Alpine and Central Europe populations have increased and expanded from 2018 until 2022 (Boitani et al. 2022; Marucco et al. 2023). Three of the non-threatened populations have been considered as NT (Iberian, Italian Peninsula and Karelian populations) because their numbers are close of the category Vulnerable, and the remaining three populations are large enough to be considered as LC. They are the Dinaric-Balkan (c.4,000 wolves), the Carpathian (c.3,460-3,840 animals) and the Baltic population, with c.1,713–2,240 wolves in the EU member states, but contiguous with Russia and Belarus wolf range (Boitani 2018).

[15] (https://www.iucnredlist.org/resources/categories-and-criteria)

National Red List assessment of the wolf in different Member States

Many EU Member States have assessed the wolf conservation status in their country according to IUCN criteria, as has been recently shown by Boitani et al. (2022). Nevertheless, these listings must be considered with some caution. On the one hand, most of the national red books in the European Union are out of date, and some of them even date from 2005 (Boitani et al. 2022, table 2). In addition, as some countries are very small, they cannot harbour large populations of wolves, so they inevitably have higher threat categories than the biological populations where they are integrated (Boitani 2018).

Almost a quarter of the EU countries do not have the wolf included in their Red Books, in some cases because they have very recent (Netherlands) or very small (Luxemburg) populations. Two countries, Austria (2005) and Belgium (2011), considered wolves as Regionally Extinct when they had not yet been established in them. Otherwise, the red books of 11 countries (44%) consider wolves threatened (CR, E, or VU) within their national territories, five as Near Threatened (Croatia, Italy, Poland, Slovak Republic and Spain) and only Romania considers it as Least Concern.

	Member States
Not included in RB	Bulgaria, Hungary, Latvia, Lithuania, Luxemburg, Netherlands
Regionally Extinct	Austria (2005), Belgium (2014)
CR	Czech Republic (2017)
EN	Finland (2019), Portugal (2022), Slovenia (2002), Sweden (2020),
VU	Denmark (2018), Estonia (2022), France (2017), Germany (2020), Greece (2009)
NT	Croatia (2014), Italy (2022), Poland (2001), Slovak Rep. (2001), Spain (2007)
LC	Romania (2002)

Table 2.3.1. Wolf threat category in each Member State according to the national Red Books (RB). From Boitani et al. (2022)

When comparing the Red List assessment with those of the art. 17 of the Habitats Directive assessments, some apparent inconsistencies appear. For example, Sweden listed their wolf population as Endangered in the national Red Book (2020), but in the last report of the art. 17 (2013-2018) the wolf conservation status in the boreal region of Sweden was considered favourable. By contrast, Poland and Spain listed the wolf as Near Threatened in their national Red Books, but in the art. 17 reporting Poland considered it as unfavourable-inadequate in the Continental region, and Spain also considered it as unfavourable-inadequate in its three biogeographic regions (Alpine, Atlantic and Mediterranean). These differences may be explained in part by the fact that red data books measure the risk of extinction of a population while the art. 17 reporting reflects the difference between the favourable reference values and the current status of wolves.

2.4. Updated information on wolf numbers in the European Union

This section presents the most recent information available on wolf numbers in the EU. It is based on several sources of information:

- The first is the report by Boitani et al. (2022), submitted to the Bern Convention which gave updated information on wolf numbers and trends in geographic Europe, using data provided by the members of the Large Carnivore Initiative for Europe (Species Survival Commission, IUCN).

- The second is based on information received in response to the European Commission's data collection exercise launched on 4 September 2023, inviting local communities, scientists and all interested parties to submit up-to-date data by 22 September 2023 on wolf population and their impacts. Over 19,000 emails were received in response to the call. Over 98% of those who sent an input wanted to express an opinion on the subject, rather than submit data. The remaining 2% provided some data on wolf populations and their impact on national, regional or district level and were analysed in detail (see Annex 1).
- Finally, data from regional and national authorities, in addition to other reliable information collected on official web pages (see section 4.4), through scientific and technical literature and consulting national experts were used.

On 17 November 2023, the information gathered from the above was sent to the Ministries of Environment of the Member States for review. Their comments and corrections have also been incorporated in Tables 2.4.1 (wolf numbers) and 3.3.1 (damage to livestock). **The latest information on wolf population in EU Member States is presented in table 2.4.1.**

As can be seen, in 2023, wolves are found in the 24 continental countries of the EU, i.e., all except Ireland, Cyprus and Malta. In all 24 countries except Luxembourg, breeding packs have been detected in 2023. Across the EU, a total of about 20,300 wolves have been estimated with the information available in 2023 (Table 2.4.1). This figure is slightly higher than the 19,400 wolves estimated by Boitani et al. (2022) and significantly higher than the 11,193 wolves estimated in 2012 (Boitani et al. 2015).

The countries with the most wolves in the EU are Italy (3,307), Romania (2,500-3,000), Spain (>2,100), Poland (1,886), Germany (1,400) and Greece (1,020). Wolf numbers in Bulgaria are uncertain. Although the official data is 2,712 wolves (Table 2.4.1), Boitani et al. (2022) suggested that this high number is likely the result of very imprecise estimates. The figure reported by the Bulgarian government to the EC in the period 2013-2018 (800-1,200 wolves) seems to be more plausible even if the precise number is unknown.

Wolf trends.

The column on wolf trends (table 2.4.1) reflects expert judgement based on information provided by the Member States competent authorities. It is important to note however that there is no consistent or common approach towards assessing trends in wolf populations across the EU. This is because assessing wolf numbers is both difficult and expensive. Some Member States assess wolf numbers every year (section 2.1), others do it every 10 years, others do it when they have the opportunity to, while still others have never undertaken a full, detailed survey of their population. As a result, the period over which the trend in wolf populations is assessed also varies considerably from one country to another and is not the same for each Member State.

Because of this diversity of circumstances across the European Union, it is difficult to establish the overall trends. This can vary depending on the period over which it is assessed as well as other factors such as how the assessment is done. In Member States where wolves are not regularly surveyed each year, the population trend is generally based on expert opinion only. In many Member States, whilst it is not known exactly how many wolves are present, there are clear signs that they are increasing because their range is expanding and new packs are settling in areas where wolves have long been absent.

Table 2.4.1. WOLF POPULATION IN THE EU MEMBER STATES.

MEMBER STATE	Packs/pairs	N. of wolves	Year	Trend	Source
Austria	7 packs	58 wolves genotyped and at least 70-80 estimated	2022	Increasing	Federal Min. Environment, EC data collection
Belgium	4 packs	[28]*	Sept 2023	Increasing	http://biodiversite.wallonie.be/fr/actualites.html?IDC=6489 Wolf Fencing Team Belgium, EC data collection
Bulgaria		2712	2021	Increasing	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47
Croatia	43 packs	243	2023	Fluctuating	Ministry of Economy and Sustainable Development Kusak, J., D. Hipolito, D. De Angelis, L. Šver, G. Gužvica (2023): Procjena parametara potrebnih za ocjenu stanja očuvanosti vuka i revizija referentnih vrijednosti. Veterinarski fakultet Sveučilišta u Zagrebu, 96 str.
Czech Republic	29 wolf territories	120-150	March 2023	Increasing	Min. Environment, EC data collection[1]
Denmark	2 packs, 4 pairs	30 wolves in spring 2023 + 14 pups born in 2023	Nov. 2023	Increasing	Sunde et al. 2023 https://dce.au.dk/fileadmin/dce.au.dk/Udgivelser/Notater_2023/N2023_41.pdf Peter Sunde (LCIE), pers. comm.
Estonia	33 packs	300-330	Nov 2022	Increasing	Game monitoring report 2023 compiled by Environment Agency. Keskkonnaagentuur (keskkonnaportaal.ee)
Finland	42 packs (40-46), 19 pairs (16-23)	310 (291-331)	March 2023	Increasing	Heikkinen S et al. (2023). Susikanta Suomessa maaliskuussa 2023. https://jukuri.luke.fi/handle/10024/553603

MEMBER STATE	Packs/pairs	N. of wolves	Year	Trend	Source
France	157 packs	1104 (1000-1210)	2023	Increasing	Office Français de la Biodiversité (OFB). https://www.caminteresse.fr/animaux/combien-y-a-t-il-de-loups-en-france-11189169/
Germany	184 packs, 47 pairs, 22 territorial individuals	[1404]*	2022/2023	Increasing	Map of territories - DBBW-E (dbb-wolf.de)
Greece	186 packs	1020	2014	Increasing	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47
Hungary		60-70	2021/2022	Increasing	National Parks directorates and Min. Agriculture
Italy		3307 (2945- 3608)	2020/2021	Increasing	Italy. First National Wolf Monitoring. https://www.isprambiente.gov.it/it/attivita/biodiversita/monitoraggio-nazionale-del-lupo
Latvia		700	2020	Fluctuating	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47
Lithuania	91 packs	728	2023	Increasing	Ministry of the Environment of the Republic of Lithuania, EC data collection. https://vstt.lrv.lt/uploads/vstt/documents/files/Vilk%C5%B3%20tyrimai/Galutine%20ataskaita%202022_23%20nuasmeninta%20fin.pdf
Luxembourg		0-2	2023	Increasing	https://www.sr.de/sr/home/nachrichten/vis_a_vis/wolf_im_osten_luxemburgs_nachgewiesen_100.html
Netherlands	9 packs with 39 pups	[63]*	Sept 2023	Increasing	https://www.bij12.nl/onderwerpen/faunazaken/diersoorten/wolf/ https://www.dutchnews.nl/2023/09/the-netherlands-is-now-home-to-nine-wolf-packs-and-39-cubs/.
Poland		1886	2021	Increasing	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47

MEMBER STATE	Packs/pairs	N. of wolves	Year	Trend	Source
Portugal	50-60 packs	300	2023	Stable	Pimenta V et al. (2023) Canis lupus lobo. https://www.icnf.pt/imprensa/livrovermelhodosmamiferosdeportugalcontinental2023
Romania		2500-3000	2019	Stable	Min. Environment, Waters and Forests- EC data collection.
Slovakia		400-600	2023	Increasing	State Nature Conservancy of the Slovak Republic
Slovenia	17 packs (5 shared with Croatia)	116**	2022/23	Stable	Ministry of National Resources and Spatial Planning of Slovenia
Spain	>300 packs	[>2100]*	2022	Stable/ Slightly increasing	Min. Environment. (MITECO, considering partial updates to the 2012-2014 national survey. EC data collection[2]
Sweden	46 packs (6 shared with Norway), 32 pairs (3 shared with Norway)	450 (356-585)	Winter 2022-2023	Increasing/ Stable	Svensson L et al. (2023). **Inventering av varg vintern 2022-2023**. Bestandsovervåking av ulv vinteren 2022-2023. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2023. 65s.
Total EU		**20,356 wolves**			

[]* Some MS estimate only the number of packs/pairs but do not provide figures on wolf numbers. For practical purposes, we have estimated the number of wolves in Belgium, the Netherlands, Germany and Spain by multiplying the number of packs by 7 (according to Boitani et al. 2022) and the number of pairs by 2.
**After correcting for transboundary wolves

[1] The Ministry of Agriculture estimates wolf numbers in Czech Republic at 986 individuals but it goes on to explain that, "*the number of wolves stated in the table is the number of wolves reported by hunters based on the statistical counts annually. It is important to mention that hunters report number of woless from their hunting grounds. Wolf home range is roughly about the size of 2-4 hunting grounds therefore some wolves could be counted multiple times*". The figures from the Ministry of Environment were therefore used for the In-depth Analysis Report as they are based on a more robust monitoring methodology.
[2] The Ministry of Environment and the Autonomous Regions have announced that they intend to carry out a national wolf survey in 2024

SOURCES AND FOOTNOTES REGARDING TRENDS

Austria: Extirpated at the mid of the 19th century. Since 2009, wolves immigrate regularly from neighbouring populations.https://www.lifewolfalps.eu/en/the-wolf-in-the-alps/the-wolf-in-austria/

Belgium: Wolves reproduced in Belgium in 2020 for the first time in more than a century. https://www.zoogdiervereniging.nl/sites/default/files/2021-10/Lutra%2064%281%29_Van%20Der%20Veken%20et%20al_2021.pdf

Czech Republic. After being exterminated in the 19th century, first wolves settled around 2014. https://wolf.org/wow/europe/czech-republic/

Denmark. The first pair of wolves in the last 200 years was detected in 2017. https://www.newsweek.com/wolves-denmark-200-years-594538

Finland. The number of packs increased from less than five in 1990 to more than 40 in 2023. Pages 10-11 in https://jukuri.luke.fi/handle/10024/553603

France. See Fig. 2.1.2.

Germany. See *https://www.dbb-wolf.de/Wolfsvorkommen/territorien/karte-der-territorien*

Hungary. In 2005, only 3–6 single wolves were estimated in Hungary. https://link.springer.com/article/10.1007/s42991-022-00287-7

Italy. About 100 wolves were estimated in the early 1970s. https://www.jstor.org/stable/2641574#:~:text=In%20Italy%20the%20population%20is,(Zimen%20%26%20Boitani%201975).

Luxembourg. First wolves were detected in 2017 after becoming extinct in 1893. https://www.degruyter.com/document/doi/10.1515/mammalia-2020-0119/html#:~:text=The%20wolves%20detected%20near%20Garnich,evidence)%20(Schley%20et%20al.

The Netherlands. The first wolf territory was established in 2018. https://www.authorea.com/doi/full/10.22541/au.169624987.70372590/v1

Poland. In western Poland, the population increased from a few wolves in 2001 to 95 packs in 2019. https://d1jyxxz9imt9yb.cloudfront.net/resource/672/attachment/original/Recovery_of_wolves_and_their_ecology_in_Western_Poland_in_2001-2019.pdf

Spain. Since 2014, the range of the breeding population has barely expanded, although the number of packs has increased at least in some peripheral areas.

Sweden. Increase in the long term, stable during the last decade (see Fig. 2.1.1).

The trend of the wolf population can also change depending on the period considered. For example, in Sweden (Fig. 2.1.1), the wolf population trend estimated from the 1990s to the present is clearly increasing; however, if one looks only at the last decade, the trend is more or less stable; and, if one looks just at the last two years (Table 2.4.2) one could think that the population is decreasing, although the small reduction from 460 to 450 wolves is not a good indicator of overall trends, especially considering the wide confidence intervals of the estimates.

While recognizing that wolf figures are approximate because, in some Member States, wolf surveys can be imprecise and because double counting of transboundary packs has not been corrected, an overall increase of the wolf population in the EU is clear. In 17 of the 24 EU Member States with wolves, populations are increasing whereas, in the remaining EU countries, there is no obvious change in the population or they are fluctuating. The increase of wolves across Europe in the last 40 years was shown by Chapron et al. (2014). In the last decade only, an increase of over 25% of wolf range has been reported in Europe (Cimatti et al. 2021, in Boitani et al. 2022), and this positive trend is confirmed by the present analysis

The country where wolves have increased the most is Germany, where from 2000 (one pack) to 2015 (47 packs) wolves experienced an annual increase of about 36% (Reinhardt et al. 2019), but the growth has been slowing down steadily to 14% for the period 2018-2020 (Singer et al. 2023). In 2022, 184 packs were detected in Germany (Table 2.4.1). Since 2017, some breeding packs have been established in small Western European countries which are densely populated, such as Denmark, the Netherlands and Belgium (Table 2.4.1). Table 2.4.2 shows wolf population data in the last two or three years in some countries where they have been annually monitored and numbers are comparable.

MEMBER STATE	Boitani et al. 2022 (year)	This report (year)
Belgium	2 packs (2022)	4 packs (2023)
Czech Republic	100 wolves (2021/22)	120-150 (March 2023)
Denmark	14 wolves (2021)	44 wolves (2023)
Estonia	240 wolves (2021)	300-330 (2022)
Finland	290 wolves (2022)	310 wolves (2023)
France	783 wolves (2021)	1104 wolves (2023)
Germany	158 packs, 27 pairs (2021/2022)	184 packs, 47 pairs (2022/2023)
Lithuania	504 wolves (2021)	728 wolves (2023)
Netherlands	15 wolves (2022)	9 packs* (2023)
Sweden	460 wolves (2022)	450 wolves (2022/23)

* Around 63 wolves (9x7)

Table 2.4.2. Wolf population data in recent years in some EU Member States

2.5. Threats and mortality

Europe is a densely populated continent, and wolves are subject to a lot of pressure from people, whether through legal hunting/culling, poaching, or traffic mortality. In addition, wolves may have genetic problems by hybridization with dogs (Salvatori et al. 2019), due to inbreeding, which is especially important in the Fennoscandian population (Liberg et al. 2005; Laikre et al. 2016), or due to the loss of genetic diversity caused by fragmentation or as a result of past persecution (Salado et al. 2023).In this section, the actual and potential threats to wolves in the European Union are reviewed using best available information. Part of this information is based on the expert judgment of specialists and part is collected from technical documents and scientific papers published in recent years. Many of these point out the great impact of poaching and the difficulties experienced in detecting it.

Threats of wolves deduced from expert judgement

In 2015, the Large Carnivore Initiative for Europe (LCIE) published a report in which the main problems of the nine biological populations of wolves were considered. The main threats identified by the European experts were "low acceptance, habitat loss due to infrastructure development, persecution, hybridization with dogs, poor management, structures and accidental mortality" (Boitani et al. 2015). The most important threat was the low acceptance of wolves by some parts of the society (mainly caused by the widespread attacks on livestock) which is likely to be the primary cause of most legal and illegal killing of wolves in Europe.

In 2022, LCIE carried out a further assessment of the threats to wolves in geographic Europe according to IUCN classification, which was again done using qualified expert judgment (Boitani et al. 2022). According to this assessment, "roads, illegal killing and disturbance from tourism-related activities are all reported in more than a quarter of all countries followed by other disturbances due to housing, industrial development and forestry. However, threats vary in strength and persistence depending on local conditions" (Fig. 2.5.1.)

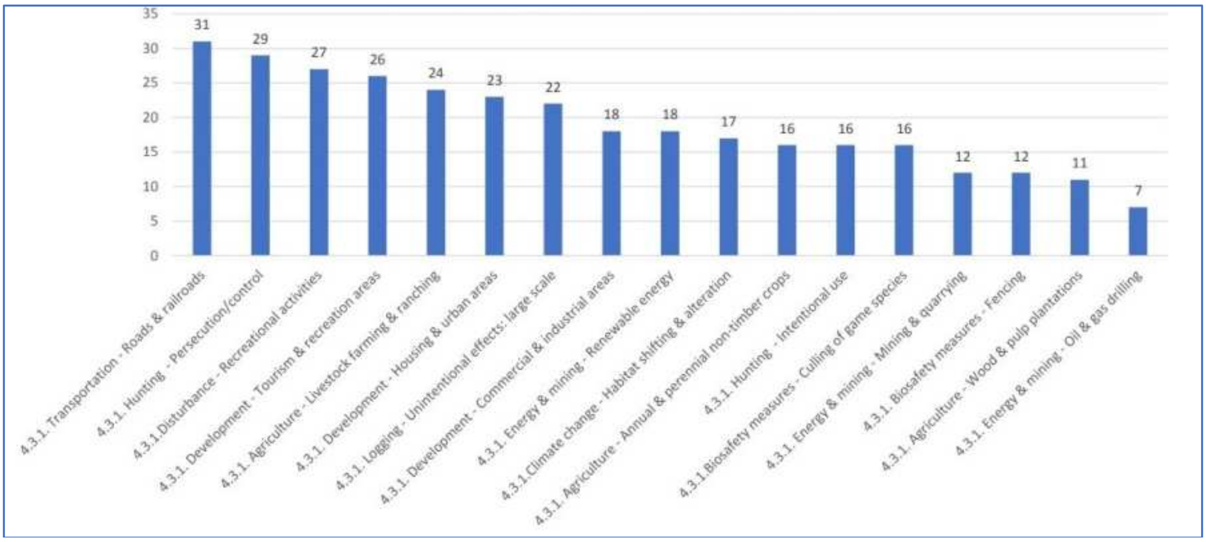

Fig. 2.5.1. Most common threats to wolves in geographic Europe, from Boitani et al. (2022). Figures represent the number of countries where the threat was detected.

Pressures and threats identified by Member States in Article 17 reports of the Habitats Directive

The Article 17 reports under the Habitats Directive also record and rank the key Pressures (current impacts) and Threats (future impacts) that affect the listed species and habitats[16]. In the case of the wolf, these have been analysed at the level of each biogeographic zone in each MS, considering only those classified as High importance/impact and those that appear in at least two different reports. In total, nine types of such pressures and threats have been reported (Fig. 2.5.2).

The most frequently reported pressure is "illegal shooting/killing" which is further supported by the pressure "Poisoning of animals", in fourth place since both are linked to the problem of wolf poaching. The "impact of roads, paths, railroads and related infrastructure" is in second place, both for the direct mortality caused by traffic accidents and for the fragmentation they can produce across populations. The "interactions with agricultural activities" (i.e., damage to livestock) occupy the third place (Fig. 2.5.2).

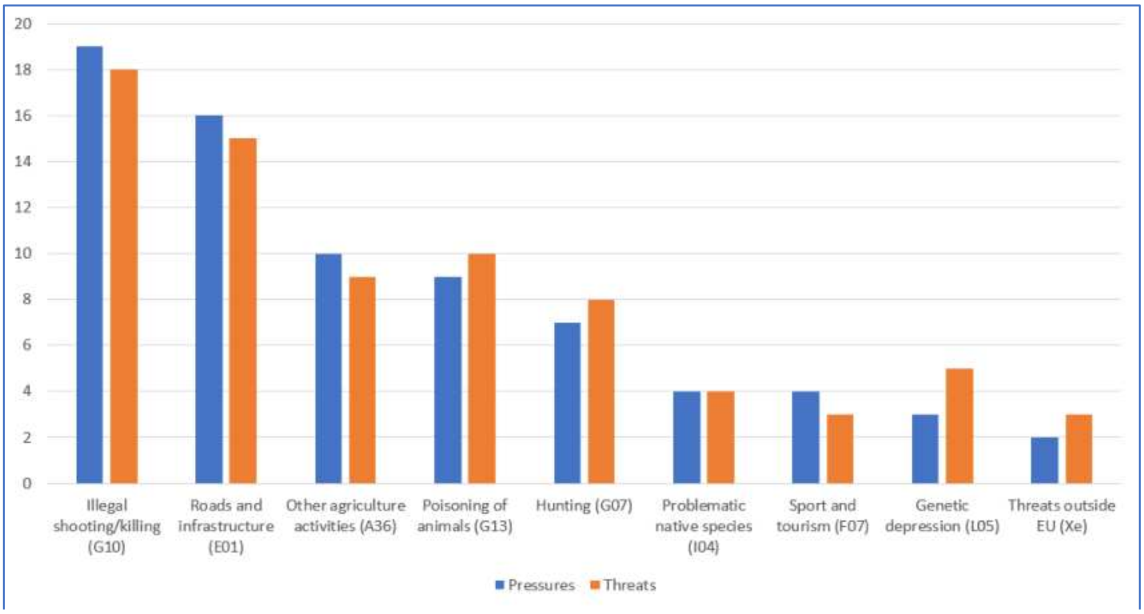

Figure 2.5.2. Frequency (number of MS) of high importance/impact Pressures and Threats reported by MS (2013-2018).

Some Member States consider G07- Hunting (as a legal activity) as a high Pressure for the wolf. This is the case, for instance, in Spain and Slovakia, where national governments have recently forbidden the legal hunting of wolves even though it is listed in Annex V of the Habitat Directive (except for the small Spanish population south of the Duero River, which is in Annex IV).

There are also seven Pressures and Threats that have only one vote each. Among those, it is worth highlighting "Closure or restricted access to site/habitat", considered as a Threat by Latvia in relation to the building of a fence along the Russian and Belorussian border to control immigration. It should be noted that several fences are currently being built between different European countries to control the movement of people, which pose a fragmentation risk for populations of wolves and other mammals (Linnell et al. 2016; Trouwborst et al. 2016; Jakes et al. 2018).

[16] https://cdr.eionet.europa.eu/help/habitats_art17

A review of wolf mortality extracted from scientific papers and technical reports

A review of causes of mortality across the EU, extracted from scientific papers or from official data also reveal several general patterns, which largely reflect those already mentioned above.

While all conclude that humans directly or indirectly are the main cause of wolf mortality in Europe (as it also happens in North America, Hill et al. 2022), the causes of mortality often depend on the method used. In studies based on the collection of 'found-dead' wolves, mortality from legal hunting/culling or traffic is much more frequent because it is more easily detected than poaching. The high importance of poaching is, on the other hand, only revealed in radiotracking studies. In these studies, poaching emerges as an important cause or as the most important cause of mortality, sometimes also in countries where hunting/culling is allowed.

A summary of the information collected in field studies across the EU (Table 2.5.1) shows that legal killing is the most frequently detected cause of mortality in the Member States where hunting or culling are legal. This is the case for example of Spain (where hunting and culling were allowed until September 2021) or Sweden.

Traffic accidents are usually the main cause of detected mortality in countries where wolves are not hunted or culled and/or where they live in densely population areas, as in Germany.

Cause of death	Alps	Spain	Italy	Germany	Poland	Sweden	Finland
Legally killed	14.0	68.0	0	1.3	27.8	66.9	3.8
Illegally killed	38.4	7.6	35.4	9.3	24.1	13.0	57.2
Traffic	36.0	15.4	49.0	74.3	38.9	5.2	4.4
Natural	3.5		9.9	8.9	7.4	14.9	1.1
Others		0.5					5.5
Unknown	8.1	8.5	5.7	6.2	1.9		
TOTAL NUMBER	86	644	212	891	54	154	91

Table 2.5.1. Causes of wolf mortality (percentages) in several EU Member States and areas. Total numbers include dead wolves in both types of studies mentioned: 'found-dead' wolf studies and radiotracking projects.

*Source: **Spain**: data from Junta de Castilla y León (2016, 2017); Principado de Asturias (2023); Blanco y Cortés (2007); Blanco et al. (2021a). From 1997 to 2022. Most of the data (635/664) corresponds to wolves found dead and only 9 to radiotracking data. Disaggregated information is shown in Table 2.5.2. **Alps**: Léonard et al. (2010); wolves found dead from 1987-2010 in France (43 wolves), Italy (34) and Switzerland (9). **Italy**: Musto et al. (2021). Wolves found dead from 2005 to 2021 in Tuscany and Emilia-Romagna regions. **Germany**: official statistic (https://www.dbb-wolf.de/wolf-occurrence/dead-wolf-finds/statistics-on-causes-of-death). Wolves found dead from 1990 to 12 April 2023. **Poland**: Nowak et al. (2008, 2021a); Nowak & Myslajek (2016). From 1996 to 2020; mainly wolves found dead (46/54), but also radiotracking data (8/54). **Sweden**: Liberg et al. (2020). Radiotracking data from 2000 to 2017. The mortality information shows only verified causes (see Poaching section); **Finland**: Suutarinen & Kojola (2017); radiotracking data from 1998 to 2013.*

Tables 2.5.2 and 2.5.3 also show that there are important differences in mortality between Member States depending on wolf management regimes. These differences are also obvious when comparing the regions of the same country. For example, in Table 2.5.2 we can see the differences in the causes of mortality in the regions of Castilla y León (hunting and culling allowed during the study period), Asturias (culling allowed during most of the study period) and Madrid, where wolves have never been hunted or culled.

In the same way, in Poland the causes of wolf detected mortality have changed with different management regimes. When hunting was legal, most (83%) known mortality was due to hunting and only 11% was caused by traffic (Table 2.5.3). After being protected in 1998, the main causes were traffic (65%) and poaching (25%) (Table 2.5.3).

Cause of death	Castile and Leon (1)	Asturias (2)	Madrid (3)	Radiotracking in Castile and Leon (4)
Legally killed	77.5	66.9	0	11.1
Illegally killed	4.5	8.7	9.5	44.5
Traffic	14.3	11.9	81.0	33.3
Other			9.5	11.1
Unknown	3.7	12.5		
TOTAL NUMBER	245	369	21	9

Table 2.5.2. Disaggregated information on wolf mortality in Spain.

Legend (1). Wolves found dead in Castile and Leon region in 2016 and 2017 (Junta de Castilla y León 2016, 2017). Hunting and culling were allowed in the study period. (2). Wolves found dead in Asturias region from 2001 to 2022 (Principado de Asturias, 2023). Culling to prevent livestock damage allowed in most of the study period. (3). Wolves found dead from 2008 to 2022 (Blanco et al. 2021a and pers. comm.). Wolves fully protected. (4). Radiotracking data in Castile and Leon from 1997 to 2006 (Blanco and Cortés, 2007). Hunting allowed in most of the study area.

Cause of death	Hunting legal (1)	Fully protected (2)	Radiotracking data (3)
Legally killed	83	0	0
Illegally killed	0	25	75
Traffic	11	65	12.5
Natural	6	7	12.5
Other			
Unknown		3	
TOTAL NUMBER	18	28	8

Table 2.5.3. Disaggregated information on wolf mortality in Poland.

Legend: Wolves found dead in western Poland (1) when hunting was legal (1996-2003)(Nowak et al. 2008) and (2) when no hunting was authorised (2001-2012) (Nowak & Myslajek et al. 2016); (3) data from radiotracking in western Poland when no hunting was authorised (Nowak et al. 2021a).

The rate of mortality can only be reliably estimated with radiotracking studies. Rates detected using "dead-found" wolves are underestimated because only some of the dead wolves are found. In Spain, the mortality rate was estimated at 18% per year in an area with few conflicts in the early 2000s, when wolves were obviously increasing (Blanco & Cortés 2007). In 2016 and 2017 (population trend unknown), 123 wolves per year were killed in Castilla and Leon (179 packs), i.e., around 10% of the total population. In Asturias region, 17.6 wolves were found dead per year from 2001 to 2021 (30-40 packs, increasing), i.e., <10% of the total population.

From 1987 to 2010 the mortality rate was estimated between 10% and 25% of the total population in the French Alps, depending on the detectability of dead wolves (Léonard et al. 2010). In recent years, the rates of culling to prevent livestock depredation is increasing in France, where 97 wolves were legally killed in 2020 (Grente, 2021).

Poaching, an important cause of mortality, but difficult to detect

Poaching is difficult to detect. Opportunistic collection of wolf carcasses can be biased and usually overestimates the rate of mortality caused by traffic and legal culling/hunting, but underestimates poaching and natural mortality, as has been deduced from research comparing the mortality of radio-collared wolves with opportunistic samples from the same population (Stenglein et al. 2015; Suutarinen and Kojola 2017).

For example, in Spain, the main cause of mortality deduced from "dead-found" wolves was legal hunting/culling (68.0%), while poaching represented only 7.6%. But, in a radiotracking study, the mortality by poaching increased to 44.5% and legal hunting dropped to 11.1% (Tables 2.5.2 and 2.5.3). In Poland, 75% of wolves dead in a radiotracking study were poached, a rate much higher than in studies using "dead-found" wolves (0-25%) (Table 2.5.4). Nowak et al. (2021a) estimated that the number of wolves illegally shot annually in Poland exceeded 147 individuals, which is 16-times higher than mean number of shot wolves discovered during 2017-2020 (9.3 wolves per year). This demonstrates again how high the "cryptic poaching" of wolves is and that collected data on illegal killing underestimates the actual number of kills.

But poaching is also difficult to detect even in studies with radio-collared wolves. In Scandinavia, 154 wolves radio-collared from 2000 to 2017 died during the study. Verified poaching accounted for 13% of the detected mortality, but most of the radio-collared wolves (n = 189) disappeared without known cause. Liberg et al. (2012b, 2020) showed that poaching was the most likely reason for the majority of these disappearances, accounting for approximately half of the total mortality. Therefore, more than two-thirds of total poaching remained undetected by conventional methods.

Poaching is probably the main cause of wolf mortality in many EU countries, and it is hindering wolf recovery in some of them. For example, simulations suggested that in Scandinavia, without poaching, the wolf population would have been almost four times as large in 2009 (Liberg et al. 2012b). In Finland, Suutarinen and Kojola (2017) showed that the poaching rate varied between years, from less than 9%–13% up to 31%–43%, with illegal killing being the primary cause of death, followed by legal hunting.

Wolves recolonized Denmark from Germany in the previous decade and reproduced for the first time in 2017, but after the breeding female of the pack was shot dead in 2018 most wolves disappeared from that country (in 2023, wolves are breeding again in Denmark: Table 2.4.1). Sunde et al. (2021) studied the mortality and disappearance rates of 35 wolves (of which three emigrated, nine died and 14 disappeared by 1 January 2020) by genetic monitoring in the heavily cultivated and densely populated Jutland peninsula. They concluded that traffic was the main cause of wolf mortality (37%) in Schleswig-Holstein, Germany, and illegal killing was the main cause in Denmark (46%).

This high mortality rate caused the decline of the population. Despite successful reproductions, the region is a wolf population sink, primarily driven by cryptic mortality, most likely illegal killing. The annual rate of disappearances and illegal killings in Denmark (most conservative estimate, 42%) exceeds the highest measured rates in Sweden (24%) (Liberg et al. 2020) and equals the highest rates measured in Finland (31%–43%) (Suutarinen & Kojola, 2017), levels which, in both countries, resulted in population declines.

2.6 Wolf-Dog hybridization

Dogs were domesticated from wolves and hybridize with them producing fertile offspring. Interbreeding between wolves and dogs has probably occurred repeatedly throughout the history of the dog's domestication, but probably to a much lesser degree than at present. Hybridization between wolves and dogs is facilitated by the large numbers of stray dogs sharing the wolf range (Salvatori et al. 2020a).

Hybridization can affect wolf populations in several ways, most of them negative. The wolf-dog hybridization may cause the introduction of non-adaptive genes in the wild wolf population and can modify the genetic identity, the ecology, morphology, behaviour and adaptations of wolves. The disruption of the genetic integrity may cause the disappearance of alleles, decreasing fitness or even threatening the existence of the parental species. Hybrids usually thrive in similar conditions as their parental species, so they are a source of competition for food and space, as has been documented in wolf dog hybridization studies (Bassi et al. 2017). If there is no selection against hybrids, these can dominate the parental species, leading to a decrease in the number of pure individuals or even extinction. Hybrids can also worsen people's perception of the wolf, reducing their societal acceptance (Leonard et al. 2015; Salvatori et al. 2020a; Dziech 2021).

Wolf-dog hybridization has been considered a conservation problem for the wolf in different European assessments (Boitani et al. 2015, 2022), and also by the Council of Europe (The Bern Convention Recommendation No. 173, 2014)[17] and the European Commission. In 2021, the European Commission acknowledged that "as a type of anthropogenic hybridisation, wolf-dog hybridisation is not a natural evolutionary process where the hybrids should be subject to conservation measures. Rather, as a threat to the genetic integrity of wolf populations, wolf-dog hybridisation is an issue of high conservation concern and should be addressed through appropriate management plans and tools" (Commission Notice C(2021) 7301)[18].

Hybridization in the European Union

Studying the wolf-dog hybridization is not an easy task, and many researchers have warned that results obtained by different laboratories are not automatically comparable since the proportion of hybrids, and consequently the perception of how severe the hybridization is, depends on the complex and fast-evolving methodological processes, including the detection power of the marker set and the threshold selected for assigning genotypes (e.g., Lorenzini et al. 2014; Salvatori et al. 2020a).

In order to identify signatures of admixture, Pilot et al. (2018) carried out a comprehensive analysis spanning the canid genome in wolves from across Eurasia and North America and compared that data to similar data from dogs. The analysis unambiguously defined wolf and dog genetic clusters without any prior information about individuals' origin, which confirms that Eurasian wolf populations are not hybrid swarms. On the other hand, 62% of genotyped wolves carried small chromosomal blocks that were inferred to originate from dogs. This suggests that most Eurasian wolves show some level of admixture with dogs, suggesting that introgressive hybridisation has occurred in distinct regions of Eurasia on a variety of timescales and is not solely a recent phenomenon.

Salvatori et al. (2020a), through a literature review and a structured questionnaire to 32 European wolf experts, found that wolf-dog hybridization is reported in all nine extant European wolf populations, and in 21 out of 28 countries for which they received information. Reports of wolf-dog hybridization have increased over the past two decades, mainly based on genetic analyses of invasive or non-invasive biological samples. However, Salvatori et al. (2020a) neither concluded nor excluded that wolf-dog hybridization is indeed increasing within and among European wolf populations.

[17] https://rm.coe.int/0900001680746351#:~:text=Take%20adequate%20measures%20to%20monitor,2

[18] https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=PI_COM:C(2021)7301

Rather than (or in addition to) wolf-dog hybridization *per se*, it is its detection that might have increased in recent years, mainly due to the increasing availability of reliable tools for the genetic identification of hybrids. Nevertheless, several authors (Galaverni et al. 2017; Donfrancesco et al. 2019) think that wolf-dog hybridization may have increased in parts of Europe during the past half century because of the recent recovery of wolf populations in Europe and their expansion into anthropogenic landscapes where densities of free-ranging dogs are higher, coupled with locally high levels of human related wolf mortality.

In 2022, the members of the LCIE were asked about wolf-dog hybridization in their countries (Boitani et al. 2022). In the 24 EU countries with wolves, 10 experts responded that they did not have wolf-dog hybrids, including those from four countries with hundreds or even thousands of wolves (Sweden, Slovakia, France, Romania). Sporadic hybridization had been detected in 10 countries, including three with more than 1,000 wolves (Bulgaria, Poland, and Germany). Finally, in four countries there was concern about the high percentage of wolf-dog hybrids detected, all of them from southern Europe (Greece, Croatia, Italy and Spain).

Member States with high hybridization rates

In Greece, the hybridization rate was unknown but expected to be >10% in periurban areas (Boitani et al. 2022) and in some agricultural areas (Iliopoulos 2023). In Croatia, Kusak et al. (2018), on the basis of phenotype of 176 wild canids, categorized 19 (10.8%) as suspected hybrids. On the basis of the Bayesian admixture tests and phenotype together, five (2.8 percent) animals were classified as wolf-dog hybrids, four of them as backcrosses with wolves, and one as a backcross with a dog. Mitochondrial DNA suggested that all hybrids originated from the mating of female wolves and male dogs. All hybrids were found in Dalmatia, where wolves settled recently and live close to humans, with a high rate of human-caused mortality.

In Spain and Portugal, Godinho et al. (2011) found 4% of hybrids, but as a disproportionate effort was devoted to locating putative hybridization events, they did not know how representative this frequency was for the whole Iberian population. They showed that Iberian wolves and dogs form two well-differentiated genetic entities, suggesting that introgressive hybridization is not a widespread phenomenon shaping both gene pools. Hybridization was apparently restricted to more peripheral and recently expanded wolf populations and they found that hybridization in wolf populations is mediated by crosses between male dogs and female wolves. Subsequently, Pacheco et al. (2017) collected wolf-like scats in Galicia (Spain) in a single breeding/pup-rearing season and found a 5.6% rate of dog introgression into the wolf population. Despite this high percentage, they found a clear maintenance of wolf genetic identity, as evidenced by the sharp genetic identification of pure individuals, suggesting the resilience of wolf populations to a small amount of hybridization.

The highest rates of wolf-dog hybridization have been found in Italy. During the national wolf survey conducted in Italy from October 2020 to September 2021, 16,000 wolf scats were collected and 1,500 of them were genetically analysed. Of the 513 wolf individuals identified in the peninsular area, 72.7% showed no genetic signs of recent or ancient hybridization with domestic dogs, 11.7% showed signs of recent hybridization and 15.6% of older hybridization (backcrossings of hybrids into the wolf population more than approximately three generations in the past)[19].

In Italy, the highest rates of hybridization have been found in the Province of Grosseto. In a study carried out in 2012–2014, Salvatori et al. (2019) found a minimum proportion of admixed individuals of 30.6%, comprising 8 out of the 13 surveyed packs; however, they suspected that the rate of recent admixture could be closer to 50%. Their results showed a widespread occurrence of admixed

[19] https://www.isprambiente.gov.it/it/attivita/biodiversita/monitoraggio-nazionale-del-lupo/risultati

individuals of older generations of backcross, and they concluded that this high level of admixture raises serious wolf conservation concerns and exemplifies the expected dynamics of wolf–dog hybridization if left unmanaged in human-dominated landscapes.

Dealing with the hybridization problem

Both the European Commission (Commission notice C(2021) 7301) and Council of Europe (The Bern Convention Recommendation No. 173, 2014) recommend removing wolf-dog hybrids from the wild, but the removal must be conducted exclusively in a government-controlled manner.

Nevertheless, the removal of hybrids is not an easy task. Donfrancesco et al. (2019) surveyed the opinion of European experts on wolf-dog hybridization on how to address the issue. To mitigate hybridization, experts agreed on adopting preventive, proactive and, when concerning small and recovering wolf populations, reactive interventions. Overall, experts' consensus waned as the issues addressed became increasingly practical, including the adoption of lethal removal. Salvatori et al. (2020a) stress that poor implementation of European recommendations of removing hybrids from the wild may be due to lack of means (e.g., resources for nationwide genetic assessment), lack of technical specificity (e.g., what is a hybrid), or the political difficulty of addressing an issue that is highly controversial on social and ethical grounds.

3. ROLE OF THE WOLF IN ECOSYSTEMS AND IMPACTS ON SOCIETY

3.1. Role in ecosystem's functioning/health/balance

This chapter reviews examples from scientific literature on the role of the wolf in ecosystems. The wolf has a clear ecological role to play as it is the largest regular predator in Europe and in many ecosystems in the northern hemisphere (Mech 1981). Over the last century, large carnivores have declined around the world, causing the loss of the ecological functions they performed, but the recent recovery of the wolf and other large carnivores in Europe (Chapron et al. 2014) may partially restore these functions if they reach ecologically effective densities (Estes et al. 2011; Ripple et al. 2014a). The main effects attributed to wolves – the reduction of herbivores and mesocarnivores – for instance, have been recorded after their removal from the environment or their reintroduction (Ripple et al. 2012; 2014b).

Trophic cascades in North American national parks

In North America, the ecological role of the wolf has been underlined on numerous occasions, creating trophic cascades following its reintroduction in Yellowstone National Park (USA). Its re-introduction seems to have reduced coyotes (*Canis latrans*) and elk (*Cervus elaphus canadensis*). The reduction in elk, led, in turn to a reduction in overgrazing, thereby creating a cascade effect on other species: natural vegetation on the banks of rivers and streams recovered leading to an increase of beavers (*Castor canadensis*) and passerines; berry-producing plants also recovered with a consequent increase in bears (*Ursus* spp.), also favoured by carrion left behind by wolves, as well as a number of other changes in the ecosystem (Beschta 2005; Beyer et al. 2007; Painter et al. al. 2015; Beschta & Ripple 2016). Most of these effects have also been demonstrated in other national parks of North America (Hebbelwhite et al. 2005).

The trophic cascades experienced in some American national parks have been possible thanks to density-mediated effects (i.e., elk reduction of densities) and to behaviourally-mediated effects in which wolves seem to have an indirect positive effect on the survival rate and growth of some bushes and trees by altering the foraging patterns of the moose and other prey species (the landscape of fear: Fortin et al. 2005; Gaynor et al. 2019).

The ecological role of wolves in ecosystem structure and functioning is becoming increasingly recognized but is often over-emphasized (Mech 2012, Allen et al. 2017). This has created strong scientific debates, which are sometimes very polarized and oversimplified. Peterson et al. (2014) conclude that the debates about whether trophic cascades exist in Yellowstone and other American national parks cannot lead to simple, precise or definitive answers. The existence of a trophic cascade largely depends on how it is defined. The main intellectual contribution of this concept is to remind us of a basic principle of ecology, which is that most species are connected to each other through a food web that, although weak, has complex indirect effects.

The ecological role of wolves in Europe

In most of Europe, humans have taken over the role of top predators in regulating both prey numbers and behaviour (Kuijper et al. 2016; Mols et al. 2021). Human effects on antipredator behaviour of prey can be stronger than those of other natural predators. For example, effects of human hunting and disturbance on the vigilance, movement rate and grouping patterns, as well as on the circadian rhythm and stress levels of cervids is significantly greater than the effects of large carnivores such as wolves (Mols et al. 2021). In the Bavarian Forest, it was found that humans rather than Eurasian lynx (*Lynx lynx*) shape browsing patterns (van Beeck Calkoen et al. 2022).

In a study conducted in Romania, wolves and bears exerted high pressure on deer (*Cervus elaphus*) and less on roe deer (*Capreolus capreolus*), but the direct and indirect impact of humans prevailed over natural processes (Dorresteijn et al. 2015). Using data on red deer density in 492 study sites across 28 European countries, van Beeck Calkoen et al. (2023) showed that a reduction in deer density only occurred when wolf, Eurasian lynx and bear co-occurred within the same site, and the strongest large carnivore effects (all three carnivore species present) on red deer occurred at sites with low human land-use activities. Moreover, hunting by humans had a stronger effect than the presence of all large carnivores in reducing red deer density.

In several Mediterranean ecosystems, the abundance of free-ranging livestock confounds the ecological role of the wolf. Free roaming livestock, on the one hand, competes with wild herbivores and, on the other, provides abundant food for wolves, altering their population dynamics and the pressure they cause on natural prey (Lagos and Bárcena 2018; Pimenta et al. 2018; Figueiredo et al. 2020). Researchers have failed to find these ecological effects in other European areas, such as in the intensively managed boreal forests of Sweden (Ausilio et al. 2021), showing again that the ecological effects of wolves in anthropogenic landscapes and the potential for trophic cascades are very much context-dependent.

Nevertheless, some studies have demonstrated that wolves can reduce the rates of increase of red deer in natural habitats in Poland (Jedrzejewski et al. 2002) and of wild boar in northwestern Spain (Tanner et al. 2019). In Białowieza Primeval Forest (Poland), the densities of red deer, especially in the case of females, were lowest in parts of the landscape intensively used by wolves (Bubnicki et al. 2019), and wolves were also found to affect the spatial patterns of ungulate browsing (Kuijper et al. 2013). In addition, wolves provide carrion for scavengers (Selva et al. 2005) and may reduce densities of golden jackals (Krofel et al. 2017).

Wolf contribution to the regulation of wild ungulates as an ecosystem service

Despite their strong influence, humans cannot always replicate in nature the indirect effects caused by wolves, and their ecological roles are not easily interchangeable. This partly explains why humans often fail to prevent or reverse some of the impacts caused by the proliferation of wild ungulates, such as overgrazing, vegetation damage, and associated biodiversity loss (Dorresteijn et al. 2015).

In recent decades, wild ungulates have dramatically recovered in Europe. Although their presence is essential for restoring ecosystem processes, wild ungulates have reached densities that probably surpass those from historical times in many parts of Europe. This is, among other reasons, because of high access to anthropogenic food sources (from agriculture, forestry, and supplementary feeding) (Linnell et al. 2020).

High-density ungulate populations have been widely shown to cause damage, particularly to crops and forestry, as well as negatively influence biodiversity, mainly through overgrazing and overbrowsing. They can also transmit disease to livestock and cause material damage, for example, traffic collisions (Carpio et al. 2020; Pascual Rico et al. 2021). Wild boar is one of the species that most often causes damage to crops and is estimated to generate an economic loss of more than 30 million euros annually in the agricultural and forestry sector in Italy and France alone (Apollonio et al. 2010).

Forestry is an important part of the national economy in Scandinavia. An increase in the moose population size can cause extensive browsing damage to young forest stands that may lead to severe economic loss for forest owners. Management objectives in Sweden includes to keep browsing damage on commercially valuable tree species at an acceptable level, while at the same time limit the moose population by harvesting at a level which results in a sustainable yield that is acceptable to hunters. The recolonization of wolves in Scandinavia has further accentuated the challenge of combining the interests of foresters, hunters and conservationists (Wikenros et al. 2020).

Wolves can reduce disease transmission and traffic collisions

Trophic cascades are only one of the ecological effects that wolves can have on the ecosystem. By selecting the most vulnerable prey - such as sick individuals (Mech et al. 2015)-, wolves may also reduce the incidence of diseases that wild ungulates transmit to livestock. Tuberculosis (TB) stands out among the diseases transmitted by wild ungulates to cattle. In the south of Spain (where wolves are extinct), several studies have shown the difficulty of dealing with the problem of tuberculosis in cattle because of the high infection rate in wild ungulates.

Wild boars from wolf-free areas in southern Spain have high rates of tuberculosis infection (52% in Doñana National Park and 58% in Sierra Morena, reaching 94% in some fenced hunting estates). In contrast, in Galicia and Asturias (northwestern Spain), where there are dense populations of wolves and much lower densities of wild ungulates, the prevalence of tuberculosis in wild boars was only 2.6% (Blanco, 2018).

A study that combined model results with field data for a system of wolves that prey on wild boar (*Sus scrofa*) in Asturias region found that wolf predation can lead to a marked reduction in the prevalence of infection without leading to a reduction in host population density since mortality due to predation can be compensated by a reduction in disease induced mortality. In Asturias, where there is a high density of wolves and a low prevalence of TB, the annual cost of compensation paid to farmers due to wolf attacks on their livestock is a quarter of the annual expenses of the cattle TB eradication scheme (Tanner et al. 2019).

In the same way, the African swine fever (ASFV) has spread among populations of wild boars and pigs in countries of Eastern and Central Europe, causing huge economic losses. It has been speculated that carnivores which are known for high daily movement and long-range dispersal ability, such as the wolf, may be indirect ASFV vectors. Nevertheless, results of field and laboratory research have shown that when wolves consume meat of ASFV-positive wild boars, the virus does not survive the passage through intestinal tract, and wolves may limit ASFV transmission by removing infectious carrion (Szewczyk et al. 2021).

Although up-to-date statistics are hard to find for the whole Europe, Linnell et al. (2020) showed that for some selected countries, more than half a million collisions with ungulates are recorded every year. A recent study has quantified the effects of restoring wolf populations by evaluating their influence on deer–vehicle collisions (DVCs) in Wisconsin (Raynor et al. 2021). The authors showed that, for the average county, wolf entry reduced DVCs by 24%, yielding an economic benefit of $10.9 million per year in aggregate across the 29 wolf counties which is 63 times greater than the costs of verified wolf predation on livestock.

Most of the reduction is due to a behavioural response of deer to wolves rather than through a deer population decline from wolf predation. This finding supports ecological research emphasizing the role of predators in creating a “landscape of fear” and suggests that wolves control economic damages from overabundant deer in ways that human deer hunters cannot replicate.

3.2. Predation on wild ungulates and implications for hunting

Hunters perceive carnivores as competitors for prey species and in some events, predation can sustainably influence traditional game harvests (Boitani et al. 2015). The competition between wolves and hunters for game species has probably been the main cause of the extinction of the wolf population in Sierra Morena since hunters perceived that wolves were incompatible with the intensive hunting of red deer in the private, fenced estates of southern Spain (López Bao et al. 2015). However, the impact of wolves on big game species is largely offset by the dramatic recovery of wild ungulates in Europe in recent decades (Linnell et al. 2020).

Wolf predation on wild ungulates is highly variable across Europe. Wolves known for their notable plasticity in diet. There is a significant positive relationship between species richness of the local ungulate community and feeding niche breadth of wolves. The degree to which wolves select a given species may depend not only on the relative abundance of that species but also on available alternative prey. For example, in central and eastern Europe where moose and/or red deer predominate, wolves notably avoid preying on wild boar.

Conversely, in southern Europe where large cervids are absent or rare, wolves often rely on wild boar and prefer it to the more numerous roe deer. Because wolves balance difficulty in killing prey with the reward in food biomass obtained, red deer was shown to be the optimal size prey for typical central European packs of 4–6 wolves (Jedrzejewski et al. 2012). Wild ungulates help reduce conflicts between predators and livestock producers as high livestock depredation rates are often linked to low wild prey densities (Linnell et al. 2020; Gervasi et al. 2021).

In any event, unlike predation on domestic livestock, predation on wild ungulates cannot be prevented or mitigated, as it is part of the natural processes that biodiversity policy aims to restore and preserve (Commission Notice C(2021) 7301)[20].

Wolves kill fewer wild ungulates than hunters

Although wolves and hunters can compete for large ungulates, at a global level ungulate mortality caused by hunting is almost twice as large as the mortality caused by all terrestrial predators combined (Darimont et al. 2015). Research conducted in Europe show that wolves kill far fewer wild ungulates than hunters. In wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*) in Italy, losses due to hunting resulted to be eight to nine times higher than those due to wolf predation and the combined removal by hunters and wolf predation did not exceed the recruitment of both ungulate populations (Bassi et al. 2020). In a study carried out across Europe, hunting by humans had a stronger effect in reducing red deer density than the presence of wolves, Eurasian lynx and bears together (van Beeck Calkoen et al. 2023).

In Białowieża Primeval Forest, daily wolf kill rate averaged 0.116 ungulates per capita (42.3 per year (Jedrzejewski et al. 2002). Multiplying this figure by the total number of wolves in Europe (20,300) it was estimated that European wolves kill a maximum of 0.86 million wild ungulates per year, far less than the more than 7.3 million wild ungulates that are harvested per year in the continent (Linnell et al. 2020).

For most ungulate species, human harvest has a larger impact on population growth compared to predation (per capita kill) as hunters generally select adult animals at a higher rate than large carnivores. Wolves usually select ungulate calves which generally have a much lower reproductive value than adults. For example, in Italy, wolves targeted the intermediate weight class (10–35 kg) in wild boar and

[20] https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=PI_COM:C(2021)7301

showed no preference for a specific class of roe deer, while hunters targeted the largest classes in both species (Bassi et al. 2020).

The increased wolf impact on wild ungulates may require adjusting harvest strategies

The wolf return may affect hunting activities in some circumstances. For example, in the absence of wolves in Sweden, and with the introduction of stand forestry practices and hunting regulations throughout the twentieth century, the Scandinavian moose (*Alces alces*) population has shown a tremendous growth and been one of the most heavily harvested ungulate populations in the world. However, after the wolf's recovery, harvest density was 51% lower in areas containing average-sized wolf territories than in areas without wolves (Wikenros et al. 2020).

The increased impact on ungulate mortality may require adjusted harvest strategies to avoid overexploitation and secure a sustainable yield. Moose management in Sweden aimed to increase productivity in the moose population, in order to compensate for the increased mortality caused by wolves. Several theoretical studies have evaluated various possible harvest strategies for moose and how harvest, for a given density, can be adjusted to reach different types of management goals such as maximizing the amount of meat, total number of harvested animals, or large males.

An alternative to reducing total moose harvest may be to change the age and sex composition of harvested animals to compensate for the increase in mortality caused by wolf predation. To harvest individuals with low reproductive value, i.e., those who have a low probability of producing calves next year, also promote high growth in the population. In general, maximizing the number of harvested animals means that harvest should mainly be directed toward calves, and this strategy also holds true in the presence of wolves. The proportion of females in the adult harvest was strongly reduced in Sweden as a response to increased wolf territory density.

3.3. Predation on farm and domestic animals

Predation on livestock has been the main cause of wolf persecution throughout history and is currently the main source of conflict between wolves and people in Europe and in most of its global range. Wolves mainly kill vulnerable wild ungulates. Since domestic livestock is vulnerable when unprotected, the wolf follows its natural tendency and kills them (Mech 1981).

Damage to livestock goes beyond a purely economic issue. In some areas, extensive livestock play a key role in the maintenance of high biodiversity grasslands, and in Mediterranean landscapes they can prevent forest fires. In addition, predation on pets, such as riding horses or hunting dogs, although is less common than damage to livestock, has a strong and growing emotional importance on the owners and the wider general public.

The resolution of the European Parliament of 24 November 2022[21] stressed that good monitoring of trends in damage occurrence for livestock breeders is a basic prerequisite for successful policies, and underscored the importance of standardised reporting formats. Monitoring of livestock damages is still very variable across the EU as gives important caveats to the info presented below.

Knowledge on livestock damage is normally derived from compensation data. But in some countries wolf damage is only partially compensated, and in other countries, it is not compensated at all. Increasing or decreasing the coverage of compensation may cause apparent, but not actual, changes in livestock damage. Damage figures from different sources sometimes do not match and comparisons

[21] https://www.europarl.europa.eu/doceo/document/TA-9-2022-0423_EN.html

from different countries not always are easy. Despite these challenges, the available data can provide a good overview of wolf depredation on livestock in the EU.

The most updated publication on the amount of damage caused by wolves has been prepared by Boitani et al. (2022) who collected the most recent available data on European countries provided by the members of the LCIE for a report submitted to the Bern Convention. A recent compilation of wolf damage on livestock in geographical Europe (Singer et al. 2023) gives fewer details on the EU countries but provides interesting complementary information. In addition, the Discussion paper on livestock depredation prepared in 2023[22] by the EU Platform on coexistence between people and large carnivores also provides useful data.

Livestock damage overview in the EU

This section presents the most recent information available on wolf damage to livestock and pets in the EU, based on several sources of information. In addition to the aforementioned publications, the results are based on information received in response to the European Commission's data collection exercise launched on 4 September 2023 (see section 2.4). Furthermore, data from regional and national authorities, reliable information collected on official web pages, through scientific and technical literature and by consulting national experts were used.

On 17 November 2023, the information gathered through the above was sent to the Ministries of Environment of the MS for review. **The resulting information on latest wolf damage to livestock in EU Member States is presented in table 3.3.1.**

In the EU, information is missing from Bulgaria and Hungary, where compensation for wolf damage is not paid, and from Romania, where only partial data are available. In table 3.3.1, disaggregate data are also lacking for a few Member States, such as France and the Netherlands. The disaggregated data in France in 2022 was estimated by applying the rates of each type of livestock killed between January and November 2023 (data from the French Ministry of Ecological Transition). In the Netherlands, we assume that most livestock killed in 2022 (973 heads) were sheep.

According to information from Table 3.3.1, in the EU wolves kill annually at least 65,500 heads of livestock, 73% of them are sheep and goats, 19% cattle and 6% horses and donkeys, most of them horses bred for meat. Semi-domestic reindeer are also killed in Finland (1,261 in 2022) and in Sweden (unknown). These figures are higher than those shown by Boitani et al. (2022) (53,530 heads of livestock). The increase of livestock killed in Spain (from 11,210 heads in 2020 to 14,309 in 2022) may be due to the expansion of damage compensation coverage following wolf protection in 2021, to an actual increase of damage or both. In any case, the results show that damage to livestock is increasing in the EU.

[22] https://circabc.europa.eu/ui/group/3f466d71-92a7-49eb-9c63-6cb0fadf29dc/library/410c2e7b-0ce8-425e-8ac2-c1c65203b476/details

Table 3.3.1 WOLF DAMAGE ON LIVESTOCK IN THE EU MEMBER STATES

Country	Year of depredation	Sheep & goats	Cattle	Horses/ donkey	Semi-domestic reindeer	Dogs	Others	TOTAL heads	Year of compensation	Amount of compensation (€)	Source
Austria	2022	860	11	0	0	0		871	2022	350,000	Federal Min. Environment, EC data collection.
Belgium[1]	2022	196	9	3	0	0	36	208	2022	50,900	Flanders: Agenschap Natuur & Bos Wallonia: Service Public de Wallonie- Agriculture, Ressources Naturelles & Environnement
Bulgaria										0	No compensation. No data on wolf damage
Croatia	2022	2777	625	61	0	48	5	3516	2022/2023	460,155	Ministry of Economy and Sustainable Development, Nature Protection Directorate
Czech Republic	2022	701	50	0	0			751	2022	390,038	https://www.navratvlku.cz/ Ministry of Environment; Min. Agriculture, EC data collection
Denmark	2022	159	2	0	0	0		161	2022	51,093	Danish Environmental Protection Agency
Estonia	2022	966	26	0	0	10	0	1002	2022	160,494	Environmental Board of Estonia

Country	Year of depredation	Sheep & goats	Cattle	Horses/ donkey	Semi-domestic reindeer	Dogs	Others	TOTAL heads	Year of compensation	Amount of compensation (€)	Source
Finland	2022	518	0	0	1,261	<50		1829	2021	2,997,413 € (semi-domestic reindeer 2,746,800 €)	2021: Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47 2022:https://www.luke.fi/fi/luonnonvaratieto/tiedetta-ja-tietoa/suurpedot/susi-0
France[2]	2022	11,981	443	23	0	79		12,526	2022	4.1M €	Office Français de la Biodiversité (OFB), EC data collection
Germany	2022	3869	260	30	0	3		4162	2022	616,413 €	Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf (2023): Wolfsverursachte Schäden, Präventions- und Ausgleichszahlungen in Deutschland 2022. 44 S
Greece	2022	2660	3474	529	0	0		6663	2022	2,301,650	Greek Agricultural Insurance Organization (ELGA) 2022
Hungary	2021	63	0	0	0	0		63	2021	0	National Parks directorates and Ministry of Agriculture
Italy[3]	2019	8480	1432	318	0	0		10,289	2019	1,918,566	Gervasi et al. 2022. Stima dell'impatto del lupo sulle attività zootecniche in Italia. Analisi del periodo 2015 – 2019.https://www.isprambiente.gov.it/public_files/StimaImpattoLupoAattivitaZootecniche.pdf

Country	Year of depredation	Sheep & goats	Cattle	Horses/ donkey	Semi-domestic reindeer	Dogs	Others	TOTAL heads	Year of compensation	Amount of compensation (€)	Source
Latvia	2021	45	2	0	0	4		51	none	none	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47
Lithuania[4]	2022	1269	137	1	0		52	1459	2022	290,571	Ministry of the Environment of the Republic of Lithuania. EU Consultation
Luxembourg	2021	0	0	0	0	0		0	2021	0	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47
Netherlands[5]	2022-2023	973[3]			0			973	2022	235,188	https://www.bij12.nl/onderwerpen/faunazaken/diersoorten/wolf/: Damage from 10.07.2022 to 09.07.2023. Alle-schademeldingen-wolf-en-geen-wolf-25-augustus-2023.xlsx (live.com).
Poland	2019				0			993	2020	351,000	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47
Portugal	2017	2064	593	395	0	7		3059	2017	332,387	Boitani et al. 2022. https://rm.coe.int/inf45e-2022-wolf-assessment-bern-convention-2791-5979-4182-1-2/1680a7fa47

Country	Year of depredation	Sheep & goats	Cattle	Horses/ donkey	Semi-domestic reindeer	Dogs	Others	TOTAL heads	Year of compensation	Amount of compensation (€)	Source
Romania	2020				0			528	2021	127,580	2020: Ministry of Environment, Water and Forests, EU data collection. 2021: Boitani et al. 2022
Slovakia	2022	1081	77	0	0	0	0	1158	2022	453,792	Ministry of the Environment of the Slovak Republic, 2022
Slovenia	2022	602	31	9	0	1	2	645	2022	121,073	Ministry of Natural Resources and Spatial Planning of Slovenia
Spain	2022	6863	5200	2273	0			14,309	2022	3,225,845	Ministry of the Environment (MITECO). EC data collection
Sweden	2022	255	5	0		22	1	283	2022	164,000 (including compensation for dogs)	Frank J, Levin M, Månsson J, Höglund L, Hensel H (2023). Viltskadestatistik 2022. Skador av stora rovdjur och stora fåglar på tamdjur, hundar och gröda. Rapport från SLU Viltskadecenter 2023-3
TOTAL[6]		**46,382**	**12,377**	**3,642**	**1,261**	**224**	**94**	**65,499**		**18,698,158€**	

[1] Some domestic species are not listed separately: 7 alpacas, 17 ponies and 12 captive fallow deer with additional amount of compensation of 10.688,79 euros.
[2] The disaggregated data in France in 2022 was estimated by applying the rates of each type of livestock killed between January and November 2023
[3] The regional administrations of Lombardy and Trento provided more up-to-date data than in the ISPRA report, it is difficult to integrate the figures with the rest of data from the other 20 regions, given that these regions have limited territories.
[4] Other includes captive fallow deer and sika deer
[5] Disaggregated data are unknown in the Netherlands. For statistical purposes, we assumed that all livestock killed were sheep. Compensation is from November 2021 to October 2022
[6] The sum of the different types of livestock is 63,980 because disaggregated data is not available in some MS

The highest damage to livestock according to available data occurs in Western European countries, but there is no complete information from some countries of Eastern Europe with large wolf populations, such as Bulgaria and Romania. Spain (about 14,000 heads killed annually), France (12,000) and Italy (10,000) represent half of all livestock damage in the EU. Considering that the number of wolves in Spain (more than 300 packs) and in Italy (about 3,300 individuals) is much higher than that of France (about 1,100 wolves in 2023), this country is the one with the highest rates of livestock killed per wolf in the European Union. Other countries, such as Germany, Greece and Croatia, also show important damage to livestock.

The different types of livestock affected

Sheep are more vulnerable to wolf attacks and are also the most depredated type of livestock. France is the country where wolf depredation on sheep is highest. Around 12,000 sheep were killed in 2022 (Table 3.3.1), which represents circa 11 sheep/wolf/ year. These large numbers are probably due in part to the many free-ranging sheep in alpine pastures. Portugal, Greece, Croatia and Italy also stand out as hot spots for wolf depredation on sheep. This is probably due to a range of factors that include husbandry, but in some cases are also associated with many areas that have low densities of wild ungulates such that wolves have no alternative prey sources (Linnell and Cretois 2018).

Cattle damage reaches its maximum in Spain. This is because in many areas of the Cantabrian Mountains sheep and goats, which were the predominant type of livestock until about 30 years ago, have been replaced by free-ranging beef cattle, which spend several months of the year in the field. Cattle are less vulnerable to predation by wolves and bears than sheep and goats (mainly calves are killed) and require less dedication, so farmers can make them compatible with other activities, such as tourism, which have become increasingly important in the economy of these areas. In addition, since the year 2000 wolves have recolonized some areas of central-western Spain, such as Ávila province, where there are huge densities of extensive beef cattle and low densities of wild ungulates. Free-ranging cattle are difficult to protect with preventive methods. Since free-ranging cattle are scattered in the field, they cannot be protected with fences, and it is not always easy to protect them with guarding dogs. In Ávila province alone, wolves kill more than 1,600 calves each year (Blanco et al. 2021b).

Damage to horses bred for meat is also widespread in northwestern Spain (2,273 killed in 2022), Portugal (395 in 2017) and Italy (317 in 2019) (Table 3.3.1), where small-sized horses (<300 kg) are raised for meat production under free-roaming systems and thus accessible to wolves, which mainly kill foals. In many of these areas, horses are more abundant than wild ungulates, which are locally scarce, and are more accessible than other livestock which are confined at night. In some studies, horses comprised >70 % of wolf diet and were positively selected in relation to other wild and domestic prey, meaning that wolves consumed horses in a higher proportion than their local availability. In Italy, wolf attacks on free-ranging horses are mostly limited to Apennine Mountain range, where they can locally reach 40% of wolf diet (Freitas et al. 2021).

Semi-domestic reindeer represent a very specific case of livestock depredation. They are grazed by Sami people in Sweden and Finland (as well as in Norway and Russia, outside of the EU). In Sweden and Finland, reindeer herding is conducted across approximately the northern 40% and 33% of the countries, respectively. Semi-domestic reindeer are free-ranging throughout the year and in most of the northern parts of the reindeer herding districts there are very low densities of alternative prey, so wolves and other large carnivores are virtually dependent on their access to reindeer as prey (Linnell and Cretois 2018). Even if wolves are not tolerated in the reindeer herding districts of Sweden and Finland, they cause significant damage. In 2022 more than 1,200 semi-domestic reindeer were killed by wolves in Finland (Table 3.3.1). In Sweden, damage statistic is unknown because the compensation system is based on paying for the risk associated with large carnivore presence and does not require documenting losses (Linnell and Cretois 2018).

Seasonal distribution of damage

The seasonal distribution of wolf-caused incidents in Europe was studied by Singer et al. (2023). Across all livestock species, incidents peaked between July and October with 48.7% of total incidents falling within these months. This pattern was particularly visible for sheep (55.2%), and for cattle (43.4%) and goats (40.9%), albeit less pronounced. In contrast, incidents involving horses peaked between April and July (51.8%) and those involving reindeer between September and December (67.5 %).

Livestock damage trends

Data from this report shows that damage is increasing in recent years in the EU. At a national level, the trend in damage has been studied in some countries where wolves have been increasing. In France, wolves were exterminated more than one century ago, and livestock breeders and herders were unprepared when wolves arrived from Italy in 1993. In 2019, 580 wolves, whose numbers are growing very fast, were present in over one third of France. According to Meuret et al. (2020), livestock deaths from wolves have grown linearly from 3,215 in 2009 to 12,451 in 2019, despite France implemented extensive damage protection measures (Fig. 3.3.1). Nevertheless, in the 2020-2022 period (not covered by the study of Meuret et al. 2020), damage has slightly decreased or stabilized but back up in 2023 (2020: 11,746 heads killed; 2021: 10826; 2022: 12,526)[23].

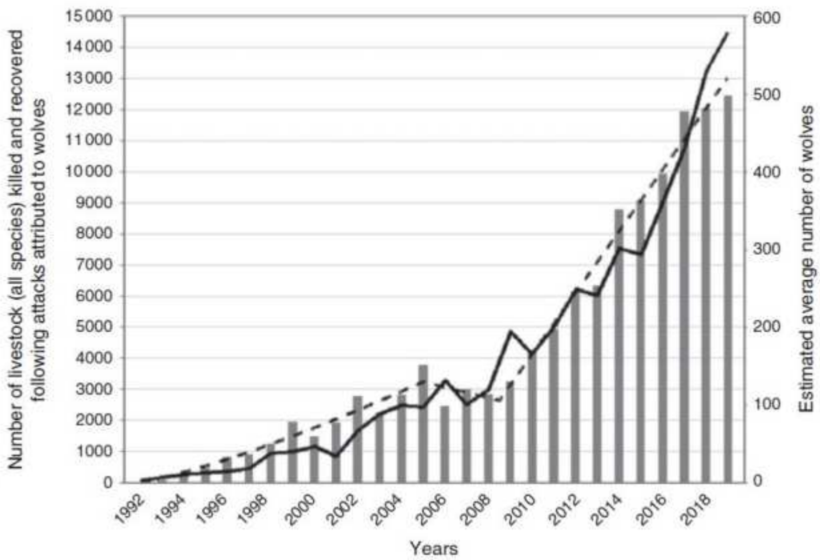

Fig. 3.3.1. Number of livestock killed by wolves in France (grey bars); number of wolves (solid line); model prediction of livestock killed by wolves (dashed lines). From Meuret et al. (2020).

In Germany also, damage to livestock has increased as the wolf population has grown (Khorozyan & Heurich 2022). Nevertheless, while the number of attacks increased in 2021 by 3.5% across Germany compared to the previous year, the number of livestock killed or injured fell by 15% (Fig. 3.3.2). The trend of the damage figures in the individual federal states was very different. In some of the federal states with the most wolves (more than 10 wolf territories in 2020), the number of wolf-caused attacks decreased significantly (e.g., Mecklenburg-Western Pomerania, Lower Saxony) or changed only moderately (Saxony, Saxony-Anhalt) while they increased significantly in Brandenburg. These data suggest that preventive measures may have been successful to reduce wolf attacks (DBBW 2022).

[23] https://www.loupfrance.fr/

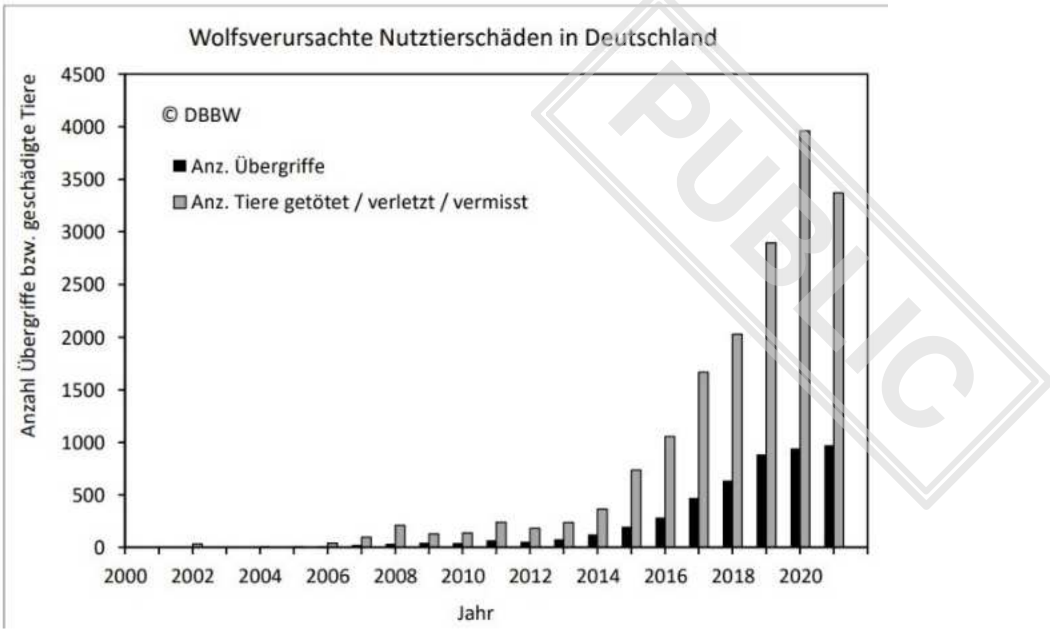

Fig. 3.3.2. Livestock damages caused by wolves in Germany 2002-2021 (black= number of attacks; grey= number of animals killed/wounded/missing). From DBBW (2022).

Dalerum et al. (2020) used a 20-year data set on wolf and three other species of large carnivores and their damages in Sweden to evaluate if temporal variation in carnivore densities has caused an equivalent variation in the number of damages to livestock. They found that wolf densities appeared to have been positively related to the number of damages more often than bear and lynx densities. Their results highlighted that large carnivore damages can be highly context dependent, and that other factors than the size of local or regional carnivore populations may be more important damage determinants. Such an interpretation implies that population reduction may not necessarily be an effective method for limiting large carnivore damages, and highlight that damage mitigation strategies need to be flexible over time and space.

Some concluding remarks

On a large scale, the impact of wolves on livestock in the EU is very small. Considering that there are 60 million sheep in the EU (Eurostat 2022), the level of sheep depredation by wolves represents an annual killing of 0.065%, a very similar figure to that previously estimated by Linnell and Cretois (2018).

Nevertheless, as Boitani et al. (2022) highlighted, although damage to livestock may be tolerable at country level, their concentration at a local level may reveal strong pressure on certain areas. Wolf attacks on livestock can also cause indirect economic losses, which are difficult to quantify, and they also have considerable emotional consequences for their owners. In some areas, recurrent damage to livestock can have a negative impact on pastoralism, the cultural heritage and the way of living of rural communities.

Throughout the European Union, a series of common characteristics related to damage to livestock have been found (see Gervasi et al. 2021 and Singer et al. 2023 for a review).

- Free-ranging livestock are more difficult to protect and account for the majority of predation by wolves.
- There is a positive relationship between wolf distribution and the number of killed sheep at a European scale.

- Depredation levels are lower in the areas where large carnivore presence has been continuous compared to areas where they disappeared and returned in the last 50 years.
- In the EU, there are many fine scale differences. A few large carnivores can produce high damage when the environmental, social, and economic systems predispose for it, whereas large populations can produce a limited impact in different circumstances.
- The availability of natural prey, landscape characteristics and the use of protection measures also shape the incidence of damage to livestock.

3.4 Attacks on hunting dogs and other pets

In addition to the attacks on livestock, wolves can also attack other animals that are considered pets. The cases are very diverse and can go from extremely rare attacks on pet wallabies[24], to the more common attacks on hunting dogs. Although the death of pets is much more uncommon than livestock depredations, they can trigger strong emotions.

This happens for instance when riding horses are attacked by wolves. In Lower Saxony, a state with high affiliation to horse keeping and breeding, the first incidents of horses allegedly injured or killed by wolves were also in 2015. A total of 43 alleged incidents of wolf attacks on horses were officially registered in Lower Saxony in 2007– 2019, and wolf involvement was confirmed in at least four cases. In 2020, 13 alleged wolf attacks on horses were reported in Lower Saxony, and seven cases, in which six horses were killed and four injured, were verifiably caused by wolves. Genetic analysis showed that a resident wolf pair experienced in attacking and killing cattle was responsible in some cases. In 2013 – 2019 a Horse & Wolf working group, comprising horse owners, biologists and members of NGOs was formed in Lower Saxony in order to help farmers and equestrians adapt their husbandry to the presence of wolves (Solmsen et al. 2021).

Wolf attacks on hunting dogs

Although the number of dogs killed by wolves may be statistically insignificant relative to other livestock predation, it can have a dramatic impact on people's perceptions and attitudes to wolves. In some cultures, humans and dogs have strong social and emotional links, and dogs are treated as family or team members. Good hunting and livestock guarding dogs are valuable and cannot be replaced quickly.

The loss of such animals triggers strong emotional responses of grief. In addition, the fact that wolves often enter villages and farmyards to take dogs close to houses may induce fear because of the threat that they also pose to human life. These incidents increase animosity toward wolves and decrease community and political support for their conservation (Butler et al. 2014).

Most commonly, wolves perceive dogs as both competitors and prey, and will kill them usually in two types of circumstances. The first is when hunting dogs are running free in wolf habitat. Wolves treat baying, free-running hunting dogs in pursuit of wild ungulates as competitors for a shared prey. Wolves are very aggressive toward other wolves that invade their territories, and they likely perceive and respond to hunting dogs in a same manner. The second one is where dogs are killed in villages or yards, often when chained to a building, suggesting that the wolf actively sought out the dog and killed it without provocation. In addition, livestock guarding or herding dogs are sometimes killed during a wolf attack on livestock. In all cases, dogs may be partially or totally consumed by wolves (Butler et al. 2014; Tikkunen 2023).

[24] https://www.euronews.com/2019/12/26/wolf-suspected-of-eating-pet-kangaroo-as-christmas-meal-in-belgium

In Croatia, the majority (64%) of dogs were killed during drive hunts on wild boar (Bassi et al. 2021), and in Finland 91% of the attacks were directed at hunting dogs during the hunting season (Tikkunen and Kojola 2020). In Poland, hunting with a dog poses a seven times greater risk of interaction with wolves compared to recreational walking (Haidt et al. 2021)

Number and trend of dogs killed by wolves

The wolf-dog conflict is more obvious in northern countries, where valuable dogs are used in moose hunting. In Finland, during 2010–2017 wolves killed an average of 38 dogs (range 24–50) per year (Tikkunen and Kojola 2020), and from 2018 to 2022, this figure increased to 45.4 dogs (Tikkunen 2023).

In Sweden, 11 dogs were killed and 11 injured by wolves in 2022, most of them, hunting dogs (Frank et al. 2023). During 2003-2018, an annual average of 29.2 dogs was killed/injured by wolves In Sweden (Dalerum et al. 2020), and damages did not show any distinct trends over time. At the national scale, the number of attacked dogs was positively related to wolf density, although the relationship was not statistically significant.

In Poland, wolves killed an average of 61 domestic dogs annually on hunting grounds from 2006 to 2011, primarily in regions where wolves are residents and live in stable packs (Wierzbowska et al. 2016). In Greece, losses averaged approximately one dog per decade and hunter, showing a positive trend (Iliopoulos et al. 2021). In Croatia, 34 dogs were killed and 14 were wounded by wolves in 2022 which is an insignificant part of the 3,516 domestic animals killed and wounded by wolves that year (Table 2.4.1). According to official statistics the number of dogs killed by wolves in Croatia is decreasing (from 154 in 2012 to 34 in 2022).

Factors influencing wolf attacks on dogs

Knowing the circumstances that determine the attacks of wolves on dogs can help to design prevention measures. The risk of interaction between wolves and a dog that is with a human depends on the distance between the dog and its owner, the number of wolves and the size of the dog. In Croatia, most of the attacked dogs were smaller than 20 kg and 86% of these attacks were fatal. In Sweden, only moose hounds heavier than 25 kg were more often injured than killed. The dog breed is also important. In Croatia, hounds that are more likely to be attacked by wolves have energetic and sometime aggressive character, while pointers, which are more vigilant, had lower risk for being attacked (Bassi et al. 2021; Haidt et al. 2021).

In Greece, dogs were more vulnerable during hare hunting and during wolf post-weaning season or in wolf territories with reproduction (Iliopoulos et al. 2021). In north-eastern Europe, wolf attacks on dogs are also linked to the scarcity of prey. In Finland a highly significant negative relationship was found between the number of dogs killed and the population density of white-tailed deer (*Odocoileus virginianus*) and the total ungulate biomass per unit area. In years when roe deer and wild boar populations are down, the risk of wolves attacking dogs in house yards was higher in Estonia. In Croatia, more dogs were attacked in counties with more livestock and fewer wild prey, but correlations were not significant (Tikkunen and Kojola 2019; Kojola et al. 2022; Bassi et al. 2021). These data suggest that wolves likely perceive dogs as potential prey.

In addition, the attacks on dogs take place near territory boundaries much more often than expected based on the position of GPS-collared territorial wolves. This pattern supports that intraguild competition is also an important motivator for wolves to kill dogs (Kojola et al. 2023).

Wolf attacks on dogs in perspective

Hunting dogs attacked by wolves account for a small part of the casualties suffered by hunting dogs from various causes. According to the report from the major insurance company Agria (40% market share) related to accidents with hunting dogs in Sweden, in 2021 238 dogs were killed/injured in traffic accidents, 9 were shot and 12 drowned. In addition to the 30 dogs killed/injured by wolves, 197 were attacked by wild boars, 17 by lynxes, 3 by bears, 4 by European adders and 2 by wasps (Frank et al. 2022; Agria Statistics).

3.5 Considerations about public safety

In the last 40 years, despite the large number of wildlife biologists collecting reliable information on large carnivores, there has not been a single verified record of a fatal wolf attack on humans in Europe and only two fatal attacks have been recorded in its wide American range (Linnell et al. 2002, 2021). In spite of this, many people who live in wolf range report that they are afraid of wolves, perhaps because of the traditional bad reputation of wolves in many cultures. This fear is also frequently used as an argument by anti-wolf advocates in efforts to undermine conservation legislation and reduce the current level of legal protection offered to wolves (Linnell and Alleau 2016).

After reviewing a vast amount of historical and current information coming from the whole wolf range, Linnell et al. (2002, 2003, 2021) concluded that there is indeed evidence that people have been killed by both healthy and rabid wolves during the last centuries, attacks in general are unusual but episodic, and humans are not part of their normal prey. In historic times, the number of cases probably was very small, but the incidence of attacks appears to have dropped dramatically during the 20th and 21st centuries.

In those extremely rare cases where wolves have killed people, most attacks have been by rabid wolves. Some predatory attacks aimed mainly at children have also been recorded in areas with an intense human pressure on the landscape, and with relatively little forest and little wild prey. Livestock (in addition to carrion and garbage) was the main prey of wolves and was only defended by unarmed child shepherds in fragmented landscapes with dispersed settlements (Linnell and Alleau 2016). When the frequency of wolf attacks on people is compared to that from other large carnivores, wolves are among the least dangerous species for their size and predatory potential.

The conditions that allowed wolf attacks in the past do not exist in Europe today, as rabies has been almost completely eradicated and children under 12 do not work as shepherds anymore. Although the risk of people being attacked by wolves is incredibly low in the modern world, the risk is not zero (Linnell and Alleau 2016).

In order to reduce even more this risk, Linnell et al. (2002) proposed to keep wolves wild by responding properly to wolves that act in an aggressive manner or have lost their shyness (see “Recommendations to address bold wolves” in section 4.7), to maintain or improve wild prey populations for wolves, and to control rabies in the countries where this is still a problem (not in most of Europe).

The current tolerance of the modern society toward wolves has allowed the emergence of fearless wolves, whose behaviour is reinforced when they obtain food from humans or are even fed on purpose. Fearless and food-conditioned wolves may be dangerous. In fact, one of the only two known lethal attacks by wolves on humans in North America was caused by food-conditioned wolves in Saskatchewan (Linnell et al. 2021).

Other documented non-lethal wolf attacks over recent decades from North America were also caused by fearless and/or conditioned wolves (Linnell et al. 2021). These fearless/bold wolves which have appeared in some countries of Europe may lead to potentially dangerous situations, as occurs with the cases of bold wolves described in Germany by Reindhart et al. (2020) or the low intensity attacks in Poland, where two wolves bit several people on the legs, hands and the buttock causing minor injuries (Nowak et al. 2021b).

These attacks were caused by yearling wolves from local packs, which appeared near households several months prior to incidents. Both individuals were positively food-conditioned and showed increasing habituation caused by irresponsible behaviour of people such as long-lasting intentional feeding or illegal keeping. Despite prolonged observations of these wolves less than 30 m to human settlements, no mitigation actions were undertaken until the attacks, after which both wolves were killed.

In the International Conference on Bold Wolves promoted by the Life project Wolf Alps on 29 April 2022[25] their presence was confirmed in Italy (23 cases over the last ten years), Slovenia (three cases from 2006 to 2022), Germany (two cases required management intervention in 22 years), and France (out of 3280 encounters from 1993 to 2000, one case of aggressive, non-defensive, behaviour without attack). More recently, a pure wolf female (DNA confirmed)[26] of central Italy, lightly bit several people on the beach or walking near the coast near the city of Vasto in summer 2023. The wolf, apparently fearless, was captured in September 2023. In these cases, the implementation of the bold wolves' protocols described in Chapter 4.7 can further minimize the risks that they pose to humans.

While previous actions focus on the real risks posed by wolves, the far greater challenge lies in managing the fear of wolves (Linnell and Alleau 2016). Apart from the propaganda of anti-wolf groups, information based on false or unconfirmed data is frequently disseminated, as demonstrated by the alleged wolf attacks that seriously injured a man in northern Italy (Caniglia et al. 2016) and killed a woman in Greece (Iliopoulos et al. 2022), which were actually caused by dogs. It is important to debunk fake news about wolves that prey on people by scientifically credible organizations.

[25] https://www.lifewolfalps.eu/en/lupi-confidenti-sintesi-della-conferenza-internazionale-2022/#:~:text=On%2029%20April%2C%20at%20the,Germany%2C%20and%20the%20management%20guidelines.

[26] https://www.isprambiente.gov.it/it/news/le-analisi-genetiche-di-ispra-confermano-che-lanimale-responsabile-degli-attacchi-a-vasto-e-una-femmina-di-lupo

4. AVAILABLE MEASURES TO IMPROVE COEXISTENCE

4.1. Prevention measures and livestock protection

The best way to reduce livestock losses after wolf recolonization is to apply measures to prevent wolf depredation. In some cases, preventing wolf attacks on livestock is a simple task requiring only inexpensive materials and minor husbandry changes. But most of the time, livestock damage prevention may imply profound modifications of husbandry practices and a corresponding increase of labour intensity (Linnell and Cretois 2018). In other cases, mainly when livestock is free-ranging and scattered over wide areas, to implement preventive measures is extremely difficult. Adopting new protection measures can be challenging for many producers, especially in countries with high labour costs.

Nevertheless, the benefits of protecting livestock become clear when comparing the different Swedish and Norwegian models of livestock and predator management (Swenson and Andrén 2005; Linnell and Cretois 2018). In Norway, sheep are free-grazed in forested and alpine-tundra habitats with very low levels of supervision, in the same way than in the past, and the recovery of large carnivore populations has not changed the husbandry system. Hence, per capita depredation rates (i.e., the number of livestock killed per large carnivore individual) in Norway and Sweden are 34 vs 0.85 for wolves, 20 vs 0.01 for bears, and 16 vs 0.1 for Eurasian lynx. The key difference is that Swedish sheep are kept behind fences (often electrified) while Norwegian sheep graze freely and unprotected. In addition of having the highest depredation rates in Europe, Norway has very small populations of large carnivores compared to Sweden (Linnell and Cretois 2018).

Information on wolf damage prevention to livestock

Every livestock's exploitation has its own needs and circumstances, and it is not possible to prescribe recipes that work for all of them. Nevertheless, dozens of papers and reports have been published in recent years on this topic, there is a journal specifically devoted to large carnivore damage prevention[27] and a lot of resources and manuals have been produced mainly by LIFE projects. Linnell and Cretois (2018) listed the main available web resources on livestock protection measures in Europe. In addition, Oliveira et al. (2021) reviewed 135 LIFE projects dealing with large carnivores between 1992 and 2019 to provide an overview of the use of damage prevention methods and their effectiveness.

The largest number of projects focused on wolves and brown bears in the Mediterranean countries and in Romania. Besides dissemination of information, carnivore-proof fencing and livestock guarding dogs were the more frequently used methods. Other methods are also efficient but demand important husbandry changes, such as changing livestock species, or moving from very vulnerable small stock (sheep and goats) to large stock (cattle, horses for meat), as has been done in many areas of the northwestern Iberian Peninsula (see section 3.3) and other parts of Europe; this change may also modify the landscape as small stocks have different grazing patterns than large ones.

Using shepherds is also a very efficient measure, because wolves are usually scared by human presence, but the cost of hiring shepherds can be challenging for many producers. Expert advice to solve problems in the early phases of the implementation of the measures is crucial to ensure their effectiveness. In the review of Oliveira et al. (2021), electric fences were reported as the most successful method for reducing damages by large carnivores, but most of the non-lethal methods used showed at least moderate effectiveness.

[27] CDPNews (protectiondestroupeaux.ch)

Effective prevention is particularly difficult in the case of free-ranging livestock, like sheep in alpine meadows, free-ranging horses for meat production in northwestern Iberian Peninsula or in Italy, or free-ranging beef cattle in some regions of Spain. This type of livestock spends much or all the year scattered in the field, so they cannot be defended with fences and it is not always easy to protect them with guarding dogs. In addition, the use of prevention methods may require significant economic investments or more labour time, which can cause costs to exceed the value of livestock not preyed on by wolves (Blanco et al. 2021b). A particular case is that of the semi-domestic reindeer in Sweden and Finland. There are few practical protection measures, and management currently rests on the strategy of using lethal-control to regulate carnivore populations and the economic compensation for losses (Linnell y Cretois 2018).

Cost and effectiveness of damage prevention in some EU countries

Some EU countries, such as France or Germany, spend a large amount of money for the prevention of damage to livestock. For example, 32.7 million euros on damage prevention and 4.1 million euros on damage compensation were spent in France in 2022[28]. France intends to spend 175M€ of CAP funds over the 2023-2027 funding period (EU LC Platform 2023). In Germany, expenditure on livestock protection measures in 2021 was €16,639,800, more than 30 times higher than expenditure on compensation payments for damage incurred (€498,433) (DBBW 2022).

In spite of the massive investment in protection measures, some French researchers are pessimistic about the outcomes of these measures. According to Meuret et al. (2020), from 2009 to 2019, the number of predated livestock increased linearly with the number of wolves, from 3215 in 2009 to 12 451 in 2019 (Fig. 3.3.1), despite France implementing extensive damage protection measures since 2004, including reinforced human presence, livestock guarding dogs, secured pasture fencing and electrified night pens. From 2009–2017, if the mean number of victims per wolf was slightly lower than during 1992–2005, the rate of increase was identical.

In the period 2009-2017, most of the increase in damages came from the historically predated area of France, invalidating the hypothesis that main damages were caused in other areas of France recently recolonized by wolves where farmers were not prepared yet to protect the livestock. In addition, in the most predated area, the majority of wolf attacks (>92%) affected the producers who had subscribed to an effectively implemented protection contract. These data allow Meuret et al. (2020) to conclude that damage prevention methods have failed. Nevertheless, in the last three years (not covered by the study of Meuret et al., 2020), damage has slightly decreased or stabilized in France (see section 3.3.) while wolves have kept increasing. This suggests that damage prevention procedures could be yielding some positive results.

In Germany, the evaluation of the results of damage prevention is more optimistic than in France. Damage to livestock has increased as the wolf population has grown, but, while the number of attacks increased in 2021 by 3.5% across Germany compared to the previous year, the number of livestock killed or injured fell by 15%, suggesting that preventive measures may have been successful to reduce wolf damage (Fig. 3.3.2, section 3.3). Sheep losses are related to the expansion of wolf population but not to increasing wolf numbers. This decreasing trend suggests that mitigation is possible, even if the number of attacks is high. Attacks on farm animals occur primarily where sheep and goat keepers have not yet adjusted to the presence of wolves and have not taken protective measures.

On the one hand, these are areas in which wolves have recently settled and established new territories. However, there are still attacks even in areas where wolves have been present for several years. A

[28] https://www.auvergne-rhone-alpes.developpement-durable.gouv.fr/IMG/pdf/infoloup40-vf-compresse.pdf

systematic and professional application of livestock protection measures in wolf areas has not yet been achieved (Bruns et al. 2020; DBBW 2022; Khorozyan & Heurich 2022; Singer et al. 2023).

A study carried out in the Iberian Peninsula illustrates the potential for prevention measures to contribute to mitigating wolf-human conflicts in the long-term. LIFE Coex (LIFE04 NAT/IT/ 00144) was implemented from 2004 to 2008 in five European countries. In Spain and Portugal, measures were focused on reducing losses of livestock to wolves at 144 holdings. These holdings were surveyed ten years after the end of the project, and 83 % were still using prevention measures at the time of the survey or had used them until ceasing farming activity. Conventional fences (93% still in use) and large guarding dogs (87%) had greater longevity than electric fences (61%). Most measures were still being used a decade after they were implemented, damage remained low and farmers continued to be satisfied (Cortés et al. 2020).

In some cases, the implementation of prevention measures may not seem satisfactory due to their high economic cost and because they do not reduce the damage sufficiently. However, the measures used to protect livestock against large carnivores will also protect them against smaller predators and theft, while the more intensive surveillance will allow earlier reaction to accidents, diseases and parasite infections. It is therefore very likely that both animal survival and welfare will be enhanced in well protected flocks (Linnell and Cretois 2018).

In most cases, there is no other alternative to prevention methods than paying large amounts of money in compensation or killing all or most of the wolves in the area, which contravene the Habitats Directive and is outrageous to a large part of society. Seeking the necessary technical, administrative, and economic improvements to make prevention measures more effective is more useful than not using prevention methods.

Preventing attacks on horses and hunting dogs

Hunting dogs, riding horses and other pets are sometimes killed by wolves. Solmsen et al. (2021) published some recommendations to prevent damages to riding horses Germany, and several studies have been carried out addressing the safety of hunting dogs.

Preventing wolf attacks on hunting dogs may lead to an increased acceptance of wolves, mainly in Finland and Sweden, where they are used for hunting moose (Tilkkunen and Kojola 2020). The studies cited in the section 3.3 (Predation on farm and domestic animals) recommend keeping hunting dogs on a short distance from hunters, using dogs heavier than 25 kg in wolf areas, or releasing multiple dogs at the same time. In addition, protective vests and other means that protect dogs from wolf bites can be functional (Fedderwitz 2010). In 2021, SEK 626,000 (€55,391) was paid in Sweden to prevent wolf damage to hunting dogs, which was mostly used by hunters to purchase protective vests for dogs (Frank et al. 2022).

In Finland and other European countries, dogs are more frequently attacked by wolves when wild ungulates are scarce (Kojola et al. 2023), so abundant wild prey would decrease the risk of attacks. Nevertheless, it must be considered that higher densities of wild ungulates could increase the risk of traffic collisions and browsing damages in forests. In addition, one of the main wild prey of wolves in Finland, the white-tailed deer (*Odocoileus virginianus*), is an alien species.

The most effective protection measure is to avoid releasing hunting dogs in hunting grounds that are being used by wolves. To obtain this information, hunters scout for wolf tracks and signs or are informed about wolf presence through social networks. To help moose hunters, the Natural Resources Institute of Finland (Luke) made accessible to the public positions of GPS-collared wolves during several hunting seasons (see chapter 3.3). This information decreased the risk, but did not completely protect dogs from wolf attacks. The negative side of this initiative is that it may increase the risk of wolf poaching in some cases (Tikkunen and Kojola 2020).

4.2. Compensatory measures

In most of the EU countries, the damage caused by wolves to livestock is compensated to the producers by the regional or national governments to alleviate the economic burden of coexisting with wolves, increase tolerance toward them and avoid retaliatory poaching. Compensation is paid by different agencies in different countries, and the compensation systems are also diverse. There are three main methods:

The classical ex post facto system is the most widespread in the EU. This system usually requires documenting losses, and producers have to face the challenge of finding fresh carcasses for examination. In some cases, compensation is only granted when at least some damage prevention measures are implemented (Boitani et al. 2010; Marino et al. 2016).

Some countries, such as Sweden in the case of semi-domestic reindeer, pay incentives ex ante for carnivore presence rather than paying ex post facto compensation for damage. This system is based on paying for the risk associated with large carnivore presence and does not require documenting losses. Rather, the focus is on documenting the presence of reproducing populations of large carnivores. Such incentive systems encourage depredation prevention rather than documentation and have significantly lower transaction costs than compensation and insurance systems (Linnell and Cretois 2018). This system is not accepted by many farmers, and economic costs can be much higher than ex post payments.

Insurance programs are also used in some countries or regions, where producers pay premiums to insure their stock against losses. Governments can partially subsidise these programs. This system has been used in some regions of Spain, but farmers prefer the ex post facto compensation system (Blanco 2003).

Of the 24 countries of the European Union with wolves, 20 pay compensations for documented losses, some of them (e.g., Croatia, Portugal, Slovakia and Germany) conditioned to the implementation of some protective measures, and in the remaining four countries (Bulgaria, Hungary, Latvia and Luxemburg), damage compensation is not paid or other methods are used for compensation (Boitani et al. 2022).

The cost of compensation

Throughout the European Union (excluding Latvia, Bulgaria and Hungary), 18.7 million euros per year are paid to compensate for wolf damages. The countries that paid the most compensation are France (4.1M euros in 2022), Spain (3.2M euros in 2022), Finland (almost 3M euros in 2021, more than 90% for semi-domestic reindeer), Greece (2.3M euros) and Italy (about 2M euros in 2019) (Table 3.3.1).

The compensation for damage caused by wolves on semi-domestic reindeer is different in Sweden and in Finland. In Finland, the compensation system is based on paying for losses, requiring at least partial documentation of large carnivore kills. In 2021, more than 2.7 million euros were paid for 1,516 reindeer killed by wolves. In Sweden, the system is based on paying for the risk associated with large carnivore presence. This system does not require documenting losses but focuses on the presence of reproducing populations of large carnivores. Although no similar data are available for Sweden, Linnell y Cretois (2018) estimated that compensation payments have been made for the equivalent of between 20,000 and 40,000 reindeer lost by the four species of large carnivores living in the country.

Wolf attacks on dogs are not compensated in many EU countries, so there are no figures to quantify such attacks. But they are compensated in Sweden and Finland. In 2021, 49,670€ were paid as compensation for attacks by large carnivores on 55 hunting dogs in Sweden; 30 of these attacks were caused by wolves (Frank et al. 2022). In Finland, more than 160,000 euros were paid to the owners of the 52 hunting dogs attacked by wolves in 2022 (Tikkunen 2023).

According to data shown in Table 3.3.1, the average compensation paid annually per wolf in the EU (18.7M euros/ 20,300 wolves) is €920, a lower figure than previous estimations (€2,400: Bautista et al. 2019). This ratio can show huge differences in different EU countries. For example, in France, it is around €3,700 per wolf and year, and in Romania, this figure is as low as €46. In any case, these figures must be taken with reservations because the compensation paid probably does not represent accurately the actual damages caused by the wolves.

Differences in compensation costs among countries are largely related to husbandry practices. In areas with free-ranging livestock, damage caused by wolves and compensation costs escalate (Linnell and Cretois 2018; Bautista et al. 2019; Singer et al. 2023). In addition, previous research has found that the annual compensation cost per individual carnivore is positively related to national economic wealth measured as gross domestic product per capita. This association is not due to differences in the price of livestock or agricultural products across countries. The link between wealth and conservation expenditures has been reported at a European level and globally. In wealthier countries, damage management policies receive more institutional support to cover the costs of damage compensation (Bautista et al. 2019).

The ex-post compensation schemes in several countries of Europe have been criticized because of fraudulent claims, high transaction costs, and because they can discourage the adoption of damage prevention measures thus promoting farmers' perpetual reliance on compensation. On the other side, farmers claim that compensations are sometimes received a long time after the attacks, are only granted when the carcass of the livestock killed is recovered and the predation by the wolf is proved, and do not consider the indirect costs of damage. The challenge for the future is to improve the compensation schemes to optimize their cost-effectiveness, being more proactive and linking compensation with prevention-based policies in an adaptive manner (Boitani et al. 2010; Marino et al. 2016; Linnell and Cretois 2018; Bautista et al. 2019).

4.3. Opportunities for nature-based tourism, education, research

In addition to being an integral part of Europe's ecosystems, the wolf has also shaped the cultural heritage and local identity of many regions and brings educational and research benefits. Alternative income for local communities generated through wolf tourism can lead to increased tolerance toward wolves at the local level.

Moreover, tourism can educate visitors about wolf ecology and coexistence and promoting awareness raising and conservation efforts on an international level. This activity allows urban visitors to learn on the ground some concepts that are much better assimilated during field experiences than through articles or websites. In these experiences, wild ungulates are often observed, which allows tourists to understand the important role that wolves can play in ecosystems, limiting wild ungulate numbers, changing prey behaviour and distribution, and thereby reducing pressure on vegetation (Kavcic et al. 2022).

The wolf-related tourism in Europe is a relatively new activity, but it has been developing for many years in North America, where the economic benefits it entails have been quantified. Different forms of tourism associated with wolves, such as wolf watching, photography, or observing signs of their presence have already been practiced for a couple of decades in North America.

In Montana, wildlife viewing is listed by both visitors and state residents as one of the top activities. The economic contribution of such activities has been studied in detail in certain parts of North America. For example, in 2005, some 94,000 visitors from outside of the three states that surround Yellowstone (Montana, Wyoming and Idaho) travelled to the National Park specifically to see or hear wolves, spending an average of $375 per person, or a total of $35.5 million in the three states (Duffield et al. 2008).

In Denali National Park and Preserve (DNPP, Alaska), a report on the economic value provided by wolves was completed in 2016 (Loomis 2016). The conclusions highlight that wildlife viewing is clearly a source of socio-economic value in the state of Alaska. Wildlife viewing is a driver of tourism for DNPP and the state of Alaska. For example, wildlife viewing activities in Alaska supported over $2,700 millions' worth of economic activity in 2011 (ECONorthwest 2014). In 1997, non-resident visitors who came to Alaska primarily to view wildlife had average expenditures of $6,000 per trip. The benefits per trip in excess of their expenditures were on the order of $700 to $900. From economic valuation questions found in Alaska wildlife viewing literature, it can be inferred that a non-resident visitor may have an additional value in the range of $200-$300 per wildlife viewing trip to Alaska if a wolf is seen on their trip (Loomis 2016).

In Europe, wolves are an important generator of culture, ethnography and tradition, and their presence brings educational and research benefits, income from regional and product marketing, as well as socio-economic benefits from wildlife tourism. Spain is one of the European countries where wolf-watching tourism is most developed. This type of tourism is located mainly in the Sierra de la Culebra Game Reserve (Zamora), in the Montaña de Riaño y Mampodre Regional Park (León) and in the Montaña Palentina Natural Park, the last two in the Cantabrian Mountains. Interestingly, this activity developed from wolf hunting. The baits used to attract and hunt wolves in the Culebra Game Reserve facilitated their observation, and the growing number of naturalists who came informally to observe wolves led to the appearance of several small guide companies to exploit this resource.

This business seems to contribute a significant amount of resources to the area. According to a survey conducted in 2012, wolf-watching tourists represent 46% of overnight stays in rural accommodation in the Sierra de la Culebra, with an average stay of 2.18 days. The minimum cost of accommodation and food could reach 440,000 euros per year, an amount much higher than the income derived from wolf hunting in the area (Talegón 2012), which was legal until September 2021. In the Sierra de la Culebra, an area with few landscape values, wolves are the main tourist attraction, and numerous hotel companies find their main economic resource in observing wolves. In the Riaño and Montaña Palentina parks, with greater landscape and natural resources, there are as yet no data on the contribution of wolf tourism to the total tourism in the area but, already, the evidence that wolves can be a source of income for a non-consumptive activity seems to produce a change in attitude among many locals, who go from considering the wolf as a simple source of nuisance to having an attitude, if not positive, at least neutral of this species (Blanco 2018).

In some areas of Europe, there is also a flourishing tourism around agriculture and livestock production. In these areas, the potential of the wolf as an attraction may complement (and in some cases, clash with) the existing business.

In some wolf-related tourism experiences in the Sierra de la Culebra (Zamora, Spain), tourists interact with producers who use mastiff dogs (livestock guarding dog breed) and other prevention measures, which allow them to understand the wolf-people conflict, to look at the cultural differences between urban and rural environments and to respect local identities. The visit to old stone-made structures intended to capture wolves and other traditional facilities for livestock protection enable tourists to appreciate the rich cultural heritage related to the long history of coexistence between wolves and humans in Europe.

Although tourism can increase the value of the species locally, such activities can also have negative impacts on wolves and their habitat, especially with the growing demand for wildlife tourism. The wolf watching tourism can indeed also have a negative side. The direct impact caused by responsible companies guiding tourists may be low, since they usually take it upon themselves to minimize it in order to avoid losing their permits and make the business sustainable. But the inevitable impact caused by the disclosure of the locations of dens, rendezvous sites and other sensitive spots, which facilitates the invasion of these usually secret places by photographers, observers and even by poachers, may be much higher.

There are some best practices manuals that can help to prevent such issues. In Spain, the Ministry for the Ecological Transition (2017) published a good practice guide for the observation of large carnivores where some elementary rules of behaviour are recalled [29]. More recently, Kavcic et al. (2022) have published the Guidelines for responsible wolf tourism, a valuable document developed within the LIFE WOLFALPS EU project, reviewed and endorsed by the Large Carnivore Initiative for Europe (IUCN/SSC Specialist Group).

4.4. Information, advice, awareness raising

The return of large carnivores, as with a number of different topic areas (climate change, vaccinations), is in many countries subject to treatment by the media ranging from sensationalisation of real news to misinformation campaigns. Broad use of social media means that stories are often not fact-checked before reposting and some false stories relating especially to damages caused by wolves have been widely spread (Arbieu et al 2021)[30].

In the EU, websites of public institutions of certain Member States provide information on basic aspects of the wolf population, such as distribution, number of wolves or packs and their trends, monitoring methods, and other aspects of interest to the public and professionals. For example, data on the Scandinavian wolf population, collected by a team of Swedish and Norwegian scientists working together, can be found on the webpage of SKANDULV[31], where technical reports and scientific papers of great interest are also available[32]. In France, the webpage Le loup en France, managed by the Office Français de la Biodiversité (OFB)[33], performs the same function. In Italy, the webpage of the public agency ISPRA (Italian Institute for Environmental Protection and Research) has provided extensive information on the Italian wolf survey carried out in 2020-2021[34].

In Germany, an outstanding public website on wolves[35] gives comprehensive information on the distribution of packs and pairs from the year 2000 to the present, including the breeding status of the packs, the minimum number of pups in each pack and other details about wolf management in the Member State. Other EU member states, like Austria[36], the Netherlands[37] and Czech Republic[38] also have official web pages on wolves.

Likewise, the European Commission has its own webpage on large carnivores[39] that includes information on conservation status, the dialogue with stakeholders, best practices, publications, etc. The

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[29] https://www.miteco.gob.es/es/biodiversidad/temas/conservacion-de-la-biodiversidad/bp_oso_lobo_lince_tcm30-441194.pdf

[30] News selection and framing: the media as a stakeholder in human–carnivore coexistence. Environmental Research letter https://iopscience.iop.org/article/10.1088/1748-9326/ac05ef

[31] SKANDULV - the Scandinavian Wolf Research Project | Externwebben (slu.se)

[32] https://www.slu.se/centrumbildningar-och-projekt/viltskadecenter/publikationer/inventeringsrapporter/inventeringsrapporter-varg/

[33] https://www.loupfrance.fr/

[34] https://www.isprambiente.gov.it/it/attivita/biodiversita/monitoraggio-nazionale-del-lupo/

[35] https://www.dbb-wolf.de/

[36] https://baer-wolf-luchs.at/verbreitungskarten/wolf-verbreitung

[37] https://www.bij12.nl/onderwerpen/faunazaken/diersoorten/wolf/

[38] https://www.navratvlku.cz/

[39] https://environment.ec.europa.eu/topics/nature-and-biodiversity/habitats-directive/large-carnivores_en#stakeholder-cooperation

webpage of the Large Carnivore Initiative for Europe (IUCN SSC Specialist Group)[40] shows updated information on large carnivore distribution in the continent, reports, publications, news, and much other information for the scientific conservation of large carnivores.

Information and advice on damage prevention in LIFE projects

Since 1992, a large number of LIFE projects have focused on wolves and other large carnivores, and most of them have included livestock prevention measures. LIFE projects must include a strategy for the successful replication and/ or transfer of project solutions and results elsewhere. They need to include tasks that ensure the multiplication of the impact of the project's solutions. A clear reporting of the results and a careful evaluation of the effectiveness of prevention measures is crucial to obtain sound information to improve the coexistence between people and wolves in the EU.

Oliveira et al. (2021) reviewed 135 LIFE projects dealing with large carnivores between 1992 and 2019 to provide an overview of the use of damage prevention and their effectiveness (section 4.1). Dissemination of information to the stakeholders was included in 32 of the 34 LIFE projects (92%) on wolves analysed by these authors. The perceived effectiveness of these actions was high or very high in 87% of the cases, and low in 13%. A large number of websites provide information and advice on preventive measures in different parts of the EU collected in LIFE projects (see section 4.1).

Information to prevent wolf attacks on hunting dogs

In some cases, specific information for specific problems has been provided by public agencies. Hunting dogs are attacked by wolves across the EU, but the problem is particularly important in Sweden and Finland, where dogs are very appreciated for moose hunting (see sections 3.3 and 4.1). In Finland, in order to decrease the risk of attacks, the last seven positions (one position per hour) of GPS-collared wolves were made accessible to the public by the Natural Resources Institute of Finland (Luke); the locations had a 5×5 km resolution during the hunting seasons of 2013-2018 (Kojola and Tikkunen 2020). The link was visited more than one million times in 3 of the 4 seasons.

Both the wolf attacks on hunting dogs and visits peaked in September–November, which is the primary hunting season in Finland. The number of daily visits to the website was higher on days when fatal attacks occurred. Kojola and Tikkunen (2020) highlights that the most remarkable benefit of this kind of information service might be the message to the public that management is not overlooking hunters' concerns about wolf attacks on their dogs. Wolves were last radiocollared in the winter of 2019, but hunters have requested that this public service be reinstated (Tikkunen 2023).

Awareness raising by NGOs

The increase of the European wolf population and the subsequent increase of livestock damage have reinforced the negative perception of wolves by some stakeholders. A review of the academic literature that assessed the socioeconomic impact of wolves revealed a bias toward investigations of negative economic impacts (Rode et al. 2021). Positive impacts were underrepresented, in particular benefits from wildlife tourism and commercial activities, benefits from ungulate population control by wolves, cultural heritage and identity, etc. To counteract this trend, awareness raising is being carried out by numerous NGOs in Europe that normally disseminate their products from their websites.

[40] https://www.lcie.org/

4.5. Dialogue with, and involvement of, stakeholders

It is often said that conflicts between wolves and people are in the end conflicts between people and people. Beyond damage to livestock, the main characteristic of the wolf conflict is that it elicits strong mixed opinions among broad sectors of society, which often results in clashes between stakeholders with differing values toward wolves and their management.

These conflicts often disclose unmet social and psychological needs, including status and recognition, dignity and identity, and unveil deeper antagonism between rural and urban areas, between modern and traditional values, or between different political positions. Stakeholder participation processes can be very useful to address these conflicts (Marchini 2014; Madden and McQuinn 2014; Linnell and Cretois 2018; von Hohenberg and Hager 2022).

The EU Platform on Coexistence between People and Large Carnivores

To support implementation of the Habitats Directive on the ground, the Commission has for many years been carrying out a range of measures to encourage and facilitate dialogue and cooperation between stakeholders and to promote best practices on coexistence. In this spirit, the European Commission supported the establishment of the EU Platform on Coexistence between People and Large Carnivores[41] in 2014.

Representatives of different interest groups take part in the meetings, including hunters, land owners, reindeer herders and nature protection NGOs, and all of them have agreed a joint mission: “to promote ways and means to minimise, and wherever possible find solutions to, conflicts between human interests and the presence of large carnivore species, by exchanging knowledge and by working together in an open-ended, constructive, and mutually respectful way”.

The platform collates information and good practice from different Member States and promotes the findings on their website and through their information channels. Promoting and supporting the adoption of damage prevention measures through EU rural development funding and the collection and evaluation of case studies have been long-standing strands of the platform’s work.

The platform communication plan describes the lessons learnt to date. Joint activities are most successful as it is easier to engage with a range of different stakeholders if they feel their interests are represented.

Having international representatives from the platform and the European Commission in the regional events helps both in terms of the subjects covered and in the participants’ feeling that their concerns are being listened to by a wider group. Joint statements are generally agreed after events that set a marker for future events and enable them to build on previous activities.

Regional and local Platforms

The conflicts surrounding wolves and agriculture, and the actions needed to mitigate them, should be viewed within their social, cultural, economic and political context. As these contexts vary dramatically across the EU, the solutions should be tailored at a regional or local scale (Linnell and Cretois 2018).

Since 2018, an EU-Parliament funded pilot project helped establishing regional and local stakeholders’ platforms[42], following the same model as the EU Platform. Until 2023, projects with regional platforms

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[41] [EU Large Carnivore Platform (europa.eu)]

[42] https://environment.ec.europa.eu/topics/nature-and-biodiversity/habitats-directive/large-carnivores/eu-large-carnivore-platform_en#regional-and-local-platforms

have been carried out in six Member States to deal with long-term conflicts with wolves, in five cases, and with bears in one case.

The assessment of the regional platforms (Salvatori et al. 2020b, 2021) concluded that collaboration among different and generally contrasting groups is possible. Even in situations where large-carnivore impacts were seen as unsatisfactorily managed for many years, people were still willing and eager to be involved in alternative discussion processes hoping this would lead to concrete solutions.

Lack of trust between stakeholders and the relevant authorities as well as the lack of genuine communication among stakeholders were the key features that characterized social conflicts related to large carnivores. The support of the competent authorities and the scaling of this process have been important challenges that should be resolved in the very preliminary stages of coming projects. This is a crucial necessity since a consistent message of the stakeholders across all platforms was that support and engagement from relevant management institutions were pivotal for the effective management of conflicts over large carnivores.

Participatory processes with stakeholders are being increasingly used in wildlife management in the EU, as they are expected to increase the level of compliance with management decisions by fostering a sense of ownership among the parties involved in the decision process (Redpath et al. 2013, 2017; Salvatori et al. 2021). For example, in Spain, the wolf conflict has been addressed with participatory techniques by Grupo Campo Grande[43], an NGO which since 2021 has collaborated with the regional government of La Rioja in a mediation process between stakeholders. As a result, the *Wolf Management Plan in La Rioja and its coexistence with extensive livestock* was legally approved in April 2023.

4.6. Lethal control/culling of wolves

As established by the European Commission in its Guidance document on the strict protection of animal species of Community interest under the Habitats Directive (Commission Notice C(2021) 7301)[44], under the current policy and related legislation, the conflicts associated with the conservation of wolves in Europe's multi-functional landscapes cannot be addressed only or mainly through culling/lethal control. Lethal control was widely used in the past, and derogations to authorise lethal control are still a tool for the Member States, but actions to deal with livestock damage or other conflicts generated by wolves can be based on livestock damage prevention methods and other management measures presented in this document.

Wolves in the EU are strictly protected in the Habitats Directive under Annex IV in most member states, but in seven MS they have Annex V status in all or in part of their territories (section 1.2). The prohibition of killing wolves in MS where wolves are in Annex IV may be derogated to prevent serious damage to livestock or in the interests of public safety (*inter alia*), under the terms and conditions of the Directive.

The use of derogations depends on each Member State. Some Member States where wolves are protected under the Annex IV have never used derogations to remove wolves (e.g., Portugal), other Member States use these derogations in a very limited way (e.g. Germany) and some other Member States make use of derogations in a regular way (e.g. Sweden and France). For example, in Germany, 921 wolves are known to have died from 2000 to 6 June 2023, of which only 13 have been legally killed under derogation. Eight of them were killed because of livestock predation, four were removed because of bold behaviour and one because of suspected hybridization with dogs (DBBW, 2023; Ilka Reinhardt pers. comm.).

[43] http://www.grupocampogrande.org/tag/lobo/
[44] https://eur-lex.europa.eu/legal-content/ES/TXT/?uri=PI_COM:C(2021)7301

A dedicated online dashboard, on the website of the European Environment Agency, provides detailed information on individual derogations/exceptions, as extracted from the national reports that have been submitted to the European Commission in relation to protected species[45].

Wolf lethal control in France

France is the EU country that invests the most money in prevention measures (section 4.1; more information, in Meuret et al. 2020). France is also one of the countries with the highest livestock damage in the entire EU (chapter 3.3), perhaps due to the difficulty of protecting free-ranging sheep in alpine meadows.

Lethal measures to protect flocks from wolf depredation are legally applied in France since 2004 (Meuret et al. 2020; Grente 2021). In 2004 the ceiling for derogations was set at 10% of the population size, half of the annual growth (20%) of the wolf population at that time. This ceiling was maintained in the period 2008-2012, and in the period 2013-2017, the method to calculate the ceiling was adapted to take into account the uncertainty about population size and growth rate. The ceiling was set at 24 wolves for 2013-2015, and increased to 36 wolves for 2015-2017, which allowed the stability or increase of the wolf population.

At the end of 2018, the wolf population in France reached 500 individuals (OFB 2019), the threshold above which the population was considered viable, and the ceiling was increased to 19% on an 'experimental basis'. Despite this increase, the wolf growth rate remained at 9% in 2019 and 8% in 2020, so the ceiling was formalised, and even extended in 2021 to 21% for the simple livestock defence culling (it remains at 19% for the other culling classes) (https://www.loupfrance.fr/; Meuret et al. 2020; Grente 2021). In 2022, 162 wolves were killed under derogation and at least 7 illegally[46]. The national action plan has set a maximum limit of 174 wolves to be culled in 2023.

Each year, the maximum number of wolves that can be culled is updated, based on the winter estimates of the wolf population size. The lethal measures are implemented by governmental agents, hunters and livestock owners, who target wolves approaching flocks and any wolf in areas with high depredation levels. Several wolves can be culled at the same time, but not with the aim to remove an entire pack (Grente 2021).

Wolf lethal control in Sweden

In Sweden, wolves are in Annex II (requiring the designation and management of Natura 2000 sites) and Annex IV (strictly protected species) of the Habitats Directive. Wolves living in the reindeer husbandry area (the half north of the country) may cause serious damage, but conflicts with other types of livestock south of this area are rather small.

A number of wolves are killed every year under protective hunting (to protect livestock) and under licensed hunting (Table 4.5.1). The aim of the licensed hunting is to limit population growth in order to reduce damage to livestock and the negative socio-economic and psychosocial impact which dense wolf populations can have on people who share the area with wolves (Epstein 2017).

[45] https://www.eea.europa.eu/data-and-maps/dashboards/derogations-and-exceptions-table
[46] https://www.auvergne-rhone-alpes.developpement-durable.gouv.fr/IMG/pdf/infoloup40-vf-compresse.pdf

Year[1]	Wolf population size	Number of wolves killed			
		Protective hunting	Licensed hunting	Other causes[2]	TOTAL
2014-15	415	21	44	12	**77**
2015-16	340	20	14	17	**51**
2016-17	355	15	25	11	**51**
2017-18	305	24	15	9	**48**
2018-19	300	9	0	7	**16**
2019-20	365	21	0	15	**36**
2020-21	395	23	27	10	**60**
2021-22	460	8	28	10	**46**
2022-23	450	23	57	8	**88**

1. From May to April next year; 2. Traffic, natural causes, poaching, etc.

Table 4.5.1. Wolves killed by protective and licensed hunting in recent years in Sweden. The wolf population size in Sweden, the number of wolves found dead by other causes and the total known number of wolves dead are also shown. Data from reports of Svensson et al. (2015, 2017, 2019, 2021, 2023) and Wabakken et al. (2016, 2018, 2020, 2022). https://www.slu.se/centrumbildningar-och-projekt/viltskadecenter/publikationer/inventeringsrapporter/inventeringsrapporter-varg/

Wolf culling in Sweden is controversial for several reasons. First, the Swedish wolf population numbers less than 500 individuals and has remained more or less stable since 2014-2015. In addition, Scandinavian wolves are severely inbred which causes high concern in terms of their long-term viability (Laikre et al. 2022).

Secondly, a relatively large number of wolves are allowed to be killed each year (Table 4.5.1). For example, during the 2022-2023 winter, 57 wolves have been legally killed under licensed hunting, including all or parts of five all-Swedish family groups and two Swedish-Norwegian family groups. In a third Swedish-Norwegian family group, parts of the group were killed during Norwegian license hunting. In Sweden, three territory-marking pairs and a group with offspring without parents were also killed (Svensson et al. 2023).

In relation to the use of derogations to cull wolves, the Commission has opened an infringement procedure regarding Sweden's compliance with the relevant provisions of the Habitats Directive. Sweden performs outstanding population monitoring and has excellent scientific knowledge on the species, which would probably make it possible to quickly detect a deterioration of the state of the population.

Wolf management under Annex V of the Habitats Directive

Wolf populations included in Annex V of the Habitats Directive can be managed as far as exploitation is compatible with their being maintained at a favourable conservation status (Article 14 of the directive). In some of the countries where wolves are in Annex V, they are managed as a game species (i.e., Estonia, Latvia, Lithuania and Bulgaria). In contrast, four MS where wolves are partially or totally included in Annex V have fully protected their populations through national legislation (Poland, Slovakia, Spain and Greece).

In Spain, the wolf is listed in Annex V of the Habitats Directive north of the river Duero (i.e., most of the wolf range) and in Annex IV south of the river Duero. Spain is a decentralized country and the autonomous regions are responsible for wildlife management. In September 2021, wolves were strictly protected throughout Spain by decision of the central government. Before protection, the different ways of managing the wolf north of the river Duero in the four autonomous regions that harbour most of the Spanish wolves can show the different options of wolf management where they are included in Annex V. More than half of the Spanish wolves (some 179 packs in 2014) live in Castile and Leon autonomous region. They have been managed as a hunting resource regardless of damage to livestock. Before wolf protection in 2021, permits were issued to kill about 140 wolves a year, although fewer animals were actually hunted.

In the autonomous region of Cantabria, with some 13 packs in 2014 and high damage to livestock, wolves were culled by official rangers and they also were hunted as a game species. The goal was to reduce wolf densities throughout the entire region in view of limiting damage to livestock. In 2020, 34 wolves were legally killed in Cantabria. In the autonomous region of Asturias, with some 40 packs in 2022 and high damage to extensive livestock, the wolf was not a hunting species, although official rangers culled about 20 wolves each year in areas where the highest livestock damage occurred. The sole purpose of culling in Asturias was to reduce damage. Finally, in the autonomous region of Galicia, the wolf is nominally a hunting species, but since 2014 no one wolf has been legally killed, so it has been managed *de facto* as a protected species. All the regions had approved management plans which include maximum quotas of culling/harvest.

In addition, in the small part of the Castile and Leon region located south of the river Duero (Annex IV), a few wolves were culled under derogation (7 in 2019 and 2 in 2020) by official rangers in areas where damage to cattle was very high. After being fully protected by the central government in 2021, no wolves have been legally hunted nor culled in Spain at least until December 2023.

Is lethal control useful to reduce damage to livestock? Targeted *vs.* non-targeted wolf culling

Lethal control is the most controversial aspect of wolf management among the general public and even among conservation professionals (Lute et al. 2018). Lethal control is frequently aimed at mitigating social conflicts by empowering afflicted parties (Woodroffe and Redpath 2015), and the benefits may be mainly social or psychological if it manages to appease livestock producers (Linnell and Cretois 2018). When lethal control is aimed at reducing wolf depredations, at best, only solves conflicts temporarily, unless the wolf population is exterminated or severely reduced over large areas (Bradley et al. 2015; Linnell and Cretois 2018). Where wolves are killed, their territories will usually be rapidly filled by other wolves and it will be necessary to continue killing wolves year after year. For example, in Scandinavia, lost wolf territories were re-occupied in less than one year when wolf population density was high. The re-occupation was faster after legal culling of individuals as compared to territories where both individuals disappeared for unknown reasons (Sand et al. 2022).

There may be benefits of lethally removing wolves that have a particular tendency to kill livestock, but it is very difficult to target these problematic individuals particularly for group-living carnivores (DeCesare et al. 2018; Linnell and Cretois 2018). For example, in Germany 8 cull permits have been granted for special individuals genetically identified from livestock kills from 2000 to May 2023. But 7 out of the 8 wolves shot for this reason were the wrong individual (Ilka Reinhardt, personal communication), showing how difficult is to target the offender wolves.

The results of studies that assess the effect of lethal removal on damage to livestock are sometimes contradictory, and the arguments provided by pro-wolf and anti-wolf sectors are deeply biased, which add a social complexity to a process that already is very complex from an ecological point of view. The contention that killing wolves increases damage to livestock maintained by Wielgus and Peebles (2014) has been discredited by two independent studies that reanalysed their data and found the opposite trend (Poudyal et al. 2016; Kompaniyets and Evans 2017).

Similarly, the studies of Bradley et al. (2015) and DeCesare et al. (2018) in the same area further question the results of Wielgus and Peebles (2014). Fernández-Gil et al. (2017), in a growing population of Asturias (Spain), found that the more wolves were culled during the current or previous year, the more depredations occurred. Nevertheless, the growth in the depredation levels was probably explained by the growth of the wolf population itself, and not by the use of lethal removals (Kompaniyets and Evans 2017). In addition, this is a correlational study and cannot provide a reliable interpretation of the cause-and-effect directionality of the relationship between depredation and removal (Linnell and Cretois 2018; Gentre 2021). The authors interpreted that more wolf lethal removals were causing more livestock depredations, but maybe the opposite is true: more livestock depredations cause more wolf culling, especially in a region such as Asturias where wolves were legally killed only to reduce damage to livestock (see previous section).

In addition, two studies carried out in the west of USA have shown that increasing levels of targeted lethal removal of wolves following depredations reduced the probability of their recurrence (Bradley et al. 2015; DeCesare et al. 2018). In contrast, DeCesare et al. (2018) in North America and Kutal et al. (2023) in Europe found no evidence that removing wolves through public harvest (non-targeted removals) affected livestock depredations by wolves. Anyway, DeCesare et al. (2018) warn that partial pack targeted removals (2.2 wolves killed/pack) were relatively ineffective as a response to wolf livestock depredations compared to the removal of the entire pack (Bradley et al. 2015). And they conclude that "in areas with recurrent conflicts, removing a relatively low number of wolves, whether through targeted control or public harvest, may do little to prevent future depredations" (DeCesare et al. 2018).

Considering these results, it appears that, wolf control has to be targeted at individuals or packs attacking livestock, and the effect of the removal must be evaluated in the long-term (Meuret et al. 2020). In recent years, Grente (2021) analysed the effect of wolf culling on the depredation levels in France using official data and concluded that the effect of culling was highly variable according to contexts. Most of the results involved a reduction of the depredations but could also involve no effect or an increase of the depredations. In summary, there is not a clear answer to the question of the effects of culling in France. Results on depredation in culling events were varied across space and time, whether these variations were linked to the environment, to pastoral practices or to the wolves. According to Grente (2021), "it is hopeless to seek a general and unique tendency of the effect of culling wolves on depredation for the French Alpine Arc, let alone at the global scale."

In summary, the research on targeted wolf culling carried out in Europe is inconclusive, and non-targeted culling (i.e., hunting) does not seem to reduce wolf depredations on livestock unless it is carried out with such intensity that it effectively reduces the density of wolves over large areas. However, this type of hunting may not be compatible with the Habitats Directive and is socially rejected by much of the public in Europe.

4.7. Recommendations to address "bold wolves"

As shown in the section 3.4, the improvement of social tolerance towards wolves enabled the emergence of fearless or bold wolves, that many times are also food-conditioned wolves. These individuals would have been quickly removed in the past, and their presence is a new challenge to wolf-human coexistence.

A bold wolf is a wolf that repeatedly tolerates recognizable people (i.e., not people in a car) within 30m or even actively approaches people repeatedly within this distance. Sometimes, wolves that are repeatedly seen close to inhabited houses are often perceived as bold. However, it is important to distinguish between wolves approaching /tolerating people at close distance (where the wolf sees the person and knows that the person sees them) and wolves approaching a house (where people are not visible directly, and where they don't know that they are being seen). Wolves living in proximity to people are not automatically a danger (Reinhardt et al. 2020; LCIE, 2019).

Bold behaviour may become dangerous to humans if it escalates, and at the least requires attention, but can also be deemed serious or critical. Every situation in which a wolf is perceived as bold or is behaving conspicuously needs to be assessed on a case-by-case basis.

To deal with bold wolves, four kinds of actions are needed (Reinhardt et al. 2020; LCIE, 2019):

- *Prevent.* To avoid habituation and food conditioning of wolves, the two basic principles are "do not approach, do not feed".
- *Document* every suspected case of bold wolf behaviour**,** routinely recording and archiving reports of sightings using standard protocols.
- *React,* removing attractants and implementing aversive conditioning. The last resort is lethal removal.
- *Communicate* properly to the public the necessity of not feeding wolves, and where appropriate the need for deterrence measures or lethal removal.

The protocol for dealing with bold wolves starts with opening a case file, conducting a field investigation to assess how many and which wolves are involved in the case, confirming reported information and identifying potential attractants. In addition, it is necessary to encourage locals to send reports of sightings and intensify wolf monitoring in the area.

Behavior	Assessment	Recommendation for action
Wolf passes close to settlements in the dark.	Not dangerous.	No need for action.
Wolf moves within sighting distance of settlements / scattered houses during daylight.	Not dangerous.	No need for action.
Wolf does not run away immediately when seeing vehicles or humans. Stops and observes.	Not dangerous.	No need for action.
Wolf is seen over several days <30m from inhabited houses (multiple events over a longer time period).	Demands attention. Possible problem of strong habituation or positive conditioning.	Analyze situation. Search for attractants and remove them if found. Consider aversive conditioning.
Wolf repeatedly allows people to approach it within 30m.	Demands attention. Indicates strong habituation. Possible problem of positive conditioning.	Analyze situation. Consider aversive conditioning.
Wolf repeatedly approaches people by itself closer than 30m. Seems to be interested in people.	Demands attention / critical situation. Positive conditioning and strong habituation may lead to an increasingly bold behavior. Risk of injury.	Consider aversive conditioning. Remove the wolf if appropriate aversive conditioning is not successful or practical.
Wolf attacks or injures a human without being provoked.	Dangerous.	Removal.

Fig. 4.6.1. Protocol of bold wolves' assessment (Reinhardt et al. 2020; LCIE, 2019).

4.8 Support for large carnivores under the Common Agricultural Policy (CAP)

The following provides a first overview of measures used by various Member States under the second Pillar of the Common Agricultural Policy (CAP) (2023 -2027)

For this analysis, all 27 CAP Strategic plans (SPs)[47] adopted at the end of 2022 for the period 2023-2027 were examined for measures relating to large carnivores, and wolves in particular. As the Strategic Plans are huge documents the search was done using the following key words "large carnivores, predators, wolf/wolves, guard dogs". The search using "fencing" was abandoned as it highlighted hundreds of references to 'ring fencing" which is not relevant.

Of the 24 Member States with wolf populations, 9 did not have any measures for large carnivores (Bulgaria, Denmark, Estonia, Hungary, Latvia, Netherlands, Poland, Romania, Sweden). This includes a number of countries with significant populations of wolves (Romania, Poland). In the Baltic states, only Lithuania has proposed measures for large carnivores, whereas Estonia[48] and Latvia have not.

Of the remaining 15 Member States, large carnivores were mentioned in the Strategic Plans of 5 Member States but no schemes were proposed specifically for them. Instead, indirect sub-measures were proposed that could help, amongst others, address the need to protect the grazing herd from wolves even if the overall objective is something different (animal welfare, seasonal grazing).

In particular:

- *Austria and Slovakia* have proposed animal welfare schemes to encourage farmers to put livestock out to pasture for a minimum number of days per year. Under this, AT offers an optional supplement for using livestock guarding dogs to protect the flock. SK compensates for loss of income due to lower yields resulting from grazing in "difficult-to-reach terrains". Here farmers must 'protect the flock from predators from grazing'**.**
- *Spain* has a similar animal welfare measure requiring dogs to protect the flock in traditional grazing systems (but only La Rioja has taken up the measure it seems).
- *Czechia* offers income aid for sheep and goat farming amongst other to improve the profitability of these farms so 'they can invest in protection from predation' (but not with CAP funding)
- *Germany* has included an AECM for management commitments to biodiversity which funds different types of measures, including nature orientated grazing. Within this sub scheme LPR5 offers compensation for "grazing in wolf scenery" but it appears that only Baden-Württemberg has invoked this measure (budget unclear). The CAP also makes clear that national funds are available for protection measures and compensation related to large carnivores (4,600,000€ /yr. federal funds).

Thus, in total, 10 Member States have included specifically targeted interventions for large carnivores/ predators under Pillar II in their CAP Strategic Plans (Belgium, Croatia, Finland, France, Greece, Italy, Lithuania, Portugal, Slovenia, Spain). For three Member States (Belgium, Finland, Portugal) the intervention focus specifically on wolves. For the remainder they cover other large carnivores as well (e.g., bear, jackal, lynx).

[47] Based on English translations received from DG ENV end 2022

[48] Estonia mentions the protection of large carnivores as an 'eligible investment' under 4.6.1 of the CSP but none of investments measures under Article 73 pick this up.

Agri-Environment-climate measures (article 70)

Six Member States have included Agri-Environment-Climate measures (AECMs) for large carnivores as follows:

Finland has an AECM primarily aimed at supporting the management and restoration of traditional biotopes with grazing and mowing as defined in a management plan. Predator fencing alone is not allowed unless it is part of the management/ restoration works (and then only for one year). Animal welfare also given as reason for anti-predator fencing.

France has an AECM for the reinforced guarding of herds in large carnivore areas. It is an annual payment for additional costs incurred by extra work needed to graze herds in large carnivores' areas (30.75€/day) and to maintain sheepdogs (815€/yr./dog). **The scheme is by far the largest of all Member States at 152,250,000€ for 2023-2029 (total public expenditure)**.

Italy has an AECM for specific commitments to encourage cohabitation with large carnivores (4 regions apply it). It offers an annual payment per ha of grazed area in large carnivore areas in compensation for the extra work needed for continued custody (within fencing, night shelters). There is an optional extra for presence of guard dogs (total public expenditure 2023-2029 is 10,113,333 €).

Portugal also has an AECM to support farmers to better protect their herds from wolf attacks but this only covers the maintenance of guard dogs (ca 350€/y per dog – max 2 dogs). 15% extra is offered for support from an NGO for advice on wolf and for training the dogs. Total budget 19,620,000€ for 2023-2029 (total public expenditure).

Spain has no direct AECM for large carnivores. Instead, the two schemes that mention large carnivores are more focused on promoting grassland management through grazing and mowing (6501.3) or preserving traditional agricultural activities (6501.6). 6501.3 can include temporary sequestration of livestock, guard dogs, monitoring, etc. but only Castilla y Leon and Galicia mention use of a large carnivore sub-measure. In case of latter public expenditure budget is 7.500.000€ for 2023-2029 (covering 20,000ha/yr.). For 6501.6, only Navarra seems to use this for activities in areas with a high presence of mammals (including use guard dogs, overnight shelters, geolocalisers, etc.) Total public expenditure budget 1,602,000 € for 2023-2029.

Slovenia has an all-encompassing AECM that covers two relevant sub-measures: "living with large carnivores" and "Maintain pastures". The former offers an annual payment for using fencing, active shepherding and/or guard dogs (at least 3) provided there is at last 0.2-1.8 LU /ha (overall public expenditure budget 1,378,000€ for 2023-2029). The latter sub measure is for grazing mountain pastures at least 80 days/yr (different rates if done with or without shepherds) (overall public expenditure budget 7,050,000€ for 2023-2029), Slovenia has also included protection of grazing animals in its investment scheme for small farms (provided this is no more than 50% of the total investment).

Non-productive Investments (Article 73)

Nine Member States have proposed investment schemes to protect against predators under article 73/74. Four Member States (BE, HR, EL, LI) offer only investment schemes, while the others offer also Agri Environmental Climate Measures (AECMs) (or only an AECM in the case of FI).

These investments cover one or more of the following expenses:

- Purchase of guard dogs (often requiring a specified breed and certificate of origin) associated costs (Belgium (Flanders), Croatia, France, Greece, Italy, Lithuania, Slovenia)
- Installation of fencing, mostly electric fencing and/or mobile fences (Belgium (Wallonia), Croatia, France, Greece, Portugal, Italy, Lithuania, Slovenia, Spain)

- Shelters for herds (at night) (Belgium (Wallonia), Croatia, Italy, Spain?

The total annual budget for investments is difficult to estimate as often there is no breakdown of costs (e.g., for Italy) but **France** is investing the most with 22,750,000€ for the period 2023-2029 (total public expenditure). This also includes costs for vulnerability assessments and technical support incl training (which other schemes don't offer.)

Lithuania has a total public expenditure foreseen of €2.3 mil. **Greece** planned also ca 3 mil until 2025. **Croatia** has foreseen a budget of 4.3 mil for majority of which goes to shelters. **Slovenia's** investment budget is more modest at 960,000€.

The large carnivore investment budget for **Spain** depends on the region. It is therefore difficult to estimate as there are lots of sub-measures available and it is up to each region to decide if they want to use them. For Andalucía a total public expenditure of 1,050,000€ is foreseen for 2024-2029.

EU State Aid Guidelines

The European Union Guidelines for State Aid in the agricultural sector[49] also allows EU Member States to grant full compensation to farmers for damage caused by protected animals, such as wolves. This makes it possible to fully reimburse the costs of investments made to prevent such damage, such as the installation of electric fences, acquisition of guard dogs, and hiring of shepherds.

[49] : https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:52022XC1221(01)

REFERENCES CITED

Agria Statistics. https://www.agria.se/pressrum/statistik-om-djur-djurvard-och-djurhalsa/vad-sager-statistiken-om-skador-vid-jakt/

Åkesson, M., Svensson, L., Flagstad, Ø., Wabakken, P. & Frank, J. (2022). Wolf monitoring in Scandinavia: evaluating counts of packs and reproduction events. Journal of Wildlife Management. DOI: 10.1002/jwmg.22206.

Allen et al. (2017). Can we save large carnivores without losing large carnivore science? Food Webs 12:64-75.

Apollonio M, Andersen R, Putman R (2010). European Ungulates and Their Management in the 21st Century. Cambridge University Press, Cambridge, UK (604p).

Ausilio G, Sand H, Månsson J, Mathisen KM and Wikenros C (2021). Ecological Effects of Wolves in Anthropogenic Landscapes: The Potential for Trophic Cascades Is Context-Dependent. Front. Ecol. Evol. 8: 577963. doi: 10.3389/fevo.2020.577963.

Barrios-Garcia MN, Ballari SA (2012). Impact of wild boar (Sus scrofa) in its introduced and native range: a review. Biological Invasions 14 (11): 2283–2300.

Bassi, E., Canu, A., Firmo, I., Mattioli, L., Scandura, M., and Apollonio, M. (2017). Trophic overlap between wolves and free-ranging wolfdog hybrids in the Apennine Mountains, Italy. Global Ecol. Conserv. 9, 39–49. doi: 10.1016/j.gecco. 2016.11.002.

Bassi E, Gazola A, Bongui P, Scandura M and Apollonio M (2020). Relative impact of human harvest and wolf predation on two ungulate species in Central Italy. Ecological Research. DOI: 10.1111/1440-1703.12130

Bassi E, Pervan I, Ugarkovic D et al (2021) Attacks on hunting dogs: the case of wolf-dog interactions in Croatia. Eur J Wildl Res 67: 4. https:// doi. org/ 10. 1007/ s10344- 020- 01451-5.

Beschta RL (2005). Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. Ecology 86: 391–403.

Beschta RL, Ripple WJ (2016). Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. Biological Conservation, 198: 93-103.

Beyer, H. L., Merrill, E. H., Varley, N., and Boyce, M. S. (2007). Willow on Yellowstone's northern range: evidence for a trophic cascade? Ecol. Appl. 17, 1563–1571. doi: 10.1890/06-1254.1.

Blanco JC (2003). Wolf damage compensation in Spain. Carnivore Damage Prev News 6: 7–9.

Blanco JC (2017). La gestión del lobo en España. Controversias científicas en torno a su caza. Arbor, vol. 193 nº 786.

Blanco JC (2018). Aspectos esenciales del lobo y su gestión. Report for WWF in the Project Life Southern Wolves. www.lifelobo.es.

Blanco y Cortés (2007). Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. Journal of Zoology 273: 114–124.

Blanco JC, Laso R and Alonso O (2021a). Diez años tras los lobos madrileños [10 years monitoring wolves in Madrid. In Spanish]. Quercus 423: 12-19.

Blanco JC, Herraiz P, Barroso A and Olmeda C (2021b). Extensive beef cattle grazing and wolf damage in Ávila province (Spain). The search for solutions. Report for the Regional Platform of the European Union on the wolf in Ávila. Istituto di Ecologia Applicata, Roma.

Boitani L (2003). Wolf conservation and recovery. Pp. 317-340, in LD Mech & L Boitani: Wolves. Behavior, Ecology, and Conservation. The University of Chicago Press, Chicago and London

Boitani, L. (2018). *Canis lupus (Europe assessment)* (errata version published in 2019). *The IUCN Red List of Threatened Species* 2018: e.T3746A144226239. Accessed on 24 April 2023.

Boitani L, Ciucci P, Raganella-Pelliccioni E (2010). Ex-post compensation payments for wolf predation on livestock in Italy: a tool for conservation? Wildlife Res 37:722–730. doi:10.1071/WR10029.

Boitani L et al. (2015). Key actions for Large Carnivore populations in Europe. Institute of Applied Ecology (Rome, Italy). Report to DG Environment, European Commission, Bruxelles. Contract no. 07.0307/2013/654446/SER/B3.

Boitani, L., Phillips, M. & Jhala, Y. (2018). *Canis lupus* (errata version published in 2020). *The IUCN Red List of Threatened Species* 2018: e.T3746A163508960. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T3746A163508960.en. Accessed on 24 April 2023.

Boitani L et al. (2022). Assessment of the conservation status of the Wolf (*Canis lupus*) in Europe. *Document prepared for the Convention on the Conservation of European Wildlif and Natural Habitats by Large Carnivore Initiative for Europe, a Specialist Group of the IUCN Species Survival Commission, with assistance of the Istituto Ecologia Applicata, Roma.*

Bradley, E. H.,Robinson, H. S.,Bangs, E. E., Kunkel,K., Jimenez, M. D.,Gude, J. A., and Grimm, T. (2015). Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. Journal of Wild Management 79, 1337–1346. doi:10.1002/jwmg.948.

Bruns A, Waltert M, Khorozyan I (2020). The effectiveness of livestock protection measures against wolves (*Canis lupus*) and implications for their co-existence with humans. Global Ecology and Conservation 21: e00868.

Bubnicki JW, Churski M, Schmidt K, Diserens TA, Kuijper DPJ (2019). Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. eLife 2019; 8:e44937.

Butler, J.R.A., Linnell, J.D.C.,Morrant, D., Athreya, V., Lescureux, N., McKeown, A. (2014). Dog eat dog, cat eat dog: social-ecological dimensions of dog predation by wild carnivores. In: Gompper, M.E. (Ed.), Free-Ranging Dogs and Wildlife Conservation. Oxford University Press, Oxford, pp. 117–143.

Caniglia R, Galaverni M, Delogu M, Fabbri E, Musto C, Randi E (2016). Big bad wolf or man's best friend? Unmasking a false wolf aggression on humans. Forensic Science International. Genetics 24: e4–e6. https://doi.org/10.1016/j.fsigen.2016.06.009.

Carpio AJ, Apollonio M, Acevedo P (2020). Wild ungulate overabundance in Europe: contexts, causes, monitoring and management recommendations. Mammal Review 51: 95-108.

Chapron G, Kaczensky P, Linnell J.D.C et al. (2014). Recovery of large carnivores in Europe's human dominated landscapes. Science 346: 1517-1519. DOI: 10.1126/science.1257553.

Cimatti M, Ranc N, Benitez-Lopez A, Maiorano L, Boitani L, Cagnacci F, Cengic M, Ciucci P, Huijbregts MAJ, Krofel M, Lopez-Bao JV, Selva N, Andren H, Bautista C, Cirovic D, Hemmingmoore H, Reinhardt I, Marence M, Mertzanis Y, Pedrotti L, Trbojevic I, Zetterberg A, Zwijacz-Kozica T, Santini L (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. Diversity and Distributions. https://doi.org/10.1111/ddi.13219.

Cortés Y, Ribeiro S, Petrucci-Fonseca F, Blanco JC (2020). A decade of use of damage prevention measures in Spain and Portugal. Carnivore Damage Prevention News 20: 32-47.

Dalerum F, Selby LOK, Pirk CWW (2020). Relationships between livestock damages and large carnivore densities in Sweden. Front. Ecol. Evol. 7:507. doi: 10.3389/fevo.2019.00507.

Darimont CT, Fox CH, Bruan HM and Reimchen TE (2015). The unique ecology of human predators. Science, vol 349, Issue 6250: 858-860. DOI: 10.1126/science.aac4249

DBBW, Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf (2022): Wolfsverursachte Schäden, Präventions- und Ausgleichszahlungen in Deutschland 2021. 41 S.

DeCesare, N. J., Wilson, S. M., Bradley, E. H., Gude, J. A., Inman, R. M., Lance, N. J., Laudon, K., Nelson, A. A., Ross, M. S., and Smucker, T. D. (2018). Wolf-livestock conflict and the effects of wolf management. The Journal of Wildlife Management 82, 711–722. doi:10.1002/jwmg.21419

Donfrancesco, V., Ciucci, P., Salvatori, V., Benson, D., Andersen, L.W., Bassi, E. et al. (2019). Unravelling the scientific debate on how to address wolf-dog hybridization in Europe. Front. Ecol. Evol. 7, 175. https://doi.org/10.3389/fevo.2019.00175.

Dorresteijn et al. (2015). Incorporating anthropogenic effects into trophic ecology: predator– prey interactions in a human-dominated landscape. Proc. R. Soc. B 282:20151602.

Duchamp C & Simon RN (2022). Wolf monitoring in France. Pp. 11-14 in Wolf Alpine Group (2022). The integrated monitoring of the wolf alpine population over 6 countries. Report for LIFE WolfAlps EU project LIFE18 NAT/IT/000972, Action A5.

Duchamp C, Boyer, J., Briaudet, P.-E., Leonard, Y., Moris, P., Bataille, A., Dahier, T., Delacour, G., Millisher, G., Miquel, C., Poillot, C., and Marboutin, E. (2012). A dual frame survey to assess time- and space-related changes of the colonizing wolf population in France. Hystrix, the Italian Journal of Mammalogy 23(1): 14-28.

Duffield, JW.; Neher, CJ.; y Patterson, DA. (2008). Wolf recovery in Yellowstone: park visitor attitudes, expenditures, and economic impacts. Yellowstone Sci. 2008; 16: 20–25.

Dziech, A. (2021). Identification of wolf-dog hybrids in Europe – an overview of genetic studies. Front. Ecol. Evol. Vol 9. https://doi.org/10.3389/fevo.2021.760160.

ECONorthwest (2014). The Economic Importance of Alaska's Wildlife in 2011. Summary report to the Alaska Department of Fish and Game, Division of Wildlife Conservation. Contract No. IHP-12-053. Portland, Oregon.

Epstein Y. (2017). Killing Wolves to Save Them? Legal Responses to 'Tolerance Hunting' in the European Union and United States. Review of European, Comparative & International Environmental Law, vol. 16(1).

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., and Jackson, J. B. (2011). Trophic downgrading of planet Earth. Science 333, 301–306.

EU Platform for Large Carnivores (2023). Livestock depredation and large carnivores in Europe: overview for the EU Platform. Discussion paper. https://circabc.europa.eu/ui/group/3f466d71-92a7-49eb-9c63-6cb0fadf29dc/library/410c2e7b-0ce8-425e-8ac2-c1c65203b476/det

Eurostat (2022) https://ec.europa.eu/eurostat/web/products-eurostat-news/-/ddn-20220517-2#:~:text=The%20EU%20has%20a%20sizeable,million%20goats%20in%20December%202021.

Fabbri, E., Miquel, C., Lucchini, V., Santini, A., Caniglia, R., Duchamp, C., et al. (2007). From the Apennines to the Alps: colonization genetics of the naturally expanding Italian wolf (Canis lupus) population. Mol. Ecol. 16, 1661–1671. doi: 10.1111/j.1365-294x.2007.03262.x

Fedderwitz F (2010). Protecting Dogs Against Attacks by Wolves (Canis lupus), with Comparison to African wild Dogs (Lycaon pictus) and Dholes (*Cuon alpinus*). Master Thesis. University of Linköping, Sverige, 32 pp. http://www.diva-portal.org/smash/get/diva2:322325/fulltext01.pdf

Figueiredo AM, Valente AM, Barros T, Carvalho J, Silva DAM, Fonseca C, et al. (2020). What does the wolf eat? Assessing the diet of the endangered Iberian wolf (*Canis lupus signatus*) in northeast Portugal. PLoS ONE 15(3): e0230433.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T. and Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86, 1320–1330. doi: 10.1890/04-0953.

Frank J, Levin M, Månsson J, Höglund L, Hensel H (2022). Viltskadestatistik 2021. Skador av stora rovdjur och stora fåglar på tamdjur, hundar och gröda *[Game damage statistics 2021. Damage by large predators and large birds to domestic animals, dogs and crops]*. Rapport från SLU Viltskadecenter 2022–2. Grimsö.

Frank J, Levin M, Månsson J, Höglund L, Hensel H (2023). Viltskadestatistik 2022 Skador av stora rovdjur och stora fåglar på tamdjur, hundar och gröda. Rapport från SLU Viltskadecenter 2023-3. https://pub.epsilon.slu.se/31119/1/frank-j-et-al-20230615.pdf

Freitas J, Lagos L, Álvares F (2021). Horses as prey of wolves: worldwide patterns and management implications. CDP news 23: 1-11.

Galaverni, M., Caniglia, R., Pagani, L., Fabbri, E., Boattini, A., and Randi, E. (2017). Disentangling Timing of Admixture, Patterns of Introgression, and Phenotypic Indicators in a Hybridizing Wolf Population. Mol. Biol. Evol. 34, 2324–2339. doi: 10.1093/molbev/msx169.

Gaynor, K. M. et al. (2019). Landscapes of fear: spatial patterns of risk perception and response. Trends Ecol. Evol. 34: 355–368.

German Statistics. https://www.dbb-wolf.de/wolf-occurrence/dead-wolf-finds/statistics-on-causes-of-death

Gervasi J, Linnell JDC, Boitani L et al (2021) Ecological correlates of large carnivore depredation on sheep in Europe. Global Ecol Cons 30. e0179. https:// doi. org/ 10. 1016/j. gecco. 2021. e01798.

Godinho, R., Llaneza, L., Blanco, J. C., Lopes, S., Álvares, F., García, E. J., et al. (2011). Genetic evidence for multiple events of hybridization between wolves and domestic dogs in the Iberian Peninsula. Mol. Ecol. 20, 5154–5166. doi: 10.1111/j.1365-294x.2011.05345.x

Grente O (2021). Understanding the depredation process in grey wolf (*Canis lupus*) and its interactions with lethal measures: focus on the French Alpine Arc. Ph. D. thesis, University of Montpellier, France.

Haidt A, Gawrýs R, Szewczyk M (2021). Human decision-making as a key factor in the risk of wolf–dog interactions during outdoor activities. Animals 11: 2497. https://doi.org/10.3390/ani11092497.

Hebbelwhite M., White C.A., Nietvelt C.G., et al. (2005). Human activity mediates a trophic cascade caused by wolves. Ecology, 86, 8: 2135-2144.

Hill et al. (2022). Quantifying anthropogenic wolf mortality in relation to hunting regulations and landscape attributes across North America. Ecology and Evolution. 2022; 12:e8875; https://doi.org/10.1002/ece3.8875

Hoag D, Breck SW, Crooks K and Niemic B (2022). Economic Consequences of the Wolf Comeback in the Western United States. Western Economics Forum 20 (1): 61-70.

Iliopoulos Y (2023). Wolf ecology in agricultural areas at the Axios-river basin national park in northern Greece. Oral Presentation in Wolves across Borders Conference. 8-11 May 2023, Stockholm, Sweden.

Iliopoulos Y, Antoniadi E, Kret E, Zakkak S, Skarts T (2021). Wolf–Hunting Dog Interactions in a Biodiversity Hot Spot Area in Northern Greece: Preliminary Assessment and Implications for Conservation in the Dadia-Lefkimi-Soufli Forest National Park and Adjacent Areas. Animals 11. 3235. https://doi.org/10.3390/ani11113235.

Iliopoulos Y, Astaras C, Chatzimichail E (2022). Dogs, not wolves, most likely to have caused the death of a British tourist in northern Greece. Nature Conservation 50: 115–143. doi:10.3897/natureconservation.50.81915. https://natureconservation.pensoft.net

Jakes AF, Paul F. Jones, L. Christine Paige, Renee G. Seidler, Marcel P. Huijser (2018). A fence runs through it: A call for greater attention to the influence of fences on wildlife and ecosystems. Biol Conservation.

Jędrzejewski W, Schmidt K, Theuerkauf J, Jędrzejewska B, Selva N, Zub K, et al. (2002). Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). Ecology 83(5): 1341–56.

Jędrzejewski W, Niedziałkowska M, Hayward MW, Goszczyński J, Jędrzejewska B, Borowik T, et al. (2012). Prey choice and diet of wolves related to ungulate communities and wolf subpopulations in Poland. J Mammalogy 93(6): 1480–1492.

Junta de Castilla y León 2016. Plan de conservación y gestión del lobo en Castilla y León. Memoria anual 2016.

Junta de Castilla y León 2017. Plan de conservación y gestión del lobo en Castilla y León. Memoria anual 2017. https://gobiernoabierto.jcyl.es/web/jcyl/GobiernoAbierto/es/Plantilla100Detalle/1284216489702/Programa/1284749944918/Comunicación

Kavcic I, Álvares F, Boitani L et al. (2022). Non-consumptive use of wolves in tourism: Guidelines for responsible practices. Ljubljana, Biotechnical faculty, Biology Department: 36 pp

Khorozyan, I. & Heurich, M. (2022). 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. 10, 1.

Kojola I, Hallikainen V, Kübarsepp M, Männil P, Tikkunen M, Heikkinen S (2022). Does prey scarcity increase the risk of wolf attacks on domestic dogs? Wildlife Biology 2022:e01038. https:// doi. org/ 10.1002/ wlb3. 01038.

Kojola I, Hallikainen V, Nivala V, Heikkinen S, Tikkunen M, Huhta E, Ruha L, Pusenius J (2023). Wolf attacks on hunting dogs are negatively related to prey abundance in Finland: an analysis at the wolf territory level. European Journal of Wildlife Research 69: 26. https://doi.org/10.1007/s10344-023-01652-8.

Kompaniyets, L., and Evans, M. A. (2017). Modelling the relationship between wolf control and cattle depredation. PLoS One 12, e0187264. doi:10.1371/journal.pone.0187264

Krofel M, Giannatos G, Cirovic D et al. (2017). Golden jackal expansion in Europe: a case of mesopredator release triggered by continent-wide wolf persecution? Hystrix: Italian journal of mammalogy, 28(1): 9-15.

Kuijper DPJ, de Kleine C, Churski M, van Hooft P, Bubnicki J, Jedrzejewska B. (2013). Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Bialowieza Primeval Forest, Poland. Ecography36:1263–1275. DOI: https://doi.org/10.1111/j.1600-0587.2013.00266.x

Kuijper DPJ, Sahlén D, Elmhagen B, Chamaillé-Jammes S, Sand H, Lone K, Cromsigt JPGM (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proceedings of the Royal Society B: Biological Sciences 283:20161625

Kusak, J., E. Fabbri, A. Galov, T. Gomerčić, H. Arbanasić, R. Caniglia, M. Galaverni, S. Reljić, Dj. Huber, E. Randi (2018).Wolf-dog hybridization in Croatia. Vet. arhiv 88: 375-395. doi: 10.24099/vet.arhiv.170314.

Kutal M, Dula M, Selivanova AR & López-Bao JV (2023). Testing a conservation compromise: No evidence that public wolf hunting in Slovakia reduced livestock losses. Conservation Letters. 2023; e12994.

Lagos L & Bárcena F (2018). F. Spatial variability in wolf diet and prey selection in Galicia (NW Spain). Mammal Res 63: 125–139.

Laikre L, Olsson F, Jansson E, Hössjer O and Ryman N (2016). Metapopulation effective size and conservation genetic goals for the Fennoscandian wolf (Canis lupus) population. Heredity 117: 279–289; doi:10.1038/hdy.2016.44.

Laikre L, Allendorf FW, Aspi J, Carroll C, Dalén L et al. (2022). Planned cull endangers Swedish wolf population. Science vol 377, issue 6602: 162.

LCIE, Large Carnivore Initiative for Europe (2019). Management of bold wolves. Policy Support Statement. https://lciepub.nina.no/pdf/636870453845842163_PPS_bold%20wolves.pdf

Léonard Y., F. Marucco, E. Avanzinelli, J. M. Weber, C. Duchamp (2010). *Analyse descriptive des causes de mortalité du loup sur le massif Alpin.* Bulletin Reseau Loup n. 23: 20- 22. (https://www.loupfrance.fr/pdf/Bulletin-Reseau-Loup-2010-N23_mortal-ite;CMR.pdf).

Leonard, J.A., Echegaray, J., Randi, E., Vilà, C. (2015). Impact of hybridization with domestic dogs on the conservation of wild canids. In: Gompper, M.E. (Ed.), Free-ranging Dogs and Wildlife Conservation. Oxford University Press, Oxford, pp. 170–184. https://doi.org/10.1093/acprof:osobl/9780199663217.003.0007.

Liberg O, André H, Pedersen C-H, Sand H, Sejberg D, Wabakken P et al. (2005). Severe inbreeding depression in a wild wolf *Canis lupus* population. Biol Lett 1: 17–20.

Liberg, O., Aronson, Å., Sand, H (2012). Monitoring of wolves in Scandinavia. Hystrix 23: 29–34. https://doi.org/10.4404/hystrix-23.1-4670.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H (2012b). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B. http://dx.doi.org/10.1098/rspb.2011.1275.

Liberg, O., Suutarinen, J., Åkesson, M., Andrén, H., Wabakken, P., Wikenros, C., & Sand, H. (2020). Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling. Biological Conservation, 243, 108456. https://doi.org/10.1016/j.biocon.2020.108456.

Linnell JDC, Andersen R, Andersone Z, Balciauskas L, Blanco JC, Boitani L, Brainerd S, Breitenmoser U, Kojola I, Liberg O, Løe J, Okarma H, Pedersen HC, Promberger C, Sand H, Solberg EJ, Valdmann H, Wabakken P (2002). The fear of wolves: A review of wolfs attacks on humans. NINA Oppdragsmelding 731, Norsk institutt for naturforskning NINA.

Linnell JDC, Solberg EJ, Brainerd S, Liberg O, Sand H, Wabakken P, Kojola I (2003) Is the Fear of Wolves Justified? A Fennoscandian Perspective. Acta Zoologica Lituanica 13(1): 34–40. https://doi.org/10.1080/13921657.2003.10512541

Linnell, J.D.C., Salvatori, V. & Boitani, L. (2008) Guidelines for population level management plans for large carnivores in Europe. A Large Carnivore Initiative for Europe re-port prepared for the European Commission (contract 070501/2005/424162/MAR/B2).

Linnell JDC, Odden J, Mertens A (2012). Mitigation methods for conflicts associated with carnivore depredation on livestock. In: Boitani L, Powell RA (eds) Carnivore ecology and conservation: a handbook of techniques. Oxford University Press, NewYork, pp 314–332. doi: 10.1093/acprof:oso/9780199558520.003.0014.

Linnell JDC, Alleau J (2016) Predators that kill humans: Myth, reality, context and the politics of wolf attacks on people. Problematic Wildlife: A Cross-Disciplinary Approach, 357–371. https://doi.org/10.1007/978-3-319-22246-2_17.

Linnell JDC, Trouwborst A, Boitani L, Kaczensky P, Huber D, Reljic S, Kusak J, Majic A, Skrbinsek T, Potocnik H, Hayward MW, Milner-Gulland EJ, Buuveibaatar B, Olson KA, Badamjav L, Bischof R, Zuther S, Breitenmoser U (2016). Border Security Fencing and Wildlife: The End of the Transboundary Paradigm in Eurasia? PLoS Biol 14(6): e1002483. https://doi.org/10.1371/journal.pbio.1002483

Linnell JDC, Cretois B, Nilsen EB, Rolandsen CM, Solberg EJ, Veiberg V, Kaczensky P, Van Moorter B, Panzacchi M, Rauset GR, Kaltenborn B (2020). The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. Biological Conservation 244: 108500.

Linnell JDC, Kovtun E, Rouart I (2021) Wolf attacks on humans: an update for 2002–2020. NINA Report 1944, Norwegian Institute for Nature Research.

Loomis, L. (2016). Economic Values of Wolves in Denali National Park and Preserve (DNPP): Concepts, Literature Synthesis, Data Gaps and Study Plan March 3, 2016. Available at IRMA Portal, National Park Service, U.S. Department of the Interior.

López-Bao JV, Blanco JC, Rodríguez A, Godinho R, Sazatornil V, Alvares F, García EJ, Llaneza L, Rico M, Cortés Y, Palacios V, Chapron G (2015). Toothless wildlife protection laws. Biodiversity and Conservation 24: 2105-2108.

Lorenzini, R., Fanelli, R., Grifoni, G., Scholl, F., and Fico, R. (2014). Wolf–dog crossbreeding: "Smelling" a hybrid may not be easy. Mamm. Biol. 79, 149–156. doi: 10.1016/ j.mambio.2013.07.080.

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

Madden F and McQuinn B (2014). Conservation's blind spot: The case for conflict transformation in wildlife conservation. Biological Conservation 178: 97-106.

Marchini S (2014). Who's in conflict with whom? Human dimensions of the conflicts involving wildlife. In: Verdade, L., Lyra-Jorge, M., Piña, C. (eds) Applied Ecology and Human Dimensions in Biological Conservation. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-54751-5_13

Marino A, Braschi C, Richi S, Salvatori V, Ciucci P (2016). Ex post and insurance-based compensation fail to increase tolerance for wolves in semi-agricultural landscapes of central Italy. Eur J Wildl Res 62: 227–240. DOI 10.1007/s10344-016-1001-5.

Marucco, F.; Reinhardt, I.; Avanzinelli, E.; Zimmermann, F.; Manz, R. et al. (2023). Transboundary Monitoring of the Wolf Alpine Population over 21 Years and Seven Countries. Animals 13: 3551. https://doi.org/10.3390/ani13223551

Mech LD (1981) The Wolf: Ecology and Behavior of an Endangered Species. University of Minnesota Press, Minneapolis.

Mech LD (2012). Is science in danger of sanctifying the wolf? Biological Conservation 150:143-149.

Mech LD, Smith DW, MacNulty DR (2015). Wolves on the Hunt. The Behavior of wolves hunting. Chicago University Press, Chicago and London.

Meuret M, Moulin C-H, Bonnet O, Garde L, Nozières-Petit M-O, Lescureux N (2020). Missing shots: has the possibility of shooting wolves been lacking for 20 years in France's livestock protection measures? The Rangeland Journal 42, 401-413. https://doi.org/10.1071/RJ20046.

Mols B, LAmbers E, Cromsigt J, Kuijper DPJ, Smit C (2022). Recreation and hunting differentially affect deer behaviour and sapling performance. Oikos 2022, e08448.

Musto 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*

Nowak, S., Myslajek, R.W. (2016). Wolf recovery and population dynamics in Western Poland, 2001–2012. Mammal Res. 61, 83–98. https://doi.org/10.1007/s13364-016- 0263-3.

Nowak, S., Myslajek RW, Jedrzejewska B. (2008). Density and demography of wolf, Canis lupus population in the western-most part of the Polish Carpathian Mountains, 1996–2003. Folia Zool. – 57(4): 392–402.

Nowak S, Zmihorski M, Figura M, Stachyra P, Myslajek RW (2021a). The illegal shooting and snaring of legally protected wolves in Poland. Biological Conservation 264, 109367.

Nowak S, Szewczyk M, Tomczak P, Calus I, Figura M, Myslajek RW (2021b). Social and environmental factors influencing contemporary cases of wolf aggression towards people in Poland. European Journal of Wildlife Research 67(4): 69. https://doi.org/10.1007/s10344-020-01455-1.

OFB Office Français de la Biodiversité (2019). Bilan hivernal de la population de loup. Hiver 2018-2019. https://www.loupfrance.fr/bilan-du-suivi-hivernal-de-la-population-de-loups-hiver-2018-2019/.

Oliveira T, Treves A, López-Bao JV, Krofel M (2021). The contribution of the LIFE program to mitigating damages caused by large carnivores in Europe. Glob. Ecol. Conserv. 31 https://doi.org/10.1016/j.gecco.2021.e01815.

Pacheco C, López-Bao JV, García EJ, Lema FJ, Llaneza L, Palacios V y Godinho R. (2017). Spatial assessment of wolf-dog hybridization in a single breeding period. *Scientific Reports* volume 7, Article number: 42475. doi: 10.1038/srep42475.

Painter, L. E., Beschta, R. L., Larsen, E. J., and Ripple, W. J. (2015). Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? Ecology 96, 252–263. doi: 10.1890/14-0712.1.

Pascual-Rico R, Morales Reyes Z, Aguilera Alcalá N, Olzanska A, Sebastián González E, Naidoo R, Monleón M, Lozano J, Botella F, von Wehrden H, Martín-López B, Sánchez-Zapata JA (2021). Usually hated, sometimes loved: A review of wild ungulates' contributions to people. Science of Total Environment 801: 149652.

Peterson, R. O., Vucetich, J. A., Bump, J. M. & Smith, D. W. (2014). Trophic Cascades in a Multicausal World: Isle Royale and Yellowstone. *Annu. Rev. Ecol. Evol. Syst.* **45**, 325–345.

Pilot, M., Greco, C., Vonholdt, B. M., Randi, E., J.edrzejewski, W., Sidorovich, V. E., et al. (2018).Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for the conservation status of hybrids. Evol. Appl. 11, 662–680. doi: 10.1111/eva.12595.

Pimenta V., Barroso I., Boitani L., & Beja P. (2018). Risks a la carte: Modelling the occurrence and intensity of wolf predation on multiple livestock species. Biol Conserv. 228: 331–342.

Poudyal, N., Baral, N., and Asah, S. T. (2016). Wolf lethal control and livestock depredations: counter-evidence from respecified models. PLoS One 11, e0148743. doi:10.1371/journal.pone.0148743.

Principado de Asturias (2023). Framework program for the development of wolf extractions in the Principality of Asturias, 2022-2023. Principality of Asturias [in Spanish].

Raynor JL, Grainger CA, Parker DP (2021). Wolves make roadways safer, generating large economic returns to predator conservation. Proc. Natl. Acad. Sci. 118, e2023251118.

Redpath SM, Young J, Evely A, Adams WM, Sutherland W, Whitehouse A, Amar A, Lambert RA, Linnell JDC, Watt A, Gutiérrez RJ (2013). Understanding and managing conservation conflicts. Trends Ecol. Evol. 28: 100–109. doi:10.1016/j.tree.2012.08.021.

Redpath SM, Linnell J, Festa-Bianchet M, Boitani L, Bunnefeld N, Dickman A, Gutiérrez R, Irvine J, Johansson M, Majic A et al. (2017). Don’t forget to look down—Collaborative approaches to predator conservation. Biol. Rev. 92: 2157–2163.

Reinhardt I (2022). Wolf monitoring in Germany. Pp. 22-25 in Wolf Alpine Group (2022). The integrated monitoring of the wolf alpine population over 6 countries. Report for LIFE WolfAlps EU project LIFE18 NAT/IT/000972, Action A5.

Reinhardt, I., Kaczensky, P., Knauer, F., Rauer, G., Kluth, G., Wölfl, S., Huckschlag, D. & U. Wotschikowsky (2015). Monitoring von Wolf, Bär und Luchs in Deutschland. BfN-Skripten 413.

Reinhardt, I., Kluth, G., Nowak, C., Szentiks, C. A., Krone, O., Ansorge, H., & Mueller, T. (2019). Military training areas facilitate the recolonization of wolves in Germany. Conservation Letters, 12(3), e12635. https://doi.org/10.1111/conl.12635.

Reinhardt I, Kaczensky P, Frank J, Knauer F, Kluth G (2020). How to deal with bold wolves – Recommendations of the DBBW. Translation of the original BfN-Skript 502 (2018). BN Federal Agency for Nature Conservation.

Ripple WJ, Beschta RL (2012). Large predators limit herbivore densities in northern forest ecosystems. European Journal of Wildlife Research 58:733–742.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014a). Status and ecological effects of the world's largest carnivores. Science, Vol 343, Issue 6167. DOI: 10.1126/science.1241484

Ripple, W. J., Beschta, R. L., Fortin, J. K. & Robbins, C. T. (2014b). Trophic cascades from wolves to grizzly bears in Yellowstone. *J. Anim. Ecol*. **83**, 223–233.

Rode J, Flinzberger L, Karutz R, Berghöfer A, Schröter-Schlaack C (2021). Why so negative? Exploring the socio-economic impacts of large carnivores from a European perspective. Biological Conservation 255(1): 108918.

Salado I, Preick M, Fernández A, Lupiáñez N, Vilà C, Hofreiter M, & Leonard J A (2023). Loss of Mitochondrial Genetic Diversity despite Population Growth: The Legacy of Past Wolf Population Declines. *Genes*, *14*(1), 75. https://doi.org/10.3390/genes14010075

Salvatori, V., Godinho, R., Braschi, C., Boitani, L., and Ciucci, P. (2019). High levels of recent wolf dog introgressive hybridization in agricultural landscapes of central Italy. Eur. J. Wild. Res. 65:73. doi: 10.1007/s10344-019-1313-3.

Salvatori et al. (2020a). European agreements for nature conservation need to explicitly address wolf-dog hybridisation. Biological Conservation 248, 108525.

Salvatori V, Balian E, Blanco JC, Ciucci P, Demeter L, Hartel T, Marsden K, Redpath SM, von Korff Y and Young JC (2020b). Applying participatory processes to address conflicts over the conservation of large carnivores: understanding conditions for successful management. Front. Ecol. Evol. 8: 182. doi: 10.3389/fevo.2020.00182

Salvatori V, Balian E, Blanco JC, Carbonell X, Ciucci P, Demeter L, Marino A, Panzavolta A, Sólyom A, von Korff Y and Young JC (2021). Are large carnivores the real issue? Solutions for improving conflict management through stakeholder participation. Sustainability 13: 4482. https://doi.org/10.3390/su13084482.

Sand H, Liberg O, Wikenros C, Åkesson M, Zimmermann B, Wabakken P (2022). Spatial dynamics in the Scandinavian wolf population. Effects of increased population size and culling. Report by SLU on behalf of the Swedish Environmental Protection Agency. https://publications.slu.se/?file=publ/show&id=117905.

Sarenbo S, Svensson PA (2021). Bitten or struck by dog: A rising number of fatalities in Europe, 1995–2016. Forensic Science International 318: 110592

Selva N., Jedrzejewska B., Jedrzejewski W., Wajrak A. (2005). Factors affecting carcass use by a guild of scavengers in European temperate woodland. Canadian Journal of Zoology-revue Canadienne De Zoologie, 83: 1590-1601.

Singer L, Wietlisbach X, Hickisch R, Schoell EM, Leuenberger C et al. (2023). The spatial distribution and temporal trends of livestock damages caused by wolves in Europe. Biological Conservation 282: 110039.

Solmsen E-H, Bathen M, Grüntjens T, Hempel E, Klose M, Krüger K, Martin H, Meyer A, Schütte P, Vogel L, Wiezorek S, Witto B (2021). Protecting horses against wolves in Germany. CDP news 23: 12-19.

Stenglein JL, Van Deelen TR, Wydeven AP, Mladenoff DJ, Wiedenhoeft JE, Businga NK, Langenberg JA, Thomas NJ, Heisey DM. (2015). Mortality patterns and detection bias from carcass data: an example from wolf recovery in Wisconsin. J Wildl Manage 79: 1173–1184.

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

Suutarinen, J., & Kojola, I. (2017). Poaching regulates the legally hunted wolf population in Finland. Biological Conservation, 215, 11–18. https://doi.org/10.1016/j.biocon.2017.08.031

Suutarinen, J., & Kojola, I. (2018). One way or another: predictors of wolf poaching in a legally harvested wolf population. Animal Conservation, 21(5), 414–422. https://doi.org/10.1111/acv.

Svensson L, Wabakken P, Maartmann E, Åkesson M & Flagstad Ø. 2015. Bestandsovervåking av ulv vinteren 2014-2015. Bestandsstatus for store rovdyr I Skandinavia 1-2015.

Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M & Flagstad, Ø. 2017. Inventering av varg vintern 2016-2017. Bestandsovervåking av ulv vinteren 2016-2017. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2017. 49 s.

Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., Flagstad, Ø. & Hedmark, E. 2019. Inventering av varg vintern 2018-2019. Bestandsovervåking av ulv vinteren 2018-2019. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2019. 53 s. Reviderad utgåva, korrigendum: Sid 15 & 32: Version 1: 65-67 helnorska vargar. Reviderad version: 64-66 helnorska vargar

Svensson, L., Wabakken, P., Maartmann, E., Cardoso Palacios, C., Flagstad, Ø. & Åkesson, M. 2021. Inventering av varg vintern 2020-2021. Bestandsovervåking av ulv vinteren 2020-2021. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2021. 55 s.

Svensson, L., Wabakken, P., Maartmann, E., Nordli, K., Flagstad, Ø., Danielsson, A., Hensel, H., Pöchhacker, K. & Åkesson, M. 2023. Inventering av varg vintern 2022-2023. Bestandsovervåking av ulv vinteren 2022-2023. Bestandsstatus for store rovdyri Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2023. 65s.

Swenson, J.E. & Andrén, H. (2005) A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. People and wildlife: conflict or coexistence? (eds R. Woodroffe, S. Thirgood & A. Rabinowitz), pp. 323-339. Cambridge University Press, Cambridge.

Szewczyk M., Lepek K., Nowak S., et al. 2021. Evaluation of the presence of ASFV in wolf feces collected from areas in Poland with ASFV persistence. Viruses 13(10): 2062.

Talegón, J.; Espíritu-Santo, C.; García, S.; y otros (2012). El (eco)turismo de lobos en la Península Ibérica: una aproximación al caso de la Reserva Regional de Caza “Sierra de la Culebra”. lIII Congeso Ibérico del Lobo, Lugo 23-25 de noviembre de 2012. Abstracts Book, p. 76.

Tanner E., White A., Acevedo P., et al. (2019). Wolves contribute to disease control in a multi-host system. Scietific Reports, 9, 7940. https://doi.org/10.1038/s41598-019-44148-9.

Tikkunen M (2023). Wolf attacks on dogs in Finland and a potential solution to mitigate the conflict. Oral Presentation in Wolves across Borders Conference. 8-11 May 2023, Stockholm, Sweden.

Tikkunen M, Kojola I (2019). Hunting dogs are at biggest risk to get attacked by wolves near wolves' territory boundaries. Mamm Res 64:581–586. https:// doi. org/ 10. 1007/ s13364- 019- 00444-3.

Tikkunen M, Kojola I (2020) Does public information about wolf (*Canis lupus*) movements decrease wolf attacks on hunting dogs (*C. familiaris*)? Nat Conserv 42:33–49. https:// doi. org/ 10. 3897/natureconservation. 42. 48314.

Trouwborst A, Fleurke F, Dubrulle J (2016). Border Fences and their Impacts on Large Carnivores, Large Herbivores and Biodiversity: An International Wildlife Law Perspective. RECIEL 25(3): 291-306.

Trouwborst A & Fleurke FM (2019) Killing wolves legally: exploring the scope for lethal wolf management under European nature conservation law. Journal of International Wildlife Law & Policy 22(3): 231-273. DOI: 10.1080/13880292.2019.1686223.

Van Beeck Calkoen STS, Deis MH, Oeser J, Kuijper DPJ, Heurich M (2022). Humans rather than Eurasian lynx (Lynx lynx) shape ungulate browsing patterns in a temperate forest. Ecosphere 13(2)

Van Beeck Calkoen STS, Kuijper DPJ, Apollonio M et al. (2023). Numerical top-down effects on red deer (*Cervus elaphus*) are mainly shaped by humans rather than large carnivores across Europe. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.14526

Von Hohenberg BC and Hager A (2022). Wolf attacks predict far-right voting. Proc Natl Acad Sci USA, 119(30): e2202224119. doi: 10.1073/pnas.2202224119.

Wabakken, P., Svensson, L., Maartmann, E., Åkesson, M & Flagstad, Ø. (2016). Bestandsovervåking av ulv vinteren 2015-2016. Bestandsstatus for store rovdyr I Skandinavia 1-2016. 49 s.

Wabakken, P., Svensson, L., Maartmann, E., Åkesson, M & Flagstad, Ø. (2018). Bestandsovervåking av ulv vinteren 2017-2018. Bestandsstatus for store rovdyr i Skandinavia 1-2018. 54 s.

Wabakken, P., Svensson, L., Maartmann, E., Nordli, K., Flagstad, Ø. & Åkesson, M. (2020). Bestandsovervåking av ulv vinteren 2019-2020. Inventering av varg vintern 2019-2020. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2020. 55 s.

Wabakken, P., Svensson, L., Maartmann, E., Nordli, K., Flagstad, Ø. & Åkesson, M. (2022). Bestandsovervåking av ulv vinteren 2021-2022. Inventering av varg vintern 2021-2022. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2022. 59s.

Wielgus, R. B., and Peebles, K. A. (2014). Effects of wolf mortality on livestock depredations. PLoS One 9, e113505. doi:10.1371/journal.pone.0113505.

Wierboska IA, Hedrzak M Popczyk B, Okarma H, Crooks K (2016). Predation of wildlife by free-ranging domestic dogs in Polish hunting grounds and potential competition with the grey wolf. Biological Conservation 201: 1-9.https://doi.org/10.1016/j.biocon.2016.06.016

Wikenros C, Sand H, Månsson J, Maartmann E, Eriksen A, Wabakken P, Zimmermann B (2020). Impact of a recolonizing, cross-border carnivore population on ungulate harvest in Scandinavia. Scientific Reports 10: 21670.

Woodroffe R, Redpath SM (2015). When the hunter becomes the hunted. Science 348:1312–1314. doi:10.1126/science.aaa8465.

ANNEX

TARGETED DATA COLLECTION ON THE WOLF POPULATION AND ITS IMPACTS IN THE EU

Launched through the Commission's Press Release of 4 September 2023

SUMMARY OF FINDINGS

18 December 2023

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INTRODUCTION

On 4 September 2023, the Commission "invited local communities, scientists and all interested parties to submit up-to-date data on the EU's wolf population and their impacts"[50]. This targeted data collection was launched in the framework of the in-depth analysis on the situation of the wolf in the EU (hereinafter called the "In-depth Analysis") which the Commission committed to carry out in response to the European Parliament Resolution of 24 November 2022[51].

In total, over 19,000 emails were sent to the Commission's dedicated email address by the deadline of 22 September 2023. Emails that were not related to the subject, or submitted after the deadline or considered repetitions[52] were removed, leaving just under 18,500 emails to analyse.

OVERVIEW OF EMAILS RECEIVED

Emails were sent from 24 Member States, 23 of which have a wolf population. No emails were sent from Luxembourg, but 4 emails were sent from Ireland where the wolf is not present.

A further 30 emails were sent from countries outside the EU (including Norway, Switzerland, US, Mexico). For some 360 emails, it was not possible to identify the country of the person because the email was sent from a generic account and the person did not indicate their place of origin in their reply. The majority of these were written in German (218), with some also in English (49), French (25) and Dutch (11). Two thirds were in favour of maintaining the protection status of the wolf, one third were against.

Finally, 20 emails were sent from an EU level or international organisation and were therefore not counted amongst the Member State emails. They are also reported on separately in this report.

Over 90% of the emails came from five Member States (Sweden, Belgium, Germany, Finland and Italy). 42% came from Sweden alone. On the other end of the scale, fewer than 10 emails were sent from each of the following ten Member States (Bulgaria, Croatia, Estonia, Greece, Hungary, Ireland, Latvia, Lithuania, Romania and Slovakia).

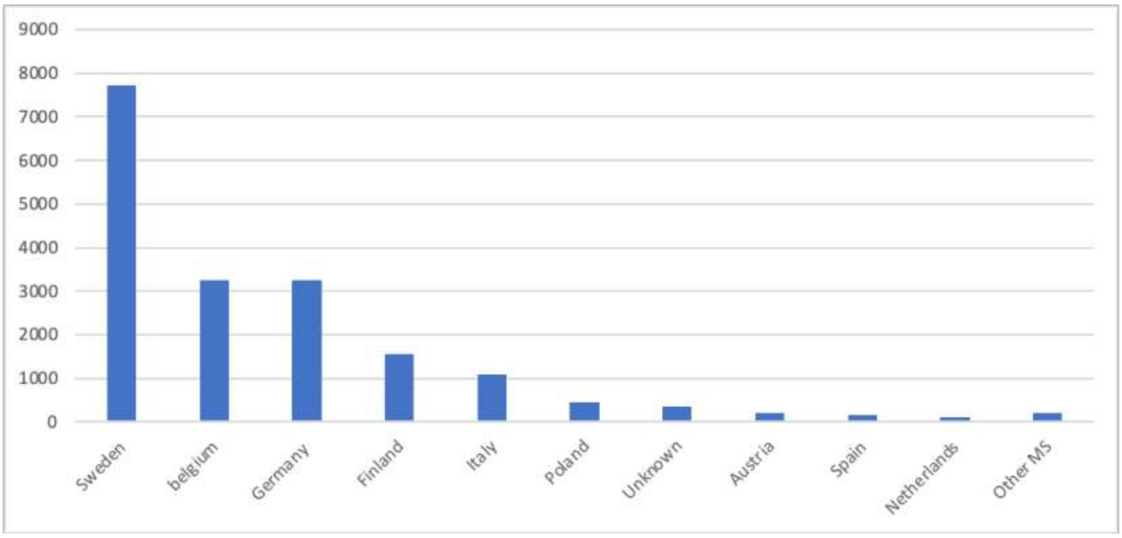

Figure 1: emails received according to Member State

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[50] https://ec.europa.eu/commission/presscorner/detail/en/ip_23_4330

[51] https://www.europarl.europa.eu/doceo/document/TA-9-2022-0423_EN.html

[52] For instance, the same email was sent two or more times, or was sent once in the original language and a 2nd time in English. Some people also sent several emails with photos, newspaper articles or videos to accompany their first email because they were too big to send in one go. These were all counted as one email.

The vast majority of those who sent an input to the targeted data collection (over 98%) wanted to express an opinion on the subject, rather than submit data on wolf populations and their impacts. As illustrated in the graph below, the majority (71%) expressed an opinion in favour of maintaining the existing protection status of the wolf, while less than one third (28%) asked to reduce its protection status. The remainder (less than 1%) made other comments on the data collection exercise or on the wolf in Europe.

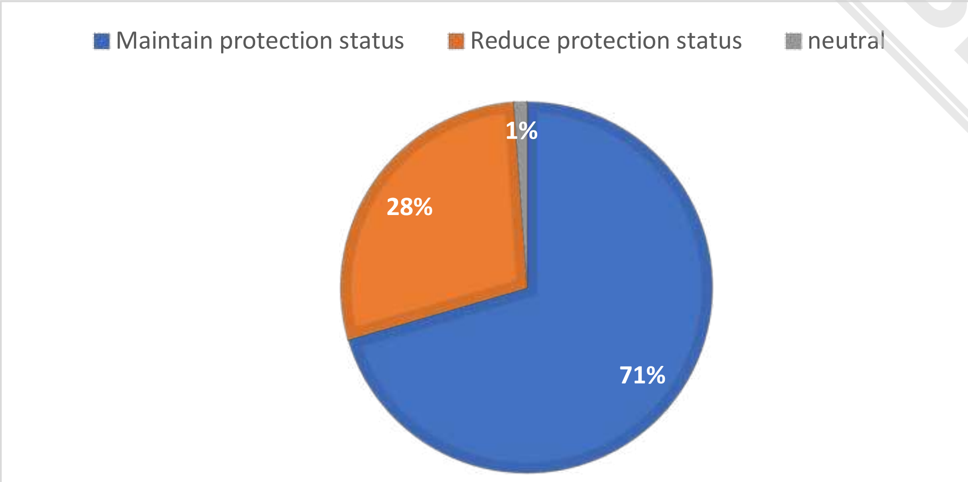

Figure 2: opinion on the protection status of the wolf

The opinions varied significantly according to Member State. Those who sent an input from Belgium, Italy, Poland, Spain, Portugal and France were overwhelmingly in favour of maintaining the protection status of the wolf. By contrast, those who sent an input from Finland, Netherlands, Austria, Czechia and Slovenia were overwhelmingly in favour of reducing its protection status. In Sweden and Germany, the views were more evenly spread, although in both cases more were in favour rather than against maintaining the protection status.

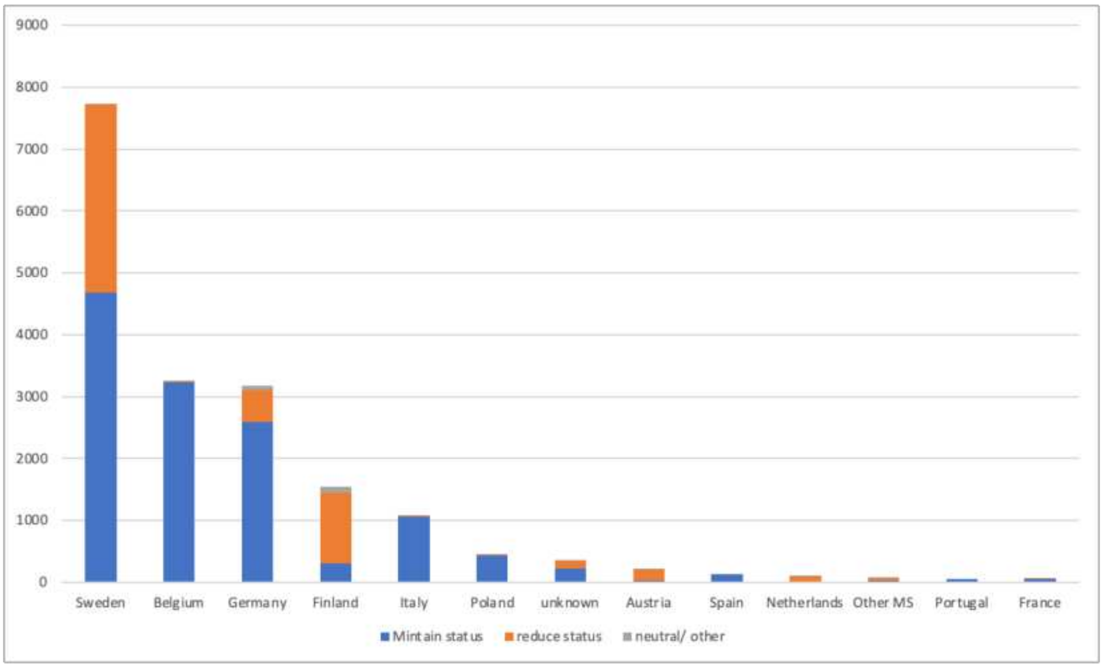

Figure 3: opinion according to Member State

Of the emails expressing an opinion on the subject, three quarters were very similar in content, suggesting that they may have been generated in response to a coordinated national campaign, whether from environmental, hunting or farming organisations or other civil society groups.

Over 90% of the emails from Belgium, Italy, Poland, Portugal and over half of those from Sweden, Germany and Spain had a similar content (but varying from one country to another). All expressed their support for maintaining the protection status of the wolf.

Likewise, most of the emails from those supporting a reduction in protection status used a standardised text. This was especially the case for emails coming from Sweden, Finland and Germany which, together, make up over 90% of the emails calling for a reduction in protection status. In both Sweden and Germany, the text varied depending on whether they came from people with a hunting interest or with farming or other interests.

Finally, for some countries like Austria, Netherlands, Czechia and Slovenia, and to a lesser extent Germany, the emails all varied in content. The majority came from small scale farmers and or hobby farmers (with rare livestock breeds, horses, ponies, alpacas, etc..). In general, they described: a) their farming context, b) any wolf encounters they have experienced or loss/injuries incurred due to predator attacks c) complications in installing protection measures (especially in alpine or coastal areas), d) their fears for their livestock, pets and children and the emotional stress this causes them as well as e) often their concerns over their future capacity to continue farming in the presence of the wolf.

TYPE OF DATA PROVIDED

The Commission's press release invited local communities, scientists and all interested parties to submit **up-to-date data on the wolf population and their impacts**. The Commission webpage on large carnivores further specified that this "data must be based on agreed national monitoring methodologies or other official procedures/ methodologies" and that such "data will also be transferred to the relevant Member States before finalising the analysis." As shown above, while the majority of emails sent gave an opinion on the issue, only **a small percentage of emails (less than 2%) provided data** on the wolf population and their impact (excluding those given personal experiences and sightings at a very local level).

Those emails containing data were analysed in detail and compared to the official data on wolf population and impacts on livestock provided to the Commission by the competent Member State authorities (or identified through other sources of information where official data was not available) and subsequently used for the In-depth Analysis Report (tables 2.4.1 and 3.31).

As stated above, a significant number of the emails contained personal sightings, observations or experiences on the wolf and/or wolf attacks and livestock losses/damages at a local level (eg at farm level, in a conservation area, over a local hunting range or within their local community). While the information gives a clear indication of the problems encountered, the data is at too local a scale to be comparable with the national data on wolf population and impacts included in the In-depth Analysis Report. They are also based on personal observation rather than agreed national monitoring methodologies or other official procedures/methodologies. The experiences were nevertheless reflected in other sections of the In-depth Analysis Report.

Finally, some emails provided links to scientific articles, reports and studies on the wolf in their country or in Europe, or internationally. These were also screened for any new relevant information for the In-depth Analysis.

ANALYSIS OF DATA PROVIDED

The following provides a summary of the emails received per Member State and, more specifically, of those providing data on wolf populations and impacts on livestock.

AUSTRIA

A total of 217 emails were sent from Austria. The majority (80%) were from farmers and farmers' organisations, especially small-scale alpine farmers, sharing their negative experiences with wolf attacks on their livestock. Many also gave explanations for why anti predator measures were considered too expensive and unworkable, especially in mountain areas. Some considered they did not receive sufficient support from the authorities for protection measures and compensation. All were in favour of reducing the protection status of the wolf.

A further 15 emails provided data on wolf populations and/or damages. Two emails from the Federal Ministry for Climate Protection, Environment, Energy, Mobility, Innovation and Technology and the Federal Ministry of Agriculture, Forestry, Regions and Water Management provided the same data on wolf populations and livestock damage which comes from a central data source (https://baer-wolf-luchs.at/). This same data source was used in the In-depth Analysis Report.

Three emails from the Provincial Governments of Carinthia, Tyrol and Voralberg provided data on wolf numbers within their province. The numbers at provincial level are compatible with the official data used for the In-depth Analysis Report. Two emails from the Provincial Governments of Carinthia and Salzburg also provided data on wolf damage, one for their province and the other for the whole country. In the case of the former, the data matches the official data for 2022 (but is a bit lower than official data for 2023). In the case of the latter, the data provided on wolf populations in whole country is slightly lower than the official data for 2022. The official data remains the most reliable since all provinces must, anyway, submit their data to the same central source (https://baer-wolf-luchs.at/).

Four farming associations, one hunting association and one association for the protection of cultural landscapes all provided data of wolf damage in their provinces or for the whole country. Again, these were largely consistent with the official data for 2022. One animal welfare organisation also referred to the official data on wolf damage.

One environmental organisation compared the number of sheep on farms in Austria with the percentage of sheep lost due to the wolf (0,79%). One individual provided a report on the alpine wolf population over 7 countries. The data for Austria for 2021 is very similar to the official data. The person also submitted a number of scientific papers that were screened for any relevant information for the In-depth Analysis.

BELGIUM

A total of 3250 emails were sent from Belgium. All were in favour of maintaining the protection status of the wolf. Three emails provided some data on the wolf population and impacts.

Both emails from an environmental NGO and an equestrian NGO provided data on the wolf population at a regional level which agrees with the figures given in the official data submitted by the competent national authority in the context of the In-depth Analysis Report. In the case of the latter, the information on wolf predation refers to the official data records kept by the Flemish Agency for Nature and Forests which is at a regional level. In the case of the former, the number of attacks on livestock was given for a total of five years with no annual breakdown but is overall lower than the official estimates. This may be because it covers damage recorded in one region only.

A third local professional association considered there are 10 wolves in Belgium after having been re-introduced to the country. This figure is not supported by documentary evidence and does not concord with the official figures. In reality, the wolf was not re-introduced in Flanders, but expanded its range naturally into Belgium from Germany. The figures given for the number of animals killed and injured and over a 5-year period are within the range given by the official data.

BULGARIA

Three emails were received from Bulgaria. Two expressed their support for maintaining the protection status of the wolf. The third, from an environmental NGO, stated that, according to latest reliable data, the wolf population in Bulgaria is approximately 800-900 individuals. This is significantly lower than the data provided by Boitani et al in 2022, but the figures have not been substantiated by documentary evidence. In the absence of reliable data for the wolf population in Bulgaria, the figures provided by Boitani at al have been used for the In-depth Analysis Report. Further, the NGO's comment that there is no official registration of wolf damage in Bulgaria concords with the findings of the Analysis Report. No data was found on wolf damage or information on compensation.

CROATIA

One email was sent by an environmental NGO from Croatia outlining its views on the management of wolf in Croatia and drawing attention to the high level of illegal killing of wolves. It called for a better implementation of the Habitats Directive rather than a reduction in wolf numbers by shooting. The data provided for wolf population agrees with the data sent by the competent authorities within the context of the In-depth Analysis Report.

CZECHIA

17 emails were sent from the Czech Republic, the majority came from individuals (mostly farmers) expressing their support for a reduction in the protection status of the wolf, principally due to its negative impact on small scale (sheep) farming in their regions.

Four emails contained data on wolf population and impacts. The first two came from the Ministry of the Environment and the Ministry of Agriculture respectively. As regards the wolf population, the data diverges significantly between the two Ministries. But, as the Ministry of Agriculture explains, "*the number of wolfs stated in the(their) table is the number of wolfs reported by hunters based on the statistical counts annually. It is important to mention that hunters report number of wolfs from their hunting grounds. Wolf home range is roughly about the size of 2-4 hunting grounds therefore some wolfs could be counted multiple times".* The figures from the Ministry of Environment were used for the In-depth Analysis Report as they are based on a more robust monitoring methodology. As regards wolf damage and compensation, both Ministries provided the same updated figures which were used for the In-depth Analysis.

The remaining two emails were sent from the authority of Hradec Kralove region and an association of municipalities of the Jablunkov region. Both provided data on wolf populations and/or damage at the level of their region or municipalities and expressed their concern over the impact of the wolf on farming in their region. While this information has been noted, the data provided is on too local a scale to be comparable with the national population estimates or compensation levels provided by the Ministry of Environment in the context of the In-depth Analysis Report.

DENMARK

17 emails were sent from Denmark, two thirds were in favour of reducing the protection status of wolves, often because of negative experiences with attacks on their livestock. One third were in favour of maintaining the protection status of wolves and called, in particular, for a reduction in illegal hunting. Two emails from private individuals contained data. In both cases, the data matched the official data submitted by the competent national authority in the context of the In-depth Analysis Report.

ESTONIA

Two emails were sent by environmental NGOs from Estonia, both containing the same data. This data is however less up to date (2021) than the official data submitted by the competent national authority in the context of the In-depth Analysis Report.

FINLAND

A total of 1551 emails were sent from Finland. Almost three quarters (74%) were in favour of reducing the protection status of the wolf, while 20% of emails were in favour of maintaining its protection status, 6% reported personal experiences and sightings or submitted links to reports, newspaper articles etc., but did not give an opinion on the wolf's protection status.

Of the emails supporting a reduction in the protection status of the wolf, almost 80% came from local hunting clubs (Metsästysseura) or Game Conservation Associations (Riistanhoitoyhdistys). The emails generally followed the same overall structure in which they described all or some of the following a) location and characterization of the hunting club's operating area, b) the activities of the hunting club, c) the wolf situation in the clubs area of operation (based mainly on sightings), d) social impact and safety e) hunting stocks and game stocks f) production or livestock damage and/or g) proposals for solutions to the wolf situation to the Commission (inter alia reducing the protection status of the wolf).

While the different observations and concerns provided in these emails have been noted, especially in relation to the danger posed by wolves to hunting dogs, the individual sightings of wolves are at too local a scale to be compared with the overall wolf population data at national level. Such observations cannot be aggregated since the information does not systematically cover the entire range of the wolf in the country and leads to double counting since wolf territories are large and move between different hunting ranges. The figures are also based on observations only which is not in line with agreed national monitoring methodologies.

13 of the emails provided some data on wolf populations and livestock predation. Seven emails provided the same data on the Finnish wolf population as the official data submitted by the competent national authority in the context of the In-depth Analysis Report (291-331 wolves, March 2023). The farming organization and national hunting organization claim that the real time population in Finland is larger after the breeding season. The environmental NGOs point out the severe risk of in-breeding which can further fragilise the wolf population.

Three environmental NGOs provided figures for sheep damage caused by the wolf, estimated at 30-50 sheep each year. These figures are however out of date. The official data submitted by the competent authorities in the context of the In-depth Analysis indicate that the number of sheep damaged by wolves has risen to over 518 in 2021. Four farming associations reported the same official figure of 518 sheep, adding that there are altogether 130,000 sheep in Finland.

Three dog associations and a national hunting organization provided a figure for the number of dogs killed by wolves in 2022-2023. The figure is the same as the one provided by the public authorities (over 50 dogs) and used in the In-depth Analysis Report.

One administration in charge of the management of wild forest reindeer considered that the wolf has been the principal cause of its decline in one region of Finland in the early 2000s.

FRANCE

63 emails were sent from France. Over 80% were in favour of the protection of wolf. Eight emails contained some data on wolf population and/or damage.

Two emails from a national farmers' association and a national federation of hunters both provided data on wolf populations and livestock damage that matches the official data from the Office Francais de la Biodiversité (OFB). The former noted, in particular, the sharp increase in damage to bovines over the last 3 years and the high cost of protection measures (29,76 mil€ in 2020.).

Another farming organisation considered that the official data on the wolf population in France are significantly under-estimated (quoting a scientific article from 2013 by mathematicians on "Modèles à variables latentes et modèles de mélange"). It also considered that the official figures for livestock damage should be increased by a third because, according to studies done by “Cerpam”, for every two specimens identified a third is not (eg disappeared). These data are however based on extrapolations.

An email from the public authority of the Département of Aveyron provided data on the increase in wolf numbers and livestock damage in its Département. It also provided a figure for the number of wolves in France as a whole, which concurs with the official data used for the In-depth Analysis Report. The data on wolf damage is also from the official OFB website. The email emphasizes the high cost of protecting livestock against wolf attacks in its department (estimated at €22-35 million for one area alone) and their apparent lack of effectiveness according to researchers from INRAE and COADAPHT « Des loups en France depuis 30 ans: quel bilan en élevage et quelle piste de solution?».

One animal welfare organisation provided data on the wolf population and livestock damage, noting that the number of attacks decreased in 2021 compared to 2020. According to the email, the decrease in attacks were observed in areas where the wolves were long established, and livestock protection methods seemed to be better implemented on the field. The figures for wolf population and livestock damage come from the same official source as for the In-depth Analysis Report. The decrease in damage in 2021 compared to 2020 does not seem to have repeated itself in 2022.

The NGO also considered that shooting measures have not been scientifically proven to be effective when it comes to protecting livestock and preserving wolf populations, as illustrated by various scientific studies.

Another animal welfare foundation also referred to the official data on wolf population and livestock damage from OFB which was used for the In-depth Analysis Report. It noted, however, that the wolf population’s growth rate varied from year to year and was much lower in 2020 compared to 2019, also that livestock damage occurred most often in areas where there is a lack of protection or insufficient surveillance.

Regarding the number of wolves for 2023, the NGO criticized the fact that OFB apparently revised its figures upwards (from 906 to 1104) after criticism from agricultural organisations. It considered this revision to have been done arbitrarily. The NGO also criticized the way in which the French authorities have used the derogation system under the Habitats Directive since 2018 to kill a number of wolves based on a percentage of the total population. It considers this is not conform to the provisions of the Directive. According to the NGO, the ceiling for the annual kill of wolves has now been raised to 19-

21% of the wolf population under 'the Plan National d'Actions 2018-2023 sur le loup et les activités d'élevage". This is higher than the ceiling recommended by the scientists but, so far, there has been no evaluation of the effectiveness of this annual cull on the wolf population.

A third animal welfare organization gave the same figure on the wolf population in France as used in the In-depth Analysis Report. As with other environmental NGOs, it criticized the annual killing of a percentage of the total wolf population, the efficacy of which has not been proven scientifically.

One regional association for the wolf noted that the wolf had recently been sighted in its region, but is not yet breeding there.

GERMANY

3240 emails were sent from Germany. Over 80% supported the continued protection of the wolf, while 17% supported a reduction in its protection status and 3% offered other types of comments. 71 emails provided information on the wolf population and/or impacts on livestock.

Of the 71 emails, 46 came from authorities at a district level (Landkreise of which there are 294 in Germany). 24 stated that they had no resident wolves in their district. A further nine stated they had one established wolf pack or one lone wolf. Of the remaining 13 emails, several referred to official regional websites or the official Dokumentations- un Beratungsstelle des Bundes zum Thema Wolf (DBBW) (http://www.dbb-wolf.de/the-dbbw) for latest data on wolf packs and livestock damage. Others gave figures for wolf populations and/or wolf attacks in their district, but did not support these figures with substantiating evidence. It is not possible to know whether the figures are based on agreed national or regional damage assessment methodologies.

Data on wolf numbers at district level cannot be aggregated since wolf territories are often located across borders in two or more districts. The issue of transboundary territories is instead addressed at regional level and the regional authorities meet regularly to discuss and coordinate their wolf population data precisely to avoid double counting. The damage data of the Landkreise are also summarized at the level of the Bundesländer which is in turn summarised at national level once a year by DBBW.

Of the remaining 25 emails (out of 71 with data), 15 provided data on the wolf population and livestock damage extracted from the DBBW website or the Länders' official websites and are therefore consistent with the official data submitted by the competent national authority in the context of the In-depth Analysis Report. Some, however, provided data for 2021 which are not the latest figures used for the In-depth Analysis Report (figures for 2022). Others provided data for 2023, but as the year is not complete yet, these data could not be used.

One email from a regional Ministry of Environment of Niedersachsen provided data on the number of packs, pairs and individuals for its region based on data that matches those on DBBW, but then extrapolated this to estimate that there are 400-600 animals in the region. There is however no scientifically agreed method for estimating individual numbers based on wolf territories and pack numbers. Even if a conversion factor of 7 wolves per pack is used this would result in 303 wolves. The projected figures for 2023/2024 are also not substantiated and appear to be based on observations from the regional hunting association which is not in line with agreed monitoring methodologies. On the other hand, the figures on livestock damage match the official figures on DBBW.

One email from a national farming organisation also used the wolf population data on DBBW to estimate that the total Germany population consisted of 1500 -2700 wolves for 2022/2023.As stated above, this extrapolation is not supported since there is no scientifically agreed method for estimating individual numbers. The number of animals in a pack has also been exaggerated (8-14 animals).

Two emails from regional farming organisations and one from a regional hunter's organisation provided data on wolf populations and livestock damage that are higher than the official data for their region. The data appears to be based on wolf observations from a national hunting association which can lead to double counting since wolves cross between different hunting ranges, it is also not in line with agreed monitoring methodologies.

One of the emails also considered that, because 30% of the wolves killed by road traffic could not be assigned genetically to a specific pack, there were more wolves than officially inventoried. This does not take into account that not all wolf packs in Germany are genetically identified. Wolves killed on the roads that could not be genetically assigned to a certain pack are likely to be offspring from those packs that were not genetically identified. In another of these emails, the figures for livestock damage were not consistent with the information on the official website for the Region. No evidence is given for the higher figures provided.

One email from a regional farming organsation provided data on wolf numbers in the region which are lower than the official data but without providing any substantiating evidence. The data on livestock damage matches the official data.

Two emails from a local hunting organsiation and a local environmental NGO provided data on wolf population (in the case of the former) and livestock damage (in the case of the latter) for their area. While noted, the data is at too local a scale to be comparable with the official data.

Two environmental NGOs, in addition to referring to the official data on DBBW, also pointed out that according to official reports 70% of attacks happen on unprotected or poorly protected livestock, in one region this went up to 89%.

One individual estimated from an online google map that there are 270 wolf territories in Germany. But this is not otherwise substantiated and appears to be a significant overestimate.

GREECE

Six emails were sent from Greece. One email from the National Environmental & Climate Change Agency referred to the report by Boitani et al 2022 as a source of information and provided links to selected case studies on wolves and their effect on human activities in Greece. The data in Boitani et al was also used for the Analysis Report. The selected case studies were screened for any relevant information for the In-depth Analysis Report.

Four emails come from hunting and livestock associations informed of local wolf sightings in their area and the negative impact this is having on local farmers. The information on wolf sightings is noted, but could not be taken into account for the In-depth Analysis Report as it is at too local a scale, not substantiated and not based on any agreed monitoring methodology as requested.

The final email came from a coalition of Greek Environmental NGOs objecting to the statements made in the Commission's press release and the short period given in which to collect data. It also stated that, instead of re-opening the issue of suitability of the Nature Directives, the Commission should insist more on the effective utilization, by the EU Member States, of tested and verified good practices and financial tools that will contribute to the more effective implementation of the Habitats Directive. It also provided a list of recent works and reports, which it considered useful. These were screened for any relevant information for the In-depth Analysis Report.

HUNGARY

One email was sent from Hungary in support of maintaining wolf protection status. No data was provided.

ITALY

In total, 1101 emails were sent from Italy, over 90% were in favour of maintaining the protection status of the wolf. 13 emails provided data on wolf populations and/or livestock damage. Four of these presented data from the First National Wolf Monitoring 2020-2021(ISPRA) which is the same source of information used for the In-depth Analysis Report.

The regional administrations of Lombardy and Trento provided up-to-date and documented data on damages and compensation in their regions. While the data is more up-to-date (2022) than the data in the ISPRA report, it is difficult to integrate the figures with the rest of data from the other 20 regions, given that these regions have limited territories.

The public forest administration for the Bolzano region provided an estimate of the wolf population in its region. The accompanying report, however, also stated that there is no detailed technical scientific documentation available on population dynamics in that region. This data has therefore not been substantiated.

One regional farming committee provided data on wolf populations for its region which are higher than the official figures, but they are based mainly on sightings and camera traps which can lead to significant double counting. The data is not in line with agreed monitoring methodologies.

One hunting association provided estimates of the wolf population and livestock damage for the Appenine belt. It considered that the latest data from ISPRA are not complete because the monitoring was only carried out in certain regions and estimates were made in others. Whilst these concerns are noted, the data provided has not been substantiated and is too local scale to be comparable with the official figures.

A regional civil society cooperative and a regional farmers association both provided an estimate of the number of wolves in their province but did not provide substantiating evidence. It is therefore not possible to know if the numbers are based on an agreed monitoring methodology. The figures for wolf damage in both cases are either the same as, or only slightly different from, those provided by the regional authority.

Another regional civil society cooperative provided data for wolf numbers and damage for its region for 2018 and 2019 – this data is both very local and out of date.

One email from a private citizen considered the data for the wolf population in Tuscany from 2016 to be an underestimate. The latest ISPRA monitoring report provides more up-to-date figures which are no longer based on expert-based estimates.

LATVIA

Three emails were sent from Latvia. One email reported data on the wolf population in a National Park. The other two came from environmental NGOs.

The first gave data on wolf predation on sheep (115 a year) which it considered very low compared to the number of sheep dying from diseases etc. The figure of 115 is higher than the figure given in Boitani et al 2021 (45 sheep) which was used for the In-Depth Analysis Report, but is lower than the figure given by the State Forest Service data (129 sheep). The NGO further pointed out that the authorities do not offer compensation for large carnivore damage or subsidies for predator protection measures. The NGO considered that the killing of 300 wolves every year (even more illegally) is too high and does not justify the government's statement that the wolf has a favourable conservation status in Latvia according to the last Article 17 report (2013-2018).

The second NGO asked the Commission to investigate the reliability of the wolf Baltic population assessment and conservation status in Latvia. According to a recent State Audit report on game management, there is a lack of reliable and unverifiable government data on wolf populations. The NGO also considers that the figure of Latvian wolf population of 700 individuals given in Boitani et all 2022 is questionable because it might be distorted by the figures given in the Article 17 report. According to expert opinion there are no more than 200-300 wolves in Latvia, but this is not substantiated by any supporting evidence.

The information used in Boitani et al 2022 was based on figures by the Latvian State Forest Research Institute Silava, supported by a scientific paper by Suba et al 2021. It remains the most reliable source of wolf population data for Latvia and has therefore been used for the In-depth Analysis Report. The NGO also considers that during the long hunting season (8.5 months), more than 50% of the Latvian wolf population is killed. However, Suba et al 2021 indicates that there is a mean annual culling mortality of 37.3% which is considered to be a moderate hunting pressure by the authors.

LITHUANIA

Two emails were sent from Lithuania. The one from the Ministry of the Environment provided data on wolf population and damage which was used for the In-depth Analysis Report. The second email from a farming organization provided higher figures for the wolf population, but without substantiating evidence. The figures for wolf damage and compensation are the same as those provided by the competent national authority.

NETHERLANDS

A total of 101 emails were sent from the Netherlands. The majority (80%) called for a reduction in the protection status of the wolf due to the threat to livestock and pets, the impact on local farmers, the safety of local communities, and the overall social and economic burdens caused by wolves.

Five emails provided data on wolf populations and/or damage. The email from the Ministry of Agriculture, Nature and Food Quality and the two from Provincial authorities of Drenthe and Gelderland all quote the same source of data that was used in the In-depth Analysis Report.

One environment NGO considered there were only 30-35 wolves in the Netherlands (excluding wandering wolves), but did not provide any substantiating evidence to support this. Regarding wolf damage they quote the same source as was used for the Analysis Report (http://www.bij12.nl). Contrary to the NGO's claim, the data does identify the different species of predator (based on DNA sampling).

Another environmental NGO stated, giving reference to a recent study, that over the past nine years, 693 claims for compensation were related to farmers that did not implement wolf fencing measures. Only 9 claims were made by farmers that did implement wolf fencing measures.

The remaining two emails were sent by an organisation responsible for a National Park and an association representing two municipalities in which they inform about local wolf sightings and their impact. While the information is noted, it is at too local a scale to be compared with the national data used in the context of the In-depth Analysis Report.

POLAND

A total of 450 were sent from Poland, over 90% came from people expressing an opinion in favour of maintaining the protection status of the wolf.

A further 8 emails provided some data on wolf populations and/or damage. Three were sent by the local municipalities of Cisna, Usztrzyki and Zary giving reports of local sightings and incidents with wolf and bear in their municipality and expressing their concern at the increase in wolf incidents and the lack of effective procedures for dealing with conflict situations. One organization also provided data on the number of incidents with wolves in the last 5 years in the Subcarpathian province. While their concerns were noted, the data is based on observations only which is not in line with agreed monitoring methodologies and is on too local a scale to be compared with the national data on wolf numbers and impacts.

One hunter and one hunting association estimated the Polish population of wolf to be 2 to 7 times higher than of the official figures. The figures are based on a hunter's census for 2022/2023, and, as the association itself states, it cannot be excluded that animals are counted twice. The data is also not based on agreed national monitoring methodologies or other official procedures/methodologies. Data was given on the number of game species (and mouflon) found killed by wolves during the last hunting season. These are again based on observations only and not further substantiated.

One coalition of environment NGOs considered there were 2000 wolves in Poland which is in a similar range (albeit slightly higher) than the figures used for the In-Depth Analysis Report. They also stated that, according to an analysis done recently, wolf predation on livestock is responsible for the mortality of only 0.08% of cattle, about 0.12% of calves, and a few percent of sheep.

Further, compensation from the State Treasury is paid to livestock farmers for damage caused by five protected species (beavers, bison, bears, lynx, and wolves). In 2020, PLN 32.3 million was paid out but compensation for damage caused by wolves accounts for less than 5% of this amount. The figure for compensation by wolf (ca 370,000 €) is similar to the figure used for the Analysis Report. The figures for mortality of different types of livestock give only percentages rather than real figures and so it not comparable.

Another environmental NGO considered the wolf population in Poland to be made up of 1900 individuals which is consistent with the figures in In-depth Analysis Report. It also considered the share of damages caused by wolves in relation to damages caused by all protected species covered by the compensation system is small. The value of paid compensation for damage caused by wolves is only 3.1% of the total in 2017 to 4.9% in 2021 of the damage caused by all protected species. The amounts paid out ranged from 758,400.00 PLN (177,923.75 euros) in 2017 to 1,676,900.00 PLN (367,177.58 euros) in 2021. These figures concord with those used for the Analysis Report.

PORTUGAL

56 emails were sent from Portugal. All expressed their support for the protection of the wolf. Three letters from Environmental NGOs also provided links to numerous scientific references and studies to support their position in favour of the protection of the wolf. These were screened for any relevant information that could be used for the In-depth Analysis Report.

ROMANIA

A total of 8 emails were sent from Romania, three were in favour of maintaining the conservation status of the wolf, two were against. One email from a County Council raised concerns about the poor implementation of derogations for wolves (in relation to livestock damages) and proposed to establish a preventive quota instead of using individual derogations. Three emails provided data on wolf numbers and livestock damage. The first email came from the Ministry of Environment and provided an update on the wolf population and the compensation paid for damage caused by wolf. These figures were used for the In-depth Analysis Report. Two environmental NGOs also quote the same official data on wolf numbers which were used for the Analysis Report.

SLOVAKIA

Two emails were sent from Slovakia. The Ministry of Agriculture and Rural Development provided up-to-date information on the wolf population in Slovakia and impacts on livestock. Their estimation of wolf population (365-524 individual) was very similar to the figures provided by the Ministry of Environment (400-600) and used in the In-depth Analysis Report. They do however distinguish between winter and summer populations, the latter being higher because of the high number of new wolf cubs every year (135-194). Regarding the livestock damage, the figures for 2022 are somewhat higher than those provided by the Ministry of Environment (1143 sheep,117 bovine, 75 goats). The figures are derived from Central evidence administration of livestock in the Slovak Republic, state enterprise. The second email from the state enterprise provided the same data.

SLOVENIA

19 emails were sent from Slovenia, all expressed their support for downlisting the wolf to Annex V of the Habitats Directive. Two provided data. The first email from a coalition of farmer organisations provided data on the wolf population that corroborates with the official data provided by the competent authorities and used in the In-depth Analysis Report. The email also stressed that low densities of grazing animals, rugged terrain, steepness, shallow soils and remoteness of pastures make protection against carnivores particularly difficult and, in the vast majority of cases, impossible.

The second email from a farming organisation stated that, according to unofficial data, there are around 200 wolves in Slovenia. This was not substantiated and, as the email itself said, it is based on unofficial data.

SPAIN

167 emails were sent from Spain. 95% supported the continued protection of the wolf. 28 emails provided data on wolf populations and livestock damage.

The Ministry of Environment provided an overview table of the number of known wolf packs per region for the first semester of 2021. They also listed the year in which the data was recorded, the number of shared packs (across two or more regions) and the estimated number of lone wolves. The total number of wolf packs is estimated at 324 (of which 30 are shared packs). However, the Ministry also pointed out that these figures are based on data collected opportunistically using different methodologies and time scales and are not the result of a nationwide survey. Much of this information comes from the national survey carried out in 2012-2014, so it is outdated. In addition, double counting of shared (transregional) packs has not been addressed which could lead to an over-estimation of the total wolf population. The Ministry and the autonomous communities intend to carry out a national survey that will be completed in 2024.

Emails were also sent from ten Autonomous Regions:

The Autonomous Region of Castilla Leon reported that they have located 214 wolf packs in the region in the period 2012-2018, but they cannot confirm that all the packs are present in any specific year. They are currently carrying out an official survey for 2022-2023. The number of wolf packs is higher than the data provided by the Ministry of Environment, but is difficult to use as it is somewhat old and covers a seven-year period. The region also provided detailed information on livestock damage for 2022 (5104 livestock) which matches the figure provided by the Ministry. Since the protection of the wolf north of the Duero in 2021, the level of compensation has increased significantly, and the regional government now receives almost 10 million € a year from the government to pay for livestock damage and for prevention measures. However, the increase in compensation does not necessarily imply an increase in livestock damage over the past 2 years, rather a higher number of claims for compensation since the compensation coverage has been expanded to many areas north of the river Duero where before wolf protection (2021) damage was not compensated.

The Autonomous Region of Rioja reported that there were four packs (18-38 wolves) in 2021/2022 which is one pack higher than the data provided by the Ministry of Environment. 696 heads of livestock were killed by wolves in 2022, most of them (682) sheep, resulting in a total of 105,761€ spent in compensation. This data matches that provided by the Ministry.

The Autonomous Region of Extremadura reported that there was one female in the north of the region in 2021 and one male hybid in 2022. In the west of the region there was also one wolf on the border with Portugal.

The Autonomous Region of Madrid reported that in 2022 there were 5 wolf packs and 104 attacks on livestock; 55,702€ was spent on compensation. The figures on compensation are lower than the data provided by the Ministry of Environment.

The Autonomous Region of Cantabria reported that there were 20 packs in the region in 2022 which matches the data provided by the Ministry of Environment. The region also reported wolf attacks and livestock damage since 2019. In 2022, livestock damage amounted to 2456 animals which matches that provided by the Ministry.

The Autonomous Region of Castilla-La Mancha provided data for one province only: 4 wolf packs and 81 attacks on livestock in 2022. The data on wolf data is one pack higher than the data provided by the Ministry of Environment. The data on livestock damage is slightly lower than the data provided by the Ministry.

The Autonomous Region of Aragon reported one wolf pair and a few lone wolves in 2023. 16 livestock were killed or wounded in 2022. No data was provided by the Ministry of Environment for this Region.

The Autonomous Region of Galicia carried out a survey in 2020-2021 which identified 93 wolf packs, 21 of which are shared with other Spanish regions or with Portugal. This data is similar to the data provided by the Ministry of Environment although the number of shared wolf packs is significantly higher (21 compared to 7). The region also provided detailed data on damage to livestock: in 2022, this amounted to 2251 livestock, the majority being sheep (1332). The data matches the figures provided by the Ministry of Environment.

The Autonomous Region of Asturias reported the presence of 40 packs, and reproduction in 35 packs, which matches the data provided by the Ministry of Environment. The figures for livestock damage (3225 head for 2022) match the data provided by the Ministry.

The Autonomous Region of Andalusia confirmed that no wolves have been found in recent years.

The province of Barcelona reported that a single male had settled in the area, killing or wounding 15 goats. The data is noted, but is at too small scale to be comparable with the official statistics provided by the Ministry of Environment in the context of the In-depth Analysis Report.

Two national farmers' associations sent a large number of reports on damage to livestock covering most of the Autonomous Regions. This material was derived from statistics provided by the Autonomous Regions and the Ministry of the Environment and is therefore the same as the official data used for the In-depth Analysis Report.

A third national farmer's association also provided data on livestock damage for the different regions. It is largely consistent with the official data submitted by the Ministry of Environment with slight variations and an overall figure that is slightly lower than the official data.

Two environmental NGOs, four regional farmer's associations and one regional research body all refer to the same statistics on wolf populations and/or livestock damage as provided by the Autonomous Regions and the Ministry of Environment.

One hunting organisation and one hunting foundation referred to a report prepared by the Foundation which provides data on wolf populations per region. Overall, they estimate that the wolf population in Spain is in the range of 370-380 herds, although future studies should confirm these figures. The regional figures are based on data collected on pack surveys carried out by the Autonomous Regions and is mostly consistent with the official data provided by the Regions and the Ministry of the Environment, but the overall aggregation is likely to be exaggerated because, as the report points out, the packs shared between Regions and lone wolves are not systematically excluded. The figures are also based on collected data and not derived from any agreed monitoring methodology.

Regarding the figures provided for livestock damage caused by the wolf in Spain (10,000 heads), these are overall lower than the figures provided by the Ministry of Environment (14,300 heads). Also, according to the report 3 million heads of livestock were lost for a variety of reasons over the last six years (ie average 500,000/year).

One local farmer's association sent data on livestock damage for some municipalities within a region, but they are at too local a scale to be compared with regional or national data.

One regional political party provided individual handwritten forms submitted by farmers reporting livestock damage. There is no summary overview. The data is at too local a scale to be comparable with the data submitted by the Autonomous Region and the Federal Ministry of Environment.

One hunting association provided data on wolf numbers for 2007 which is out of data.

One regional farmers union provided data on the wolf population and livestock damage in its region. It estimated that the total population is around 736 to 828 wolves, distributed in 93 groups. Whilst this figure is similar to the data provided by the Region and the Ministry of Environment, it does not take into account the fact that several wolf packs are shared with two or more regions. The data on livestock damage matches that provided by the Region and the Ministry of Environment.

SWEDEN

A total of 7727 emails were sent from Sweden. Two thirds (62%) were in favour of maintaining the protection status of the wolf, while one third (38%) asked for the protection status to be reduced. In the case of the former, the majority estimated the Swedish wolf population to be 450 wolves in the winter of 2022-2023 and stated that 250 sheep were attacked by wolves in 2022. Both figures match the official data provided by the competent authorities which was used for the In-depth Analysis Report.

The emails in favour of protecting the wolf also expressed concern that the wolf population had decreased to 368 wolves by 2023, according to the Swedish University of Agricultural Sciences and that the species had not reached a favourable conservation status in Sweden. Due to its small population size, it was also in danger of genetic inbreeding. Yet, the wolf has a positive effect on Swedish nature and ecology according to several research projects.

The emails requesting a reduction in the protection status of the wolf considered that the Swedish wolf population had reached a favourable conservation status and should no longer be listed as strictly protected. They considered that the wolf had been increasing and expanding in Sweden for forty years and are now spreading into more densely populated areas of the country which is leading to increasing conflicts and higher costs for farmers, as well as fear in local communities.

9 emails contained data on wolf populations and livestock damage. The email from the Swedish Environment Protection Agency submitted official data for wolf population and livestock damage for the Winter 2022/2023 which was used for the In-depth Analysis.

Five emails came from national environmental NGOs. Three provided the same population data as the official data (450 wolves), but all considered that the Swedish population is small, isolated and heavily in-bred, having originated from only three individuals in the 1980s and with little influence from outside immigrants since. They also considered that the population remained in danger due to decisions on licensed hunting (57 wolves - 12% of the population in 2023), illegal hunting, accidents, and natural mortality. The same reference source was quoted claiming that the Swedish wolf population drastically decreased to 368 wolfs in the autumn of 2023 according to the Swedish University of Agricultural Sciences.

One of the environmental NGOs considered that the Scandinavian wolf population now only has around 300 individuals (counted in March 2023) before breeding with the correct multiplication factor 7,67 but this latter figure has not been substantiated.

All five emails disagreed that the wolf has reached favourable conservation status as stated by the Swedish authorities and they contest the figure of 300 wolves which was given by SEPA as a favourable reference value. According to 18 scientists this should be higher (600 wolves) in order to fulfill the criteria of ecological viability.

Three emails were sent from a farming organization, hunting organization and business association. All provided the same data for the wolf population and livestock damage as used for the In-depth Analysis Report. All expressed concern over the fact that the wolf is concentrated in the centre of the country and is spreading to more densely populated areas which risks increasing wolf attacks on livestock and affects hunting, especially traditional hunting with dogs. It also creates fear amongst local communities. They consider that preventive measures for protecting livestock are expensive and would be prohibitive if predator repellent fences had to be put in place for all sheep in Sweden.

EU LEVEL ORGANISATIONS

20 emails were sent from organisations operating at EU level or internationally (environmental, animal welfare or youth organisations or farming or hunting organisations). 17 were in favour of maintaining the protection status of the wolf, 3 asked for its protection status to be lowered. All gave explanations for their position, supported by relevant documentation.

In the case of environmental NGOs, the following are some of the key points were raised:

a) the wolf has not reached a favourable conservation status within the EU and remains vulnerable, the current positive trend can easily be reversed; many populations are still threatened by illegal hunting (and hunting quotas in some Member States), hybridisation, road accidents and genetic in-breeding;

b) wolf monitoring is very uneven across the different Member States which gives an unclear overall picture of the EU population and status– it is a priority to improve monitoring standards;
c) any policy decisions must be evidence- and science-based and not based on anecdotal evidence delivered through an irregular consultation process;
d) the existing derogation system under the Habitats Directive provides sufficient flexibility to deal with ‘problem’ wolves;
e) many tools are already available to protect livestock and compensate for losses; these have been shown to work, but are insufficiently and very unevenly applied;
f) instead of reducing the protection status of the wolf, the focus should be instead on significantly improving the use of existing tools to protect livestock eg by using the exceptions available under State aid rules and funding from CAP;
g) attacks on humans are extremely rare;
h) wolves, as an apex species, have an important positive role to play in Europe’s ecosystems;
i) lethal controls of wolf populations have not been scientifically proven to be effective in reducing livestock depredations;
j) the overall livestock loss in the EU is very low 0,1- 0.05% of the total sheep stock.

Most of the emails from the environmental NGOs also expressed serious concern at the tone of the press release which they consider misleading and could pre-empt the outcome. The consultation period of 18 days was also considered to be too short and not in line with the Commission’s own better regulation rules.

In the case of the <u>hunting and farming organisations</u>, the following are some of the key points raised:

a) Increasing wolf populations are leading to increasing conflicts with livestock and threatening the livelihoods of farmers – especially extensive livestock farming (which contributes positively to biodiversity);
b) the data from the Article 17 Habitats Directive’s Reports do not paint a correct picture of the conservation status of the wolf in the EU; there should instead be a science-based population level assessment of the wolf that more appropriately recognizes their biology and ecology;
c) listing the wolf in Annex V instead of Annex IV of the Habitats Directive allows for a more active and flexible management of the species;
d) the present derogation system under the Habitats Directive is too strict and presents a significant bureaucratic burden in many countries. It does not allow for instant and efficient conflict resolution;
e) the wolf also has a negative impact on wild ungulates and on hunting activities (especially with hunting dogs);
f) the wolf has changed behaviour and is not as afraid of humans as before;
g) the cost of protection measures and compensation is exorbitant and will only continue to increase;
h) the EU platform on coexistence between people and large carnivores should continue to facilitate dialogue between different stakeholders and Member State authorities.

Six emails also provided data on wolf populations and livestock damage.

One environmental organisation and one hunting organisation referred to the assessment made by the Large Carnivore Initiative for Europe in 2022 which stated that there are currently around 19,000 wolves distributed across 27 EU Member States. Two other environmental NGOs referred to the figure of over 17,000 wolves based on figures for 2018 (cf Wildlife Comeback Report, 2022). According to the latest official data collected from competent national authorities or other reliable sources as part of the In-depth Analysis the population is currently estimated at 20,300 wolves for EU-27 (2023).

One environmental organisation also considered that wolves kill between 30,000 and 40,000 European livestock animals annually, of which the majority are sheep. This figure is lower than the latest data collected from competent national authorities or other reliable sources as part of the In-depth Analysis. According to the latest figures, livestock damage is currently estimated at 65,000 head for EU-27 (2023); this includes not only livestock killed, but also those reported as injured.

Another environmental organisation stated that between 2012 and 2016, the annual number of sheep compensated because of wolf depredation corresponded to 0.05% of the over-wintering sheep stock. Member States presenting higher depredation rates such as Portugal, France, Italy or Croatia, appeared to be countries with husbandry systems that leave livestock unprotected, or where there are low densities of wild prey.

Several hunting organisations provided data on wolf populations and livestock predation at Member State level:

- Germany: the figures quoted by one hunting organisation are based on official data from DBBW and concord with those used in the In-depth Analysis Report. A second hunting organisation provided figures that are lower than the data presented in the In-depth Analysis Report but without substantiating its data;
- Poland: The figure given by one hunting organisation of 2154 wolves for Poland is based on information collected from hunting clubs and corrected for possible double counts. This is higher than the figure of 1886 wolves identified in the In-depth Analysis report (Boitani et al 2022). The organisation's estimation is however based on sightings and, even if corrected, it does not follow agreed monitoring standards;
- Spain: Two hunting organisations provided a figure for the wolf population in Spain of 2800 (400 wolf packs) based on estimation done by a hunting foundation which collected data on pack surveys carried out by the autonomous communities. The data is not consistent with the official data provided by the autonomous authorities in the context of the In-depth Analysis (eg Asturias:53 wolf packs according to NGO, 40 according to regional government; Cantabria 27 packs according to the NGO, 20 according to the regional government). The overall figure of 2800 is therefore likely to be overestimated. It is also based on collected data and not derived from any agreed monitoring methodology. Regarding the figures provided for livestock damage caused by the wolf in Spain, this varies from one hunting organisation to the other. In one case, the figure (8000 attacks) is lower than the official data provided in the In-depth Analysis (14,300 animals, 2022). The other organisation gives a figure of 10,000 cattle lost in 2022. This is double the official figures for cattle provided in the In-depth Analysis, but it has also not been substantiated (and is possibly meant to say 10,000 livestock);
- Netherlands: the hunting organisation quoted the same official figures for wolf population that were used for the Analysis Report but then goes on to state that, based on observations, the actual numbers appear to be much higher: more like 100. This is however not substantiated and is based on observation only;
- Czech Republic, Belgium, Sweden: The figures provided for wolf population and/or livestock damage match the official figures provided in the In-depth Analysis Report;
- Austria: the figures given for livestock damage caused by the wolf are double the official data available on https://baer-wolf-luchs.at/ and have not been substantiated.

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im Fachbereich Wald und Umwelt

Studiengang „Forstwirtschaft“

Entwicklung der Schalenwildbestände im Fläming vor dem Hintergrund der Besiedlung durch den europäischen Wolf

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und
Antje Weber

Eberswalde, den 02.08.2022

Abbildung 1: *links oben: Wolfswelpe im Revier Göritz (Quelle: Heiko Anders), links unten: Wolfsriss im Revier Göritz (Quelle: Nils Schumann), mittig: Buchensaatkultur im Revier Göritz (Quelle: Nils Schumann), rechts oben: Damhirsch im Revier Göritz (Quelle: Nils Schumann), rechts unten: Wolf im Revier Göritz (Quelle: Heiko Anders)*

Eidesstattliche Erklärung

Hiermit erkläre ich, dass ich die vorliegende Bachelorarbeit mit dem Titel „Entwicklung der Schalenwildbestände im Fläming vor dem Hintergrund der Besiedlung durch den europäischen Wolf“ selbständig verfasst habe, dass ich sie zuvor an keiner anderen Hochschule und in keinem anderen Studiengang als Prüfungsleistung eingereicht habe und dass ich keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Alle Stellen der Arbeit, die wörtlich oder sinngemäß aus Veröffentlichungen oder aus anderweitigen fremden Äußerungen entnommen wurden, sind als solche kenntlich gemacht.

Eberswalde, der 02.08.2022 E. Schumann

Ort, Datum, Unterschrift

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1. Einleitung

Die Waldflächen im Fläming sind in den letzten Jahren durch Stürme, Insektenkalamitäten, Waldbrände, Dürre, Hitze und Pilzkrankheiten stark geschädigt wurden. Zur Wiederherstellung der vielfältigen Nutz- und Schutzfunktionen der Wälder sollen die entstandenen Schadflächen möglichst schnell wieder natürlich verjüngt oder aufgeforstet werden. Ein wichtiger Faktor ist dabei, auf den umfangreichen Verjüngungsflächen die Wildschäden möglichst gering zu halten.

In den letzten Jahren sind wieder Wölfe (*Canis lupus*) in den Fläming eingewandert und haben hier reproduzierende Rudel gegründet. In welchem Umfang und in welchem Tempo haben die Wölfe ihren ursprünglichen Lebensraum im Untersuchungsgebiet wiederbesiedelt? Wie haben sich die Schalenwildbestände im Fläming seit der Rückkehr der Wölfe entwickelt? Und wie haben sich die Wildschäden auf den Kulturen der Flämingreviere im Landesforstbetrieb Sachsen-Anhalt verändert?

Die vorliegende Arbeit versucht Zusammenhänge zwischen dem Beutegreifer Wolf, der Schalenwildpopulation und den Wildschäden auf den Verjüngungsflächen im Landesforstbetrieb darzustellen und die Frage zu beantworten, ob Wölfe durch die Regulierung der Wildbestände indirekt einen positiven Einfluss auf die Verjüngungssituation im Wald ausüben können.

2.Untersuchungsgebiet

2.1 Naturraum/Landschaft Fläming

Der Fläming ist ein eiszeitlich gebildeter Höhenzug und eine historisch gewachsene Kulturlandschaft. Der Name des Gebiets entstand durch die Besiedlung durch Flamen im frühen Mittelalter.
Während der Saalekaltzeit waren die Hauptvorstöße des Eises verantwortlich für die wesentliche Formung des Höhenzuges. Der Hauptteil des Flämings ist dabei aus Sedimenten des Drenthe-Vorstoßes aufgebaut.
Der Fläming wird im Norden und Süden jeweils durch Urstromtäler begrenzt. Die Nordgrenze bildet das Baruther Urstromtal. Im Süden endet der Fläming im Breslau-Magdeburg-Bremer-Urstromtal sowie an der Elbe. Die Westgrenze bildet das Elbtal bei Magdeburg. Der Fläming wird unterteilt in die Bereiche „Hoher Fläming" im Westen und „Niederer Fläming" im Osten. Das Untersuchungsgebiet befindet sich im Hohen Fläming sowie im sogenannten Roßlau-Wittenberger Vorfläming.
Die Böden im Fläming sind entsprechend der kaltzeitlichen Ablagerungen des skandinavischen Inlandeises sehr vielseitig aufgebaut. Neben nährstoffarmen Böden gibt es auch sehr fruchtbare Bereiche.
Das Landeszentrum Wald Sachsen-Anhalt hat für die Waldgebiete im Bundesland Klimastufen definiert. Der Fläming ist in die Klimastufe „Tiefland mäßig trocken" eingeordnet. Diese Klimastufe entspricht einer Jahresdurchschnittstemperatur von 8,0 – 8,7 °C und einem durchschnittlichem Jahresniederschlag von 550-600 mm (vgl. Landeszentrum Wald Sachsen-Anhalt)
Eine Besonderheit im Fläming sind die sogenannten „Rummeln". Dabei handelt es sich um Trockentäler ohne Fließgewässer, die zum Ende der Eiszeit beim Abschmelzen der Gletscher entstanden sind. Fließgewässer wie Bäche und kleine Flüsse findet man dagegen im zentralen Bereich des Hohen Fläming fast gar nicht, da die Niederschläge in den groben Sedimenten leicht versickern. Grundwasserschichten findet man häufig erst in 30 Meter Tiefe. Dafür existieren am Flämingrand sowie im Vorfläming zahlreiche Quellregionen, Feuchtgebiete und kleine Bäche.
Der Fläming ist eine sehr waldreiche Region, vor allem im Hohen Fläming findet man große geschlossene Waldkomplexe. Die Siedlungsdichte im Fläming ist dagegen gering.

Im Fläming existieren zwei Naturparke. Im Bundesland Brandenburg existiert der Naturpark „Hoher Fläming" mit dem Naturparkzentrum in Raben. In Sachsen-Anhalt wurde der Naturpark „Fläming" mit Sitz in Coswig (Anhalt) gegründet (vgl. Helm, Joachimi 2010).

2.2 Flämingreviere im Landesforstbetrieb

Der Landesforstbetrieb Sachsen-Anhalt bewirtschaftet seit 01.01.2006 die Landeswaldflächen im Bundesland Sachsen-Anhalt. Er ist untergliedert in die fünf Teilbetriebe Altmark, Anhalt, Oberharz, Ostharz und Süd. Der Forstbetrieb Anhalt bewirtschaftet die Landeswälder im Ostteil Sachsen-Anhalts auf einer Fläche von 38.700 ha und ist aufgeteilt in zwölf Reviere. Das Untersuchungsgebiet besteht aus den vier Flämingrevieren Nedlitz, Hoher Fläming, Stackelitz und Göritz, die sich im Norden und Nordwesten des Betriebsterritoriums befinden (vgl. Abb. 2).

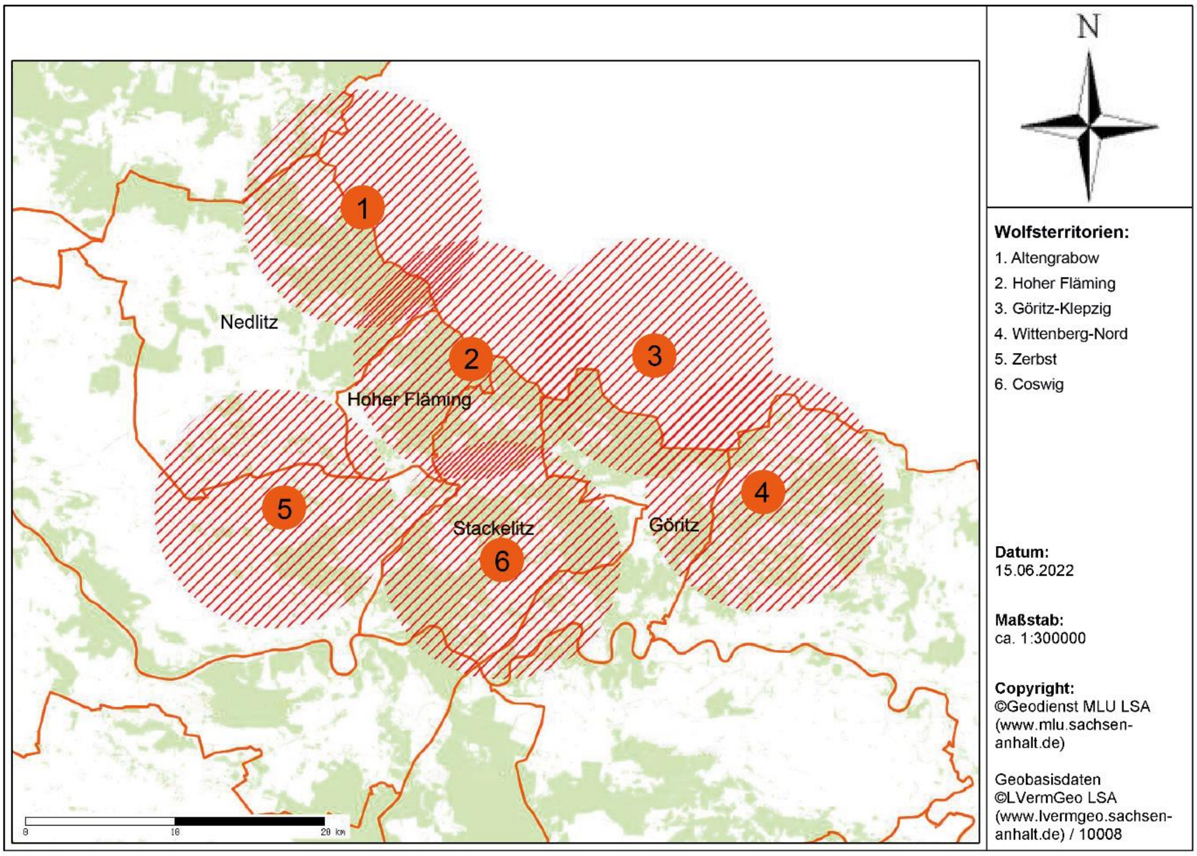

Abbildung 2: *Übersichtskarte der Landeswaldreviere und der Wolfsterritorien im Untersuchungsgebiet (Quelle: LAU Sachsen-Anhalt, LFB Sachsen-Anhalt FB Anhalt)*

Die Hauptbaumart in den Revieren ist die Kiefer. Sie stockt auf etwa 70% der Waldfläche.

Daneben gibt es in allen Revieren größere Buchen- und Eichenkomplexe.

Im Warthestadium der Saaleeiszeit kam es im Gebiet zu den letzten eiszeitlichen

Ablagerungen. Daraus entwickelte sich überwiegend die Nedlitzer Sandbraunerde mit einer mittleren Nährstoff- und Wasserversorgung für die Waldbestände.

Auf Grund der Trockenjahre 2018 bis 2020 sind in allen Revieren und bei allen Baumarten und Altersklassen Absterbeerscheinungen zu verzeichnen. Bei der Wiederaufforstung der Schadflächen werden Mischwälder aus drei bis fünf Baumarten angelegt, die den künftigen waldbaulichen Anforderungen durch den Klimawandel gerecht werden sollen. Folgende Baumarten werden für den Aufbau klimatoleranter Wälder im Untersuchungsgebiet verwendet und je nach kleinstandörtlichen Gegebenheiten gemischt: Traubeneiche, Stieleiche, Roteiche, Winterlinde, Hainbuche, Rotbuche, Esskastanie, Bergahorn, Feldahorn, Wildapfel, Wildbirne, Kiefer, Douglasie, Küstentanne und Weißtanne.

Durch den großen Umfang der Schadflächen in den Waldbeständen der Region ist es nicht möglich, alle Kulturen durch Zäune vor Wildschäden zu schützen. Deshalb ist eine Verringerung der Verbiss- und Fegeschäden aktuell eine Hauptaufgabe der Förster im Fläming. Dazu ist eine weitere Reduzierung der Schalenwildbestände in der Region erforderlich.

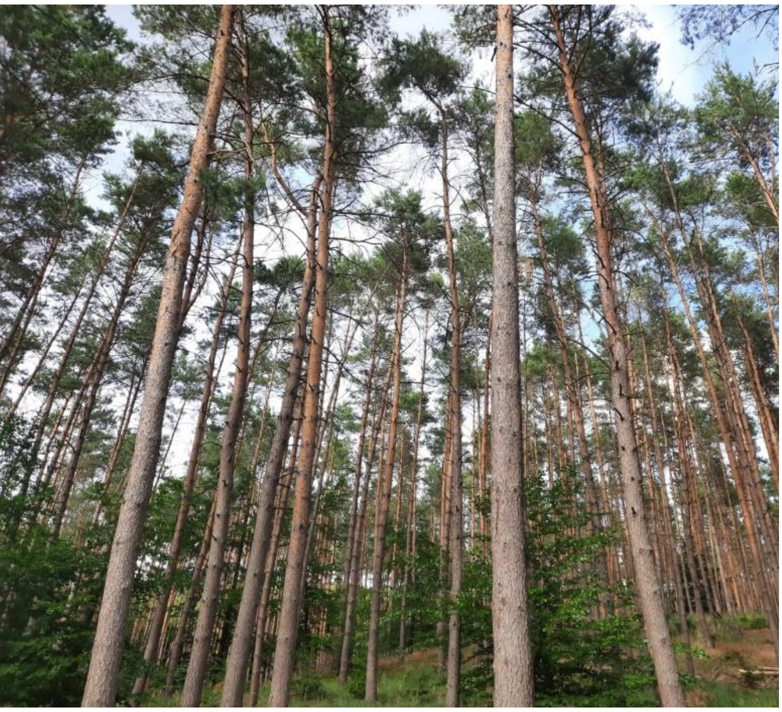

Abbildung 3: links: Kiefernbestand, rechts: mehrschichtiger Buchen-Eichen-Komplex im Revier Göritz (Quelle: Nils Schumann)

3. Material und Methoden

Grundlage der vorliegenden Arbeit ist die Aufarbeitung und Auswertung von Datenmaterial zu den Themenbereichen: Entwicklung der Wolfspopulation, der Abschussergebnisse beim Schalenwild und der Wildschäden auf den Forstkulturen im Untersuchungsgebiet.
Die Daten zur Entwicklung der Wolfspopulation im Fläming stammen aus den Jahresberichten des Landesamtes für Umweltschutz Sachsen-Anhalt, erarbeitet vom Wolfskompetenzzentrum Iden für die Monitoringjahre 2012/2013 bis 2020/2021 sowie aus persönlichen Mitteilungen von Frau Antje Weber vom Wolfskompetenzzentrum Iden.
Zur Ermittlung der Abschussergebnisse beim Schalenwild wurde durch den Forstbetrieb Anhalt umfangreiches Datenmaterial zur Verfügung gestellt. Wesentliche Grundlage für die Zusammenstellung war die jährliche Streckenmeldung des Forstbetriebes an die jeweils zuständigen Unteren Jagdbehörden der Landkreise. Die Streckenmeldung basierte auf den Wildursprungsscheinen für erlegtes Wild, Unfallwild und sonstiges Fallwild (Krankheit, Wolfsriss).
Die Daten zur Auswertung der Wildschäden auf den Forstkulturen im Untersuchungsgebiet beruhen auf den Ergebnissen des Kulturqualitätsmanagments (KQM) des Landesforstbetriebes Sachsen-Anhalts. In den Jahren 2008, 2012, 2016 und 2021 wurden jeweils alle vier- bis sechsjährigen Forstkulturen durch eigene Mitarbeiter und externe Gutachter kontrolliert. Dabei erfolgte u. a. die Erfassung der Pflanzenzahlen, der Höhe der Pflanzen, der Baumartenanteile und der Verbissschäden. Auf der Basis dieses umfangreichen Datenmaterials wurden nach der Digitalisierung entsprechende Auswertungen durch Herrn Jörg Köhler vom Landesforstbetrieb Sachsen-Anhalt durchgeführt. Herr Köhler stellte diese Auswertungen zur Verfügung und anschließend erfolgte in der vorliegenden Arbeit eine graphische Bearbeitung.

4.Wolfsrudel im Untersuchungsgebiet

4.1 Einführung zum Wolf

Der Wolf gehört wie auch der Haushund zur Art *Canis lupus* und damit zur Familie der Hunde. Canidae gehören zur Unterordnung der Landraubtiere. Sie gelten als größter Vertreter der Caniden. Es besteht ein leichter Geschlechtsdimorphismus, wodurch die Männchen (Rüden) generell größer und schwerer sind als die Weibchen (Fähen). Außerdem bestehen je nach geographischer Lage, wie durch die Bergmannsche Regel beschrieben, Größenunterschiede zwischen den verschiedenen Wolfspopulationen.

Abbildung 4: *Wolfsportrait im Revier Göritz (Quelle: Heiko Anders)*

Die Fellfarbe der Wölfe unterliegt je nach Lebensraum einer sehr großen Varianz. So ist die graue Fällfärbung im mitteleuropäischen Raum am häufigsten vertreten (vgl. Okarma/Langwald 2002: 1). Das Fell schützt den Wolf mit seiner mehrlagigen Beschaffenheit vor verschiedenen Umwelteinflüssen und isoliert sowohl bei Hitze als auch bei Kälte. Im Zeitraum zwischen April und Mai verlieren die Wölfe ihr Winterfell, welches ab August wieder nachwächst.

Das Erscheinungsbild des Wolfes ist geprägt durch einen gut proportionierten, kräftigen Körperbau, welcher auf die Fortbewegung über lange Strecken angepasst ist. Der Rücken beschreibt eine fast gerade Linie und endet in einer leicht abfallenden Kruppe. Die Beine sind hoch und schlank. Die Vorderpfoten sind besonders kräftig. Darüber hinaus besitzt der Wolf einen sehr langen und breiten Brustkorb, welcher sich im Bereich der Vorderbeine verschmälert. Dadurch entsteht das für den Wolf charakteristische geradlinige Fährtenbild. Der Kopf des Wolfes erscheint im Verhältnis zu seinem Körper schwer und groß. Seine Schnauze ist lang, aber nicht spitz und er besitzt kräftige Kiefer (vgl. Bibikow 1990: 6). Die Zahnformel des Wolfes lautet I3/4 C1/1 P4/4 M2/3 = 42. Besonders die Eckzähne (Canini) sind beim Reißen und Fangen der Beute von großer Bedeutung. Die Backenzähne (Prämolaren und Molaren) können aufgrund ihrer starken Hebelkraft hinten im Kiefer zum „Brechen" von Knochen verwendet werden. Die Stirn ist breit und liegt zwischen zwei aufrechtstehenden, dreieckigen Ohren, welche in der Regel nach vorne gerichtet getragen werden. Auch sein Hals erscheint muskulös und kräftig. Normalerweise hält der Wolf seinen Hals waagerecht, so dass sein Kopf nur wenig höher als der Widerrist gehalten wird. Mit gesenktem Kopf erreicht die Nase des Wolfes fast den Boden (vgl. Okarma/Langwald 2002: 8-15).

Das Gehör der Wölfe ist sehr gut ausgeprägt. Sie hören Töne bis zu einer Frequenz von 42000 Hertz. Die beweglichen Ohren helfen außerdem bei der genauen Lokalisierung der Schallquellen. Die Nase ist das am besten ausgeprägte Sinnesorgan des Wolfes. Die Oberfläche des Riechephitels hat eine Größe von 130 cm². Die vom Menschen im Vergleich dazu nur 5 cm². Somit kann der Wolf die Witterung von Beutetieren und Artgenossen über Entfernungen von zwei bis drei Kilometern wahrnehmen. Die Augen der Wölfe sind an die Abend- und Morgendämmerung besonders gut angepasst. Ihre Farbwahrnehmung ist begrenzt. Ihr Wahrnehmungsvermögen für Bewegungen ist sehr ausgeprägt.

Wölfe sind territoriale Tiere. Die Verteilung der Rudel als auch die Stellungen der einzelnen Wölfe innerhalb dieser Rudel ist genau geregelt und folgt einer geordneten Struktur. Die Rudel sind immer Familienverbände, bestehend aus den Elterntieren und den Welpen des aktuellen Jahres. Teilweise gehören auch noch Welpen vom Vorjahr zeitweise mit zum Rudel. Zur Aufrechterhaltung dieser Struktur bedienen sie sich eines komplexen Informations- und Kommunikationssystems. Auch hierbei ist der Geruchssinn die wichtigste Informationsquelle. Die Informationsübertragung geschieht in diesem Fall hauptsächlich über Harn, Anal- und Genitaldrüsen. Bei der visuellen Kommunikation werden Informationen sowohl durch die Mimik, die Haltung als auch die Bewegung weitergegeben. Die akustische

Kommunikation der Wölfe wird in zwei Grundtypen zum Zweck der Fernsignalgebung unterteilt. Dabei handelt es sich um das Heulen und um das Bellen. Ersteres dient der Reviermarkierung und wohlmöglich dazu anderen Tieren Standorte mitzuteilen. Das Bellen ist ein Warnlaut und ist vor allem charakteristisch für Jungwölfe im ersten Sommer und Herbst (vgl. Bibikow 1990: 1-30).

4.2 Rudel Altengrabow

Das Rudel Altengrabow war das erste Rudel, das sich wieder in Sachsen-Anhalt angesiedelt hat. Es lebt seit 2009 auf dem Truppenübungsplatz Altengrabow und angrenzenden Gebieten. Bei der ersten Verpaarung hatte der Rüde die Bezeichnung GW187m. Seine Herkunft ist unbekannt. Die Fähe (GW016f) stammt aus dem Rudel Neustadt nahe der deutsch-polnischen Landesgrenze. Die Elterntiere haben von 2009 bis 2015 in jedem Jahr Welpen aufgezogen. Da auch einige ein- und mehrjährige Wölfe im Territorium verblieben, wuchs das Rudel Altengrabow stetig an und erreichte 2014/15 eine Stärke von 20 Individuen.

Seit 2013/14 gab es vermehrt Wölfe mit Räudesymptomen. Im Monitoringjahr 2016/17 war eine deutliche Abnahme der Rudelgröße zu verzeichnen. Es wurden nur zwei Welpen nachgewiesen und insgesamt waren nur noch acht Rudelmitglieder vorhanden. Von den ursprünglichen Elterntieren gab es seit Juni 2016 keine genetischen Nachweise mehr. Im Monitoringjahr 2017/18 vollzog sich höchstwahrscheinlich ein vollständiger Generationswechsel, der im folgenden Jahr auch genetisch nachgewiesen werden konnte. Die zweite Verpaarung im Territorium Altengrabow bestand aus dem Rüden GW519m, der aus dem Rudel Göritz-Klepzig stammt, sowie der Fähe GW1092f. Dieses Weibchen stammt aus dem alten Rudel Altengrabow. Die beiden Wölfe zogen bis zum Jahr 2019/20 jährlich Welpen auf. Seit dem Monitoringjahr 2020/21 sind sie jedoch nicht mehr nachweisbar. Nach dem zweiten Generationswechsel im Rudel Altengrabow sind die Elterntiere der Rüde GW1569m, welcher aus dem Territorium Hoher Fläming stammt, sowie die Fähe GW1083f, wahrscheinlich aus dem Territorium Altengrabow stammend. Die Reproduktion des Rudels konnte für das Monitoringjahr 2020/2021 aufgrund fehlender Welpennachweise nicht bestätigt werden (vgl. Tab. 1).

Das Streifgebiet des Rudels Altengrabow erstreckt sich vor allem auf den nordwestlichen Teil des Untersuchungsgebietes dieser Arbeit. Von den jagdlichen Aktivitäten des Rudels ist vor allem das Forstrevier Nedlitz betroffen, da es direkt an den Truppenübungsplatz Altengrabow angrenzt (vgl. LAU 2012-2021).

Tabelle 1: *Mindest-Individuenzahl des Territoriums Altengrabow, Zeitraum 2012-2021 (Quelle: LAU Sachsen-Anhalt)*

Monitoring-Jahr	2012/13	2013/14	2014/15	2015/16	2016/17	2017/18	2018/19	2019/20	2020/21
Anzahl nachgewiesener Wölfe	11	16	20	18	8	4	8	9	4
Anzahl Welpen	6	8	6	11	2	0	6	2	0

4.3 Rudel Göritz-Klepzig

Erste Hinweise auf die Existenz des Rudels Göritz-Klepzig gab es im Monitoringjahr 2012/13. Das Streifgebiet des Rudels lag ursprünglich im Grenzgebiet Sachsen-Anhalt/Brandenburg im Waldgebiet zwischen den Ortschaften Göritz und Klepzig. Die genetischen Rudelstrukturen wurden im darauffolgenden Monitoringjahr aufgelöst. Die Herkunft des Rüden GW237m war nicht bekannt. Die Fähe GW196f stammt aus dem Rudel Altengrabow und wurde dort 2010 geboren. Im Jahr 2013/14 war außerdem ein erster Reproduktionsnachweis möglich. Es wurden dabei zwei bis drei Welpen bestätigt (vgl. Tab. 2). Des Weiteren gehörten dem Rudel noch zwei Jährlinge an, so dass davon ausgegangen werden kann, dass es auch schon im Vorjahr im Rudel Göritz-Klepzig Welpen gab. In den Monitoringjahren 2014/15 und 2015/16 wurde ebenfalls die Aufzucht von Welpen im Rudel durch Fotofallenbilder und genetische Nachweise bestätigt. Im Monitoringzeitraum 2016/17 konnten keine Welpen nachgewiesen werden. Seit 2017/18 verlagerte sich das Rudelterritorium zeitweise mehr nach Brandenburg. Ursache dafür kann die Verschiebung des Rudelterritoriums über die Landesgrenze Brandenburg sein. Außerdem

Abbildung 5: *Welpen aus dem Rudel Göritz-Klepzig (Quelle: Heiko Anders)*

gab es in diesem Monitoringjahr einen Generationswechsel. Das ergaben Ergebnisse genetischer Untersuchungen in den Folgejahren. Der neue Rüde GW599m stammte aus Rosenthal in Sachsen, die Fähe GW496f aus dem Rudel Hoher Fläming. Durch den illegalen Abschuss des Rüden im Monitoringjahr 2019/20 wurde der nächste Generationswechsel im Rudel ausgelöst. Die Verpaarung bestand aus GW615f X GW237m. Die neue Verpaarung im Monitoringjahr 2020/2021 besteht aus einem unbekannten Rüden und der Fähe GW1830f. Die Aktivitäten des Rudels beeinflussen vor allem den Schalenwildbestand im Forstrevier Göritz im Osten des Untersuchungsgebiets dieser Arbeit (LAU: 2012-2021).

Tabelle 2: *Mindest-Individuenanzahl des Territoriums Göritz-Klepzig, Zeitraum 2012-2021 (Quelle: LAU Sachsen-Anhalt)*

Monitoring-Jahr	2012/13	2013/14	2014/15	2015/16	2016/17	2017/18	2018/19	2019/20	2020/21
Anzahl nachgewiesener Wölfe	0	7	7	9	3	10	4	3	5
Anzahl Welpen	0	2	5	6	0	6	2	0	3

4.4 Rudel Hoher Fläming

Das Rudel Hoher Fläming existiert nachweislich seit dem Monitoringjahr 2014/15. Zu diesem Zeitpunkt gelang der Aufzuchtnachweis von drei Welpen. Das Streifgebiet des Rudels Hoher Fläming liegt genau zwischen den Rudelterritorien Altengrabow und Göritz-Klepzig und damit zentral im Untersuchungsgebiet der Arbeit. Das Rudel ist vor allem im Forstrevier Hoher Fläming sowie in den Nachbarbereichen der Forstreviere Nedlitz und Stackelitz jagdlich aktiv. Die Elterntiere des Rudels sind GW233m und GW227f. Der Rüde stammt aus dem Rudel Göritz-Klepzig und wurde 2012 geboren. Die Fähe des Rudels Hoher Fläming ist in Altengrabow aufgewachsen. Vom Monitoringjahr 2015/16 bis zum Monitoringjahr 2019/20 wurden jährlich erfolgreich Welpen aufgezogen (vgl. Tab. 3). Die Rudelstärke betrug in diesem Zeitraum bis zu 12 Exemplare, da sich immer noch Jährlinge im Rudel aufhielten. Im Monitoringjahr 2020/21 wurde der Rüde des Rudels überfahren. Auch die Fähe konnte genetisch nicht mehr nachgewiesen werden (LAU: 2014-2021).

***Tabelle 3:** Mindest-Individuenanzahl des Territoriums Hoher Fläming, Zeitraum 2014-2021 (Quelle: LAU Sachsen-Anhalt)*

Monitoring-Jahr	2014/ 15	2015/ 16	2016/ 17	2017/ 18	2018/ 19	2019/ 20	2020/ 21
Anzahl nachgewiesener Wölfe	5	5	6	10	12	12	4
Anzahl Welpen	0	3	4	6	6	4	0

4.5 Rudel Coswig

Im Territorium Coswig wurden im Mai 2015 gezielte Untersuchungen aufgenommen und die Anwesenheit eines territorialen Paares basierend auf Rückschlüssen auch für 2014 bestätigt. Zu diesem Zeitpunkt befanden sich im Territorium zwei Tiere.
Zuvor wurde das Gebiet als Randbereich des Rudels Göritz-Klepzig eingeordnet. Aufgrund der Überschneidungen des Territoriums mit denen der Rudel Göritz Klepzig im Nordosten und Hoher Fläming im Norden ist die Abgrenzung des genauen Gebietes schwierig. Räumlich ist das Territorium Coswig im Süden des Untersuchungsgebietes gelegen. Im Monitoringjahr 2015/16 konnten die Territorien allerdings aufgrund der frühzeitigen Welpennachweise in allen drei Rudeln genauer abgegrenzt werden. Auch die Reproduktion konnte durch Welpenbeobachtungen erstmals nachgewiesen werden. Damit befanden sich im Monitoringjahr 2016/17 sieben Wölfe im Territorium (vgl. Tab. 4). Darunter fünf Welpen. Auch im Folgejahr wurden drei Welpen des Rudels Coswig bestätigt. Zwischenzeitlich wurde eine Verlagerung des Territoriums Richtung Norden vermutet. Diese wurde später mithilfe genetischer Nachweise des Vaterrüden im ehemaligen Göritz Klepziger Territorium und Fotofallendokumentation von innerartlichen Auseinandersetzungen bestätigt. Diesen Umständen geschuldet war eine genaue Zahl der anwesenden Tiere sowie die Reproduktion für das Monitoringjahr 2017/18 nicht festlegbar. Im folgenden Jahr wurde eine neue Elternkombination festgestellt. Der Rüde, abstammend aus dem Rudel Rosenthal (Sachsen), bildete zusammen mit einer Fähe aus dem Rudel Hoher Fläming das neue Elternpaar. Durch das Auffinden zwei toter Welpen (Autounfall und illegaler Abschuss) konnten diese dem Paar genetisch zugeordnet werden. Im Monitoringjahr 2019/20 wird aufgrund einer tot aufgefundenen, säugenden Fähe die Doppelreproduktion vermutet. Weiterhin konnten zwei Welpen bestätigt und die Anwesenheit von insgesamt fünf Tieren belegt werden. Im

Folgejahr 2020/21 kam es erneut zur Neuverpaarung aus GW 1091f und GW1829m. Die Fähe stammt aus dem Rudel Oranienbaumer Heide. Die Herkunft des Rüdens ist bis dahin noch ungeklärt. Damit handelt es sich mittlerweile um die dritte Elternkombination in dem Territorium Coswig. Drei Welpen konnten bestätigt werden, wovon aber zwei überfahren und tot aufgefunden wurden. Somit waren in diesem Jahr sechs Wölfe im Territorium Coswig anwesend (vgl. LAU 2014-2021).

***Tabelle 4:** Mindest-Individuenanzahl des Territoriums Coswig, Zeitraum 2014-2021 (Quelle: LAU Sachsen-Anhalt)*

Monitoring-Jahr	2014/ 15	2015/ 16	2016/ 17	2017/ 18	2018/ 19	2019/ 20	2020/ 21
Anzahl nachgewiesener Wölfe	2	7	5	-	4	5	6(-2)
Anzahl Welpen	0	5	3	-	2(-2)	2	3(-2)

4.6 Rudel Wittenberg-Nord

Das Territorium Wittenberg-Nord wurde erstmals im Monitoringjahr 2019/20 anhand von Fotofallenbildern eines morphologisch auffallenden Rüden entdeckt. Eine mittlerweile verheilte Verletzung am Hals gibt dem Rüden Wiedererkennungswert. Zu Beginn wurden die Aktivitäten des Rudels den Nachbarterritorien zugeordnet, doch nach Abgleich der Daten mit denen des Landesamtes für Umweltschutz Brandenburg wurde ein eigenständiges Territorium ersichtlich. Im ersten Monitoringjahr 2019/20 wurde die Reproduktion von zwei Welpen nachgewiesen. Insgesamt waren fünf Tiere in diesem Jahr anwesend (vgl. Tab. 5). Schlussfolgernd aus dieser Rudelstruktur bestand das Territorium schon im Jahr 2018/19 als Paarterritorium.

Auch im Folgejahr wurden vier Welpen bestätigt, womit insgesamt neun Tiere für das Monitoringjahr 2020/21 belegt wurden. Für die genaue genetische Aufklärung des Rudelkonstrukts sind weitere Analysen notwendig.

Das Territorium liegt im südöstlichen Teil des Untersuchungsgebietes und betrifft somit das Revier Göritz (vgl. LAU 2019-2021).

***Tabelle 5:** Mindest-Individuenanzahl des Territoriums Wittenberg-Nord, Zeitraum 2019-2021 (Quelle: LAU Sachsen-Anhalt)*

Monitoringjahr	2019/20	2020/21
Anzahl nachgewiesener Wölfe	5	9
Anzahl Welpen	2	4

4.7 Rudel Zerbst

Das Territorium Zerbst wurde im Monitoringjahr 2020/21 entdeckt. Hinweis dafür war ein überfahrener Welpe an der B184, welcher als erster Welpennachweis galt. In den Jahren zuvor wurden die in diesem Territorium gesichteten Wölfe den Nachbarterritorien zugeordnet: Hoher Fläming im Osten, Rudel Coswig im Südosten und Rudel Steckby-Lödderitzer Forst im Südwesten. Diese Lage macht die eindeutige Zuordnung von Spurenfunden sehr schwierig. Die Fähe GW1082f, aus dem Rudel Coswig abstammend, wurde bereits genetisch identifiziert. Die Herkunft des Rüden war noch nicht eindeutig ermittelt. Der überfahrene Welpe stellt bis dato den einzigen Welpennachweis dar. Im Jahr 2020/21 wurden drei Wölfe belegt (vgl. Tab. 6).

Das Territorium Zerbst liegt im südwestlichen Teil des Untersuchungsgebiets. Das Rudel bejagt Teiles des Reviers Nedlitz (vgl. LAU 2020-2021).

Tabelle 6: *Mindest-Individuenanzahl des Territoriums Zerbst, Zeitraum 2020-2021 (Quelle: LAU Sachsen-Anhalt)*

Monitoringjahr	2020/21
Anzahl nachgewiesener Wölfe	4
Anzahl Welpen	0

4.8 Auswertung

Die Anzahl der Rudel im Untersuchungsgebiet ist während des Untersuchungszeitraumes kontinuierlich gestiegen. Oft bestehen zwischen den einzelnen Rudeln verwandtschaftliche Beziehungen. Einige Jungwölfe wandern nicht ab, sondern besetzen mit einem zugewanderten Partner in der Nähe des Herkunftsrudels ein neues Territorium. Außerdem durchstreifen einzelne Jungwölfe aus der Region und von außerhalb regelmäßig das Untersuchungsgebiet.

Eine Sättigung des Lebensraums ist an der Anzahl der durchschnittlich pro Jahr und Rudel nachgewiesenen Welpen zu erkennen (vgl. Abb. 6). Dieser Wert ist im Untersuchungszeitraum deutlich zurückgegangen. In den letzten beiden Jahren wurden im Durchschnitt nur noch etwa zwei Welpen pro Rudel nachgewiesen.

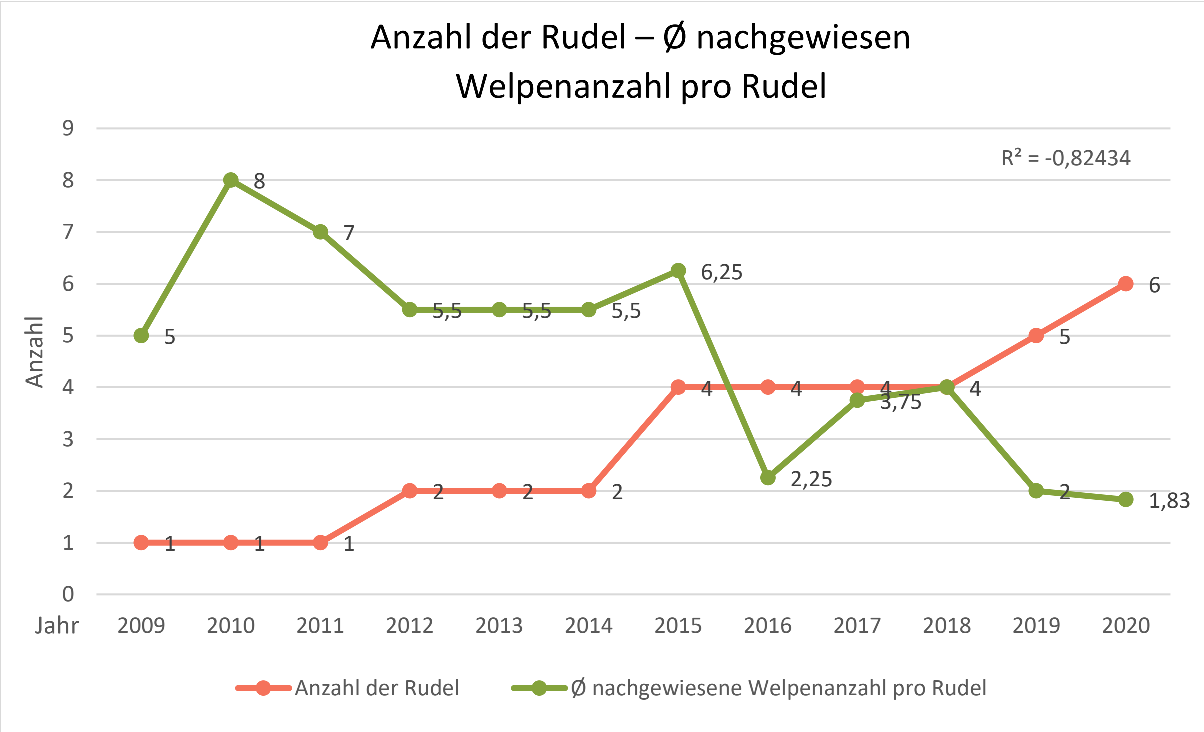

Abbildung 6: *Vergleich Anzahl der Rudel - Ø nachgewiesene Welpenanzahl pro Rudel im Untersuchungsgebiet, Zeitraum 2009-2021 (Quelle: LAU Sachsen-Anhalt)*

Abbildung 7: *Damhirsch im Revier Göritz (Quelle: Heiko Anders)*

5. Auswertung der Abschussergebnisse des Schalenwildes im Untersuchungsgebiet

5.1 Einführung

Der Landesjagdbezirk Fläming des Landesforstbetriebs Sachsen-Anhalt besteht aus den vier Flämingrevieren im Forstbetrieb Anhalt. Er besitzt eine Jagdfläche von insgesamt 12516 Hektar. Seit dem Jagdjahr 2011/2012 existiert eine Aufteilung entsprechend den Landkreisen Wittenberg und Anhalt-Bitterfeld in die Bezirke „Fläming-Ost“ und „Fläming-West“. Die Gesamtfläche der beiden neuen Landesjagdbezirke ist jedoch identisch mit dem Wert des ursprünglichen Landesjagdbezirk „Fläming“. Der Landesjagdbezirk „Fläming-Ost“ besteht aus den Forstrevieren Stackelitz und Göritz und besitzt eine Größe von 6139 Hektar. Der Landesjagdbezirk „Fläming-West“ beinhaltet die Forstreviere Nedlitz und Hoher Fläming und ist 6377 Hektar groß. Zur besseren Vergleichbarkeit in der gesamten Zeitreihe wurden die Daten der Landesjagdbezirke „Fläming-Ost“ und „Fläming-West“ überwiegend zusammengefasst zum Landesjagdbezirk „Fläming“, auch wenn dieser formell nicht mehr existiert.

Die Hauptwildarten im Untersuchungsgebiet sind Damwild, Schwarzwild und Rehwild. Als Wechselwild kommt in einigen Bereichen Rotwild vor. Zu Beginn des Untersuchungszeitraums existierte in einem Teil des Reviers Göritz im Landesjagdbezirk „Fläming-Ost“ eine größere Muffelwildpopulation. Dieses Vorkommen ist jedoch seit ungefähr 5 Jahren erloschen.

Seit den 1960er Jahren bestand im Bereich des heutigen Landesjagdbezirk „Fläming-West“ ein Damwildforschungsgebiet. Daraus entstand eine Damwildpopulation, die zu einer hohen Individuendichte im gesamten Untersuchungsgebiet führte.

5.2 Entwicklung der Abschusszahlen im Landesjagdbezirk Fläming beim Schalenwild insgesamt

Im Durchschnitt der Jagdjahre 2007/2008 bis 2021/22 wurden insgesamt 1507 Stück Schalenwild erlegt. Vom Beginn der Zeitreihe bis zum Jagdjahr 2013/2014 lagen die Abschusszahlen über dem Durchschnittswert. Seitdem wurde weniger Schalenwild geschossen als das durchschnittliche Ergebnis. In den letzten beiden Jagdjahren ist dabei ein deutlicher Rückgang der Abschusszahlen zu verzeichnen.

Die Trendlinie zeigt, dass sich die Streckenergebnisse beim Schalenwild vom Anfang bis zum Ende des Untersuchungszeitraumes halbiert haben (vgl. Abb. 8).

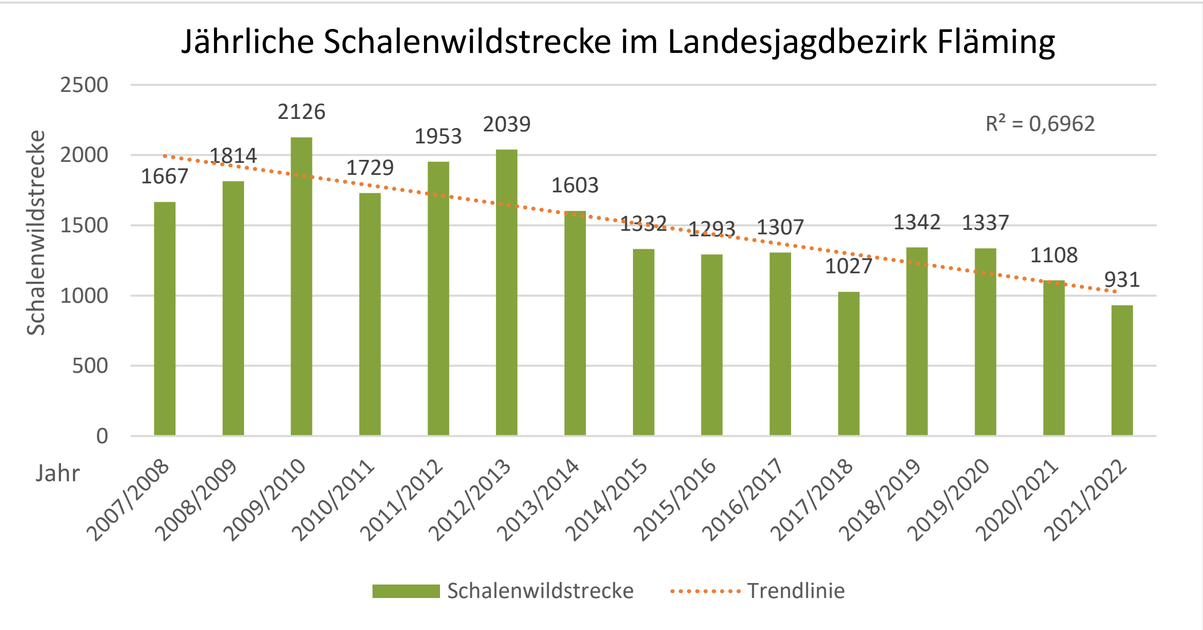

***Abbildung 8:** Jährliche Schalenwildstrecke im Landesjagdbezirk Fläming, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

5.3 Entwicklung der Abschusszahlen beim Rotwild

Die durchschnittliche Rotwildstrecke betrug im Untersuchungszeitraum acht Stück pro Jagdjahr. In den ersten vier Jagdjahren pendelte das Abschussergebnis um diesen Durchschnittswert. In den folgenden drei Jagdjahren stiegen die Abschusszahlen stark an. Seit dem Jagdjahr 2014/2015 wurde weniger als der Durchschnittswert erlegt. In den letzten Jahren ist dabei eine Stabilisierung auf niedrigem Niveau zu verzeichnen.
Anhand der Trendlinie kann man dagegen erkennen, dass über den gesamten Untersuchungszeitraum betrachtet eine deutliche Tendenz zum Rückgang der Jahresstrecken besteht (vgl. Abb. 9).

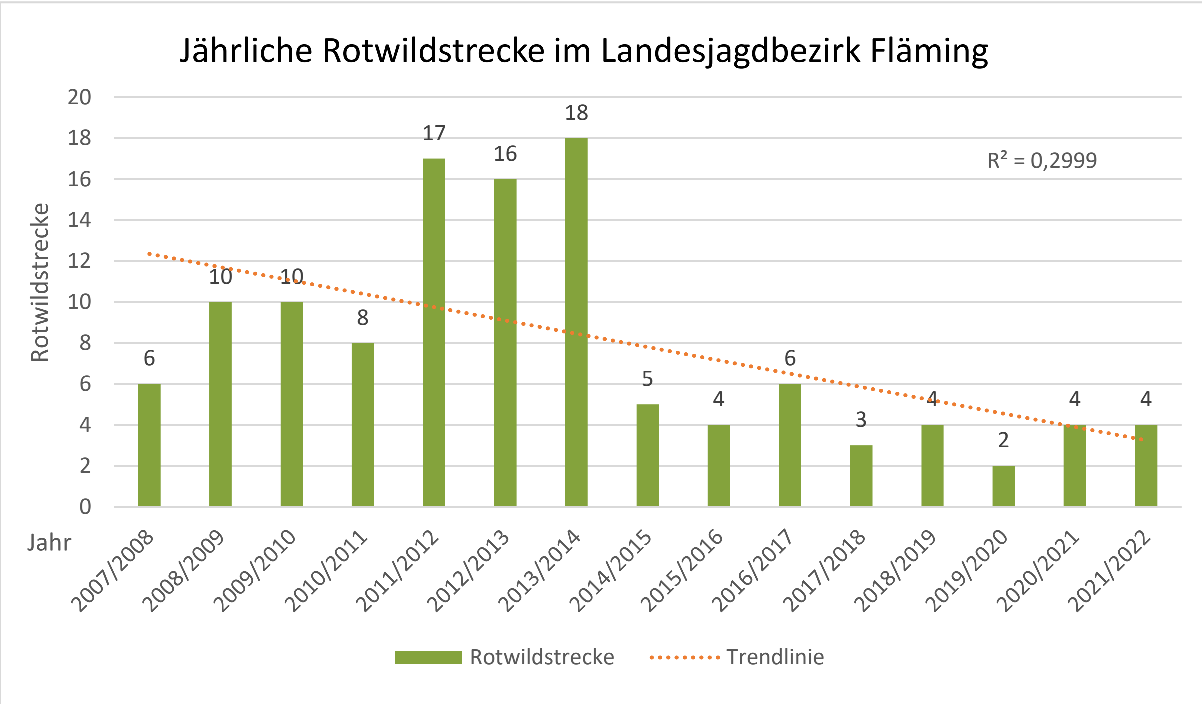

Abbildung 9: *Jährliche Rotwildstrecke im Landesjagdbezirk Fläming, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

5.4 Entwicklung der Abschusszahlen beim Muffelwild

Die durchschnittliche Muffelwildstrecke lag bei sechs Stück pro Jagdjahr. In den ersten vier Jagdjahren war die Strecke stark schwankend. In den darauffolgenden Jahren lag die Strecke über der durchschnittlichen Muffelwildstrecke (vgl. Abb. 10). Ab dem Jagdjahr 2016/2017 wurden keine Tiere mehr erlegt, da die lokale Population erloschen ist.

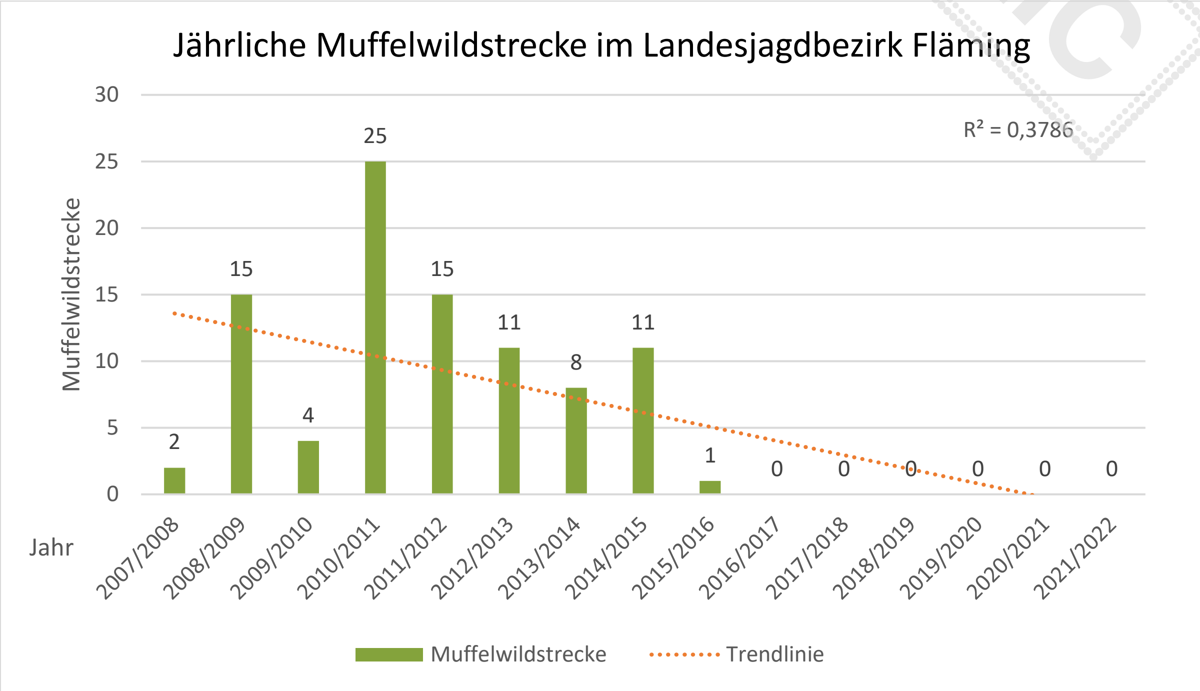

Abbildung 10: *Jährliche Muffelwildstrecke im Landesjagdbezirk Fläming, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

5.5 Entwicklung der Abschusszahlen beim Damwild

Der Mittelwert der jährlichen Damwildstrecke in der untersuchten Zeitreihe betrug 508 Stück. Ausgehend von einem Wert in der Nähe des Durchschnitts im Jagdjahr 2007/2008 lagen die Abschussergebnisse in den folgenden sechs Jahren deutlich darüber (vgl. Abb. 11). Ab dem Jagdjahr 2014/2015 fiel die jährliche Strecke unter den langfristigen Durchschnittswert. Nach sinkenden Werten von 2014/2015 bis 2017/2018 ist seit dem Jagdjahr 2018/2019 ein gleichbleibendes Abschussergebnis mit nur noch leichten Schwankungen festzustellen.

Die Trendlinie verdeutlicht den starken Rückgang der jährlichen Damwildstrecken über den gesamten Untersuchungszeitraum betrachtet.

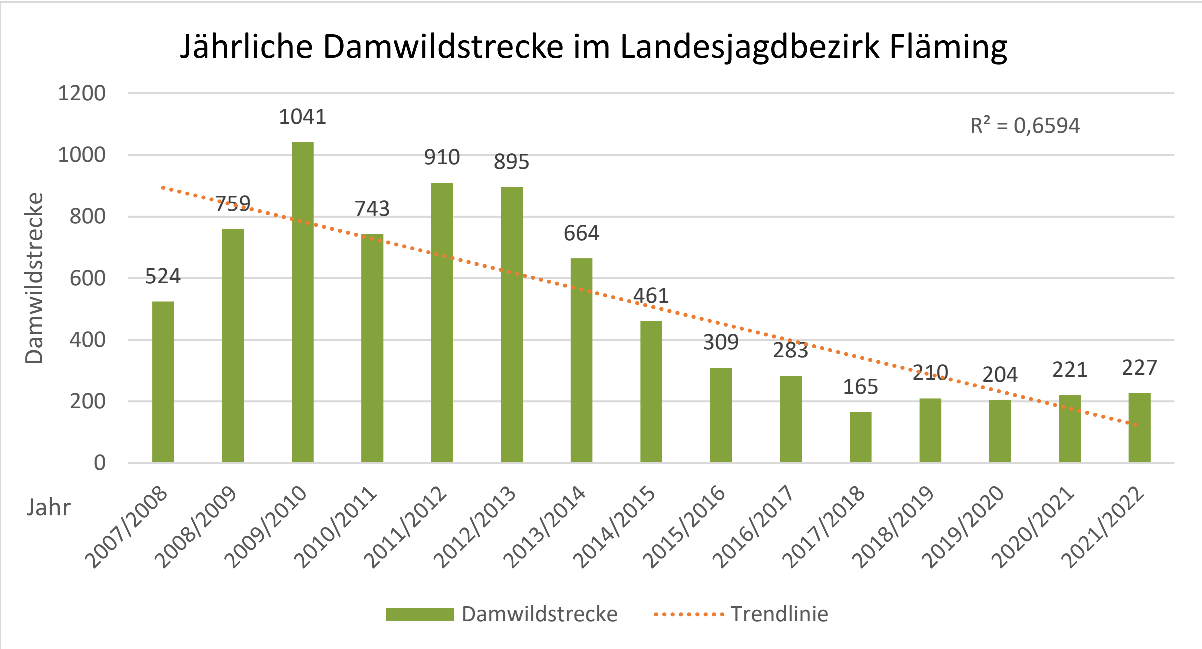

Abbildung 11: *Jährliche Damwildstrecke im Landesjagdbezirk Fläming, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

Auffallend bei der Damwildstrecke ist die unterschiedliche Entwicklung in den Landesjagdbezirken Fläming-Ost und Fläming-West. Im Landesjagdbezirk Fläming-Ost hat sich die jährliche Damwildstrecke seit 2016 auf einen Wert von ungefähr 200 Stück pro Jagdjahr eingependelt (vgl. Abb. 12). Im Landesjagdbezirk Fläming-West ist der Abschuss beim Damwild deutlich stärker zurückgegangen, so dass hier aktuell Damwild nur noch als Wechselwild vorkommt.

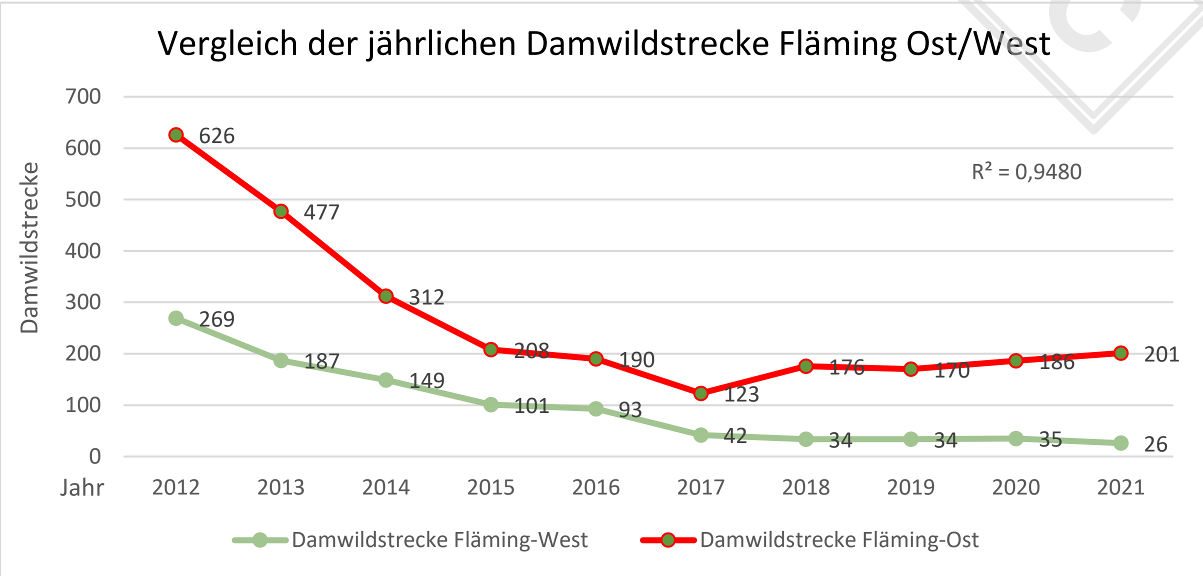

Abbildung 12: *Vergleich Damwildstrecke Fläming Ost/West, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

5.6 Entwicklung der Abschusszahlen beim Rehwild

Die durchschnittliche Jahresstrecke im Untersuchungszeitraum betrug beim Rehwild 546 Stück pro Jagdjahr. Im ersten Jagdjahr lag die Jahresstrecke unter dem Mittelwert. In den folgenden fünf Jagdjahren war eine steigende Tendenz zu verzeichnen. Ab dem Jagdjahr 2013/2014 pendeln sich die Jahresstrecken um den Mittelwert ein, wobei in den letzten drei Jahren eine fallende Tendenz zu verzeichnen ist (vgl. Abb. 13).

Anhand der Trendlinie erkennt man, dass sich im Gegensatz zu den anderen verbeißenden Schalenwildarten die Jahresstrecken beim Rehwild im Untersuchungszeitraum insgesamt nur leicht reduziert haben.

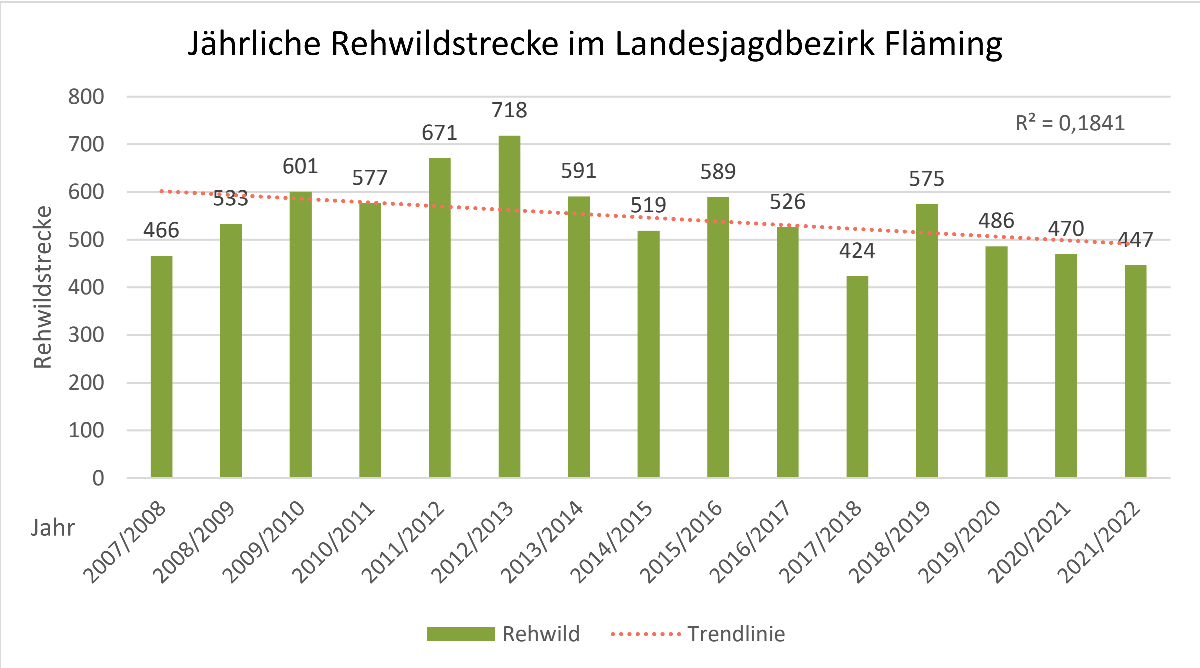

Abbildung 13: *Jährliche Rehwildstrecke im Landesjagdbezirk Fläming, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

5.7 Entwicklung der Abschusszahlen beim Schwarzwild

Die durchschnittliche Schwarzwildstrecke im Untersuchungszeitraum betrug 439 Stück pro Jagdjahr. In den ersten fünf Jagdjahren nahm die Jahresstrecke deutlich ab. Ab dem Jagdjahr 2014/2015 nahm die Schwarzwildstrecke wieder zu (vgl. Abb. 14). In den letzten zwei Jagdjahren ist ein sehr starker Abfall der Jahresstrecke zu erkennen.

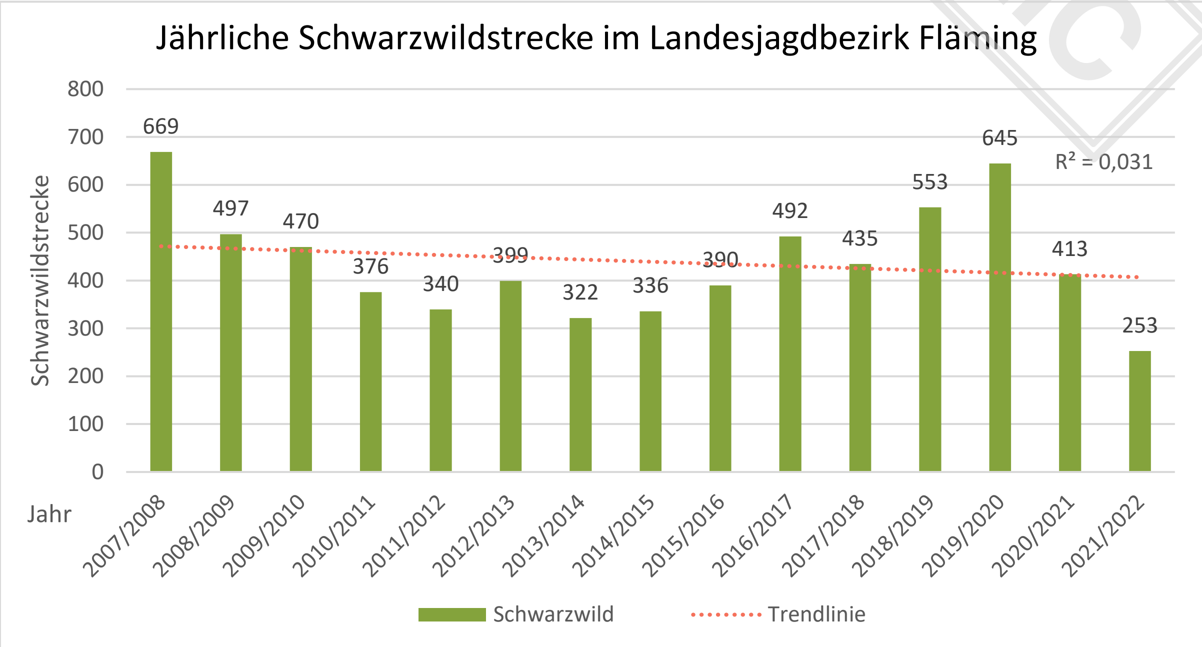

Abbildung 14: *Jährliche Schwarzwildstrecke im Landesjagdbezirk Fläming, Zeitraum 2007-2022 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

5.8 Diskussion der Schalenwildstreckenentwicklung

Bei den Wildarten Rotwild und Damwild sind die jährlichen Abschusszahlen im Untersuchungszeitraum deutlich zurückgegangen.

Die lokale Muffelwildpopulation ist im Untersuchungsgebiet seit 2017 erloschen.

Die Rehwildstrecke ist bei leichten Schwankungen relativ stabil geblieben, wobei in den letzten Jagdjahren eine leicht sinkende Tendenz zu verzeichnen ist.

Die Schwarzwildpopulation im Untersuchungsgebiet zeigt ausgeprägte Schwankungen, da sie sehr stark von natürlichen Faktoren wie strengen Wintern und regelmäßigen Eichel- und Bucheckernmasten abhängig ist. Die in den letzten beiden Jagdjahren wegen der Ausbreitung der afrikanischen Schweinepest getroffenen Vorkehrungen wie die Einführung von Abschussprämien und die Erlaubnis zur Verwendung von Nachtsichttechnik haben zu einer deutlichen Reduzierung der Schwarzwildpopulation geführt.

6. Entwicklung der Verbissschäden, der Pflanzenanzahl und des Anteils gezäunter Kulturen im Untersuchungsgebiet von 2008 bis 2021

6.1 Einführung

Die Entwicklung der Verbissschäden im Landesjagdbezirk „Fläming“ wird mit Hilfe der Ergebnisse des Kulturqualitätsmanagements (KQM) des Landesforstbetriebs Sachsen-Anhalt dargestellt. Das waldbauliche Kulturqualitätsmanagement dient zur Qualitätsüberprüfung der getätigten Aufforstungen im Landeswald und zur Dokumentation von Schäden durch Wildverbiss.

Die Kontrolle der Aufforstungen wird im Abstand von vier beziehungsweise fünf Jahren durchgeführt. Dabei werden zunächst die vier- bis sechsjährigen (oder vier- bis siebenjährigen) Aufforstungen durch die Revierleiter und externe Dienstleister überprüft und dokumentiert. Es erfolgt eine Aufnahme der Pflanzenzahlen und Pflanzenhöhen je Baumart sowie eine Erfassung der Verbissschäden pro Baumart. Abschließend schätzt der Erfasser nach den Kriterien Pflanzenzahl, Verbissschäden, Mindesthöhe und Vitalität der Hauptbaumarten ein, ob die Kultur „gesichert“ oder „ungesichert“ ist. Pro Aufforstungsfläche wird dabei ein Erfassungsbeleg erstellt und anschließend durch die Betriebsleitung digitalisiert. Damit sind umfangreiche Auswertungen nach Revier, Forstbetrieb, Baumart und so weiter möglich.

Das waldbauliche Kulturqualitätsmanagement (KQM) wurde im Untersuchungsgebiet in den Jahren 2008, 2012, 2016 und 2021 durchgeführt. Die Erfassung und Auswertung der Daten erfolgte revierweise. Auf Grund der unterschiedlichen Anzahl und Größe der Flächen pro Revier ist die Ermittlung von statistischen Durchschnittswerten für das gesamte Untersuchungsgebiet nicht möglich. Deshalb werden die Ergebnisse des KQM für die vier Flämingreviere getrennt dargestellt.

Bei der Auswertung der prozentualen Verbissschäden in den Flämingrevieren ist zu beachten, dass die einzelnen Baumarten unterschiedlich stark verbissen werden und die Baumartenverteilung bei der Aufforstung in jedem Jahr variiert. Außerdem ist es für die Verbissschäden von großer Bedeutung, ob die Kultur gezäunt ist. Die ermittelten Verbissprozente sind also relative Werte, die aber ausreichen, um bestimmte Tendenzen aufzuzeigen.

Die Entwicklung der Pflanzenzahlen zeigt auf, wie sich die aufgeforstete Kultur mit Naturverjüngung angereichert hat. Die Naturverjüngung besteht dabei oft nicht aus den ursprünglich gepflanzten Baumarten. Also zu einer Eichen-Hainbuchen-Kultur mischt sich dann Naturverjüngung aus Birke, Kiefer und Aspe bei und alle Pflanzen werden bei der Erfassung baumartenweise gezählt. Nicht erfasst werden lediglich die Baumarten ohne wirtschaftliche Bedeutung wie zum Beispiel Eberesche und Spätblühende Traubenkirsche. Der Anteil gezäunter Kulturflächen an der gesamten Aufforstungsfläche ist abhängig von den verwendeten Baumarten sowie vom aktuellen Verbissdruck. Werden also verstärkt Baumarten mit einer geringen Verbissgefährdung wie zum Beispiel Kiefer gepflanzt, dann sinkt der Anteil gezäunter Kulturflächen automatisch.

6.2 Kulturqualitätsmanagementergebnisse im Revier Stackelitz

Der durchschnittliche Verbiss im Revier Stackelitz lag 2008 und 2012 jeweils bei ungefähr 20%. Bei der Erfassung 2016 war ein starker Rückgang der Verbissschäden auf ungefähr 2% zu verzeichnen (vgl. Abb. 15). Ein ähnlicher Wert wurde auch 2021 ermittelt.

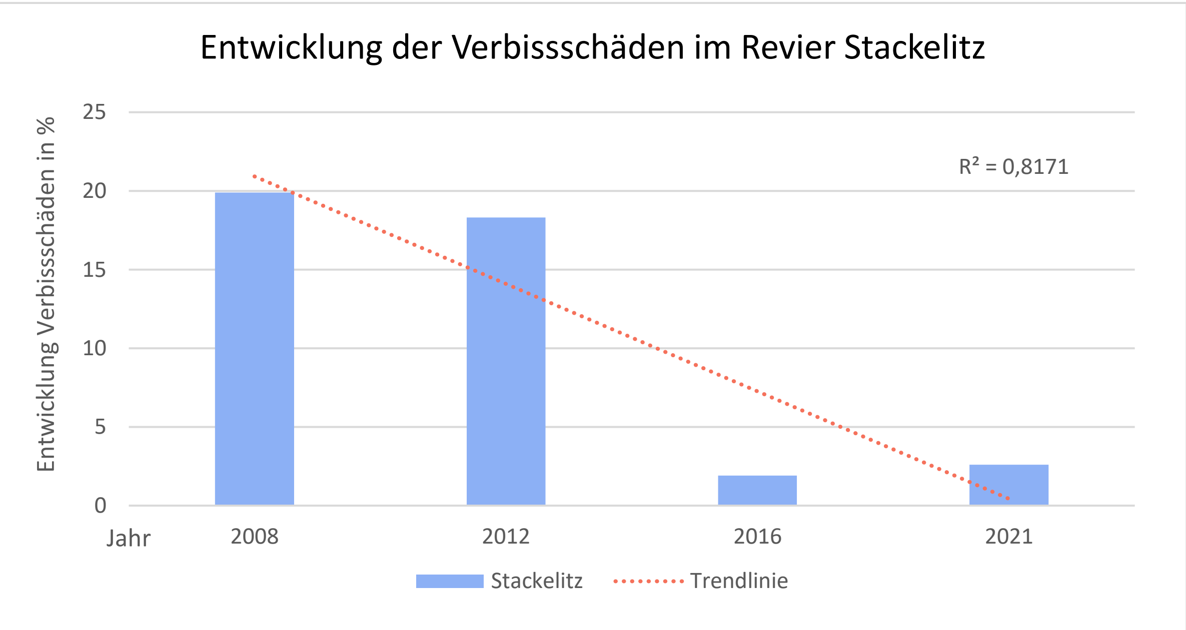

Abbildung 15: *Entwicklung der Verbissschäden im Revier Stackelitz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

Die Anzahl der Pflanzen auf den Kulturen ist durch die Anreicherung der Aufforstung mit Naturverjüngung von 2012 bis 2016 leicht angestiegen. Bei der

Kulturqualitätsmanagementerfassung 2021 hat sich dieser Wert verdoppelt (vgl. Abb. 16). Damit beträgt die aktuelle Pflanzenzahl auf den Kulturen des Reviers Stackelitz durch die Anreicherung der Aufforstung mit Naturverjüngung fast das Dreifache der ursprünglichen Pflanzenmenge.

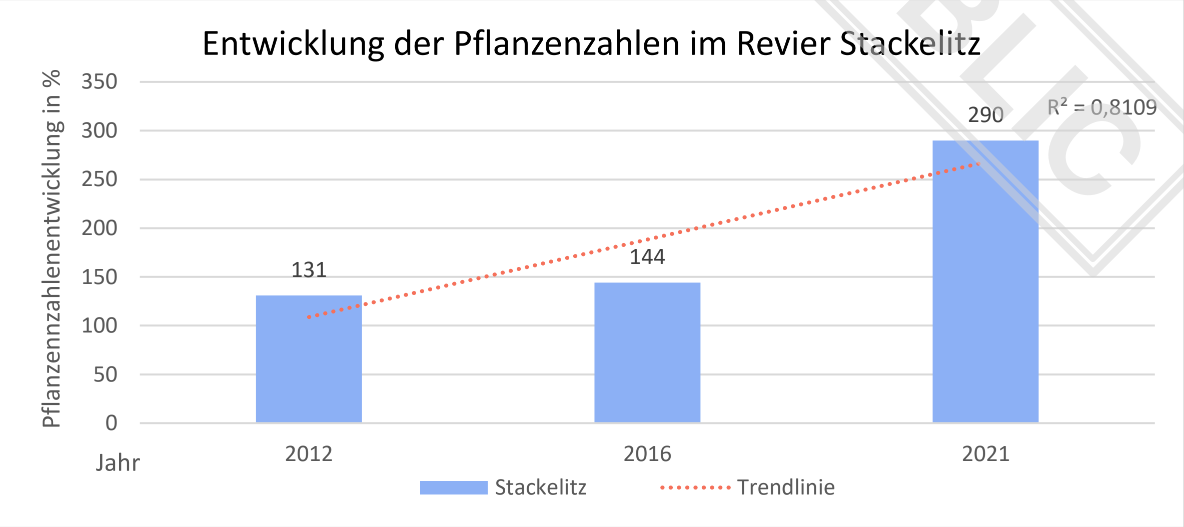

Abbildung 16: *Entwicklung der Pflanzenzahlen im Revier Stackelitz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

Der Anteil der gezäunten Kulturflächen an der gesamten Aufforstungsfläche betrug zunächst 68%. Nach einem ähnlichen Wert im Jahr 2012 gab es 2016 eine deutliche Reduzierung auf 22% (vgl. Abb. 17). Bei der Kulturqualitätsmanagementerfassung im Jahr 2021 war der Wert wieder leicht angestiegen auf 34%.

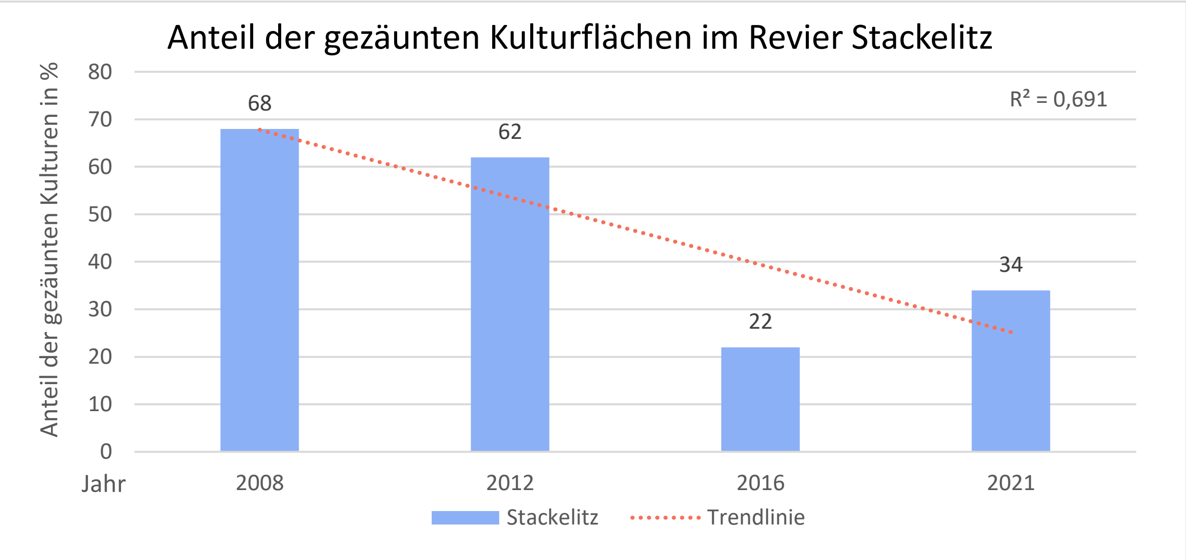

Abbildung 17: *Anteil der gezäunzten Kulturflächen im Revier Stackelitz, 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

6.3 Kulturqualitätsmanagementergebnisse im Revier Nedlitz

Der durchschnittliche Verbissprozent im Revier Nedlitz betrug 2008 etwa 29% (vgl. Abb. 18). Bei den Aufnahmen im Jahr 2012 ist ein klarer Rückgang der verbissenen Pflanzen auf ungefähr 1% zu verzeichnen. Dieser Trend setzte sich ebenso bei den Kulturqualitätsmanagementerfassungen in den Jahren 2016 und 2021 fort.

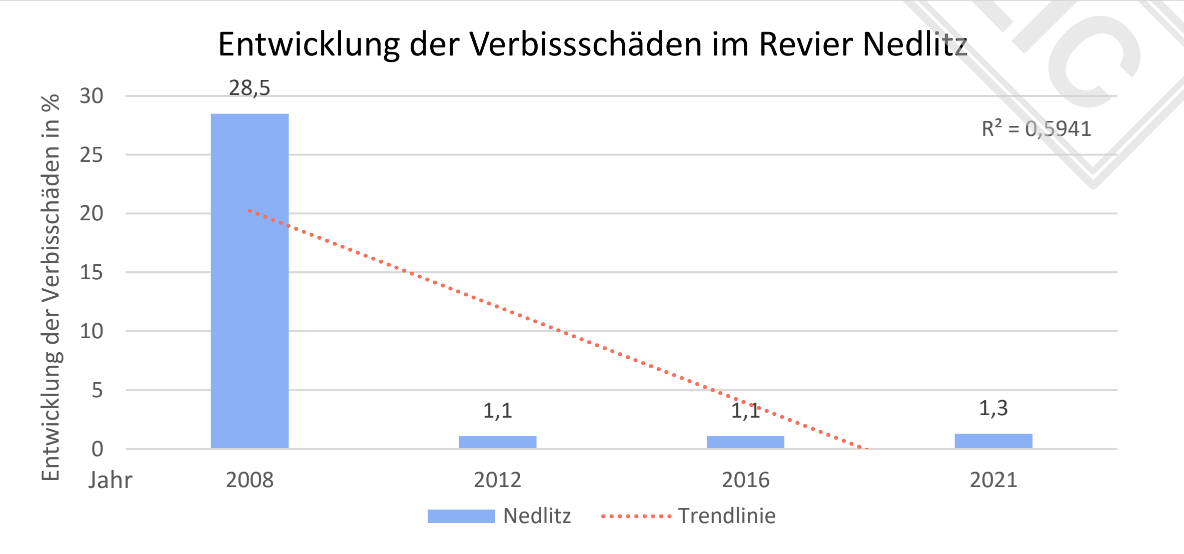

Abbildung 18: Entwicklung der Verbissschäden im Revier Nedlitz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)

Die Entwicklung der Pflanzenzahlen auf den Kulturen im Revier Nedlitz lag bei den Aufnahmen im Jahr 2012 bei 198%. Dieser Wert stieg bei der Datenerfassung im Jahr 2016 auf 294% an, worauf im Folgejahr ein ähnlicher Wert ermittelt wurde (vgl. Abb. 19).

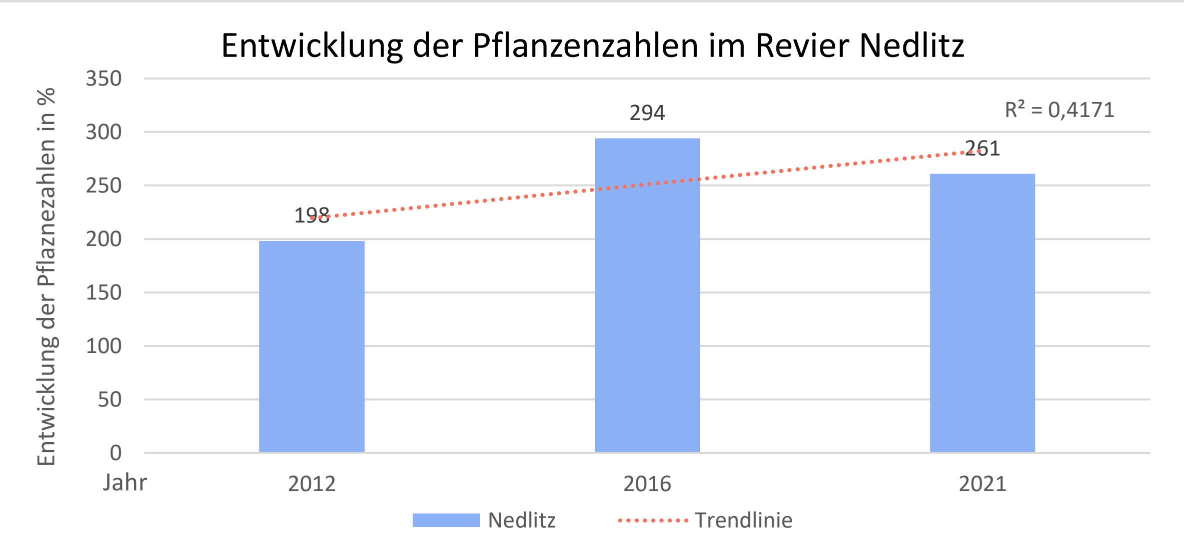

Abbildung 19: Entwicklung der Pflanzenzahlen im Revier Nedlitz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)

Im Revier Nedlitz lag der prozentuale Anteil der gezäunten Kulturfläche an der gesamten Aufforstungsfläche im Jahr 2008 bei 72%. Bereits bei den Aufnahmen im Jahr 2012 war ein deutlicher Rückgang auf 28 % zu verzeichnen (vgl. Abb. 20). Nach einem leichten Anstieg bei der Kontrolle 2016 gab es im Jahr 2021 noch einmal einen deutlichen Rückgang auf 14%.

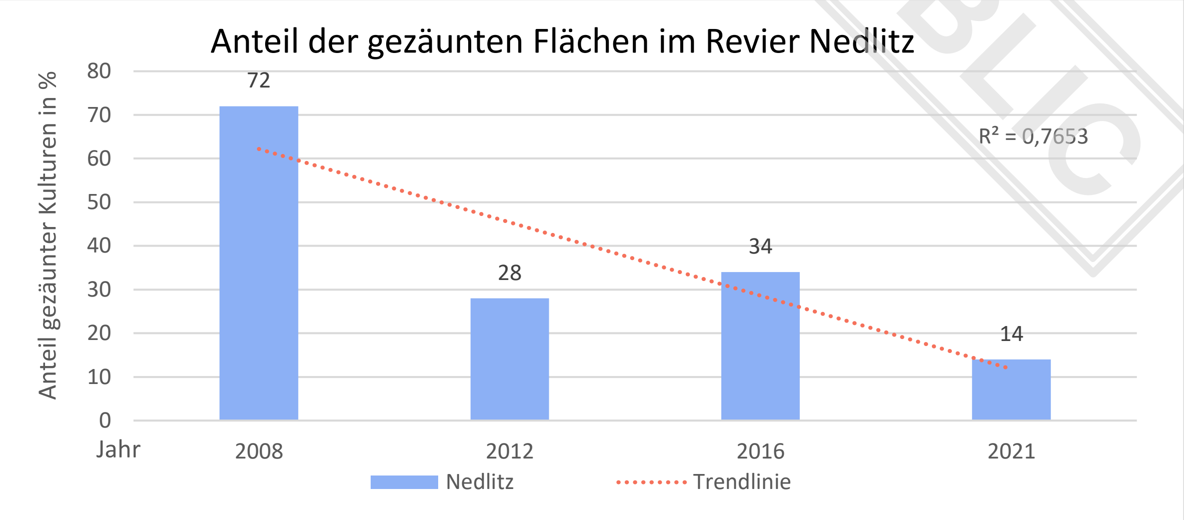

Abbildung 20: *Anteil der gezäunten Flächen im Revier Nedlitz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

6.4 Kulturqualitätsmanagementergebnisse im Revier Hoher Fläming

Lag der durchschnittliche Verbissprozent im Jahr 2008 noch bei circa 14%, so reduzierte sich dieser bei der folgenden Datenerfassung auf knapp 2% (vgl. Abb. 21). Dieser Trend setzte sich auch bei den Aufnahmen in den Jahren 2016 und 2021 fort, wo die durchschnittlichen Verbissprozente bei circa 1% lagen.

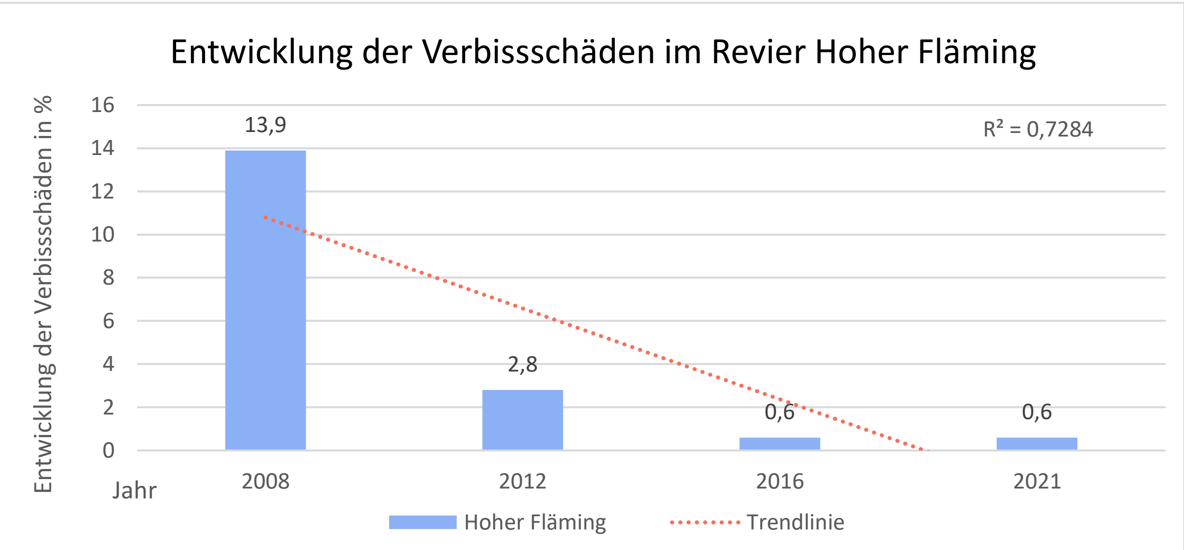

Abbildung 21: *Entwicklung der Verbissschäden im Revier Hoher Fläming, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

Die Entwicklung der Pflanzenzahlen im Revier Hoher Fläming zeigt einen stetigen Anstieg über den Zeitraum der Aufnahmen. Im Jahr 2012 war die Pflanzenzahl bereits leicht gestiegen. In den Folgejahren konnte sich die Pflanzenzahl auf 225% vom Ausgangswert steigern (vgl. Abb. 22).

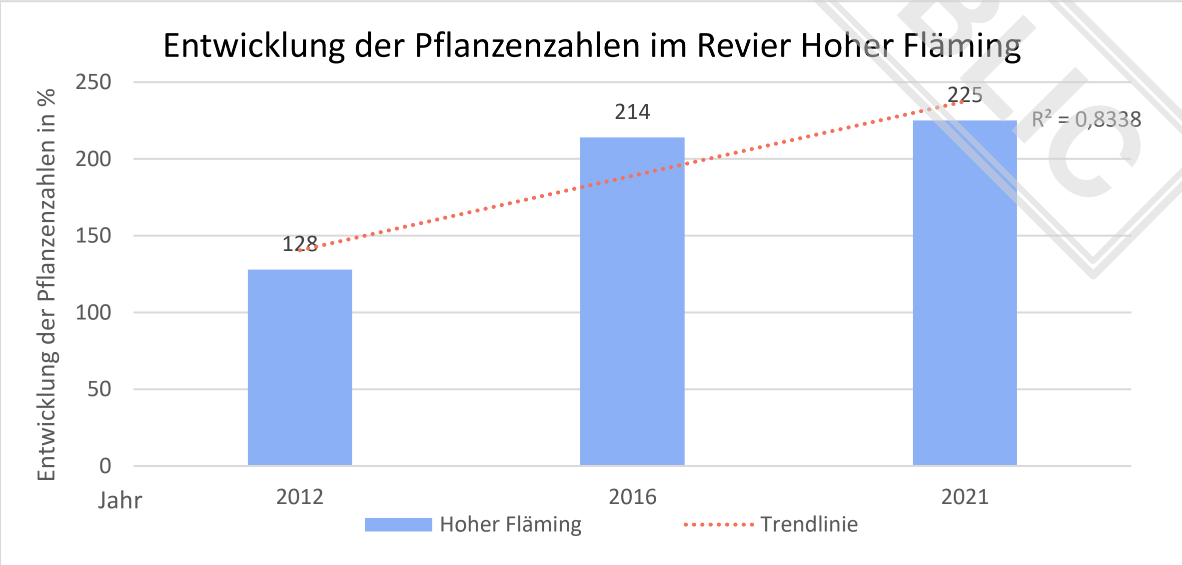

Abbildung 22: *Entwicklung der Pflanzenzahlen im Revier Hoher Fläming, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

Der Anteil der gezäunten Kulturflächen an der gesamten Aufforstungsfläche lag zunächst bei 60% (vgl. Abb. 23). Bei den folgenden Aufnahmen machte sich eine Absenkung auf 23% deutlich bemerkbar. Stieg dieser Wert im Jahr 2016 wieder auf 56% an, so sank er im Jahr 2021 erneut deutlich auf 14%.

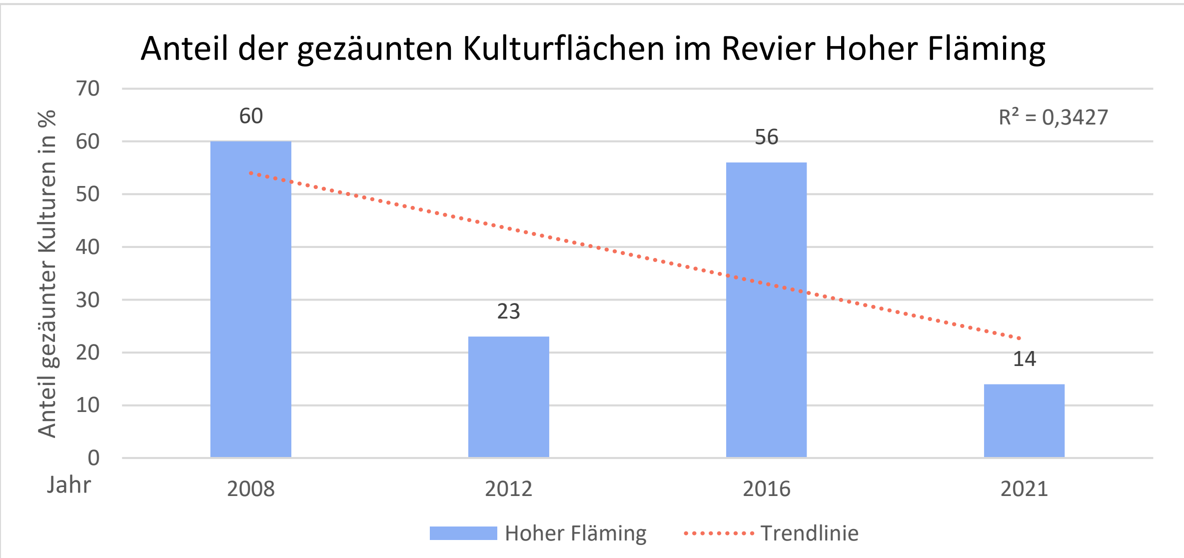

Abbildung 23: *Anteil der gezäunten Kulturflächen im Revier Hoher Fläming, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

6.5 Kulturqualitätsmanagementergebnisse im Revier Göritz

Der durchschnittliche Verbissprozent im Revier Göritz lag im Jahr 2008 bei 9,7%. Die Datenerfassung aus dem Jahr 2012 zeigt einen verringerten Verbissdruck mit etwa 4% Verbissprozent (vgl. Abb. 24). Ein weiterer Rückgang ist auch bei den Erfassungen 2016 und 2021 deutlich zu verzeichnen.

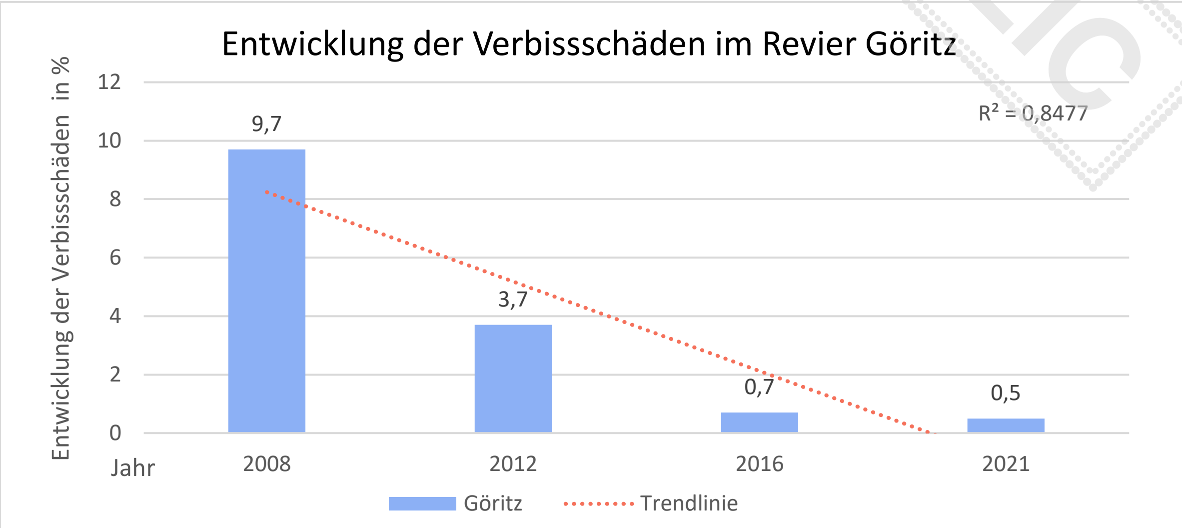

Abbildung 24: *Entwicklung der Verbissschäden im Revier Göritz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

Die Entwicklung der Pflanzenzahlen auf den Kulturen zeigt eine starke Anreicherung der Kulturen mit Naturverjüngung. Dieser Wert stieg von 2012 bis 2016 auf 310% an (vgl. Abb. 25). Bei den letzten Kulturqualitätsmanagementaufnahmen ergab sich eine Entwicklung auf 775%.

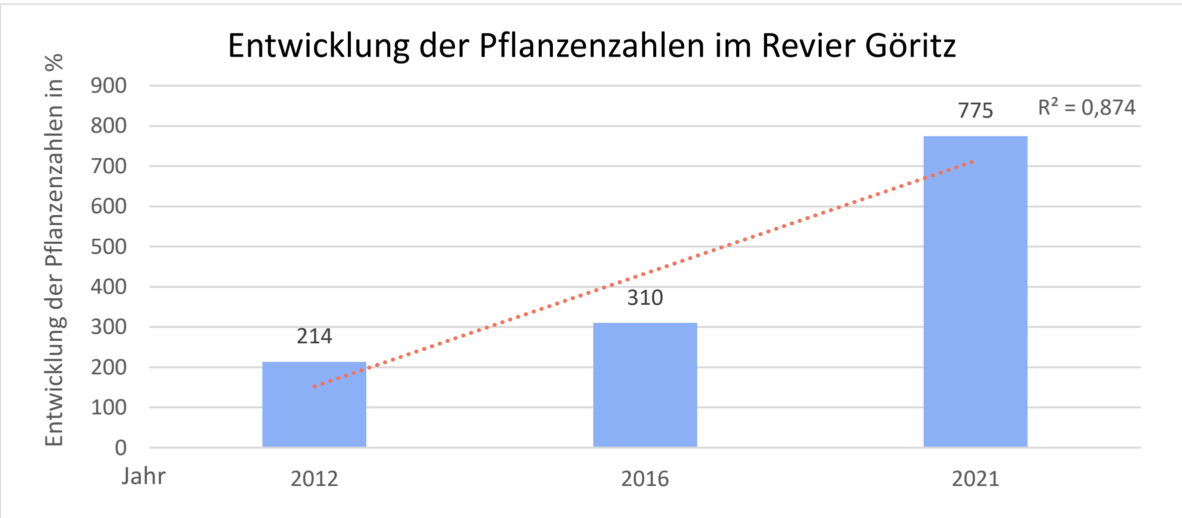

Abbildung 25: *Entwicklung der Pflanzenzahlen im Revier Göritz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

Die gezäunten Kulturflächen machten im Jahr 2008 92% der gesamten Aufforstungsfläche aus (vgl. Abb. 26). Dieser Wert blieb auch bei den Aufnahmen 2012 und 2016 ähnlich. Im Jahr 2021 ist die Anzahl der gezäunten Kulturflächen auf 18% gesunken.

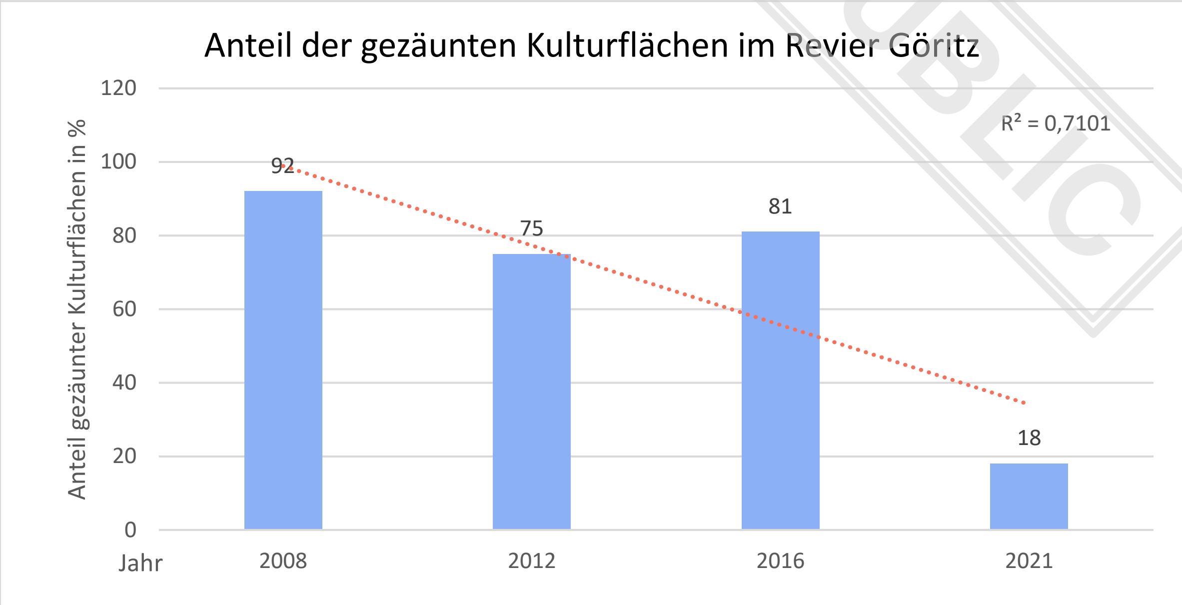

***Abbildung 26:** Anteil der gezäunten Kulturflächen im Revier Göritz, Zeitraum 2008-2021, Kulturqualitätsmanagement (Quelle: SG Waldbau/Forsteinrichtung J. Köhler)*

6.6 Diskussion der Ergebnisse der Kulturqualitätsmanagement-Erfassung

Abbildung 27: *Buchen-Douglasien-Jungbestand unter Altkiefern im Revier Göritz (Quelle: Nils Schumann)*

Die Verbissschäden auf den Kulturen haben sich im Untersuchungszeitraum in allen vier Forstrevieren deutlich reduziert und auf niedrigem Niveau stabilisiert. Während der starke Rückgang in den westlichen Revieren im Zeitraum 2008 bis 2012 erfolgte, war die deutliche Reduzierung der Schäden in den östlichen Revieren erst im Zeitraum 2012 bis 2016 zu verzeichnen.
Ähnlich verhält es sich mit der Entwicklung der Pflanzenzahlen auf den Kulturen und dem Anteil der gezäunten Flächen an der gesamten Aufforstungsfläche. Als indirekte Folge der stark sinkenden Verbissschäden sind die Pflanzenzahlen auf den Kulturen in allen vier Revieren kontinuierlich gestiegen. Gleichzeitig ist der Anteil der Aufforstungsflächen, die durch einen Zaun geschützt werden müssen, im Untersuchungszeitraum in allen Revieren gesunken. Damit kann man feststellen, dass sich die Bedingungen für die erfolgreiche Etablierung von Kulturen im Untersuchungszeitraum deutlich verbessert haben. Neben der Verringerung der Kosten für Zaunbau, Zaunkontrollen, Zaunreperatur und Zaunabriss sowie für Nachbesserung und Wiederholung von Kulturen ist eine erhebliche Verbesserung der waldbaulichen Situation im Untersuchungsgebiet zu verzeichnen.

7. Zusammenhänge zwischen den Entwicklungen der Wolfspopulation, der Entwicklung der Schalenwildpopulation und dem Zustand der Kulturen im Untersuchungsgebiet

Die Anzahl der Wolfsrudel und damit die Populationsdichte der Wölfe haben im Untersuchungszeitraum kontinuierlich zugenommen (vgl. Abb. 28). Gleichzeitig reduzierten sich die Streckenergebnisse beim Schalenwild in diesem Zeitabschnitt. Für einen daraus abzuleitenden Rückgang der Schalenwildpopulation im Untersuchungsgebiet spricht auch die deutliche Reduzierung der Verbissschäden auf den Kulturen sowie die Entwicklung weiterer Parameter aus der Kulturqualitätsmanagementerfassung. Es besteht also ein direkter Zusammenhang zwischen der Zunahme der Wolfspopulation, einer sinkenden Schalenwildpopulation und der Reduzierung der Verbissschäden auf den Kulturen.

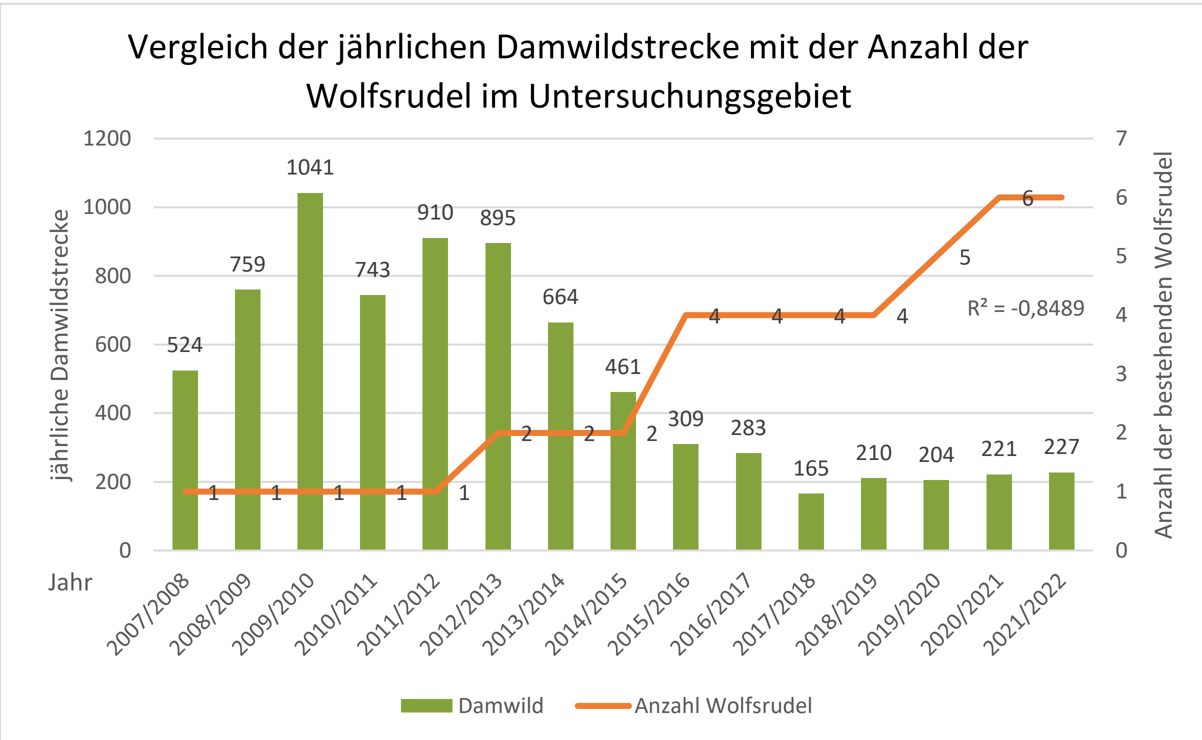

Abbildung 28: *Vergleich der jährlichen Damwildstrecke mit der Anzahl der Wolfsrudel im Untersuchungsgebiet, Zeitraum 2007-2021 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt, LAU Sachsen-Anhalt)*

Am Beispiel des Damwildes, einer Hauptwildart im Untersuchungsgebiet, erkennt man gut den Zusammenhang zwischen Wolfspopulation, Damwildpopulation und Verbissschäden auf den Kulturen. In den Revieren Nedlitz und Hoher Fläming wirkte sich schon zu Beginn des Untersuchungszeitraums die Anwesenheit des Rudels Altengrabow aus. Im Jagdjahr 2012/2013 betrug die Damwildstrecke hier nur noch circa 43% des Wertes der Reviere Stackelitz und Göritz, obwohl zu Beginn der Zeitreihe die Werte in beiden Teilen des Untersuchungsgebietes etwa gleich hoch waren (vgl. Abb. 29). Dementsprechend waren die Verbissschäden im Revier Nedlitz und Hoher Fläming bei der Kulturqualitätsmanagementaufnahme 2012 schon sehr stark zurückgegangen. Eine deutliche Reduzierung der Damwildstrecke und der Verbissschäden war in den Revieren Stackelitz und Göritz erst im Zeitraum 2012 bis 2016 zu verzeichnen, zeitgleich mit der Entstehung des Rudels Göritz-Klepzig.

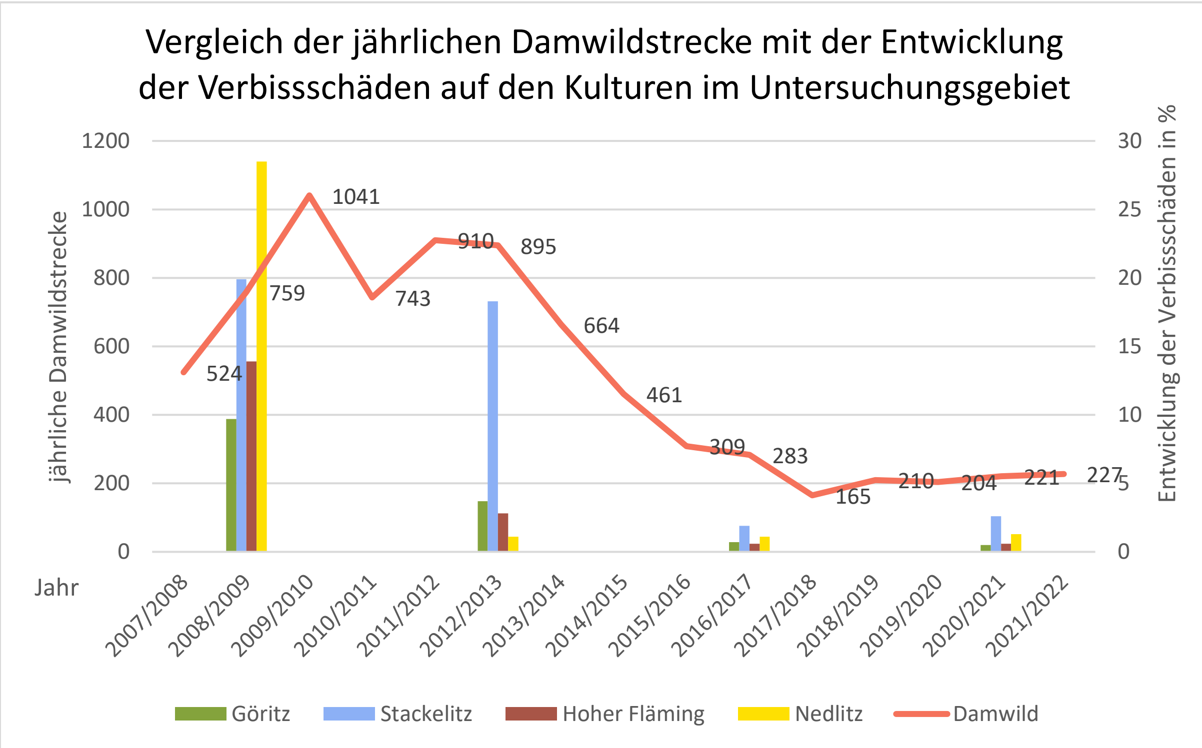

Abbildung 29: *Vergleich der jährlichen Damwildstrecke mit der Entwicklung der Verbissschäden auf den Kulturen im Untersuchungsgebiet, Zeitraum 2007-2021 (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt, SG Waldbau/Forsteinrichtung J. Köhler)*

8. Fehlerdiskussion

Die Aussagen zur Entwicklung der Wilddichte im Untersuchungsgebiet basieren auf den jährlichen Streckenergebnissen der vier Flämingreviere. Es wird angenommen, dass die Abschussergebnisse die tatsächliche Größe der Schalenwildpopulation widerspiegeln. Das bedeutet, je mehr Wild vorhanden ist, umso größer ist die Jagdstrecke. Änderungen in der Wilddichte bewirken veränderte Abschusszahlen, wenn man von gleichbleibendem Jagddruck ausgeht. Nach Aussagen einiger Revierleiter wurde jedoch die Intensität der Bejagung in den ersten Jahren des Untersuchungszeitraumes deutlich erhöht. So fanden u. a. verstärkt Bewegungsjagden mit Stöberhunden in den Revieren statt. Außerdem erfolgt seitdem ein intensiver Gästejagdbetrieb und für die örtlichen Jäger im Landesforstbetrieb wurde eine Art Prämiensystem nach persönlicher Jagdstrecke eingeführt. Deshalb kann man davon ausgehen, dass die steigenden Abschusszahlen zu Beginn des Untersuchungszeitraumes nicht auf wachsenden Wilddichten basieren, sondern durch den verstärkten Jagddruck entstanden sind. Im weiteren Verlauf des Untersuchungszeitraumes sinken die Jagdstrecken kontinuierlich. Da die Intensität der Bejagung nicht nachgelassen hat, kann man jetzt von einer sinkenden Schalenwilddichte im Untersuchungsgebiet ausgehen.

Neben der Bejagungsintensität und dem Beutegreifer Wolf bestehen noch weitere Einflussfaktoren auf die Wilddichte. Zu nennen sind hier vor allem Wildkrankheiten wie die Blauzungenkrankheit beim Damwild und die Aujeszkysche Krankheit beim Schwarzwild. Die Blauzungenkrankheit trat im Untersuchungsgebiet nur über einen kurzen Zeitraum von ein bis zwei Jahren vor Beginn der Zeitreihe auf. In den Jahren 2003 und 2004 wurde im Untersuchungsgebiet regelmäßig an Blauzungenkrankheit verendetes Damwild gefunden. Der Schwerpunkt lag dabei im Revier Nedlitz. Seit Beginn des Untersuchungszeitraumes wurden keine Fälle der Blauzungenkrankheit in der Region festgestellt, sodass ein Einfluss der Krankheit auf die Damwildpopulation in diesem Zeitraum unwahrscheinlich ist.

Die Aujeszkysche Krankheit (Pseudowut) wird durch ein Herpesvirus hervorgerufen und kann fast alle Säugetiere befallen. Der Hauptwirt sind jedoch Schweine. Frischlinge verenden, wenn sie bei der Infektion jünger als vier Wochen sind. Sind die Wildschweine schon älter als vier Wochen, so überleben sie die Infektion normalerweise, tragen das Virus jedoch lebenslang im Körper (Urbach 2020: 619). Im Untersuchungsgebiet ist die Pseudowut in der Schwarzwildpopulation seit Anfang des Untersuchungszeitraumes vorhanden. Bei den

durchgeführten Untersuchungen der Veterinärämter an erlegten Wildschweinen wurden regelmäßig Antikörper auf die Aujeszkysche Krankheit nachgewiesen. Nach mündlicher Mitteilung von Revierleiter Tobias Weke von der Forstverwaltung Hohenlohe, die unmittelbar an das Untersuchungsgebiet angrenzt, haben die Nachweise von Pseudowut in seinem Betrieb stetig zugenommen. Im letzten Jahr waren nach seiner Aussage bei 25 untersuchten Wildschweinen 23 Proben positiv auf Pseudowut getestet, also 92% der beprobten Stücke hatten entsprechende Antikörper ausgebildet. Bei dieser Durchseuchung der Schwarzwildpopulation im Fläming mit dem Aujeszkyvirus kann man von einer hohen Ansteckungsrate bei Frischlingen in den ersten vier Lebenswochen und einer entsprechend hohen Mortalität ausgehen. Die Pseudowut hat also vermutlich einen Einfluss auf die Größe der Schwarzwildpopulation im Untersuchungsgebiet. Die Höhe des Einflusses lässt sich jedoch im Rahmen dieser Arbeit nicht genau feststellen.
Es ist außerdem zu vermuten, dass sich die Pseudowutdurchseuchung der Schwarzwildpopulation im Untersuchungsgebiet auch auf die Wolfspopulation auswirkt. Nach einer Infektion durch die Aufnahme von erbeuteten Wildschweinen erkranken auch Wölfe an der Pseudowut. Dabei ist von einer hohen Mortalität der infizierten Wölfe unabhängig von ihrem Alter auszugehen (vgl. DBBW).
Das Kulturqualitätsmanagement (KQM) im Landesforstbetrieb Sachsen-Anhalt basiert auf einem Stichprobenverfahren. Auf allen Kulturflächen werden Probekreise ausgewählt und die hier ermittelten Daten werden auf die gesamte Fläche hochgerechnet. Dadurch kann es eventuell zu leichten Abweichungen der Ergebnisse vom realen Zustand auf den Flächen kommen. Außerdem variiert die Anzahl und Größe der Kulturflächen in den Revieren in den Untersuchungszeiträumen, sodass die errechneten Durchschnittswerte nicht immer absolut vergleichbar sein können. Die Baumartenzusammensetzung auf den Aufforstungsflächen ist in jedem Jahr anders und die einzelnen Baumarten werden unterschiedlich stark verbissen. Veränderungen in den Verbissprozenten während der Zeitreihe können daher teilweise auch auf eine veränderte Baumartenzusammensetzung zurückzuführen sein.
Abschließend soll noch die Frage diskutiert werden, wie sich die Jahresstrecken beim Schalenwild außerhalb des Untersuchungsgebietes im Vergleich zum Landesjagdbezirk Fläming verändert haben. Auf der Grundlage der vom Landesverwaltungsamt Sachsen-Anhalt aktuell veröffentlichten Zahlen der Oberen Jagdbehörde wird die Entwicklung der Streckenergebnisse in Sachsen-Anhalt von 2011 bis 2021 mit den Werten im

Untersuchungsgebiet im gleichen Zeitraum verglichen.

In Sachsen-Anhalt haben die Jahresstrecken in den letzten zehn Jahren beim Rotwild, Damwild und Rehwild eine leicht rückläufige Tendenz. Das Abschussergebniss beim Muffelwild ist dagegen deutlich zurückgegangen. Die Jahresstrecken beim Schwarzwild sind im Zehn-Jahres-Vergleich leicht angestiegen (vgl. Tab. 7).

Tabelle 7: *Streckendaten der Schalenwildarten in Sachsen-Anhalt, Zeitraum 2011-2021, (Quelle: Landesverwaltungsamt Sachsen-Anhalt Obere Jagdbehörde)*

Wildart	Rotwild	Damwild	Muffelwild	Rehwild	Schwarzwild
LSA Jahresstrecke 2011 in Stück	5178	5075	729	48118	26801
LSA Jahresstrecke 2021 in Stück	4734	4214	306	42656	32430

Im Untersuchungsgebiet sind die Rückgänge der Jahresstrecken in diesem Zeitraum beim Rotwild, Damwild und Muffelwild deutlich stärker ausgefallen. Auch beim Rehwild sind die Rückgänge der Jahresstrecken etwas stärker. Beim Schwarzwild sind die Jahresstrecken im Land Sachsen-Anhalt von 2011 bis 2021 leicht angestiegen. Im Untersuchungsgebiet sind die Wildschweinstrecken in diesem Zeitraum dagegen leicht zurückgegangen. Dabei ist zu erwähnen, dass es sowohl landesweit als auch im Landesjagdbezirk Fläming bei dieser Wildart zwischenzeitlich deutlich höhere Abschüsse gab (vgl. Tab. 8).

Tabelle 8: *Streckendaten der Schalenwildarten im Untersuchungsgebiet Landesjagdbezirk Fläming, Zeitraum 2011-2021, (Quelle: Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt)*

Wildart	Rotwild	Damwild	Muffelwild	Rehwild	Schwarzwild
Jahresstrecke im Untersuchungsgebiet 2011 in Stück	17	910	15	671	340
Jahresstrecke im Untersuchungsgebiet 2021 in Stück	4	227	0	447	253

Es bleibt festzuhalten, dass bei allen Schalenwildarten außer dem Schwarzwild landesweit eine ähnliche Tendenz in der Streckenentwicklung wie im Untersuchungsgebiet zu verzeichnen ist. Allerdings sind die Rückgänge der Streckenergebnisse im Untersuchungsgebiet wesentlich stärker ausgeprägt.

9. Zusammenfassung

Der Forstbetrieb Anhalt als Teil des Landesforstbetriebs Sachsen-Anhalt bewirtschaftet im Fläming in vier Forstrevieren eine Jagdfläche von insgesamt 12516 Hektar. Die Hauptwildarten sind Damwild, Rehwild und Schwarzwild. Als Nebenwildarten kommen beziehungsweise kamen Rotwild und Muffelwild vor. Von 2008 bis 2021 haben sich im Territorium insgesamt sechs Wolfsrudel angesiedelt. Die Streifgebiete der Rudel tangieren jeweils ein oder mehrere Forstreviere.

Mit der Zunahme der Wolfspopulation im Untersuchungsgebiet reduzierten sich die Abschussergebnisse der Schalenwildarten. Dabei variierte der Rückgang der Jahresstrecken von Wildart zu Wildart deutlich. So ist die Muffelwildpopulation im Gebiet mittlerweile erloschen. Deutliche kontinuierliche Rückgänge im Abschussergebnis gab es beim Damwild sowie beim Rotwild als Nebenwildart. Dagegen war beim Rehwild nur eine geringere Reduzierung der Jahresstrecken zu verzeichnen.

Von 2008 bis 2021 wurden durch den Landesforstbetrieb Sachsen-Anhalt im Rahmen des Kulturqualitätsmanagement (KQM) revierweise alle vier- bis sechsjährigen Aufforstungen kontrolliert. Dabei erfolgte die Erfassung der vorhandenen Pflanzenzahlen, der durchschnittlichen Pflanzengröße, der Vitalität und der Verbissschäden.

Im Untersuchungsgebiet ergab sich ein sehr starker Rückgang der Verbissschäden, eine deutliche Zunahme der Pflanzenzahlen auf den Kulturen durch Anreicherung mit Naturverjüngung und ein Rückgang des Anteils von gezäunten Kulturen an der Aufforstungsfläche in allen vier Revieren. Damit hat sich im Flämingbereich des Forstbetriebs Anhalt die waldbauliche Situation deutlich verbessert und es wurden in erheblichem Umfang Kosten für Kulturzäune, sowie für Nachbesserungen und Wiederholung von Kulturen eingespart.

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Literaturverzeichnis

Michael Helm, Jens Joachimi (2010): Das Große Buch über den Fläming: Das schöne Land zwischen Elbe und Dahme
Dimitry Bibikow (1990): Der Wolf
Henryk Okarma, Dagmar Langwald (2002): Der Wolf: Ökologie, Verhalten, Schutz
Egbert Urbach (2020): Krebs – Vor und nach der Jägerprüfung
LAU – Landesamt für Umweltschutz Sachsen-Anhalt (2013): Wolfsmonitoring Sachsen-Anhalt. Bericht zum Monitoringjahr 2012/2013
LAU – Landesamt für Umweltschutz Sachsen-Anhalt (2014): Wolfsmonitoring Sachsen-Anhalt. Bericht zum Monitoringjahr 2013/2014
LAU – Landesamt für Umweltschutz Sachsen-Anhalt (2015): Wolfsmonitoring Sachsen-Anhalt. Bericht zum Monitoringjahr 2014/2015
LAU – Landesamt für Umweltschutz Sachsen-Anhalt (2016): Wolfsmonitoring Sachsen-Anhalt. Bericht zum Monitoringjahr 2015/2016
LAU/WZI – Landesamt für Umweltschutz Sachsen-Anhalt (2017): Wolfsmonitoring SachsenAnhalt. Bericht zum Monitoringjahr 2016/2017
LAU/WZI – Landesamt für Umweltschutz Sachsen-Anhalt (2018): Wolfsmonitoring SachsenAnhalt. Bericht zum Monitoringjahr 2017/2018
LAU/WZI – Landesamt für Umweltschutz Sachsen-Anhalt (2019): Wolfsmonitoring SachsenAnhalt. Bericht zum Monitoringjahr 2018/2019
LAU/WZI – Landesamt für Umweltschutz Sachsen-Anhalt (2020): Wolfsmonitoring SachsenAnhalt. Bericht zum Monitoringjahr 2019/2020
LAU/WZI – Landesamt für Umweltschutz Sachsen-Anhalt (2021): Wolfsmonitoring SachsenAnhalt. Bericht zum Monitoringjahr 2020/2021
Landeszentrum Wald Sachsen-Anhalt : Naturräumliche Grundlagen – Klimastufen
Online verfügbar unter https://landeszentrumwald.sachsen-anhalt.de/fuer-waldbesitzende/waldbauportal/naturraeumliche-und-standoertliche-grundlagen/klimastufen/ , zuletzt geprüft am 02.08.2022.
DBBW-Dokumentations- und Beratungsstelle des Bundes zum Thema Wolf : Welche Krankheiten können Wölfe bekommen? Online verfügbar unter https://www.dbb-wolf.de/mehr/faq/welche-krankheiten-koennen-woelfe-bekommen , zuletzt geprüft am 02.08.2022.
SG Waldbau/Forsteinrichtung Jörg Köhler (2008): Kulturqualitätsmanagementerfassung 2008
SG Waldbau/Forsteinrichtung Jörg Köhler (2012): Kulturqualitätsmanagementerfassung 2012
SG Waldbau/Forsteinrichtung Jörg Köhler (2016): Kulturqualitätsmanagementerfassung 2016
SG Waldbau/Forsteinrichtung Jörg Köhler (2021): Kulturqualitätsmanagementerfassung 2021
Landesforstbetrieb Sachsen-Anhalt Forstbetrieb Anhalt (2021): Streckenergebnisse der Schalenwildarten von 2007/2008 bis 2021/2022
Landesverwaltungsamt Sachsen-Anhalt Obere Jagdbehörde (2021): Streckenergebnisse der Schalenwildarten im Land Sachsen-Anhalt für 2011 und 2021

Abbildung 1
Sicherungsverhalten gegenüber möglichen Gefahren eines Rothirsches auf einer Versuchsfläche (alle Fotos/Abbildungen: Suzanne van Beeck Calkoen).

Suzanne van Beeck Calkoen und Marco Heurich

Einfluss von großen Beutegreifern auf die Nahrungssuche des Rothirschs

Große Beutegreifer werden häufig als Retter der Funktionsfähigkeit von Ökosystemen dargestellt, da sie das Verhalten von Huftieren und dadurch das Wachstum von Pflanzen beeinflussen können. Welche Effekte unterschiedliche Beutegreifer auf die Nahrungssuche ihrer Beute haben, ist bislang wenig erforscht. Wir zeigen Ergebnisse am Beispiel des Rothirsches (*Cervus elaphus*) auf.

In den letzten Jahrzehnten haben große Beutegreifer Teile ihres historischen Verbreitungsgebietes in Europa wieder besiedelt (Chapron et al. 2014). Grundlage dieser Entwicklung war ein Wandel in der gesellschaftlichen Einstellung gegenüber großen Beutegreifern in westlichen Industrienationen, welcher schließlich auch zu einem strengen gesetzlichen Schutz führte (Chapron et al. 2014; Kuijper et al. 2016). Aus diesem Grund konnten sich Wölfe (*Canis lupus*) in Ländern wie Polen, Finnland, Schweden, Italien sowie in Deutschland auf natürliche Weise ausbreiten. Andere große Beutegreifer, wie der Eurasische Luchs (*Lynx lynx*) und der Braunbär (*Ursus arctos*), konnten in einigen Gebieten Mitteleuropas durch aktive Maßnahmen zurückkehren.

Die Rückkehr der großen Beutegreifer erfolgt in stark vom Menschen veränderte Kulturlandschaften mit hoher Einwohnerdichte (Chapron et al. 2014). In den letzten Jahren wurde eine steigende Zahl Studien veröffentlicht, die darauf hindeuten, dass große Beutegreifer Effekte auf Ökosysteme haben können, indem sie über ihre Beutetiere auch die Vegetationsentwicklung beeinflussen (siehe Übersicht in Heurich 2015; Kuijper et al. 2016). Dabei wirken große Beutegreifer über zwei Wege auf ihre Beutetiere ein: Zum einen direkt, indem sie Beutetiere töten und so ihre Anzahl verändern (letale Effekte; zum Beispiel Messier 1994). Zum anderen können sie das Verhalten der Tiere ändern (nicht letale Effekte), wenn diese ihre räumlichen Nutzungs- und Aktivitätsmuster verändern (Lima & Dill 1990; Bonnot et al. 2020) oder ihre Wachsamkeit und/oder die Gruppengröße erhöhen (Brown 1999; Périquet et al. 2010). Diese letalen und nicht letalen Wirkungen der großen

Beutegreifer beeinflussen auch das Nahrungsverhalten ihrer Beutetiere dahingehend, dass sich die Verbissintensität generell reduziert und die räumlichen Muster des Verbisses und der Nahrungsselektion verändern (Brown & Kotler 2004; Kuijper et al. 2013).

In Gebieten, in denen wieder große Beutegreifer vorkommen, sehen sich ihre Beutetiere, zum Beispiel Reh und Rothirsch, einer größeren Wahrscheinlichkeit ausgesetzt, von ihren Fressfeinden entdeckt zu werden. Wie die Beutetiere darauf reagieren, hängt von ihrer Fähigkeit ab, diese Bedrohung zu erkennen oder auf Hinweise zu reagieren, die auf die Anwesenheit von Prädatoren hinweisen (Gaynor et al. 2019).

Das Ziel dieser Studie war es, den Einfluss eines Lauerjägers (Luchs) und eines Hetzjägers (Wolf) auf das Nahrungsverhalten von Huftieren (Rotwild) zu untersuchen. Die Präsenz großer Beutegreifer wurde mittels Gerüchen simuliert, indem sowohl Kot als auch Urin auf Versuchsflächen ausgebracht wurden. Rothirsche sind eine wichtige Beuteart sowohl für Wölfe als auch für Luchse (Okarma et al. 1997; Jędrzejewski et al. 2002; Belotti et al. 2015), deshalb erwarteten wir, dass Rothirsche auf den Versuchsflächen mit dem Geruch von großen Beutegreifern (1) ihr Sicherungsverhalten verstärken und die Versuchsflächen weniger häufig und wenn, dann nur kurz besuchen, was (2) zu einer geringeren Verbissintensität, aber (3) zu einer stärkeren Selektion der von ihnen bevorzugten Baumarten führt, um die höheren Kosten der möglichen Prädation auszugleichen. Zuletzt (4), erwarteten wir, dass die oben genannten Effekte stärker auf den Versuchsflächen mit Luchsgeruch sind, der seine Beute durch einen Überraschungsangriff tötet, als auf Flächen mit dem Geruch des Hetzjägers Wolfs.

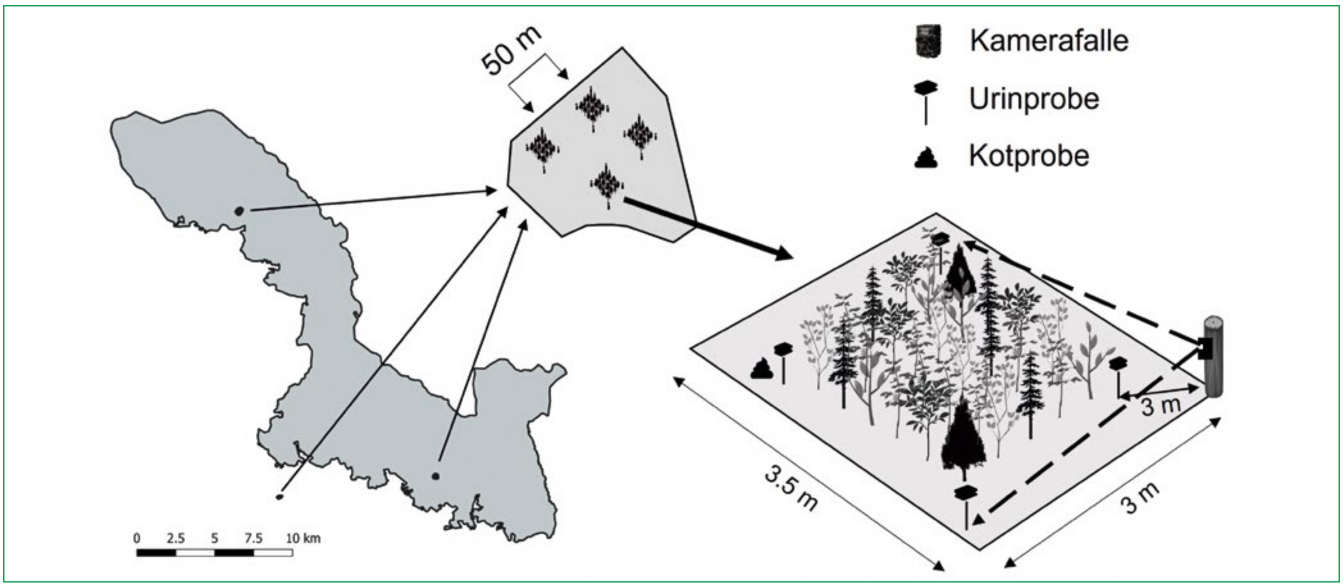
Methodik

Die Auswirkungen des Prädationsrisikos auf die Nahrungswahl und das Sicherungsverhalten des Rotwilds wurden in drei verschiedenen Rotwildgehegen im und um den Nationalpark Bayerischer Wald untersucht. Innerhalb jeden Geheges wurden vier Versuchsflächen angelegt, die entweder mit Urin und Kot von Wolf, Luchs und Kuh oder mit Wasser behandelt wurden. Der Geruch von Rindern wurde verwendet, um einen unbekannten, ungefährlichen Geruch darzustellen. Auf jeder Versuchsfläche wurden insgesamt 30 Bäume der jeweils fünf häufigsten Baumarten des Nationalparks Bayerischer Wald gepflanzt (Fichte, Weißtanne, Rotbuche, Vogelbeere und Bergahorn), die sich in ihrer Beliebtheit als Rothirschnahrung unterscheiden. An jeder Ecke wurde ein Schwamm platziert, an dem der Urin aufgetragen wurde (Abbildung 2).

Aufzeichnung des Verhaltens vom Rothirsch mit Kamerafallen

Auf jeder Versuchsfläche wurde das Verhalten von Rothirsch mit einer Kamerafalle erfasst (Abbildung 1). Jede Kamera wurde bei Bewegung ausgelöst und zeichnete kurze Videos bei Tag und Nacht auf. Es wurde neben der Bewegung, dem Nahrungsverhalten und der Anzahl der Besuche, auch das Sicherungsverhalten aufgezeichnet.

Abbildung 2 Sicherungsverhalten gegenüber möglichen Gefahren eines Rothirsches auf einer Versuchsfläche.



Erfassung des Verbisses

Für jeden Baum innerhalb einer Versuchsfläche wurde zweimal täglich der Verbiss gemessen, indem erfasst wurde, 1) ob der Leittrieb und 2) wie viele der obersten 10 seitlichen Triebe verbissen wurden (nach Kuijper et al. 2013). Die Verbissintensität wurde anhand der Gesamtzahl der verbissenen Triebe und der Gesamtzahl am Baum vorhandener Triebe (maximal 11) ermittelt. Zusätzlich wurden Baumart und Baumhöhe für jeden Baum erfasst. Um zu testen, ob sich die von Rothirsch gewählten Baumarten unter Prädationsrisiko veränderten, wurden Vogelbeere und Weißtanne als bevorzugte Baumarten und Bergahorn und Fichte als weniger bevorzugte Baumarten definiert.

Ergebnisse

Rothirsche hielten sich in Anwesenheit des Geruchs großer Beutegreifer kürzer auf den Probeflächen auf (Abbildung 4), ohne aber ihr Sicherungsverhalten zu erhöhen. Gleichzeitig führt die Anwesenheit des Geruchs großer Beutegreifer (sowohl von Luchs als auch Wolf) zu einer geringeren Verbissintensität (Abbildung 4). Obwohl die Rothirsche eine deutliche Präferenz für bestimmte Baumarten zeigten, kompensierten sie die reduzierte Nahrungsaufnahme bei Anwesenheit von Großraubtiergeruch nicht dadurch, dass sie verstärkt die bevorzugten Baumarten fressen.

Schließlich fanden wir im Gegensatz zu unserer Erwartung stärkere Effekte durch Wolfsgeruch (Hetzjäger) als durch Luchsgeruch (Lauerjäger), obwohl andere Studien stärkere Effekte durch Lauerjäger gefunden haben (Preisser, Orrock & Schmitz 2007; Wikenros et al. 2015). Wir führen das darauf zurück, dass Rothirsche nicht die Hauptbeutetiere von Luchsen, aber von Wölfen sind (Jędrzejewski et al. 2012; Belotti et al. 2015). Dementsprechend sind ihre Reaktionen gegenüber Luchsen geringer als gegenüber Wölfen.

Fazit

Unsere Forschung zeigt, dass große Raubtiere das Nahrungssuchverhalten ihrer Beutetiere auf kleinen räumlichen Skalen verändern können. Unterschiede in der Verhaltensreaktion und der Verbissintensität als Reaktion auf ein unterschiedliches Prädationsrisiko könnten zu einer höheren Variabilität in der Regeneration von Wäldern führen, was langfristig Konsequenzen für die Struktur von Wäldern haben könnte.

Abbildung 3
Beispiel Leittriebverbiss einer Buche.

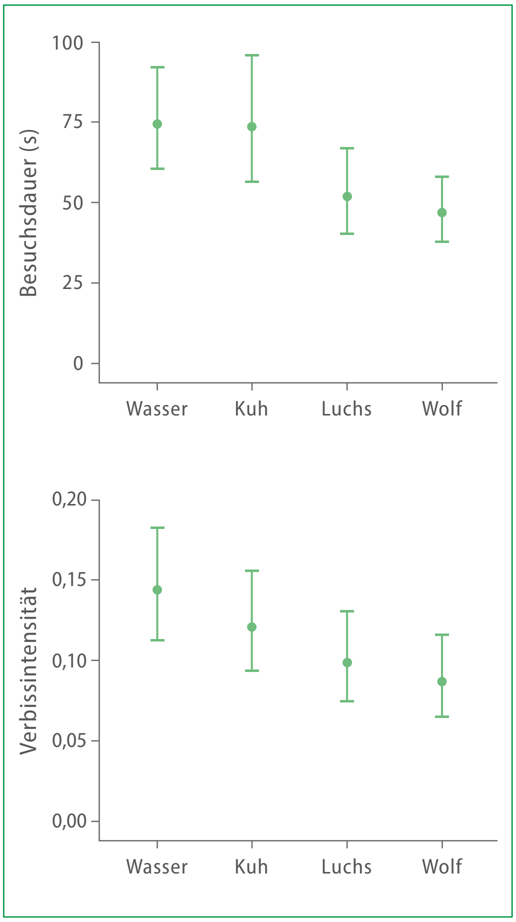


Abbildung 4
Ergebnisse der statistischen Modelle. **Oben** die Besuchsdauer (s) und **unten** die Verbissintensität (die Anzahl der verbissenen Triebe an einem einzelnen Baum), mit den unterschiedlichen Geruchshinweisen von Wolf, Luchs, Kuh und Wasser als Kontrolle. Für jede Behandlung werden die angepassten Werte (Punkte) und ihre 95 %-Konfidenzintervalle angezeigt (Linien).

Literatur

Belotti, E. et al. (2015): Patterns of Lynx Predation at the Interface between Protected Areas and Multi-Use Landscapes in Central Europe. – Plos One, 10(9): p. e0138139; doi:10.1371/journal.pone.0138139.

Bonnot, N. C. et al. (2020): Fear of the dark? Contrasting impacts of humans versus lynx on diel activity of roe deer across Europe. – Journal of Animal Ecology, 89(1): pp. 132–145; doi:10.1111/1365-2656.13161.

Brown, J. S. (1999): Vigilance, patch use, and habitat selection: foraging under predation risk. – Evolutionary ecology research, 1(1): pp. 49–71.

Brown, J. S. & Kotler, B. P. (2004): Hazardous duty pay and the foraging cost of predation. – Ecology Letters, 7(10): pp. 999–1014; doi:10.1111/j.1461-0248.2004.00661.x.

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

Gaynor, K. M. et al. (2019): Landscapes of Fear: Spatial Patterns of Risk Perception and Response. – Trends in Ecology & Evolution, 34(4): pp. 355–368; doi:10.1016/j.tree.2019.01.004.

Heurich, M. (2015): Welche Effekte haben große Beutegreifer auf Huftierpopulationen und Ökosysteme? – Naturschutz und Landschaftsplanung: p. 10.

Jędrzejewski, W. et al. (2002): Kill Rates and Predation by Wolves on Ungulate Populations in Białowieża Primeval Forest (poland). – Ecology, 83(5): pp. 1341–1356; doi:https://doi.org/10.1890/0012-9658(2002)083[1341:KRAPBW]2.0.CO;2.

Jędrzejewski, W. et al. (2012): Prey choice and diet of wolves related to ungulate communities and wolf subpopulations in Poland. – Journal of Mammalogy, 93(6): pp. 1480–1492; doi:10.1644/10-MAMM-A-132.1.

Kuijper et al. (2016): Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. – Proceedings of the Royal Society B: Biological Sciences, 283(1841): p. 20161625; doi:10.1098/rspb.2016.1625.

Kuijper, D. P. J. et al. (2013): Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest – Poland. – Ecography, 36(12), pp. 1263–1275.

Lima, S. L. & Dill, L. M. (1990): Behavioral decisions made under the risk of predation: a review and prospectus. – Canadian Journal of Zoology, 68(4): pp. 619–640; doi:10.1139/z90-092.

Messier, F. (1994): Ungulate Population Models with Predation: A Case Study with the North American Moose. – Ecology, 75(2): pp. 478–488; doi:10.2307/1939551.

Okarma, H. et al. (1997): Predation of Eurasian lynx on roe deer and red deer in Bialowieza Primeval Forest, Poland. – Acta theriologica, 42: pp. 203–224; doi:10.4098/AT.arch.97-22.

Périquet, S. et al. (2010): Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. – Animal Behaviour, 79(3): pp. 665–671; doi:10.1016/j.anbehav.2009.12.016.

Preisser, E. L., Orrock, J. L. & Schmitz, O. J. (2007): Predator Hunting Mode and Habitat Domain Alter Nonconsumptive Effects in Predator-Prey Interactions. – Ecology, 88(11): pp. 2744–2751; doi:10.1890/07-0260.1.

Wikenros, C. et al. (2015): Behavioural responses of ungulates to indirect cues of an ambush predator. – Behaviour, 152(7–8): pp. 1019–1040.

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BRITISH ECOLOGICAL SOCIETY Ecological Solutions and Evidence

RESEARCH ARTICLE

Wolf reintroduction to Scotland could support substantial native woodland expansion and associated carbon sequestration

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Abstract

1. Large carnivores, including the grey wolf (*Canis lupus*), play an important role in the carbon cycle through modifying the behaviour and population of wild herbivores. Large carnivores have been eradicated from much of their former range and are now absent from the UK, contributing to increased herbivore populations, which can prevent natural regeneration of trees and woodland. A reintroduction of wolves to the UK could reduce deer populations and associated browsing of tree saplings, but the potential impacts on woodland expansion and carbon sequestration have not been assessed.
2. Here we estimate the impact of a wolf reintroduction in the Scottish Highlands on red deer populations, native woodland colonisation and carbon sequestration. We use a Markov predator–prey model to estimate that a reintroduction would lead to a population of 167 ± 23 wolves, sufficient to reduce red deer populations below 4 deer km^{-2}, the threshold at which we assume browsing to be sufficiently suppressed to enable natural colonisation of trees.
3. Using a model of potential new native woodlands we estimate the subsequent expansion of native woodland would result in an average annual carbon sequestration of 1.0 ± 0.1 Mt CO_2, with each wolf contributing an annual carbon sequestration of 6080 t CO_2.
4. *Practical Implication*. Our analysis demonstrates the ecosystem benefit that wolves can provide through control of red deer numbers, leading to native woodland expansion. Large-scale expansion of woodlands, facilitated through the return of wolves, can contribute to national climate targets and could provide potential economic benefits to landowners and communities through carbon finance.

KEYWORDS
carnivore restoration, native woodland, natural colonisation, trophic cascade, wolf reintroduction

1 | INTRODUCTION

Large carnivores play an important role in regulating ecosystems (Estes et al., 2011; Ripple et al., 2014). They alter the abundance and behaviour of their prey (Emerson et al., 2024; Manning et al., 2009), impacting vegetation structure (Beschta & Ripple, 2009), ecosystem function (Suraci et al., 2016), biogeochemical cycling and the carbon cycle (Leroux et al., 2020; Rizzuto et al., 2024; Schmitz et al., 2018; Schmitz & Leroux, 2020; Strickland et al., 2013). Recent work has suggested that the grey wolf (*Canis lupus*) enhances annual ecosystem carbon uptake by 260 Mt CO_2 across Northern Hemisphere forests through modifying herbivore populations and behaviour (Schmitz et al., 2023). Reintroducing wolves to parts of their natural range where they are no longer present could further increase carbon sequestration, contributing to the natural climate solutions that are needed to prevent climate warming exceeding 2°C (Griscom et al., 2017).

Large carnivores have experienced substantial population declines and range contractions (Ripple et al., 2014) and are now absent from the United Kingdom (UK). Lynx were eradicated from the UK around 700 AD (Hetherington et al., 2006) and the wolf was eradicated from Scotland about 250 years ago (Nilsen et al., 2007). The loss of natural predators, in particular the wolf, has contributed to increased population of Red deer (*Cervus elaphus*) across Scotland (Clutton-Brock et al., 2004). Despite ongoing management, red deer numbers in Scotland have increased over the last century (Edwards & Kenyon, 2013) with latest estimates of 360,000–400,000 (Pepper et al., 2020).

Deer abundance has important impacts on natural ecosystems including vegetation composition and dynamics, growth and survival of tree saplings, and nutrient cycling (Côté et al., 2004). Natural regeneration and colonisation of woodland in Scotland is limited by herbivore browsing (Gullett et al., 2023; Miller et al., 1998; Rao, 2017; Tanentzap et al., 2013). Increased deer populations also have widespread impact on woodland ecology (Fuller & Gill, 2001). The maximum density of deer under which regeneration and establishment of woodland can occur depends on the tree species, vegetation, soil fertility and herbivore distribution (Miller et al., 1998; Palmer et al., 2004). Palmer and Truscott (2003) found that less than 15% of saplings were browsed for deer densities below 2 km^{-2}, increasing to 30% for deer densities of 10 km^{-2} and to 80% for deer densities of 20 km^{-2}. Tanentzap et al. (2013) suggested that <10% of seedlings can be browsed to enable tree establishment, suggesting deer density exceeding 2 to 10 km^{-2} would suppress regeneration.

Deer, in combination with sheep in some areas, prevents tree regeneration across much of Scotland. The density of red deer on open-hill ground in the Highlands and Islands of Scotland in winter 2019 was estimated as 9.35 km^{-2} (Albon et al., 2019), too high to allow natural regeneration or colonisation. Lack of tree regeneration has contributed to a long term decline and loss of native woodland, with less than 4% of Scotland currently covered by native woodland (Native Woodland Survey of Scotland, 2014). At such high deer densities, natural regeneration and colonisation of woodland is largely restricted to areas where deer are excluded by fencing (Palmer et al., 2009). More intensive deer management in some locations has been shown to facilitate tree regeneration with increasing number of tree seedlings when red deer numbers were reduced below 3.5 km^{-2} (Rao, 2017). A reduction in deer numbers to less than 6 km^{-2} over a 60,000 ha landscape in the Cairngorms in eastern Scotland, facilitated natural colonisation and created about 164 ha of new woodland each year over a 30 year period (Gullett et al., 2023). If deer numbers were reduced more widely to levels that would permit natural colonisation, Fletcher et al. (2021) estimated that more than 39,000 km^2 of the Scottish Highlands would be suitable for establishment of native woodland.

In recent decades, large carnivores have started to re-establish across areas of mainland Europe (Chapron et al., 2014; Cimatti et al., 2021). Wolves now occupy 67% of their former European historical range (Ripple et al., 2014), including human-dominated landscapes in Central Europe, demonstrating an ability to coexist close to humans (Chapron et al., 2014; Cretois et al., 2021). The wolf population in Western Europe now exceeds 12,000 (Hindrikson et al., 2017). Due to the natural barrier presented by the sea, reintroduction would be necessary to re-establish large carnivores in the UK (Seddon et al., 2014). Nilsen et al. (2007) suggested a wolf reintroduction to Scotland could result in 25 wolves per 1000 km^2. Gwynn and Symeonakis (2022) estimate a contiguous area of 10,139 to 18,857 km^2 of Scotland would be suitable for wolf and could support 200 to 376 individuals (50 to 94 wolf packs).

There is increasing acknowledgement that the climate and biodiversity crises cannot be managed in isolation (Pörtner et al., 2021), with greater interest in the potential role of natural processes, including restoring trophic cascades for ecosystem recovery (Cromsigt et al., 2018), to deliver co-benefits for climate, and nature recovery. Climate mitigation and adaptation will require large-scale changes in land management (Smith et al., 2019). Fletcher et al. (2021) estimated expansion of native woodlands across the Scottish uplands could remove nearly 700 million tons of CO_2 and make a sizeable contribution to national climate targets.

Discussions around potential large carnivore introductions to the UK (Convery et al., 2023; Wilson & Campera, 2024) and elsewhere (Gonzalez et al., 2024) are ongoing. The potential for a wolf reintroduction to reduce red deer populations in the Scottish

Highlands has already been demonstrated (Nilsen et al., 2007) but the impacts on woodland establishment and carbon sequestration have not been assessed. Here we combine a range of models to provide the first estimate of the impact of a reintroduction of wolves to Scotland on red deer population, natural colonisation of native woodlands and associated carbon sequestration. The expansion of wolves across their former range in western Europe has created substantial conflict, particularly with farmers and hunters (Martin et al., 2020). Substantial and wide-ranging stakeholder and public engagement would clearly be essential before any wolf reintroduction could be considered. Our aim is to provide new information to inform these ongoing and future discussions around human-wolf conflict and wolf reintroductions both in the UK and elsewhere.

2 | MATERIALS AND METHODS

2.1 | Wild Land Areas

We focused our analysis on the Scottish Wild Land Areas (WLAs), defined as the "most extensive areas of high wildness" in Scotland. WLAs were identified using a methodology based on the relative wildness of the landscape (NatureScot, 2014), taking into account perceived naturalness, rugged or challenging terrain, remoteness from public mechanised access, lack of built modern artefacts. WLAs are nationally important in Scottish Planning Policy, but are not a statutory designation.

Because WLAs have been identified as Scotland's more natural and remote landscapes with low levels of human influence, they represent a potential target for any future wolf reintroduction. There are 42 WLAs in Scotland covering 14,537 km^2, nearly 20% of Scotland. We selected the four largest contiguous areas of wild land in the Scottish Highlands which we defined as WLAs separated by less than 5 km in distance and not intersected by major human infrastructure such as a dual-carriageway road. These four areas are: (i) Cairngorms (Cairngorms; Lochnagar–Mount Keen), (ii) South-west Highlands (Rannoch—Nevis—Mamores—Alder, Loch Etive mountains; Breadalbane—Schiehallion; Lyon–Lochay, Ben Lawers; Ben Lui, Ben More, Ben Ledi), (iii) Central Highlands (Kinlochhourn—Knoydart—Morar, Central Highlands Fisherfield—Letterewe—Fannichs; Moidart—Ardgour; Coulin and Ledgowan Forest, Flowerdale—Shieldaig—Torridon), (iv) North-west Highlands (Rhiddoroch—Beinn Dearg—Ben Wyvis, Inverpolly—Glencanisp, Quinag; Foinaven—Ben Hee, Ben Hope—Ben Loyal, Cape Wrath, Reay—Cassley, Ben Kilbreck—Armine Forest). These areas vary in size from 2100 km^2 to 4100 km^2 with a total area of 12,167 km^2 (Figure 1). Each area is individually larger than the minimum of 600 km^2 required for viable wolf populations (Sandom et al., 2012) and match the areas previously identified as the most suitable for wolf reintroduction in Scotland (Gwynn & Symeonakis, 2022). We assumed separate reintroductions within each area. As in previous work (Nilsen et al., 2007; Sandom et al., 2012) we assumed that wolves are confined to the introduction area and are not free to spread to surrounding regions as would be the case if the area was fenced. However, we acknowledge that securely fencing large areas would be challenging and unlikely to be feasible. Future work is needed to understand how wolves might be likely to spread if they were free to move across Scotland and how this would alter both equilibrium populations and temporal development of populations.

2.2 | Red deer—Wolf population modelling

We based our red deer and wolf population modelling using the models described in Nilsen et al. (2007). The red deer population model is a density-dependent, discrete-time, age- and sex structured Markov model parameterised based on a long-term individual-based study of red deer in Scotland (Clutton-Brock et al., 1982). The deer population dynamics include interactions between density dependence, climate and age structure (Clutton-Brock & Coulson, 2002; Clutton-Brock et al., 2002; Milner-Gulland et al., 2004). This model simulates the observed population dynamics of red deer in Scotland (Nilsen et al., 2007).

Survival and fecundity probabilities were fitted as logistic functions of hind density according to $R_{i,j} = 1 - \frac{1}{1+e^{-a+bD}}$, where $R_{i,j}$ is the deterministic vital rate for sex i in age class j, a and b are coefficients, and D is the density of adult hinds (≥3 years). The proportion of males at birth (m) is calculated as $m = 0.6438 - 0.00748D$.

The stochastic adult hind mortality for hinds in age class j was calculated as $\rho_j = R_j + z\sigma_j$, where z is a standardised normal deviate with a standard deviation of σ_j. The model assumes fecundity and other class-specific mortality rates are correlated with adult hind mortality such that $\rho_{i,j} = R_{i,j} + \sigma_{i,j} z\sqrt{1-r^2} + r\sigma_{i,j}A$, where $\rho_{i,j}$ is the stochastic rate for sex i and age j, r is the correlation between the rate and adult hind mortality, and A is the average of the z-values for adult hind mortality (Clutton-Brock et al., 2002; Milner-Gulland et al. 2004). We assume $r = 0.522$ for stag mortality and $r = -0.452$ for all other rates.

The wolf population was simulated using an individual based model. The wolf population was characterised as the number of packs, the number of wolves in each pack, and the age, sex and social status of each wolf classified as juvenile (J; 6–18 months), sub-adult (Sa; 18–30 months), sub-dominant adult (A; >30 months) or dominant adult (Do). All packs that include an alpha pair are assumed to produce a litter. The discrete probability distribution for litter size had a mean of 3.5 pups and a range from zero to six. The sex of each recruit was determined as a result of a Bernoulli trial with mean 0.5. Individuals are recruited into the population at 6 months. We assume different wolf survival rates for juveniles, wolves aged 1–6 years, and older wolves (>6 years). If the pack includes one or more alpha individuals, dispersal of the rest of the pack was calculated as a binomially distributed random variable, assumed to be age-dependent, with older individuals more likely to disperse. Alpha individuals are assumed not to disperse. If both alpha individuals died, all remaining members of the pack

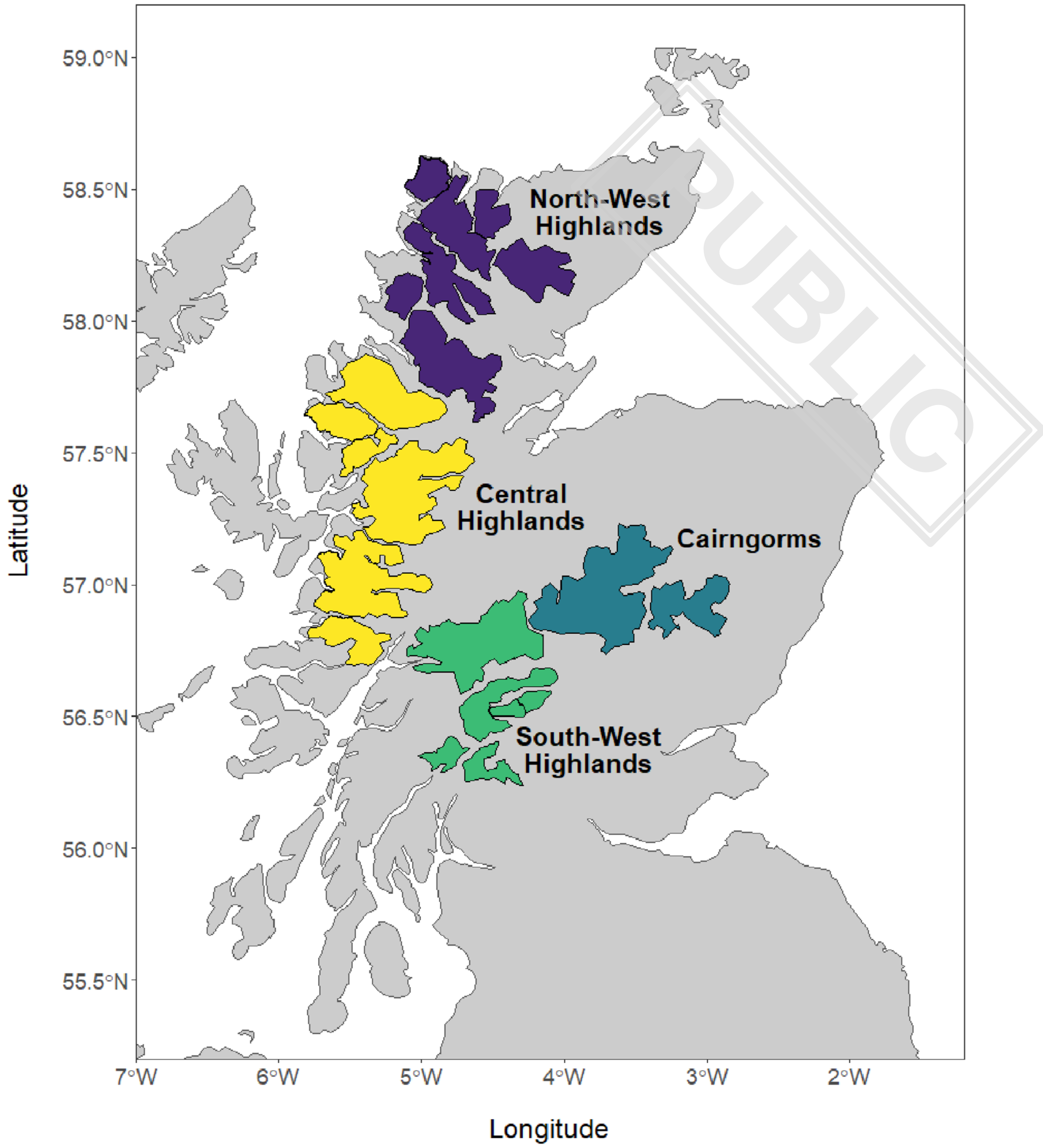

FIGURE 1 Location of the four areas where wolf reintroductions are simulated: Cairngorms, South-West Highlands, Central Highlands and North-West Highlands.

dispersed. If only one dominant individual was alive, the pack continued to occupy the territory but did not breed until a dispersing adult joined the pack.

We assume dispersing individuals can become breeders either by occupying a vacant territory that an individual of the opposite sex also dispersed into or by joining widowed alpha individuals of the opposite sex. Juvenile wolves can only breed after 1 year after dispersal, consequently the minimum age of first reproduction was 24 months. Dispersing wolves that were not successful in establishing a territory were assumed to die. We assume that dispersing wolves cannot join packs with an alpha pair.

Dispersal probabilities for juveniles, sub-adults and adults when one or both breeders were present were 0.3, 0.5 and 0.9, respectively. Dispersing wolves were assumed to actively seek a territory in which to become breeders. We assumed that 30% of the dispersing wolves were not successful in occupying a territory when vacant territories were available.

The mean density of red deer in the Highlands and Islands of Scotland has recently been estimated as 9.35 (8.01–10.69, 95% CI) deer km^{-2} (Albon et al., 2019). For each simulation, we ran the red deer model for 50 years before a wolf reintroduction. For each of the four regions simulated, we applied a hind harvest rate of 10% that results in a red deer density prior to wolf reintroduction of ~9 deer km^{-2}. We tested the sensitivity of using initial red deer density of 8–11 deer km^{-2}, and found that this did not alter our results. Nilsen et al. (2007) found that red deer populations could not support a hind harvest greater than 4%–5% as well as a viable wolf population. We assumed that hind harvest continues at 10% after wolf introduction, but reduced the hind harvest rate to 5% if deer populations are less than 8 deer km^{-2} and to 1.5% if numbers are less than 6 deer km^{-2}.

In each region simulated, we assumed a reintroduction of three wolf packs, each consisting of three wolves. For each area, we ran the model 100 times.

In our simulations, we updated the deer and wolf population annually within each of the four regions for 100 years after wolf reintroduction, based on the underlying model parameters. We calculated the mean and standard deviation of wolf and red deer density across the 100 simulations.

We tested the sensitivity of our results to uncertainty in the parameters in the wolf population model. We selected the parameters that were identified by Nilsen et al. (2007) as being the most important: the rate at which wolves kill deer when deer are abundant (a), adult wolf survival rates (s_{adult}) and the probability that a dispersing wolf is successful in establishing a territory (p_{settle}). For each parameter we completed 10 sensitivity simulations varying the parameter by up ±10% in increments of 2 percentage points. For each parameter, we calculated the standard deviation of wolf density calculated by the model across the 10 simulations. We combined the standard deviations in quadrature to estimate an uncertainty in wolf population.

2.3 | Potential for native woodland

We used the potential for native woodland model (NWM; Towers et al., 2004) to predict potential national vegetation classification (NVC) woodland types across the four areas selected in this study. The model predicts the woodland types that would be expected under current soil and vegetation conditions with no or minimal ground intervention, including fertilisation, ground preparation and drainage. The model uses information on soils from the national soils survey and the national land cover map (Towers et al., 2004).

The outputs of the model are categorised into 58 woodland types, which may be single, interchangeable or mosaics of different NVC classes. A comparison of the woodland types simulated by the NWM with on-the-ground NVC surveys, suggest that the NWM accurately predicts site suitability for a range of NVC classes spanning oakwoods, ashwoods and pinewoods (Towers et al., 2004) that are the dominant NVC classes across the areas in our study.

Previous studies have suggested that deer numbers less than 5–10 km^{-2} are required to allow tree establishment (Beaumont et al., 1995; Miller et al., 1998; Mitchell et al., 1977; Rao, 2017; Staines, 1995). We assumed that natural colonisation and tree establishment occur if deer numbers are reduced to less than 4 km^{-2}. In a sensitivity study, we assumed natural colonisation occurs below deer numbers of 7 km^{-2}.

2.4 | Carbon sequestration

We assumed carbon sequestration for mature native woodland (80% canopy cover) of 84 tonnes of carbon per hectare ($tC\,ha^{-1}$) based on data from 12 native woodland sites across Scotland (Perks et al., 2010). These were predominantly upland sites with nutrient poor soils with similar conditions and NVC types to those simulated by the NWM across the WLA that were the focus on this study including W17 (upland oak/birch with bilberry), W18 (Scots pine with heather), W11 (upland oak/birch with bluebell/wild hyacinth), W7 (alder/ash with yellow pimpernel), W9b (upland ash with birch/rowan/aspen) and W4 (birch with purple moor grass).

To provide carbon sequestration for different woodland types predicted by the NWM, we scaled carbon sequestration by the canopy cover for each woodland type. To determine the percentage canopy cover for the woodland types predicted by the NWM, each component part of the woodland types was assigned a canopy cover value based on the values in Fletcher et al. (2021): Types W4a, W6-W11 and W16-W19 were assigned 80% canopy cover; W4 (with open ground) and Sc1, Sc3, Sc6 and Sc7 were assigned 30% canopy cover; and Sc2, Sc4, Sc5 and Sc8 were assigned 10% canopy cover.

As in Fletcher et al. (2021), we assumed new woodlands take 100 years to reach maturity. We assumed carbon sequestration begins when deer numbers reduce below the threshold for natural colonisation. We calculated cumulative carbon sequestration over a 100 year period and assumed that carbon sequestration is linear across this period from the year when natural colonisation begins, which is reasonable when calculating the cumulative impact over 100 years. We did not account for potential changes in belowground and soil carbon (Tanentzap & Coomes, 2012) and so total carbon sequestration is likely to be higher than presented here.

We calculated sensitivity of our carbon sequestration estimates to parameters in the wolf population model. For each of the parameters tested we calculated the year deer populations fall below the threshold for natural colonisation and then calculated the resulting carbon sequestration for that scenario. We report the standard deviation across all the parameter combinations.

We calculated an annual financial benefit associated with carbon sequestration assuming £25.36 per tonne of CO_2 based on UK Woodland Carbon Code prices in 2023 (Woodland Carbon Code, 2023) ($31.95 per tonne CO_2 assuming GBP £1 = US $1.26). We did not apply inflation to our estimated financial benefits. We calculated a nominal value per wolf by dividing the annual financial benefit by the average wolf population. We estimated an uncertainty by combining our uncertainty in the wolf population and the uncertainty in carbon sequestered.

2.5 | Model framework

Figure 2 shows the model framework used for our study. The Wild Land Area mapping (Section 2.1) was used to determine the spatial extent of the area. We then applied a red deer–wolf model (Section 2.2) to simulate the annual dynamics of red deer and wolf populations. The annual population of red deer was used along with the native woodland model (Section 2.3) to simulate the potential expansion of native woodland. Finally, information on the carbon sequestration of new native woodlands (Section 2.4) was used to estimate the annual carbon sequestration.

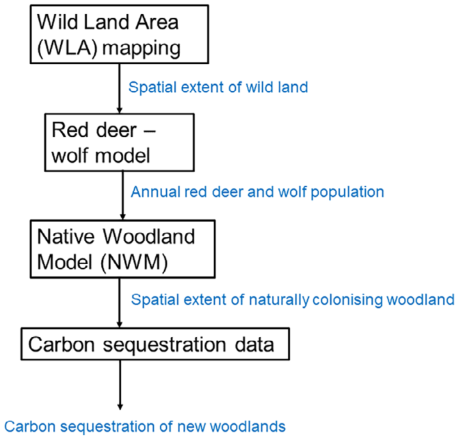

FIGURE 2 Model framework for simulating the impacts of grey wolves on red deer populations, native woodlands and carbon sequestration.

The models were coupled at an annual time-scale. Each year the red deer and wolf population was used to assess the potential for woodland expansion and the annual carbon sequestration was calculated. A simplification of our approach is that the expansion of woodland does not alter red deer–wolf population dynamics.

3 | RESULTS AND DISCUSSION

Table 1 reports the results of our simulations. Average wolf populations after reintroduction are 13–14 wolves per 1000 km^2, somewhat lower than the 20–49 wolves per 1000 km^2 recorded in unmanaged wolf populations in the Bialowieza Forest, Poland (Jedrzejewski et al., 2002) or 25–100 wolves per 1000 km^2 in the Yellowstone National Park, USA (Hobbs et al., 2024). The lower estimated carrying capacity in our study may be because we assume that wolves only predate red deer, whereas in reality there are multiple prey species. Total wolf populations vary from 27 wolves in the Cairngorms to 56 wolves in the Central Highlands. The total population across the four areas of the Scottish Highlands is estimated to be 167 ± 23 wolves, similar to previous estimates (Gwynn & Symeonakis, 2022; Nilsen et al., 2007). Our estimated total population is also similar to the viable population of 200 wolves estimated for the recent reintroduction to Colorado, USA (Hoag et al., 2023).

Deer populations decline after a wolf reintroduction (Figure 3). In our simulations, it takes 20–23 years after wolf reintroduction for deer populations to decline below 4 km^{-2} (Table 1; 11–12 years for deer populations to decline below 7 km^{-2}). Our results on wolf–deer dynamics are similar to those reported in Nilsen et al. (2007). Passoni et al. (2024) used a wolf-elk model to simulate that a population of 99 wolves was sufficient to reduce elk numbers by 61% in the Yellowstone ecosystem. In the western European Alps, a wolf density of 17–29 wolves per 1000 km^2 caused 19%–51% of annual red deer mortality sufficient to have a limiting effect on populations (Gazzola et al., 2007). In the Bialowieza Forest in Poland, wolves took 12% of red deer each year which was equivalent to 40% of annual red deer mortality (Jedrzejewski et al., 2002). In more productive habitats, where ungulates can have a very high reproduction rate the impacts of wolf predation on ungulate populations can be lower (Meriggi et al., 2011). In the Northern Apennines, Italy, wolf range expansion has followed the expansion of roe deer (Torretta et al., 2024). The high deer densities in Scotland contrast with some parts of Europe where scarcity of wild prey can be a limiting factor for large carnivores such as wolves (Rossa et al., 2023). The potential for wolves to mediate trophic cascades in human-dominated landscapes is heavily influenced by humans and their effects on the behaviour of both predator and prey (Kuijper et al., 2016). We simulated continued hind deer cull after a potential wolf reintroduction to capture such interactions. However, we did not simulate potential impacts of humans on wolf populations via legal hunting or poaching. In parts of Europe, poaching may supress wolf populations by a factor of 4 (Liberg et al., 2012) reducing the potential for wolves to regulate prey species. In forested regions of Scandinavia with intensive forestry and where deer are hunted by humans, wolves were not associated with either reduced herbivore populations or reduced browsing pressure (Ausilio et al., 2021). Future research is needed to better understand the potential for carnivores to initiate trophic cascades in human dominated landscapes. In addition to altering herbivore populations, wolves can also alter herbivore behaviour and browsing pressure (Manning et al., 2009). We did not simulate such interactions, which might further enhance the potential for wolves to increase woodland regeneration.

Figure 4 shows the potential carbon sequestration from native woodland expansion across the four areas over a 100-year period after a wolf reintroduction. Over this period, individual areas sequester between 17 and 38 Mt CO_2. On average wolf reintroduction increases carbon sequestration by 18–26 g C m^{-2} year^{-1} (Table 1) at the lower end of the 24–52 g C m^{-2} year^{-1} estimated for wolf-deer interactions in North America (Wilmers & Schmitz, 2016) or 37 ± 13 g C m^{-2} year^{-1} estimated for wolf across the boreal forest (Schmitz et al., 2023). Estimated sequestration rates in the North West Highlands and Cairngorms are lower than in the SW and Central Highlands due to higher elevations and less favourable conditions for woodland establishment. Our sequestration rates are also similar to the estimated biomass offtake by herbivore grazing at UK oak woodland sites of up to 16 g m^{-2} year^{-1} (Palmer et al., 2004).

Total carbon sequestration across the four areas after 100 years is 102 ± 10 Mt CO_2, equivalent to an annual sequestration of 1.0 ± 0.1 Mt CO_2 year^{-1}. This is equivalent to approximately 5% of the carbon removal target for UK woodlands that has been suggested by the UK's Climate Change Committee (UKCCC) as being necessary to reach net-zero by 2050. While much of the carbon sequestration considered here would occur post-2050, natural colonisation could play an important role in the maintenance of a longer term carbon sink on UK land. Based on the total carbon sequestration and the total wold population, the average annual carbon sequestration per wolf is 6080 ± 980 t CO_2.

Assuming a carbon price of £25.36 per tonne of CO_2, the carbon sequestration from native woodland establishment due to wolf

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TABLE 1 Summary of the wolf population, number of years after wolf reintroduction before tree regeneration begins, carbon sequestration and financial value following a wolf reintroduction to four areas of the Scottish Highlands (location indicated in Figure 1).

Area	Area (km^2)	Start year	Wolf population density, mean (per 1000 km^2)	Total sequestration (Mt CO_2)	Sequestration (g C $m^{-2}year^{-1}$)	Value of carbon sequestration (£Million)	Total wolf population	Annual sequestration per wolf (t CO_2 $year^{-1}$)	Annual value per wolf (£)
Cairngorms	2108	20 ± 8	13.0 ± 1.2	17.2 ± 1.8	22.3 ± 2.2	437.4 ± 44	27 ± 2	6280 ± 880	£159,400 ± 22,000
SW Highlands	2674	21 ± 5.6	14.1 ± 1.8	23.8 ± 1.7	24.6 ± 1.7	604.6 ± 42	37 ± 6	6390 ± 890	£162,000 ± 23,000
Central Highlands	4097	21 ± 8	13.9 ± 2.2	36.6 ± 4.1	25.7 ± 2.5	979.9 ± 98	56 ± 9	6800 ± 1300	£172,300 ± 34,000
NW Highlands	3316	23 ± 7	13.7 ± 2.1	21.8 ± 1.9	17.8 ± 1.4	633.4 ± 46	45 ± 7	4800 ± 820	£122,000 ± 21,000
Total	12,167	–	–	101.6 ± 9.5		2580 ± 230	167	6080 ± 980	£154,000 ± 25,000

Note: The start year of tree regeneration is determined as the number of years after wolf reintroduction before red deer populations fall below the assumed threshold for regeneration (see Section 2). Average wolf populations and total carbon sequestration are reported for the 100 years following a wolf reintroduction. The value of carbon sequestration is calculated based on GBP £25.36 per tonne of CO_2.

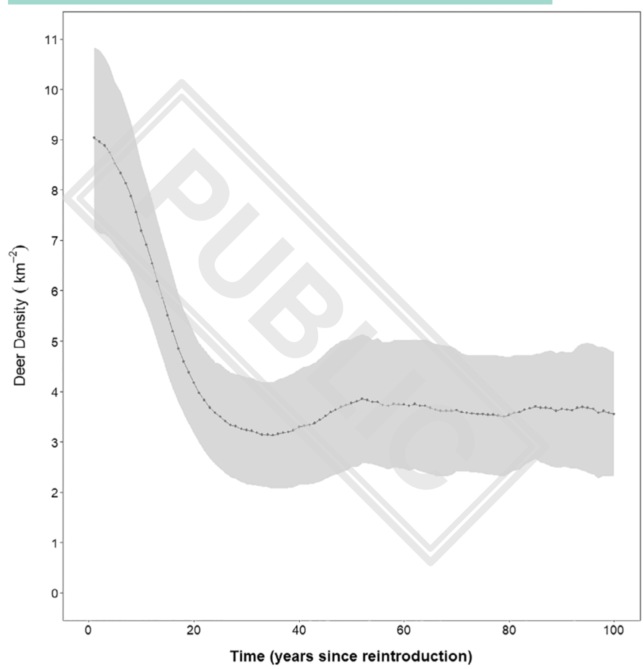

FIGURE 3 Predicted deer dynamics in the Central Highlands after a wolf reintroduction. Mean red deer density (black line) and ±1 standard deviation (grey shading).

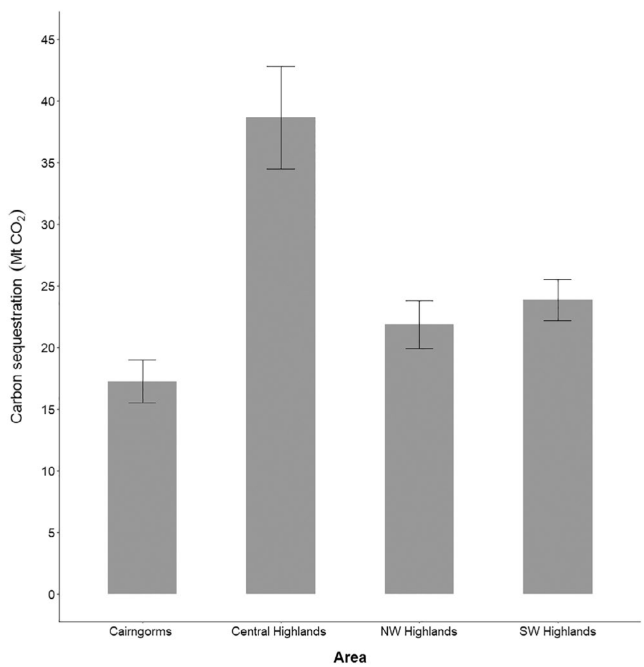

FIGURE 4 Potential carbon sequestration from native woodland expansion over a 100 year period after wolf reintroduction. Error bars show the estimated uncertainty (see Section 2).

reintroduction has an estimated value of £2580 million ± £230 million over a 100 year period (US $3250 million ± $290 million). At the annual scale, wolf reintroduction would be worth an average of £25.8 million ± £2.3 million per year (US $32.5 million ± $3 million). Assuming a population of 167 wolves, this means that each wolf would be worth an average of £154,000 ± £25,000 per year

($194,000 ± $32,000) over the 100 year period. Hoag et al. (2023) used a willingness-to-pay method to estimate an annual benefit of US$115 million for a population of 200 wolves in Colorado following a recent reintroduction, equivalent to an annual benefit of $575,000 for each wolf. We acknowledge that our financial analysis is simplistic and merely represents the potential value from carbon sequestration. As such our estimate undervalues the functional role that wolves play in sustaining the ecosystem and the wide range of resulting ecosystem services. Furthermore, our estimate does not include the upfront costs of establishing wolves in the environment, any ongoing management costs to maintain wolves in a human dominated landscape or any opportunity costs associated with the presence of wolves. Furthermore, the costs of tree planting in places without an adequate seed source for natural colonisation are not included. Future work is needed to complete a full economic valuation.

We explored the sensitivity of our analysis to several key variables. The reported uncertainty in our estimates (see Table 1) includes the key uncertainties in the wolf model as identified by Nilsen et al. (2007). Together these result in an estimated uncertainty in carbon sequestration values of approximately ±10%. We also explore uncertainties in the threshold deer population below which natural regeneration is not suppressed by browsing. If deer numbers need to be below 7 km^{-2} to facilitate natural regeneration of trees, wolves reduce deer numbers below this threshold more rapidly and the total carbon sequestration is increased by ~14% to 1.14 Mt CO_2 per year over a 100 year period. This increases the financial benefit to £29 million per year meaning each wolf would deliver an annual financial benefit of £173,000. Our financial benefits use 2023 Woodland Carbon Code Prices, but carbon prices are likely to rise in the future.

Our analysis quantifies the impacts of a potential wolf reintroduction on red deer and the subsequent impacts on vegetation, woodland regeneration and carbon storage. We note that an increased culling of red deer and improved deer management would also lead to some of the benefits outlined here (Gullett et al., 2023; Kirkland et al., 2021; Rao, 2017). However, the full functional role that wolves play in a landscape and the wide suite of benefits they provide is difficult to fully replicate through management alone (Martin et al., 2020).

The financial benefit associated with carbon would be in addition to other well documented economic and ecological impacts from wolf reintroduction, which include, ecotourism (Duffield, 2019), a reduction in deer-related road traffic accidents (Gilbert et al., 2017; Raynor et al., 2021), a reduction in Lyme disease associated with deer (Levi et al., 2014) and a broad spectrum of ecological benefits relating from the reestablishment of reduced herbivory and modified herbivore behaviour (Martin et al., 2020). A wolf reintroduction could reduce the costs of a deer culls (Nilsen et al., 2007). In this work we reduce the rate of hind harvest rate if deer populations fall below 8 km^{-2}. In Scotland, a reduction in hind harvest rate would result in reduced costs to the land owner or land manager but we do not attempt to quantify these savings. We note that this is context specific: in other regions of Europe hunters pay a fee to hunt and a reduction in hunting opportunities associated with reduced hind harvest rate would be an economic loss. A reduction in wild herbivores could improve availability of vegetation for livestock (Prowse et al., 2015). Expansion of woodland would have a range of other benefits beyond carbon sequestration, including natural flood management (Monger et al., 2022, 2024; Harvey & Henshaw, 2023) and enhanced biodiversity (Burton et al., 2018). Herbivore pressure has resulted in mountain woodland being a particularly scarce habitat in the Scottish Highlands; expansion of this habitat will bring a wide range of benefits (Watts & Jump, 2022).

Conflict between humans and wolves is substantial and there are major challenges to coexistence (Martin et al., 2020). Substantial and widespread stakeholder and public engagement would be needed prior to any wolf reintroduction to identify potentially affected groups including farmers, foresters, gamekeepers and hunters (Niemiec et al., 2020; Wilson & Campera, 2024). Human-wildlife conflicts involving carnivores are common and must be addressed, through public policies that account for people's attitudes (Huber et al., 2008), for a reintroduction to be successful. One major source of conflict is predation of livestock (Treves et al., 2004) and the impacts on farmers (Zahl-Thanem et al., 2020). Where wolves have expanded their range in Europe, farmers and hunters have particularly negative attitudes (Dressel et al., 2014). In Scotland, there would be important concerns around loss of livestock, particularly sheep (Nilsen et al., 2007). Sheep stocks have declined across much of the Scottish Highlands in the last few decades (Albon et al., 2019), but concerns are still likely to be substantial. In southern Europe the presence of wild ungulates was found to reduce wolf predation on livestock (Meriggi et al., 2011; Meriggi & Lovari, 1996). In contrast to some parts of Europe (Rossa et al., 2023), deer are abundant and widespread in Scotland which may reduce the potential for livestock-wolf conflict. Developing effective methods to reduce livestock losses might help reduce wolf-human conflicts and safeguard human livelihoods (van Eeden et al., 2018). Fear of wolves is another reason for human-wolf conflict.

Across Europe, recolonization of wolves to human dominated landscapes has caused challenges (Pettersson et al., 2021) and lessons can be learned from these experiences. Likewise understanding can be gained from wolf reintroductions that have been conducted in the USA. There are ongoing debates around wolf reintroduction in other countries that could also inform discussions in the UK. For example, there are proposals to reintroduce wolves to Japan to help control increasing deer populations and reduce forest and agricultural damage (Sakurai et al., 2023). Substantial gaps in our understanding of the ecological effects of large carnivores especially in human dominated landscapes also need to be addressed (Ausilio et al., 2021; Kuijper et al., 2016).

The financial benefits associated with expansion of native woodland and subsequent carbon sequestration following a wolf reintroduction may influence landowner and land manager opinions around large carnivores, though economic motivations are only one aspect of decision making (Thomas et al., 2015). Carefully designed benefit sharing mechanisms would be needed to ensure that financial benefits were distributed in an equitable way and that any livelihoods negatively impacted by wolves were adequately compensated. The design of these compensation schemes could be informed by policies and practices in countries where wolf populations have already recovered or where recent reintroductions have occurred (Hoag et al., 2023).

There are ongoing discussions around the interactions between predators and prey and the extent to which prey populations are controlled by predators and vice-versa. There is evidence of ecological change in landscapes that have lost or gained large carnivores (Atkins et al., 2019; Ripple et al., 2014) that demonstrates the role played by large carnivores. Long-term monitoring of wolves in Italy spanning more than four decades provides important information on the expansion of wolves and the interaction with prey species in a human-dominated landscape (Dondina et al., 2015; Meriggi et al., 1991, 1996, 2015; Torretta et al., 2024). Where deer numbers have increased they become an increasing component of wolf diet (Torretta et al., 2024).

Our work does not account for changes in nutrient cycling (le Roux et al., 2018) or behavioural adaptations of prey to the return of predators (Gerber et al., 2024) which can result in additional impacts on plant communities (Fortin et al., 2005). Predators have been shown to impact prey behaviour even when predators are at low densities (Laundré et al., 2001). This means we may underestimate the impacts of a potential return of wolves on vegetation and nutrient cycling. However, in some studies in Europe, wolves and roe deer show low spatial avoidance at a landscape scale although changes in activity patterns were documented (Torretta et al., 2016). Future work is needed to further understand behavioural adaptations of prey, particularly in human dominated landscapes (Gerber et al., 2024). Future modelling studies will then be need that include these interactions. The presence and abundance of seed sources or the impact of ground cover composition in the rate of natural colonisation was not accounted for in our analysis. The density of new saplings is typically greatest close to adult seed sources (Murphy et al., 2022), though natural colonisation is recorded at substantial distances from a seed source (Bauld et al., 2023; Spracklen et al., 2013). It is likely that in some areas, lack of suitable seed source will limit the rate of natural regeneration (Bunce et al., 2014). Ground cover composition can also hinder seedling establishment (Tanentzap et al., 2013) and some selective disturbance may be necessary for tree colonisation (Sandom et al., 2013). Tree planting or direct seeding (Willoughby et al., 2019) will be required to establish woodlands in some areas. Targeted tree planting to establish seed sources for subsequent natural colonisation and regeneration may be a way to accelerate woodland creation through natural colonisation (Williams et al., 2024). We also recognise that other conditions need to be met to facilitate natural colonisation such as the absence of prescribed moorland burning which is widespread in some parts of Scotland (Spracklen & Spracklen, 2023).

Our analysis does not consider the impacts of changing herbivore dynamics and woodland expansion on soil carbon. Total carbon stocks to 1 m depth in Scotland are estimated to be 3056 Mt (Rees et al., 2018), making it a significant national carbon store and important to consider in the context of land use change. In temperate forests the presence of ungulate herbivores has been shown to negatively affect inputs to soil C through plant litter, subsequently impacting below-ground C stocks, however responses are highly dependent on the type of vegetation and herbivores, making it difficult to generalise (Mayer et al., 2020; Tanentzap & Coomes, 2012). In contrast, soil disturbance associated with tree planting can potentially lead to soil carbon losses particularly on high carbon content soils such as those which cover much of upland Scotland (Friggens et al., 2020; Warner et al., 2022). Consequently, woodland expansion as a consequence of a wolf reintroduction may reduce the potential for loss of soil organic carbon both through a reduction in herbivore density increasing litter inputs combined with the lower soil disturbance associated with natural colonisation. A better understanding of soil carbon dynamics is critical to future projections of carbon sequestration potential from native woodland expansion, either through tree planting or natural colonisation, which are both currently constrained by a lack of UK-based evidence.

4 | CONCLUSIONS

Our analysis shows that a wolf reintroduction to the Scottish Highlands could reduce red deer numbers sufficiently to lead to natural colonisation of trees and expansion of native woodlands with associated carbon sequestration benefits. We used a model of wolf–red deer dynamics to estimate a wolf reintroduction to four areas of the Scottish Highlands covering 12,167 km^2 would lead to a total wolf population of 167 ± 23 individuals. Our modelling approach included a number of important simplifications: we assumed that wolves could not leave the reintroduction area, we did not account for alterations in behaviour of prey, changes in nutrient cycling or human-wolf conflicts. Future work is needed to address these simplifications. Wolves reduce simulated average red deer populations to less than 4 km^{-2} within 20 to 23 years after reintroduction. We used a model of native woodland potential to estimate expansion of native woodlands would sequester 100 Mt CO_2 over a 100 year period (average annual carbon sequestration of 1.0 ± 0.1 Mt CO_2) sufficient to make an important contribution to national climate targets. This substantial carbon sequestration and the potential financial benefit related to wolf reintroduction may influence landowner and land manager perspectives around large carnivores. Carefully designed benefit sharing mechanisms would be needed to ensure any financial benefits are shared equitably across landowners, land managers and local communities. Comprehensive stakeholder engagement would be needed well in advance of any proposed reintroduction to identify potentially affected groups and address challenges of co-existing with large carnivores. Our work provides further evidence of the role of large carnivores in assisting ecosystem recovery and delivering the nature-based solutions required to address the climate emergency.

AUTHOR CONTRIBUTIONS

Dominick V. Spracklen conceived the analysis; Dominick V. Spracklen and Jude V. Lane conducted the wolf–deer modelling; Tasmin

Fletcher completed the native woodland analysis; Erlend B. Nilsen advised on the wolf model; all authors contributed to discussions and commented on the paper.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no competing interests.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The Native Woodland Model data are available at https://openscience.hutton.ac.uk/dataset/native-woodland-model-2004 (Donnelly, 2004). The Wild Land Area data are available at https://gis-downloads.nature.scot/WLA_SCOTLAND_SHP_27700.zip (NatureScot Chapron et al., 2014).

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources Natural colonisation, Native woodland, Reintroduction.

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REFERENCES

Albon, S. D., McLeod, J., Potts, J., Irvine, J., Fraser, D., & Newey, S. (2019). Updating the estimates of national trends and regional differences in red deer densities on open-hill ground in Scotland. Scottish Natural Heritage Research Report No. 1149.

Atkins, J. L., Long, R. A., Pansu, J., Daskin, J. H., Potter, A. B., Stalmans, M. E., Tarnita, C. E., & Pringel, R. M. (2019). Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science*, *364*, 173–177. https://doi.org/10.1126/science.aau3561

Ausilio, G., Sand, H., Månsson, J., Mathisen, K. M., & Wikenros, C. (2021). Ecological effects of wolves in anthropogenic landscapes: The potential for trophic cascades is context-dependent. *Frontiers in Ecology and Evolution*, *8*. https://doi.org/10.3389/fevo.2020.577963

Bauld, J., Guy, M., Hughes, S., Forster, J., & Watts, K. (2023). Assessing the use of natural colonization to create new forests within temperate agriculturally dominated landscapes. *Restoration Ecology*, *30*(8), e14004. https://doi.org/10.1111/rec.14004

Beaumont, D., Dugan, D., Evans, G., & Taylor, S. (1995). Deer management and tree regeneration in the RSPB Reserve at Abernethy Forest. *Scottish Forestry*, *49*, 155–161.

Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, *142*(11), 2401–2414. https://doi.org/10.1016/j.biocon.2009.06.015

Bunce, R. G. H., Wood, C. M., Smart, S. M., Oakley, R., Browning, G., Daniels, M. J., Ashmole, P., & Cresswell, J. (2014). The landscape ecological impacts of afforestation in the British uplands and some initiatives to restore native woodland cover. *Journal of Landscape Ecology*, *7*, 5–24. https://doi.org/10.2478/jlecol-2014-0013

Burton, V., Moseley, D., Brown, C., Metzger, M. J., & Bellamy, P. (2018). Reviewing the evidence base for the effects of woodland expansion on biodiversity and ecosystem services in the United Kingdom. *Forest Ecology and Management*, *430*, 366–379. https://doi.org/10.1016/j.foreco.2018.08.003

Chapron, G., Kaczensky, P., Linnell, J. D., von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., … Boitani, L. (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., Ranc, N., Benítez-lópez, A., Maiorano, L., Boitani, L., Cagnacci, F., Čengić, M., Ciucci, P., Huijbregts, M. A. J., Krofel, M., López-Bao, J. V., Selva, N., Andren, H., Bautista, C., Ćirović, D., Hemmingmoore, H., Reinhardt, I., Marenče, M., … Santini, L. (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. *Diversity and Distributions*, *27*, 602–617. https://doi.org/10.1111/ddi.13219

Clutton-Brock, T. H., Coulson, T., & Milner, J. M. (2004). Red deer stocks in the highlands of Scotland. *Nature*, *429*, 261–262. https://doi.org/10.1038/429261a

Clutton-Brock, T. H., Coulson, T., Milner-Gulland, E. J., Armstrong, H. M., & Thomson, D. (2002). Sex differences in emigration and mortality affect optimal management of deer populations. *Nature*, *415*, 633–637. https://doi.org/10.1038/415633a

Clutton-Brock, T. H., & Coulson, T. N. (2002). Ungulate population dynamics: The devil is in the detail. *Philosophical Transactions of the Royal Society*, *357*, 1299–1306. https://doi.org/10.1098/rstb.2002.1128

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. (1982). *Red Deer: Behaviour and ecology of two sexes*. University of Chicago Press.

Convery, I., Nevin, O., Blackshaw-Crosby, E., Brady, D., & Fisher, M. (2023). The case for wolves in the UK. In *The Wolf*. Boydell and Brewer. https://doi.org/10.1515/9781805430551-031

Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C., & Waller, D. M. (2004). Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics*, *35*, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725

Cretois, B., Linnell, J. D. C., Van Moorter, B., Kaczensky, P., Nilsen, E. B., Parada, J., & Rød, J. K. (2021). Coexistence of large mammals and humans is possible in Europe's anthropogenic landscapes. *iScience*, *24*(9), 103083. https://doi.org/10.1016/j.isci.2021.103083

Cromsigt, J. P. G. M., te Beest, M., Kerley, G. I. H., Landman, M., le Roux, E., & Smith, F. A. (2018). Trophic rewilding as a climate change mitigation strategy? *Philosophical Transactions of the Royal Society B*, *373*, 20170440. https://doi.org/10.1098/rstb.2017.0440

Dondina, O., Meriggi, A., Dagradi, V., Perversi, M., & Milanesi, P. (2015). Wolf predation on livestock in an area of northern Italy and prediction of damage risk. *Ethology Ecology and Evolution*, *2015*(27), 200–219. https://doi.org/10.1080/03949370.2014.916352

Donnelly, D. (2004). The James Hutton Institute. Data from: Native Woodland Model 2004. https://openscience.hutton.ac.uk/dataset/native-woodland-model-2004

Dressel, S., Sandström, C., & Ericsson, G. (2014). A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. *Conservation Biology*, *29*(2), 565–574. https://doi.org/10.1111/cobi.12420

Duffield, J. (2019). Shopping for wolves: Using nonmarket valuation for informing conservation districts. In R. Rasker (Ed.), *People and public lands*. Headwaters Economics.

Edwards, T., & Kenyon, W. (2013). Scottish parliament information centre: wild deer in Scotland. [cited 2014 January 8]. Available from: http://www.scottish.parliament.uk/ResearchBriefingsAndFactsheets/S4/SB_13-74.

Emerson, L. D., Wittmer, H. U., Elbroch, M., Kostoglou, K., Bannister, K. J., Psaila, J. J., Whisson, D., & Ritchie, E. G. (2024). A global assessment of large terrestrial carnivore kill rates. *Biological Reviews*, *100*(1), 327–350. https://doi.org/10.1111/brv.13143

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fletcher, T. I., Scott, C. E., Hall, J., & Spracklen, D. V. (2021). The carbon sequestration potential of Scottish native woodland. *Environmental Research Communications*, *3*, 041003. https://doi.org/10.1088/2515-7620/abf467

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*, 1320–1330. https://doi.org/10.1890/04-0953

Friggens, N. L., Hester, A. J., Mitchell, R. J., Parker, T. C., Subke, J. A., & Wookey, P. A. (2020). Tree planting in organic soils does not result in net carbon sequestration on decadal timescales. *Global Change Biology*, *26*(9), 5178–5188. https://doi.org/10.1111/gcb.15229

Fuller, R. J., & Gill, R. M. (2001). Ecological impacts of increasing numbers of deer in British woodland. *Forestry*, *74*, 193–199. https://doi.org/10.1093/forestry/74.3.193

Gazzola, A., Avanzinelli, E., Bertelli, I., Tolosano, A., Bertotto, P., Musso, R., & Apollonio, M. (2007). The role of the wolf in shaping a multispecies ungulate community in the Italian western Alps. *The Italian Journal of Zoology*, *74*(3), 297–307. https://doi.org/10.1080/11250000701447074

Gerber, N., Riesch, F., Bojarska, K., Zetsche, M., Rohwer, N.-K., Signer, J., Isselstein, J., Herzog, S., Okarma, H., Kuijper, D. P. J., & Balkenhol, N. (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

Gilbert, S. L., Sivy, K. J., Pozzanghera, C. B., DuBour, A., Overduijn, K., Smith, M. M., Zhou, J., Little, J. M., & Prugh, L. R. (2017). Socioeconomic benefits of large carnivore recolonization through reduced wildlife-vehicle collisions. *Conservation Letters*, *10*, 431–439. https://doi.org/10.1111/conl.12280

Gonzalez, M. N., Berl, R. E. W., Teel, T. L., & Niemiec, R. (2024). The impact of social norms on intended individual and collective civic actions related to wolf reintroduction. *Society & Natural Resources*, *37*(8), 1–17. https://doi.org/10.1080/08941920.2024.2335400

Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamäki, J. V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R. T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M. R., … Fargione, J. (2017). Natural climate solutions. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(44), 11645–11650. https://doi.org/10.1073/pnas.1710465114

Gullett, P. R., Leslie, C., Mason, R., Ratcliffe, P., Sargent, I., Beck, A., Cameron, T., Cowie, N. R., Hetherington, D., MacDonell, T., Moat, T., Moore, P., Teuten, E., & Hancock, M. H. (2023). Woodland expansion in the presence of deer: 30 years of evidence from the Cairngorms Connect landscape restoration partnership. *Journal of Applied Ecology*, *60*(11), 2298–2308. https://doi.org/10.1111/1365-2664.14501

Gwynn, V., & Symeonakis, E. (2022). Rule-based habitat suitability modelling for the reintroduction of the grey wolf (*Canis lupus*) in Scotland. *PLoS One*, *17*(10), e0265293. https://doi.org/10.1371/journal.pone.0265293

Harvey, G. L., & Henshaw, A. J. (2023). Rewilding and the water cycle. *Wiley Interdisciplinary Reviews: Water*, *10*, e1686. https://doi.org/10.1002/wat2.1686

Hetherington, D. A., Lord, T. C., & Jacobi, R. M. (2006). New evidence for the occurrence of the Eurasian lynx (*Lynx lynx*) in medieval Britain. *Journal of Quaternary Science*, *21*(1), 3–8. https://doi.org/10.1002/jqs.960

Hindrikson, M., Remm, J., Pilot, M., Godinho, R., Vik Stronen, A., Baltrunaité, L., Czarnomska, S. D., Leonard, J. A., Randi, E., Nowak, C., Akesson, M., Lopez-Bao, J. V., Alvares, F., Llaneza, L., Echegaray, J., Vilà, C., Ozolins, J., Rungis, D., Aspi, J., … Saarma, U. (2017). Wolf population genetics in Europe: A systematic review, meta-analysis and suggestions for conservation and management. *Biological Reviews*, *72*, 248–270. https://doi.org/10.1111/brv.12298

Hoag, D. L. K., Burkhardt, J., Ghasemi, B., Breck, S., Niemiec, R., & Crooks, K. (2023). Willingness to pay for reintroducing wolves in a divided voting base. *Global Ecology and Conservation*, *46*, e02576. https://doi.org/10.1016/j.gecco.2023.e02576

Hobbs, N. T., Johnston, D. B., Marshall, K. N., Wolf, E. C., & Cooper, D. J. (2024). Does restoring apex predators to food webs restore ecosystems? Large carnivores in Yellowstone as a model system. *Ecological Monographs*, *94*(2), e1598. https://doi.org/10.1002/ecm.1598

Huber, D., Kusak, J., Majić-Skrbinšek, A., Majnarić, D., & Sindičić, M. (2008). A multidimensional approach to managing the European brown bear in Croatia. *Ursus*, *19*, 22–32.

Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva, N., Zub, K., & Szymura, L. (2002). Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). *Ecology*, *83*, 1341–1356. https://doi.org/10.1890/0012-9658(2002)083[1341:KRAPBW]2.0.CO;2

Kirkland, H., Hare, D., Daniels, M., Krofel, M., Rao, S., Chapman, T., & Blossey, B. (2021). Successful deer management in Scotland requires less conflict not more. *Frontiers in Conservation Science*, *2*, 770303. https://doi.org/10.3389/fcosc.2021.770303

Kuijper, D. P. J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 1841. https://doi.org/10.1098/rspb.2016.1625

Laundré, J. W., Hernández, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: Reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*, 1401–1409. https://doi.org/10.1139/z01-094

le Roux, E., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2018). Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*, *28*, 2493–2499. https://doi.org/10.1016/j.cub.2018.05.088

Leroux, S. J., Wiersma, Y. F., & Vander Wal, E. (2020). Herbivore impacts on carbon cycling in boreal forests. *Trends in Ecology & Evolution*, *35*(11), 1001–1010. https://doi.org/10.1016/j.tree.2020.07.009

Levi, T., Kilpatrick, A. M., & Wilmers, C. C. (2014). Deer, predators, and the emergence of Lyme disease. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(27), 10942–10947. https://doi.org/10.1073/pnas.1204536109

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Hobbs, N. T., & Sand, H. (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*, 910–915. https://doi.org/10.1098/rspb.2011.1275

Manning, A. D., Gordon, I. J., & Ripple, W. J. (2009). Restoring landscapes of fear with wolves in the Scottish Highlands. *Biological Conservation*, *142*(10), 2314–2321. https://doi.org/10.1016/j.biocon.2009.05.007

Martin, J.-L., Chamaillé-Jammes, S., & Waller, D. M. (2020). Deer, wolves, and people: Costs, benefits and challenges of living together.

Biological Reviews, *95*(3), 782–801. https://doi.org/10.1111/brv.12587

Mayer, M., Prescott, C. E., Abaker, W. E. A., Augusto, L., Cécillon, L., Ferreira, G. W. D., James, J., Jandl, R., Katzensteiner, K., Laclau, J.-P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J. A., Vanguelova, E. I., & Vesterdal, L. (2020). Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. *Forest Ecology and Management*, *466*, 118127. https://doi.org/10.1016/j.foreco.2020.118127

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

Meriggi, A., Brangi, A., Schenone, L., Signorelli, D., & Milanesi, P. (2011). Changes of wolf (*Canis lupus*) diet in Italy in relation to the increase of wild ungulate abundance. *Ethology Ecology & Evolution*, *23*(3), 195–210. https://doi.org/10.1080/03949370.2011.577814

Meriggi, A., Dagradi, V., Dondina, O., Perversi, M., Milanesi, P., Lombardini, M., Raviglione, S., & Repossi, A. (2015). Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in northern Italy. *Ethology Ecology and Evolution*, *27*, 389–411. https://doi.org/10.1080/03949370.2014.986768

Meriggi, A., & Lovari, S. (1996). A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? *Journal of Applied Ecology*, *33*(6), 1561–1571. https://doi.org/10.2307/2404794

Meriggi, A., Rosa, P., Brangi, A., & Matteucci, C. (1991). Habitat use and diet of the wolf in northern Italy. *Acta Theriologica*, *36*, 141–151. https://doi.org/10.4098/AT.arch.91-11

Miller, G., Cummings, R., & Hester, A. (1998). *Scottish forestry*. Royal Scottish Forestry Society.

Milner-Gulland, E. J., Coulson, T., & Clutton-Brock, T. H. (2004). Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*. *Wildlife Biology*, *10*(3), 187–201. https://doi.org/10.2981/wlb.2004.025

Mitchell, B., Staines, B. W., & Welch, D. (1977). *Ecology of Red Deer*. Institute of Terrestrial Ecology.

Monger, F., Spracklen, D. V., Kirkby, M. J., & Schofield, L. (2022). The impact of semi-natural broadleaf woodland and pasture on soil properties and flood discharge. *Hydrological Processes*, *36*(1), e14453. https://doi.org/10.1002/hyp.14453

Monger, F., Spracklen, D. V., Kirkby, M. J., & Willis, T. (2024). Investigating the impact of woodland placement and percentage cover on flood peaks in an upland catchment using spatially distributed TOPMODEL. *Journal of Flood Risk Management*, *17*, e12977. https://doi.org/10.1111/jfr3.12977

Murphy, T. R., Hanley, M. E., Ellis, J. S., & Lunt, P. H. (2022). Optimizing opportunities for oak woodland expansion into upland pastures. *Ecological Solutions and Evidence*, *3*(1), e12126. https://doi.org/10.1002/2688-8319.12126

Native Woodland Survey of Scotland. (2014). Forestry Commission Scotland. 978 0 85538 899 7.

NatureScot. (2014). Wild land areas 2014. Data from: NatureScot GIS Downloads. https://gis-downloads.nature.scot/WLA_SCOTLAND_SHP_27700.zip

Niemiec, R., Berl, R. E. W., Gonzalez, M., Teel, T., Camara, C., Collins, M., Salerno, J., Crooks, K., Schultz, C., Breck, S., & Hoag, D. (2020). Public perspectives and media reporting of wolf reintroduction in Colorado. *PeerJ*, *8*, e9074. https://doi.org/10.7717/peerj.9074

Nilsen, E. B., Milner-Gulland, E. J., Schofield, L., Mysterud, A., Stenseth, N. C., & Coulson, T. (2007). Wolf reintroduction to Scotland: Public attitudes and consequences for red deer management. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 995–1003. https://doi.org/10.1098/rspb.2006.0369

Palmer, S. C. F., Mitchell, R. J., Truscott, A.-M., & Welch, D. (2004). Regeneration failure in Atlantic oakwoods: The roles of ungulate grazing and invertebrates. *Forest Ecology and Management*, *192*(2–3), 251–265. https://doi.org/10.1016/j.foreco.2004.01.038

Palmer, S. C. F., & Truscott, A.-M. (2003). Browsing by deer on naturally regenerating Scots pine (*Pinus sylvestris* L.) and its effects on sapling growth. *Forest Ecology and Management*, *182*(1–3), 31–47. https://doi.org/10.1016/S0378-1127(03)00026-4

Palmer, S. C. F., Truscott, A.-M., Mitchell, R. J., & Welch, D. (2009). Regeneration in Atlantic oakwoods: Has deer management had a beneficial effect? *Botanical Journal of Scotland*, *57*(1–2), 167–178. https://doi.org/10.1080/03746600508685095

Passoni, G., Coulson, T., Cagnacci, F., Hudson, P., Stahler, D. R., Smith, D. W., & Lachish, S. (2024). Investigating tritrophic interactions using bioenergetic demographic models. *Ecology*, *105*(1), e4197. https://doi.org/10.1002/ecy.4197

Pepper, S., Barbour, A., & Glass, J. (2020). *The management of wild deer in Scotland*, Report of the Deer Working Group, ISBN: 978–1–83960-525-3. The Scottish Government.

Perks, M. P., Nagy, L., Meir, P., Auld, M., Wood, M., Atkinson, N., Staples-Scott, L., Harvey, G., McGhee, W., & Tipper, R. (2010). *Carbon sequestration benefits of new native woodland expansion in Scotland*. Scottish Forest Alliance.

Pettersson, H. L., Quinn, C. H., Holmes, G., Sait, S. M., & López-Bao, J. V. (2021). Welcoming wolves? Governing the return of large carnivores in traditional pastoral landscapes. *Frontiers in Conservation Science*, *2*, 710218. https://doi.org/10.3389/fcosc.2021.710218

Pörtner, H.-. O., Pörtner, H.-O., Scholes, R. J., Agard, J., Archer, E., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W. L., Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M. A., Handa, C., Hickler, T., Hoegh-Guldberg, O., … Ngo, H. (2021). *Scientific outcome of the IPBES-IPCC co-sponsored workshop on biodiversity and climate change*. (p. 252).

Prowse, T. A. A., Johnson, C. N., Cassey, P., Bradshaw, C. J. A., & Brook, B. W. (2015). Ecological and economic benefits to cattle rangelands of restoring an apex predator. *Journal of Applied Ecology*, *52*, 455–466. https://doi.org/10.1111/1365-2664.12378

Rao, S. J. (2017). Effect of reducing red deer *Cervus elaphus* density on browsing impact and growth of scots pine *Pinus sylvestris* seedlings in semi-natural woodland in the Cairngorms, UK. *Conservation Evidence*, *14*, 22–26.

Raynor, J. L., Grainger, C. A., & Parker, D. P. (2021). Wolves make roadways safer, generating large economic returns to predator conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(22), e2023251118. https://doi.org/10.1073/pnas.2023251118

Rees, R. M., Buckingham, S., Chapman, S. J., Jones, S., Lilly, A., Matthews, R. B., Morison, J. I. L., Perks, M., Vanguelova, E., Yamulki, S., & Yeluripati, J. (2018). Soil carbon and land use in Scotland. https://www.climatexchange.org.uk/media/3046/soil-carbon-and-land-use-in-scotland.pdf

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. (2014). Status and ecological effects of the world's largest carnivores. *Science*, *343*(6167), 1241484. https://doi.org/10.1126/science.1241484

Rizzuto, M., Leroux, S. J., & Schmitz, O. J. (2024). Rewiring the carbon cycle: A theoretical framework for animal-driven ecosystem carbon sequestration. *JGR Biogeosciences*, *129*(4), e2024JG008026. https://doi.org/10.1029/2024JG008026

Rossa, M., Torres, R. T., Linck, P., Martins, R., Couto, A., Aliácar, S., Hipólito, D., Brotas, G., Fonseca, C., & Carvalho, J. (2023). Environmental favorability models as a tool to support trophic rewilding initiatives. *Restoration Ecology*, *32*(3), e14048. https://doi.org/10.1111/rec.14048

Sakurai, R., Tsunoda, H., Enari, H., & Stedman, R. C. (2023). Public attitudes and intentions toward engaging in reintroduction of wolves to Japan. *Conservation Biology*, *37*(6), e14130. https://doi.org/10.1111/cobi.14130

Sandom, C., Bull, J., Canney, S., & Macdonald, D. W. (2012). Exploring the value of wolves (*Canis lupus*) in landscape-scale fenced reserves for ecological restoration in the Scottish Highlands. In M. J. Somers & M. Hayward (Eds.), *Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes?* (pp. 245–276). Springer New York. https://doi.org/10.1007/978-1-4614-0902-1_14

Sandom, C. J., Hughes, J., & Macdonald, D. W. (2013). Rooting for rewilding: Quantifying wild boar's sus scrofa rooting rate in the Scottish Highlands. *Restoration Ecology*, *21*(3), 329–335. https://doi.org/10.1111/j.1526-100X.2012.00904.x

Schmitz, O. J., & Leroux, S. J. (2020). Food webs and ecosystems: Linking species interactions to the carbon cycle. *Annual Review of Ecology, Evolution, and Systematics*, *51*(1), 271–295. https://doi.org/10.1146/annurev-ecolsys-011720-104730

Schmitz, O. J., Sylvén, M., Atwood, T. B., Bakker, E. S., Berzaghi, F., Brodie, J. F., Cromsigt, J. P. G. M., Davies, A. B., Leroux, S. J., Schepers, F. J., Smith, F. A., Stark, S., Svenning, J. C., Tilker, A., & Ylänne, H. (2023). Trophic rewilding can expand natural climate solutions. *Nature Climate Change*, *13*, 324–333. https://doi.org/10.1038/s41558-023-01631-6

Schmitz, O. J., Wilmers, C. C., Leroux, S. J., Doughty, C. E., Atwood, T. B., Galetti, M., Davies, A. B., Goetz, S. J. (2018). Animals and the zoogeochemistry of the carbon cycle. *Science*, *362*(6419), eaar3213. https://doi.org/10.1126/science.aar3213

Seddon, P., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, *345*(6195), 406–412. https://doi.org/10.1126/science.1251818

Smith, P., Calvin, K., Nkem, J., Campbell, D., Cherubini, F., Grassi, G., Korotkov, A., Hoang, L., Lwasa, S., McElwee, P., Nkonya, E., Saigusa, N., Soussana, J.-F., Taboada, M. A., Manning, F. C., Nampanzira, D., Arias-Navarro, C., Vizzarri, M., House, J., … Arneth, A. (2019). Which practices co-deliver food security, climate change mitigation and adaptation, and combat land degradation and desertification? *Global Change Biology*, *26*(3), 1532–1575. https://doi.org/10.1111/gcb.14878

Spracklen, B. D., Lane, J. V., Spracklen, D. V., Williams, N., & Kunin, W. E. (2013). Regeneration of native broadleaved species on clearfelled conifer plantations in upland Britain. *Forest Ecology and Management*, *310*(15), 204–212. https://doi.org/10.1016/j.foreco.2013.08.001

Spracklen, B. D., & Spracklen, D. V. (2023). Assessment of peatland burning in Scotland during 1985–2022 using Landsat imagery. *Ecological Solutions and Evidence*, *4*(4), e12296. https://doi.org/10.1002/2688-8319.12296

Staines, B. W. (1995). The impact of red deer on the regeneration of native pinewoods. In J. R. Aldhous (Ed.), *Our Pinewood Heritage* (pp. 107–114). Forestry Commission.

Strickland, M. S., Hawlena, D., Reese, A., & Schmitz, O. J. (2013). Trophic cascade alters ecosystem carbon exchange. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(27), 11035–11038. https://doi.org/10.1073/pnas.1305191110

Suraci, J. P., Clinchy, M., Dill, L. M., Roberts, D., & Zanette, L. Y. (2016). Fear of large carnivores causes a trophic cascade. *Nature Communications*, *7*, 10698. https://doi.org/10.1038/ncomms10698

Tanentzap, A. J., & Coomes, D. A. (2012). Carbon storage in terrestrial ecosystems: Do browsing and grazing herbivores matter? *Biological Reviews*, *87*(1), 72–94. https://doi.org/10.1111/j.1469-185X.2011.00185.x

Tanentzap, A. J., Zou, J., & Coomes, D. A. (2013). Getting the biggest birch for the bang: Restoring and expanding upland birchwoods in the Scottish Highlands by managing red deer. *Ecology and Evolution*, *3*(7), 1890–1901. https://doi.org/10.1002/ece3.548

Thomas, H. J. D., Paterson, J. S., Metzger, M. J., & Sing, L. (2015). Towards a research agenda for woodland expansion in Scotland. *Forest Ecology and Management*, *349*, 149–161. https://doi.org/10.1016/j.foreco.2015.04.003

Torretta, E., Brangi, A., & Meriggi, A. (2024). Changes in wolf occupancy and feeding habits in the northern Apennines: Results of Long-term predator–prey monitoring. *Animals*, *14*(5), 735. https://doi.org/10.3390/ani14050735

Torretta, E., Serafini, M., Imbert, C., Milanesi, P., & Meriggi, A. (2016). Wolves and wild ungulates in the Ligurian Alps (western Italy): Prey selection and spatial-temporal interactions. *Mammalia*, *81*, 537–551.

Towers, W., Hall, J., Hester, A., Malcolm, A., & Stone, D. (2004). *The potential for native woodland in Scotland: The native woodland model*. Scottish Natural Heritage.

Treves, A., Naughton-Treves, L., Harper, E. K., Mladenoff, D. J., Rose, R. A., Sickley, T. A., & Wydeven, A. P. (2004). Predicting human-carnivore conflict: A spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology*, *18*(1), 114–125. https://doi.org/10.1111/j.1523-1739.2004.00189.x

van Eeden, L. M., Eklund, A., Miller, J. R. B., López-Bao, J. V., Chapron, G., Cejtin, M. R., Crowther, M. S., Dickman, C. R., Frank, J., Krofel, M., Macdonald, D. W., McManus, J., Meyer, T. K., Middleton, A. D., Newsome, T. M., Ripple, W. J., Ritchie, E. G., Schmitz, O. J., Stoner, K. J., … Treves, A. (2018). Carnivore conservation needs evidence-based livestock protection. *PLoS Biology*, *16*(9), e2005577. https://doi.org/10.1371/journal.pbio.2005577

Warner, E., Lewis, O. T., Brown, N., Green, R., McDonnell, A., Gilbert, D., & Hector, A. (2022). Does restoring native forest restore ecosystem functioning? Evidence from a large-scale reforestation project in the Scottish Highlands. *Restoration Ecology*, *30*(3), e13530. https://doi.org/10.1111/rec.13530

Watts, S. H., & Jump, A. S. (2022). The benefits of mountain woodland restoration. *Restoration Ecology*, *30*(8), e13701. https://doi.org/10.1111/rec.13701

Williams, J., Sandom, C. J., & Pettorelli, N. (2024). Active management is required to regenerate the Caledonian forest: Alladale as a case study. *Ecological Solutions and Evidence*, *5*(1), e12315. https://doi.org/10.1002/2688-8319.12315

Willoughby, I. H., Jinks, R. L., & Forster, J. (2019). Direct seeding of birch, rowan and alder can be a viable technique for the restoration of upland native woodland in the UK forestry. *An International Journal of Forest Research*, *92*, 324–338. https://doi.org/10.1093/forestry/cpz018

Wilmers, C. C., & Schmitz, O. J. (2016). Effects of grey wolf-induced trophic cascades on ecosystem carbon cycling. *Ecosphere*, *7*(10), e01501. https://doi.org/10.1002/ecs2.1501

Wilson, S., & Campera, M. (2024). The perspectives of key stakeholders on the reintroduction of apex predators to the United Kingdom. *Ecologies*, *5*(1), 52–67. https://doi.org/10.3390/ecologies5010004

Woodland Carbon Code. (2023). UK Carbon Prices. https://woodlandcarboncode.org.uk/uk-land-carbon-registry/uk-carbon-prices

Zahl-Thanem, A., Burton, R. J. F., Blekesaune, A., Haugen, M. S., & Rønningen, K. (2020). The impact of wolves on psychological distress among farmers in Norway. *Journal of Rural Studies*, *78*, 1–11. https://doi.org/10.1016/j.jrurstud.2020.05.010

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OPEN

The presence of wolves leads to spatial differentiation in deer browsing pressure on forest regeneration

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With the recent return of large carnivores to forest ecosystems, an important issue for forest owners and managers is how large predators influence the behaviour of their natural prey and, consequently, cervid browsing pressure on forest regeneration. To investigate this issue, we analysed deer pressure on Scots pine and European beech plantations in northern Poland's ecosystems with and without permanent wolf populations. Two characteristics were used to describe deer browsing patterns in plantations: distance from the forest edge (spatial pattern of browsing) and number of saplings browsed (browsing intensity). Beech saplings were more intensively browsed by deer compared to pine saplings. In a forest ecosystem not inhabited by wolves, spatial variation in browsing patterns on small-sized beech plantations was the same between the edge and the center. In contrast, browsing pressure by deer was greater at the edges on large-sized pine plantations. The presence of wolves reduced deer browsing on beech and increased browsing on pine saplings. In addition, deer foraging behaviour changed in large-sized pine plantations, and browsing pressure increased only in the central areas of the plantations. We assume that the presence of wolves in a forest landscape is an important factor that alters browsing pressure on the youngest stands and their spatial pattern, and that this may be a major factor in stand regeneration, especially in small forest patches.

In recent decades, the numbers and population densities of many deer species have increased in temperate forests, including in Europe[1]. The reasons for this phenomenon lie in changes favorable to these herbivores during the twentieth century, including the disappearance of populations of large predators[1,2]. As a result, the increasing number and density of ungulates increases browsing pressure on vegetation, leading to higher losses in agricultural and forestry production[1,3]. Although it is worth noting that deer damage is not solely related to deer population density[4]. Trees and shrubs make up a significant share of the diet of wild ungulates[5,6]. Browsing of woody plants by deer is one of the major problems of modern forestry and consumes a large portion of the funds spent on tree protection in commercial forests. This problem mainly affects tree species preferred by deer, such as oaks *Quercus spp.*, hornbeams *Carpinus betulus*, silver firs *Abies alba* and Scots pines *Pinus sylvestris*[7,8].

Intense herbivore pressure on woody and shrub vegetation, while often favoring the development of herbaceous vegetation and creating favorable conditions for the maintenance of a wider range of forest plant community species[9–11], conflicts with timber production and hinders the achievement of forest management goals. Current ungulate densities in temperate and boreal forests have long-term effects on forest structure, composition and litter depth, implying that these herbivores can slow down natural succession and reduce the sapling richness[12]. Deer damage young trees primarily by browsing shoots and stripping bark. Damaged trees may die[13], develop more slowly[14], have lower biomass growth[15], and are more susceptible to damage from invertebrate infestations[16]. Loss of their main shoots also causes trees to take on a shrub form[17]. Patches of varying sizes in forest stands are attractive foraging sites for ungulates, as they find food more easily when they emerge from the closed forest[18]. Forest edges are particularly attractive to deer and thus these animals can largely shape the vegetation within them[19]. For this reason, young forest plantations are particularly vulnerable to severe damage from these herbivores. Furthermore, abundant early successional forest stands and edge habitats, together with local high deer densities, may cause significant external threats to stands near old and mature forest communities because widely wandering deer also penetrate deeply into them[20].

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In the Northern Hemisphere, large carnivores are returning to their native ecosystems[21]. In Poland, for example, the grey wolf *Canis lupus* L. populations are increasing[22,23]. With the return of wolves to forests, the question arises whether this could reduce deer pressure on forest regeneration. Predators may indirectly affect lower trophic levels by influencing prey behaviour and reducing density[24]. They limit herbivore pressure on vegetation, which creates better conditions for plant development (a trophic cascade effect[25,26]). In forest ecosystems, large carnivores can affect forest stands in this indirect way because there is a strong relationship between the extent of tree damage caused by herbivores and stand regeneration[27,28].

Large carnivores' predation risk can affect ungulate density, distribution and behaviour, probably operate at different spatial scales[29], but so far the influence of wolf presence on deer feeding behaviour at different scales (landscape, stand) has been demonstrated only in the protected Białowieża primaeval forest[29–31]. It has been argued that in natural ecosystems, like in Białowieża, large carnivores may alter the foraging behaviour of browsers at fine spatial scales (stand level), which could have long-term consequences for woody plant communities and affect forest ecosystem structure and composition[32]. In contrast, recent data from commercial forests suggest that the presence of wolves in the ecosystem does not affect or even increase damage to forest plantations caused by large herbivores such as moose *Alces alces* L. and the authors of these studies suggested that the attractiveness of the food base was the stronger factor than the risk of predation for this herbivore species[33–35]. There is limited data on the spatial pattern of foraging by deer at fine scales within gaps of different sizes. In addition, Kuijper et al.[36] concluded that in human-dominated landscapes, fear is more likely to be caused by anthropogenic disturbance (even nonlethal effects of hunter presence) than by the presence of large predators, so the intensity and spatial pattern of browsing by wild ungulates may differ from those in natural, protected ecosystems.

From a scientific and practical perspective, this knowledge is important for forest managers where deer (such as red deer *Cervus elaphus* L. and roe deer *Capreolus capreolus* L.) cause the greatest damage to young, productive stands.

The purpose of our study was to investigate whether the presence of wolves in forest ecosystems affects the intensity and spatial distribution of browsing damage by deer in pine and beech plantations, which may lead to changes in timber production and forest quality. We tested two hypotheses: (1) deer browsing intensity is lower in ecosystems where wolves are present, and (2) deer browsing intensity is higher near forest edges.

Materials and methods

Study area

The study was conducted between 2015 and 2017 in three forest districts (FD) in northern Poland: Borne Sulinowo Forest District (BS), Polanów Forest District (POL) and Manowo Forest District (MAN). BS is located near the town of Borne Sulinowo (53°34′52″ N 16°32′00″ E) and covers 204.32 km^2 of flat terrain with some slightly hilly areas. The predominant tree species is pine (about 90% of the stands). POL is located near the town of Polanów (54°07′10″ N 16°41′18″ E), covering 168.32 km2 and consists of both flat and hilly terrain. Pine and European beech (*Fagus sylvatica*) are the main tree species (together about 90% of the stands). MAN is located near the town of Manowo (54°07′30″ N 16°18′06″ E) and covers 172.03 km^2 of hilly or flat terrain. The main tree species is pine (about 84% of the stands, and 87% together with beech).

In each FD, hunting is conducted annually during the hunting season. The hunting season for red deer lasts from August 21 to February 28 (bulls), from October 1 to January 1 (does) and from January 1 to February 28 (calves), and for roe deer from May 11 to September 30 (bucks) and from October 1 to January 15 (does and fawns). In this region of Poland, 2.2–2.4 ind./km^2/year of red deer and 2.7–2.9 ind./km^2/year of roe deer were harvested. Also, the forests of each of these FDs are available for recreation (e.g. cycling, hiking). However, there are no tourist spots in any of them that can attract a particularly large numbers of tourists.

The detailed characteristics of the study area are shown in Table 1. Data on ungulate densities and hunting consist of unpublished 2016 data from official hunting and forestry statistics. In addition, single individuals of European bison *Bison bonasus* and moose occasionally appeared within the BS and single individuals of fallow deer *Dama dama* occasionally appeared within the MAN and POL. MAN and BS wolf populations were stable (about 1.2 individuals/100 km^2 each) and average pack size varied between 3.5 and 5.6 individuals[37]. One wolf pack was present in MAN and two packs were present within BS. At the beginning of the study, no permanently functioning wolf packs were recorded in POL—only single wolves were observed sporadically at the end of the study period (these were usually individuals moving through the area).

Forest district	Wolf population	Wild ungulate density (ind./km^2)		Study plots
		Red deer	Roe deer	
Borne Sulinowo BS	Present	6.8	7.9	12 pine plantations
Manowo MAN	Present	7.7	8.4	10 beech plantations
Polanów POL	Absent	7.5	8.8	6 pine plantations 6 beech plantations

Table 1. The characteristics of study plots.

Field measurements

Three- to five-year-old Scots pine plantations of 1–5 ha with the same soil characteristics and forest type and three- to five-year-old round or elliptical beech plantations of about 0.1 ha were randomly selected for the study, because they were the most common forest crops within the three sites. The selected plantations met the following criteria:

1) The saplings were unfenced and unprotected against browsing;
2) Each study plot was located at least 300 m from buildings, public roads and tourist spots and was completely or mostly surrounded by older stands. There was one unpaved forest road near each study plot (closer than 50 m), which might have limited browsing pressure on saplings by making deer avoiding them[34,38,39] and increased the wolf predation risk, as these carnivores take advantage of forest road infrastructure[40];
3) Sapling heights ranged from 20 to 150 cm, the size most susceptible to browsing[8,13,41]. Plantations with higher saplings (> 150 cm), were not selected for the measurements because we wanted to avoid the situation when saplings become too high for deer to be browsed during the 3-year study period and the plantations become unattractive for large herbivores before the study ends. Also, up to this tree height, forest plantations are still an open environment where deer can see and perceive danger. Taller trees create an entirely different forest development medium—a forest thicket with lots of cover but little visibility.

Thirty-four study plots in total were selected for measurements (Table 1).

In addition, representatives of the genera *Rubus spp*. and/or *Vaccinum spp*. were present in each plantation, increasing the likelihood of tree browsing by deer[42,43]. There were also representatives of other vegetation groups, the most numerous of which were (in varying proportions): birch *Betula pendula* seedlings, *Calluna vulgaris*, *Juncus spp.*, *Festuca spp.*, *Poa spp*. No large grasslands were present within the POL and MAN forest districts. Within the BS were two large nature reserves (moors), but none of the study plots was closer than 500 m from these open areas.

The beech plantations had an area of 0.1 ha, while the pine plantations had an area of 1–5 ha. Because of their size, the beech plantations were divided into zones less than 10 m or more than 10 m from the nearest older forest edge. Data from the pine plantations were collected in zones that were less than 10 m from forest edge and no closer than 50 m from the nearest forest edge (and close to the plantation centre). Each year four 10 m transects perpendicular to the edge of the plantation were randomly selected in each zone. We noted the number of saplings along each transect and whether traces of fresh browsing were present on the main shoots of each sapling (the freshly browsed apical shoots were noticeably softer and lighter in colour than those previously browsed). The plantations were single-species, so we analysed only pine saplings within pine plantations and beech saplings within beech plantations. If seedlings of other tree species (e.g. birch) were found in transects, which occurred very rarely, they were not included in the analysis. Traces of browsing on side shoots were not included in our analyses, as the loss of these shoots does not cause significant changes in the saplings' form and their growth rate. We then calculated the proportion of trees with traces of browsing on apical shoots among all measured trees per transect. In each forest plantation, fresh browsing pressure was evaluated annually from 2015 to 2017 in late spring (April–May), after the greatest winter and spring pressure from deer[44]. During the study period, neither tracks nor faeces of bison, moose or fallow deer were found within the study plots.

Statistical analysis

To analyse the data, we used a generalized linear mixed model fitted by maximum likelihood with binomial distribution for the response variable and logit linkage function. We calculated proportion of damaged trees as the number of browsed (apical shoot damaged) and unbrowsed trees per transect in each zone of the study plot[35]. This was our indirect indicator of browsing pressure and forest regeneration success[41]. The proportion of damaged trees was used as a response variable. All predictors were also binary coded: the apical shoot (1-browsed, 0-not browsed), presence of wolves (1-present, 0-not present), distance to forest edge (edge < 10 m-1, far > 50 m (for pine)/ > 10 m (for beech)-0), and tree species (pine-1, beech-0). The study year (2015/2016/2017) and plot (specific forest plantation) were used as random factors. Initially, all interactions between dependent variables were considered: wolf presence, distance to the forest edge, and tree species, but only significant interactions were included in the final model. All statistical analyses were performed using the lmerTest package[45] in R software[46].

The null model contained only tree species as a predictor variable. We added more predictor variables to the null model and compared subsequent models using the likelihood ratio test to see which one fits the data better. We assessed how the model fits the data using the Hosmer–Lemeshow (HL) goodness of fit (GOF) test.

Ethical approval

The authors declare that the research was carried out in compliance with the IUCN Policy Statement on Research Involving Species at Risk of Extinction and the Convention on the Trade in Endangered Species of Wild Fauna and Flora.

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Results

A total of 2 087 pine saplings (within 144 transects) and 1 664 beech saplings (within 128 transects) were analyzed. The mean number of saplings per transect were: 4.99 ± 1.25 (SD) within the close zone (< 10 m to the forest edge) and 8.75 ± 1.37 (SD) within the far zone (> 50 m to the forest edge) for pine, and 5.13 ± 0.77 (SD) within the close zone (< 10 m to the forest edge) and 5.80 ± 0.99 (SD) within the far zone (> 10 m to the forest edge) for beech.

Although the final model performed significantly better than the null (species only) model (Chi-squared = 13.97, p = 007) it did not fit data well (Hosmer–Lemeshow Goodness-of-Fit Test, Chi-squared = 30.72, df = 8, p = 0.0002). The reason why the model did not work well was due to two different effects. First, the presence of wolves mainly affected foraging distance (the location of foraging and thus its intensity depending on the size of the plantation, which varied between species). Second, the browsing intensity depended mainly on the tree species, hence the lack of interaction with the wolf. The interaction effect of wolf and species was insignificant in any of the interaction effects of factors.

The intensity of browsing differed between landscapes with and without wolf populations and by distance from the forest edge. In forests inhabited by wolves, browsing levels were higher than in forests without permanent wolf populations, but only for pine. For beech an opposite browsing pattern was observed (Table 2, Fig. 1). In both pine and beech plantations, deer preferred to browse near to the forest edge in landscapes with no wolves

Effects	Estimate	SE	z value	Pr(>|z|)
Intercept	− 2.0015	0.6904	− 2.899	0.00374
Wolf (Yes)	**0.7769**	**0.2883**	**2.695**	**0.00705**
Distance (Close)	**0.3521**	**0.1733**	**2.032**	**0.04211**
Species (Pine)	**− 1.7952**	**0.2788**	**− 6.440**	**< 0.001**
Wolf (Yes)*Distance (Close)	**− 0.7070**	**0.2280**	**− 3.101**	**0.00193**
Distance (Close) *Species (Pine)	0.4151	0.2249	1.845	0.06497

Table 2. Model output results for browsing on pine and beech saplings together (with interactions). Wolf (Yes)—wolf present in the landscape (Yes vs. No), Distance (Close)- distance from the forest edge—above 10 m in beech and 50 m in pine plantations (Far vs. Close), Species (Pine)—analysed tree species' saplings (pine vs. beech). *SE* standard error, *Pr p* value. Significant values are in [bold].

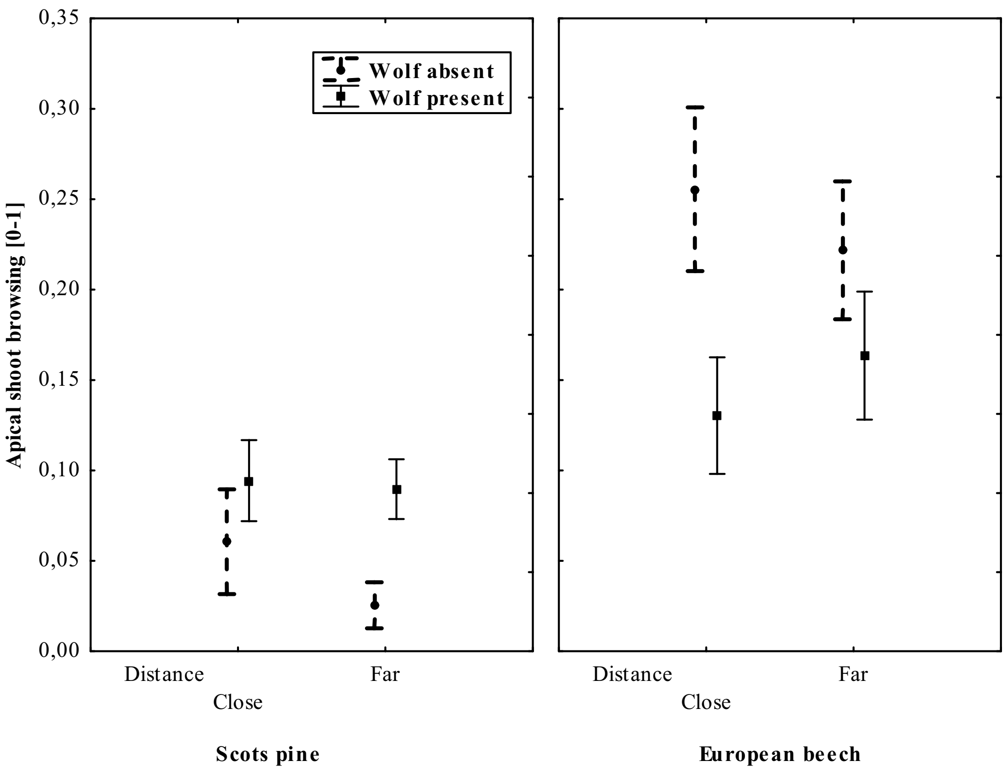

Figure 1. The proportion (mean ± SD) of freshly browsed apical shoots of Scotch pine and European beech saplings in different distances from the forest edge: in forests with (BS and MAN) and without (POL) permanent wolf populations.

(Table 2, Fig. 1). Deer browsed pine saplings less intensively than beech saplings (Table 2). The presence of wolves increased the browsing pressure of deer on pine far from the forest edge, while a decrease in browsing close to the forest edge was observed in beech plantations.

Discussion

The results of a study conducted in North America show that large carnivores can have strong effects on prey populations by reducing their density and changing their behaviour, which can lead to a chain of changes at different trophic levels, i.e., cascade effects[47,48]. In our study, we hypothesised that the presence of wolves in the forest ecosystem would reduce the browsing intensity of deer in forest plantations regardless of their main sapling species. However, the results obtained partially contradicted this prediction. It was also noted that the presence of predators altered the spatial pattern of deer foraging. In pine plantations, deer tended to consume more pine saplings in the central zone. Within beech plantations, we observed a decrease in browsing at the forest edge. These results contrast with observations in Yellowstone National Park, where 15 years after the return of wolves, a decline in the deer population was accompanied by a significant decrease in the number of young trees damaged and an increase in young tree survival[49] (but see Kauffman et al.[50]). Our results also differ from those of a study from Scandinavia, where the presence of wolves had no effect on damage caused by moose in pine plantations[35], but they are consistent with the results of other studies in which moose browsing on pines was higher in wolf territories[33,34]. However, as has been highlighted in North America, predation on large prey is sometimes wishful thinking, while a trophic cascade may be weaker than claimed and strongly dependent on adequate sampling[51].

So, the obvious question arises: why does the presence of wolves increase the browsing pressure of deer on saplings? According to the Optimal Foraging Theory, the most intuitive answer is that deer browsing pressure in wolf-inhabited landscapes may be concentrated in places with high food availability and good visibility, such as young and large forest plantations[52]. Such behaviour helps animals minimise foraging time and easily detect danger (predators). Some confirmation of the above explanation comes from the results of studies conducted in North America showing that deer minimise the risk of being preyed upon by coursing predators by relying on early detection, which is facilitated by the use of large-sized, open forest plantations[53,54]. Although dense vegetation cover near the forest edge may provide safety to deer by reducing detection[42], it may obstruct visibility and escape routes, increasing predation risk from apex predators[29,31]. This would explain why distance from the forest edge was not statistically significant factor in the case of the beech plantations—these gaps were too small (0.1 ha) to provide sufficient distance for early detection of predators by deer, so they likely felt equally safe (or unsafe) within the entire plantations. We confirmed our second hypothesis that deer foraging behaviour varies spatially, but only under specific spatial conditions. However, sometimes the forest edge is the safest location[42] or simply the most attractive location where a trade-off can be made to provide both cover for safety and open space for grazing at safer times[55]. Wolf risk is an important factor creating a landscape of fear and influencing deer foraging behaviour, even in commercial forests, where human activities (e.g., recreation, hunting) influence deer browsing behaviour at the stand and landscape level[33,36,38] and fear is triggered by anthropogenic disturbance rather than the presence of large predators[36,56]. Although the hunting pressure within our study areas was relatively high compared to other regions of Poland, it was due to alike deer densities similar for three analysed forest districts, which is why it was not included as a factor in our experimental design. It additionally suggests that risk effects caused by the wolf presence in the ecosystem may be strong enough to be found even in intensively human-disturbed landscapes.

One might wonder whether the results obtained were affected by differences in the densities of deer within the study areas, especially since the available data indicate a strong relationship between the density of deer and foraging intensity[8,57–59]. However, in the previously mentioned studies, significant differences in foraging intensity were found for deer densities ranging from a dozen to several dozen individuals/km^2. In contrast, density varied at most in the presented study by only a few individuals/km^2. Therefore, in our opinion, the effects of deer densities on levels of browsing damage were negligible.

Since the process of forest colonisation by wolves in Poland is relatively fast, it was a challenge to find suitable sites for research. We were able to locate three areas in the same region with similar (although not identical) natural conditions and different statuses of wolf populations in the landscape. Similar studies should include more areas to better analyse the effects of large predators on deer behaviour and forest regeneration, although we believe our research provided satisfactory results. This study suggests how apex predators can alter deer browsing intensity and young tree survival within forest plantations in anthropogenic forest ecosystems through spatial differentiation in the landscape of fear. However, we must remember that the earliest stand stages in commercial forests represent only a part of the total ecosystem and deer browsing pressure may be lower at other stages of forest development. Although the threat posed by human hunters is thought to be the most important determinant of cervid responses in commercial forests during the day through the hunting season[36,60–62], we have observed a pattern of changes in the distance from the forest edge selection by deer in the face of cursorial predators. We found that open-spaced centres of large-sized clearcuts and young forests, distant from older forest edges, seem to be the safest places for deer to reduce predation risk by wolves and to browse in northern Poland. However, this is not a general rule, as, for example, the results of a study conducted in Scandinavia indicated that such habitats represent the highest risk of predation on moose[61].

Our study suggests that the presence of wolves significantly affects forest regeneration by influencing the foraging behaviour and browsing of wild herbivores at a fine-scale. The conservation of temperate forests can benefit from the reduction of time deer spend browsing in forest patches with high biodiversity value[63]. Silviculture can benefit from a reduction of time deer spend browsing in forest plantations and wolves can support it. Our results are also relevant for the field of studying cascading effects of predators and how this shapes forests in general. We perceive the wolf as a factor that can reduce and modify the pressure of herbivores at fine-scale and thus help regenerate forests to some extent.

However, the inconsistent results when combining research studies on this topic highlight the need for further research on the cascading effects of large predator populations and human activities on forest regeneration (in both commercial and protected forests). Furthermore, the influence of humans should be considered simultaneously with the influence of natural predators, as it is ubiquitous and cannot be ignored. This could benefit forest management and support the sustainable management of wildlife populations[64].

Data availability

The data that support the findings of this study are available on request from the corresponding author.

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References

1. Côté, S. D., Rooney, T. P., Tremblay, J.-P., Dussault, C. & Waller, D. M. Ecological impacts of deer overabundance. *Ann. Rev. Ecol. Evol. Syst.* **35**, 114–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725 (2004).
2. Kuiters, A. T., Mohren, G. M. J. & Van Wieren, S. E. Ungulates in temperate forest ecosystems. *For. Ecol. Manag.* **88**, 1–5 (1996).
3. Bałazy, R., Ciesielski, M., Stereńczak, K. & Borowski, Z. The role of topography in the distribution and intensity of damage caused by deer in polish mountain forests. *PloS One* **11**, e0165967. https://doi.org/10.1371/journal.pone.0165967 (2016).
4. Felton, A. M. *et al.* Forage availability, supplementary feed and ungulate density: Associations with ungulate damage in pine production forests. *For. Ecol. Manag.* **513**, 120187. https://doi.org/10.1016/j.foreco.2022.120187 (2022).
5. Krojerová-Prokešová, J., Barančeková, M., Šustr, P. & Heurich, M. Feeding patterns of red deer *Cervus elaphus* along an altitudinal gradient in the Bohemian Forest: effect of habitat and season. *Wildl. Biol.* **16**, 173–184. https://doi.org/10.2981/09-004 (2010).
6. Churski, M. *et al.* How do forest management and wolf space-use affect diet composition of the wolf's main prey, the red deer versus a non-prey species, the European bison?. *For. Ecol. Manag.* **479**, 118620. https://doi.org/10.1016/j.foreco.2020.118620 (2021).
7. Boulanger, V. *et al.* Ranking temperate woody species along a gradient of browsing by deer. *For. Ecol. Manag.* **258**, 1397–1406. https://doi.org/10.1016/j.foreco.2009.06.055 (2009).
8. Borowski, Z. *et al.* Density-related effect of red deer browsing on palatable and unpalatable tree species and forest regeneration dynamics. *For. Ecol. Manag.* **496**, 119442. https://doi.org/10.1016/j.foreco.2021.119442 (2021).
9. Callan, R., Nibbelink, N. P., Rooney, T. P., Wiedenhoeft, J. E. & Wydeven, A. P. Recolonizing wolves trigger a trophic cascade in Wisconsin (USA). *J. Ecol.* **101**(4), 837–845. https://doi.org/10.1111/1365-2745.12095 (2013).
10. Tremblay, J.-P., Côté, S. D., Rooney, T., Dussault, C. & Waller, D. M. Ecological impacts of deer overabundance on temperate and boreal forests. *Ann. Rev. Ecol. Evol. Syst.* **35**, 114–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725 (2014).
11. Boulanger, V. *et al.* Ungulates increase forest plant species richness to the benefit of non-forest specialists. *Glob. Change Biol.* **24**(2), 485–495. https://doi.org/10.1111/gcb.13899 (2018).
12. Ramirez, J. I. *et al.* Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. *For. Ecol. Manag.* **432**, 478–488. https://doi.org/10.1016/j.foreco.2018.09.049 (2019).
13. Motta, R. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the western Italian Alps. *For. Ecol. Manag.* **88**(1/2), 93–98. https://doi.org/10.1016/S0378-1127(96)03814-5 (1996).
14. Boulanger, V. *et al.* Decreasing deer browsing pressure influenced understory vegetation dynamics over 30 years. *Ann. For. Sci.* **72**, 367–378. https://doi.org/10.1007/s13595-014-0431-z (2015).
15. Persson, I. L., Bergström, R. & Danell, K. Browse biomass production and regrowth capacity after biomass loss in deciduous and coniferous trees: Responses to moose browsing along a productivity gradient. *Oikos* **116**(10), 1639–1650. https://doi.org/10.1111/j.2007.0030-1299.15946.x (2007).
16. Den Herder, M., Bergström, R., Niemelä, P., Danell, K. & Lindgren, M. Effects of natural winter browsing and simulated summer browsing by moose on growth and shoot biomass of birch and its associated invertebrate fauna. *Ann. Zool. Fenn.* **46**, 63–74. https://doi.org/10.5735/086.046.0107 (2009).
17. Drexhage, M. & Colin, F. Effects of browsing on shoots and roots of naturally regenerated sessile oak seedlings. *Ann. For. Sci.* **60**, 173–178. https://doi.org/10.1051/forest:2003010 (2003).
18. Kuijper, D. P. J. *et al.* Do ungulates preferentially feed in forest gaps in European temperate forest?. *For. Ecol. Manag.* **258**(7), 1528–1535. https://doi.org/10.1016/j.foreco.2009.07.010 (2009).
19. Cadenasso, M. L. & Pickett, S. T. A. Linking forest edge structure to edge function: mediation of herbivore damage. *J. Ecol.* **88**(1), 31–44. https://doi.org/10.1046/j.1365-2745.2000.00423.x (2000).
20. Alverson, W. S., Waller, D. M. & Solheim, S. L. Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* **2**(4), 348–358. https://doi.org/10.1111/j.1523-1739.1988.tb00199.x (1988).
21. Ripple, W. J. *et al.* Status and ecological effects of the world's largest carnivores. *Science* **343**(6167), 1241484. https://doi.org/10.1126/science.1241484 (2014).
22. Jędrzejewski, W., Nowak, S., Schmidt, K. & Jędrzejewska, B. Wilk i ryś w Polsce – wyniki inwentaryzacji w 2001 roku. *Kosmos* **51**, 491–499 (2002) (**in Polish**).
23. Nowak, S. & Mysłajek, R. M. Wolf recovery and population dynamics in Western Poland, 2001–2012. *Mamm. Res.* **61**, 83–98. https://doi.org/10.1007/s13364-016-0263-3 (2016).
24. Strong, D. R. & Frank, K. T. Human involvement in food webs. *Ann. Rev. Environ. Resour.* **35**, 1–23. https://doi.org/10.1146/annurev-environ-031809-133103 (2010).
25. Carpenter, S. R., Kitchell, J. F. & Hogdson, J. R. Cascading trophic interactions and lake productivity. *BioScience* **35**(10), 634–639. https://doi.org/10.2307/1309989 (1985).
26. Pace, M. L., Cole, J. J., Carpenter, S. R. & Kitchell, J. F. Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* **14**, 483–488. https://doi.org/10.1016/S0169-5347(99)01723-1 (1999).
27. Palmer, S. & Truscott, A. M. Browsing by deer on naturally regenerating Scots Pine (*Pinus sylvestris* L.) and its effect on sapling growth. *For. Ecol. Manag.* **182**(1–3), 31–47. https://doi.org/10.1016/S0378-1127(03)00026-4 (2003).
28. Didion, M., Kupferschmid, A. D. & Bugmann, H. Long-term effects of ungulate browsing on forest composition and structure. *For. Ecol. Manag.* **258**, 44–55. https://doi.org/10.1016/j.foreco.2009.06.006 (2009).
29. Van Ginkel, H. A. L., Kuijper, D. P. J., Schotanus, J. & Smit, C. Wolves and tree logs: Landscape-scale and fine-scale risk factors interactively influence tree regeneration. *Ecosystems* **22**, 202–212. https://doi.org/10.1007/s10021-018-0263-z (2019).
30. Kuijper, D. P. J. *et al.* Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* **36**, 1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x (2013).
31. Kuijper, D. P. J. *et al.* Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. *Behav. Ecol.* **26**(6), 1558–1568. https://doi.org/10.1093/beheco/arv107 (2015).

32. Van Beeck Calkoen, S. T. S., Kreikenbohm, R., Kuijper, D. P. J. & Heurich, M. Olfactory cues of large carnivores modify red deer behavior and browsing intensity. *Behav. Ecol.* **32**(5), 982–992. https://doi.org/10.1093/beheco/arab071 (2021).
33. Van Beeck Calkoen, S. T. S. *et al.* Does wolf presence reduce moose browsing intensity in young forest plantations?. *Ecography* **41**(11), 1776–1787. https://doi.org/10.1111/ecog.03329 (2018).
34. Gicquel, M., Sand, H., Månsson, J., Wallgren, M. & Wikenros, C. Does recolonization of wolves affect moose browsing damage on young Scots pine?. *For. Ecol. Manag.* **473**, 118298. https://doi.org/10.1016/j.foreco.2020.118298 (2020).
35. Loosen, A. E. *et al.* Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia. *Ecosphere* **12**(1), e03358. https://doi.org/10.1002/ecs2.3358 (2021).
36. Kuijper, D. P. J. *et al.* Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proc. R. Soc. B Biol. Sci.* **283**, 20161625. https://doi.org/10.1098/rspb.2016.1625 (1841).
37. Mysłajek, R. *et al.* Spatial organization in wolves *Canis lupus* recolonizing north-west Poland: Large territories at low population density. *Mamm. Biol.* **92**, 37–44. https://doi.org/10.1016/j.mambio.2018.01.006 (2018).
38. Mols, B., Lambers, E., Cromsigt, J. P. G. M., Kuijper, D. P. J. & Smit, C. Recreation and hunting differentially affect deer behaviour and sapling performance. *Oikos* **1**, e08448. https://doi.org/10.1111/oik.08448 (2021).
39. Scholten, J., Moe, S. R. & Hegland, S. J. Red deer (*Cervus elaphus*) avoid mountain biking trails. *Eur. J. Wildl. Res.* **61**(1), 8. https://doi.org/10.1007/s10344-018-1169-y (2018).
40. Bojarska, K. *et al.* Opportunity and peril: How wolves use a dense network of forest roads. *Mamm. Biol.* **100**, 203–211. https://doi.org/10.1007/s42991-020-00014-0 (2020).
41. D'Aprile, D. *et al.* Effects of twenty years of ungulate browsing on forest regeneration at Paneveggio Reserve, Italy. *Forests* **11**, 612. https://doi.org/10.3390/f11060612 (2020).
42. Borowski, Z., Bartoń, K., Gil, W., Wójcicki, A. & Pawlak, B. Factors affecting deer pressure on forest regeneration: The roles of forest roads, visibility and forage availability. *Pest Manag. Sci.* **77**(2), 628–634. https://doi.org/10.1002/ps.6207 (2021).
43. Heinze, E. *et al.* Habitat use of large ungulates in northeastern Germany in relation to forest management. *For. Ecol. Manag.* **261**(2), 288–296. https://doi.org/10.1016/j.foreco.2010.10.022 (2011).
44. Jędrzejewska, B., Jędrzejewski, W., Bunevich, A. N., Miłkowski, L. & Krasiński, Z. A. Factors shaping population densites and increase of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriol.* **42**, 399–451. https://doi.org/10.4098/AT.arch.97-39 (1997).
45. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. LmerTest: Tests in linear mixed effects models. *J. Stat. Softw.* https://doi.org/10.18637/jss.v082.i13 (2017).
46. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2020)
47. McLaren, B. E. & Peterson, R. O. Wolves, moose, and tree rings on Isle Royale. *Science* **266**, 1555–1558 (1994).
48. Beschta, R. L. & Ripple, W. J. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviourally mediated trophic cascade—comment. *Ecology* https://doi.org/10.1890/11-0063.1 (2011).
49. Ripple, W. J. & Beschta, R. L. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biol. Conserv.* **145**(1), 205–213. https://doi.org/10.1016/j.biocon.2011.11.005 (2012).
50. Kauffman, M. J., Brodie, J. F. & Jules, E. S. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* **91**, 2742–2755. https://doi.org/10.1890/09-1949.1 (2010).
51. Brice, E. M., Larsen, E. J. & MacNulty, D. R. Sampling bias exaggerates a textbook example of a trophic cascade. *Ecol. Lett.* **25**(1), 177–188. https://doi.org/10.1111/ele.13915 (2021).
52. Brown, J. S. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiology* **22**, 37–47. https://doi.org/10.1007/BF00395696 (1988).
53. Kunkel, K. & Pletscher, D. H. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *J. Wildl. Manag.* **65**, 520–530. https://doi.org/10.2307/3803105 (2001).
54. Dellinger, J. A. *et al.* Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. *Oecologia* **189**, 487–500. https://doi.org/10.1007/s00442-018-4323-z (2019).
55. Fattebert, J., Morelle, K., Jurkiewicz, J., Ukalska, J. & Borkowski, J. Safety first: Seasonal and diel habitat selection patterns by red deer in a contrasted landscape. *J. Zool.* **308**(2), 111–120. https://doi.org/10.1111/jzo.12657 (2019).
56. Van Beeck Calkoen, S. T. S., Deis, M. H., Oeser, J., Kuijper, D. P. J. & Heurich, M. Humans rather than Eurasian lynx (*Lynx lynx*) shape ungulate browsing patterns in a temperate forest. *Ecosphere* **13**(2), e3931. https://doi.org/10.1002/ecs2.3931 (2022).
57. Kamler, J., Homolka, M., Barancеková, M. & Krojerová-Prokešová, J. Reduction of herbivore density as a tool for reduction of herbivore browsing on palatable tree species. *Eur. J. For. Res.* **129**(2), 155–162. https://doi.org/10.1007/s10342-009-0309-z (2010).
58. Gill, R. M. A. & Morgan, G. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry* **83**(1), 53–63. https://doi.org/10.1093/forestry/cpp031 (2010).
59. Chevrier, T. *et al.* The oak browsing index correlates linearly with roe deer denisty: A new indicator for deer management?. *Eur. J. Wildl. Res.* **58**, 17–22. https://doi.org/10.1007/s10344-011-0535-9 (2012).
60. Ciuti, S. *et al.* Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS One* **7**(11), e50611. https://doi.org/10.1371/journal.pone.0050611 (2012).
61. Ausilio, G. *et al.* Environmental and anthropogenic features mediate risk from human hunters and wolves for moose. *Ecosphere* **13**(12), e4323. https://doi.org/10.1002/ecs2.4323 (2022).
62. Ramirez, J. I. *et al.* Top-down and bottom-up forces explain patch utilization by two deer species and forest recruitment. *Oecologia* **201**(1), 229–240. https://doi.org/10.1007/s00442-022-05292-8 (2023).
63. Ramirez, J. I. *et al.* Temperate forests respond in a non-linear way to a population gradient of wild deer. *For. Int. J. For. Res.* **94**(4), 502–511. https://doi.org/10.1093/forestry/cpaa049 (2021).
64. Bobrowski, M., Gillich, B. & Stolter, C. Modelling browsing of deer on beech and birch in northern Germany. *For. Ecol. Manag.* **358**, 212–221. https://doi.org/10.1016/j.foreco.2015.08.031 (2015).

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Author contributions

A.W.—Research concept, data collection, data analysis, main text preparation. Z.B.—Research concept, supervision, data analysis, text corrections.

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Additional information
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RESEARCH ARTICLE OPEN ACCESS

Influence of Human Hunting Strategies and Large Carnivore Presence on Population Dynamics of European Facultative Scavengers

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ABSTRACT

Ungulates serve as the primary carrion source for facultative scavengers in European ecosystems. In the absence of large carnivores, such as wolves (*Canis lupus*), human hunting leftovers are the main source of carrion for these scavengers. Additionally, wild boars (*Sus scrofa*) are heavily culled in many ecosystems and are both a significant prey species for wolves as well as a key scavenger. Nowadays, wolves and wild boars are re-establishing their historical home ranges. However, it remains unclear how their presence influences the population dynamics of facultative scavengers under different scenarios of human hunting strategies. We simulated the biomass densities of all states in the trophic web including European scavengers and wolves using an ordinary differential equations (ODE) model. The presence of wolves led to a positive trend in scavenger biomass in general. However, in general, we found that plant-based resources were more important for scavenger dynamics than carrion, regardless of whether the carrion originated from human hunting or wolf predation. Only when wolves were absent but boars present, the human hunting strategy became important in determining scavenger dynamics via carrion supply. In conclusion, our model indicates that population dynamics of facultative scavengers are not mainly driven by the availability of carrion, but rather by the presence of and competition for vegetation. Furthermore, our simulations highlight the importance of adapting human hunting strategies in accordance with the re-establishment of wolf and boar as these can cause fluctuating population patterns over the years.

1 | Introduction

The decomposition of dead animal bodies – carrion – is an important ecological process that can have far-reaching consequences for ecosystem functioning (Wenting et al. 2023, 2024). Most of the carrion in terrestrial ecosystems is consumed by scavengers (DeVault, Rhodes Jr, and Shivik 2003; Wilson and Wolkovich 2011). The major source of carrion in many ecosystems, including European temperate woodlands, consists of large ungulates (Beasley et al. 2019; Moleón et al. 2019; Greenspoon et al. 2023). This includes species like red deer (*Cervus elaphus*), fallow deer (*Dama dama*), and wild boar (*Sus scrofa*). Anthropogenic hunting is one of the major causes of death of free roaming ungulates, especially in areas where large carnivores no longer occur due to extermination (Gordon 2009; Found 2016; Williams et al. 2017).

Elke Wenting and Jasper A.J. Eikelboom contributed equally to this work.

Currently, however, populations of large carnivores are re-establishing to their historical ranges across Europe (Chapron et al. 2014; Galaverni et al. 2016). An example is the grey wolf (*Canis lupus*), a social apex predator with large dispersal rates and large territories (Jędrzejewski et al. 2007), that expanded its distribution extensively over the past decades (Planillo et al. 2023). The re-establishment of the wolf has been possible due to strict legal protection and the recovery of large herbivore populations (Chapron et al. 2014). The presence of the wolf can have cascading effects on ecosystem functioning (Allen et al. 2017), for example by indirectly changing the diet of grizzly bears (*Ursus arctos horribilis*) to more plant-based (Ripple et al. 2015) and willow recovery through behavioural changes of herbivores (Marshall, Cooper, and Hobbs 2014). This is well-studied in North American wolf habitats (Lesmerises, Dussault, and St-Laurent 2012; Ripple and Beschta 2012; Ford and Goheen 2015; Gantchoff et al. 2022). The European situation is considerably less well-studied (Nowak et al. 2017; Reinhardt et al. 2019), despite that there are essential differences between the European and North American continent. Since it is generally harder to predict trophic cascades in more human-dominated landscapes such as European ecosystems (Hebblewhite et al. 2005; Muhly et al. 2013; Dorresteijn et al. 2015), insights obtained from North American wolf habitats might not be equally relevant in European wolf habitats (Focardi et al. 2017).

One of the most notable differences between European and American ecosystems is the importance of wild boar as both abundant ungulate, scavenger species, and prey species for wolves (Focardi et al. 2017). The wild boar is a widespread non-ruminant ungulate that is widely described as an ecosystem engineer due to its extensive rooting behaviour (Sandom, Hughes, and Macdonald 2013; Ballari and Barrios-García 2014; Baruzzi and Krofel 2017; Barrios-Garcia et al. 2023). It is a well-known scavenger species (Selva et al. 2005; Selva and Fortuna 2007; Focardi et al. 2008) that can contribute considerably to carrion removal from ecosystems (Wenting, Rinzema, and van Langevelde 2022; Wenting et al. 2024; Newsome et al. 2023). Although wild boars are not tolerated by humans everywhere in Europe (Boonman-Berson, Driessen, and Turnhout 2019), hence not everywhere present as prey species, they are reported as a noticeable part of the wolves' diet throughout European ecosystems in areas where they occur (Smietana and Klimek 1993; Ansorge, Kluth, and Hahne 2006; Nores, Llaneza, and Álvarez 2008; Lanszki et al. 2012; Špinkytė-Bačkaitienė and Pėtelis 2012; Barja et al. 2023). That implies that the wild boar is an important prey species for wolves (Mattioli et al. 2011; Mori et al. 2017) and also an important scavenger in wolf habitats (Focardi et al. 2017).

The presence of large carnivores like wolves can influence the process of scavenging in ecosystems. Through only partially consuming their prey, wolves can indirectly facilitate scavengers (Vucetich, Vucetich, and Peterson 2012; Focardi et al. 2017; Boczulak et al. 2023). Wolves might facilitate consumption efficiency of vultures, corvids and smaller mammals by tearing open thick-skinned carcasses (Moleón et al. 2014). Partial prey consumption is common behaviour for wolves, being the combined result of pack size, prey size, and completeness of consumption in first sitting (Sand et al. 2012; Vucetich, Vucetich, and Peterson 2012; Mech and Boitani 2019). In North America, it has been described that common ravens (*Corvus corax*) use activity patterns of wolves to benefit from wolf kills, as a feeding strategy in winter (Stahler, Heinrich, and Smith 2002; Walker et al. 2018). However, scavenger dynamics might not change in the same way in different systems because scavenger species adapt their behaviour based on the local circumstances. Klauder et al. (2021), for instance, found that red foxes (*Vulpes vulpes*) were least likely to visit wolf kills in Denali National Park and Preserve, Alaska. This contradicts to findings in Europe and elsewhere in North America, where red foxes are reported to visit up to 90% of wolf-predated ungulates (Selva 2004; Wikenros, Ståhlberg, and Sand 2014; O'Malley et al. 2018). Thus, the potential impact of re-establishing wolf populations on scavenger dynamics can be system specific (Laundré, Hernández, and Altendorf 2001; Levi and Wilmers 2012; Haswell, Kusak, and Hayward 2017; Kuijper et al. 2024), increasing the need to investigate potential influences of re-establishing wolves under different circumstances.

It has been described that different causes of death of ungulates – e.g., originated from human hunting or predated by wolves – can differently influence scavengers. For instance, predator-kills were mostly preferred by scavengers in the Białowieża Primaeval Forest, Poland (Selva 2004; Selva and Fortuna 2007). Carrion obtained from human hunting can also facilitate a wide range of scavenger species (Mateo-Tomás et al. 2015), in some cases even more than wolf kills (Ho et al. 2023). It remains unclear to which extent such differences might be due to different human hunting strategies, e.g., hunting target ('pressure') or the fraction of carrion left for scavengers. Also, the actual importance of carrion versus other resources for facultative scavengers – that frequently consume but do not depend on carrion (Wilson and Wolkovich 2011) – remains unclear.

Thus, summarising, it remains unclear how human hunting strategies and the presence of wolves and/or wild boar (henceforth 'boar') influence the population dynamics of European facultative scavengers (henceforth 'scavengers'). We focus on (vertebrate) species that consume plant-based food and carrion primarily and are flexible in their diet and behaviour (Selva and Fortuna 2007; Wenting, Rinzema, and van Langevelde 2022; Wenting et al. 2024). These include corvids like common raven and carrion crow (*Corvus corone*), and mesocarnivores, for instance red fox, European badger (*Melis melis*), raccoon (*Procyon lotor*) and other mustelids including beach marten (*Martes foina*), pine marten (*Martes martes*) and European polecat (*Mustela putorius*) (Díaz-Ruiz et al. 2013; Rooney and Montgomery 2013; Papakosta et al. 2014; Libois et al. 2019; Jain et al. 2022). In this study, we use a differential-equations modelling approach to examine how different human hunting strategies combined with the presence or absence of wolf and boar influence the population dynamics of scavengers. We address two research questions: (1) What is the influence of human hunting strategies in interaction with the presence or absence of boar and wolf, on scavenger population dynamics? and (2) What is the relative importance of carrion for scavenger population dynamics under different human hunting strategies in interaction with the presence or absence of boar and wolf?

2 | Methods

2.1 | Model Description and Assumptions

We simulated the biomass densities of a trophic web of European scavengers and wolves (Figure 1) using an ordinary differential equations (ODE) model. We based our model on the model developed by Focardi et al. (2017) for scavenger/predator systems, but changed three main things: (1) we added a separate state for scavengers, (2) implemented human hunting on boar and deer, and (3) merged adult boar and piglets into one state to simplify the model. The other details of the model by Focardi et al. (2017) are similar to our model specifications that we explain here. In our model, vegetation V is consumed by deer D, boar B and scavengers S (Equation 1), which we further subdivided here into Equations (1a)–(1d). Here, vegetation includes all plant-based materials. Deer are consumed by wolf W, killed by hunters and die of other causes (Equation 2, subdivided over Equations 2a–2d). For boar the same applies as for deer, but they also consume deer carrion instead of only vegetation (Equation 3, subdivided over Equations 3a–3e). Scavengers consume both vegetation and the carrion from deer and boar, and die of natural causes (Equation 4, subdivided over Equations 4a–4d). Wolves thus consume deer and boar and die of natural causes (Equation 5, subdivided over Equations 5a–5c). For simplicity, we assumed no scavenging behaviour by wolves, nor did we assume that scavengers consume wolf carrion (as wolf carrion only makes up a small portion of the total amount of carrion).

$$\frac{dV}{dt} = V_{\text{growth}} - V_{\text{consD}} - V_{\text{consB}} - V_{\text{consS}} \quad (1)$$

$$\frac{dD}{dt} = D_{\text{growthV}} - D_{\text{pred}} - D_{\text{hunt}} - D_{\text{death}} \quad (2)$$

$$\frac{dB}{dt} = B_{\text{growthV}} + B_{\text{growthD}} - B_{\text{pred}} - B_{\text{hunt}} - B_{\text{death}} \quad (3)$$

$$\frac{dS}{dt} = S_{\text{growthV}} + S_{\text{growthD}} + S_{\text{growthB}} - S_{\text{death}} \quad (4)$$

$$\frac{dW}{dt} = W_{\text{growthD}} + W_{\text{growthB}} - W_{\text{death}} \quad (5)$$

A description of all variables and the references underlying their parameter estimations are presented in Table 1, where in the text we only elaborate on the variables that are needed to understand the working of the equations. All vegetation biomass is modelled in one state and follows the regrowth equation of Turchin and Batzli (2001), where biomass is expressed in normalised values with respect to the carrying capacity k_0 and grows with rate R_0 (Equation 1a).

$$V_{\text{growth}} = R_0 V \left(1 - \frac{V}{k_0}\right) \quad (1a)$$

The consumption rates of vegetation by deer (Equation 1b), boar (Equation 1c) and scavengers (Equation 1d) all follow a Holling type II functional response (Holling 1966), which is often used to describe the realistic 'levelling-off' of a response with increasing resources (Skalski and Gilliam 2001).

$$V_{\text{consD}} = D\frac{A_{VD}V}{B_{XX}+V} \quad (1b)$$

$$V_{\text{consB}} = B\ddot{A}_{XB}(1-\ddot{u}) \quad (1c)$$

$$V_{\text{consS}} = S\frac{\ddot{A}_{XS}V}{(K_D - \ddot{A}_{XB}\ddot{u}B) + K_B + V} \quad (1d)$$

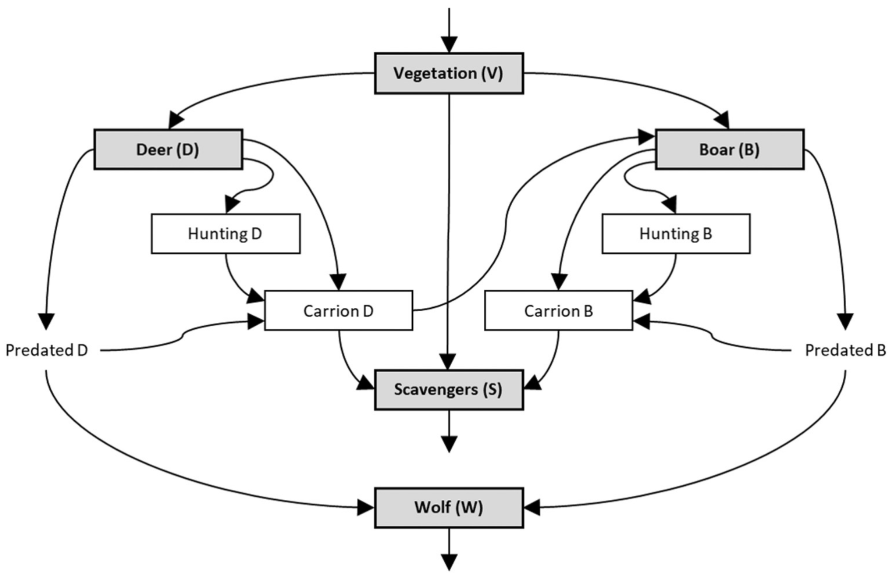

FIGURE 1 | Trophic web of European scavengers and wolves. The consumers of vegetation (V) consist of two types of ungulates – deer (D) and boar (B) – and facultative scavengers (S). V represents vegetation and all other resources, including small prey of facultative scavengers, combined. The D species represent all Cervidae species, whereas the B represents wild boar (*Sus scrofa*). The S species represent all facultative scavengers, including vertebrates and invertebrates. Both D and B populations can be hunted, e.g., regular culling practices by humans. S species consume both D and B carrion, whereas B only scavenge on D carrion, i.e., we assume no cannibalism. Carrion from D is first consumed by B, then S. The large predator wolf (W) predates both on D and B, of which a fraction enters the carrion pool and is thus not consumed by W.

A_{YZ} is the maximum amount of resources Y ingested per unit Z (e.g., A_{VD} is the maximum amount of vegetation ingested per unit of deer), with B_{YZ} being the half-saturation density of Y per unit Z (which we kept at the same value B_{XX} (Table 1) for all functional response equations in our model, as these values are very difficult to estimate (Skalski and Gilliam 2001)) to determine the actual ingestion rate via this functional response.

Equation (1b) has its functional response written in its most basic form, given that deer only consume vegetation in our model. However, boar (Equation 1c) also consume deer carrion K_D, and scavengers (Equation 1d) also consume both deer and boar K_B carrion, which influences their vegetation consumption rate per time step. Therefore, we extended upon the default Holling type II functional response equations of the vegetation consumption by boar and scavengers, which we list here as separate equations to be substituted in the main equations. For example for boar, we model the portion of deer carrion in their diet $\ddot{u}$ with a separate Holling type II functional response (Equation 1c2), based on the amount of available deer carrion.

$$\ddot{u} = \frac{u\frac{K_D}{A_{XB}B}}{B_u + \frac{K_D}{A_{XB}B}} \tag{1c2}$$

Given that carrion is more nutritious than vegetation for boar, the conversion factor from a unit consumed vegetation biomass to a unit boar C_{VB} is smaller than the conversion factor from deer carrion to boar C_{DB} (Table 1; Appendix S1). As such, we model the maximum total consumption rate by boar $\ddot{A}_{XB}$ so that it consumes less biomass, when more of its diet consists of carrion (Equation 1c1a).

$$\ddot{A}_{XB} = A_{XB}\frac{C_{VB}\left(1-u_a\right)+C_{DB}u_a}{C_{VB}(1-\ddot{u})+C_{DB}\ddot{u}} \tag{1c1a}$$

This way a unit of boar 'aims to' obtain approximately the same amount of boar biomass units in total $\ddot{A}_{XB}$ via a Holling type II functional response (Equation 1c1), independent of the fraction of carrion in its diet.

$$\ddot{A}_{XB} = \frac{\ddot{A}_{XB}\left(V(1-\ddot{u})+K_D\ddot{u}\right)}{B_{XX}+V(1-\ddot{u})+K_D\ddot{u}} \tag{1c1}$$

For scavengers, their maximum total consumption rate $\ddot{A}_{XS}$ is also computed via a Holling type II functional response (Equation 1d1), which considers the available vegetation, deer carrion and boar carrion biomass.

$$\ddot{A}_{XS} = \frac{A_{XS}\left(V+\left(K_D-\ddot{A}_{XB}\ddot{u}B\right)+K_B\right)}{B_{XX}+V+\left(K_D-\ddot{A}_{XB}\ddot{u}B\right)+K_B} \tag{1d1}$$

Given that we assume boars are the first and foremost scavengers to consume deer carrion (Wenting, Rinzema, and van Langevelde 2022; Wenting et al. 2024), only the deer carrion that is not consumed by boar are available for other scavengers. Deer (Equation 1d2) and boar carrion (Equation 1d3) are (i) produced by natural mortality, (ii) the fraction that is left by human hunters and (iii) the fraction that is left by wolves.

$$K_D = D_{\text{death}} + D_{\text{hunt}}L_D + D_{\text{pred}}\nu \tag{1d2}$$

$$K_B = B_{\text{death}} + B_{\text{hunt}}L_B + B_{\text{pred}}\nu \tag{1d3}$$

The functions that describe the growth of deer (Equation 2a), boar (Equation 3a) and scavengers (Equation 4a) from vegetation are all calculated by multiplying the consumed vegetation biomass by the conversion factor C_{VY} from a unit consumed vegetation biomass to a unit Y.

$$D_{\text{growthV}} = V_{\text{consD}}C_{VD} \tag{2a}$$

$$B_{\text{growthV}} = V_{\text{consB}}C_{VB} \tag{3a}$$

$$S_{\text{growthV}} = V_{\text{consS}}C_{VS} \tag{4a}$$

The deer carrion growth function of boar (Equation 3b) is obtained by multiplying the portion of deer carrion in the boars' diet $\ddot{u}$ by the total consumed biomass per unit boar $\ddot{A}_{XB}$, the deer carrion to boar conversion factor C_{DB} and the total units of boar.

$$B_{\text{growthD}} = \ddot{A}_{XB}\ddot{u}BC_{DB} \tag{3b}$$

The deer (Equation 4b) and boar carrion (Equation 4c) growth functions of scavengers are also obtained by multiplying the consumed carrion biomass by the carrion to scavenger conversion factor C_{XS}.

$$S_{\text{growthD}} = \min\left[\left(\ddot{A}_{XS}S\right),\left(K_D-\ddot{A}_{XB}\ddot{u}B\right)\right]C_{XS} \tag{4b}$$

$$S_{\text{growthB}} = \min\left[\left(\ddot{A}_{XS}S\right),\left(K_B\right)\right]C_{XS} \tag{4c}$$

The consumed carrion biomass by scavengers is modelled with a Holling type I functional response (Holling 1966), meaning that scavengers will consume $\ddot{A}_{XS}$ per unit S until a maximum value that is equal to the total amount of available carrion. However, do note that $\ddot{A}_{XS}$ itself is computed via a Holling type II functional response (Equation 1d1), so the overall carrion consumption by and subsequent growth of scavengers follows a Holling type II functional response in relation to resource availability.

The deer (Equation 5a) and boar growth functions of wolf (Equation 5b) are also similar in structure as the other growth functions, where the amount of predated deer D_{pred} and boar B_{pred} (both explained in the next paragraph) are multiplied by the conversion factor C_{XW} and multiplied by the fraction of the carrion that is not left behind by the wolves $(1-\nu)$.

$$W_{\text{growthD}} = D_{\text{pred}}C_{XW}(1-\nu) \tag{5a}$$

$$W_{\text{growthB}} = B_{\text{pred}}C_{XW}(1-\nu) \tag{5b}$$

The predation of deer (Equation 2b) and boar by wolves (Equation 3c) are both also modelled with a Holling type II

TABLE 1 | Parameter values.

Symbol	Meaning	Initial value	Value after sensitivity analysis	Unit	Reference/notes
R_0	Regrowth rate of V	4	4	$year^{-1}$	Focardi et al. (2017)
k_0	Carrying capacity of V	10	10	ton ha^{-1}	Normalised vegetation biomass density (as in Focardi et al. (2017)), unit is an approximation using Earth's total plant biomass (Bar-On, Phillips, and Milo 2018)
A_{VD}	Ingestion of resources by D per unit D for overwhelming V	23.5	23.5	$year^{-1}$	Based on individual food requirement of 986 kg $year^{-1}$ (Mulley 2002) and average individual weight of 42 kg (Moore, Littlejohn, and Cowie 1988)
B_{XX}	Half-saturation density of resources in the foraging of D, B, S and W	10	10	ton ha^{-1}	Based on Focardi et al. (2017)
C_{VD}	Conversion factor from consumed resource V to D	0.017	0.025	—	Based on Flajšman, Jerina, and Pokorny (2017), Mulley (2002), and Moore, Littlejohn, and Cowie (1988), see conversion coefficient calculations (Appendix S1)
M_D	Death rate of D in the absence of hunting or predators	0.125	0.125	$year^{-1}$	Based on Müller et al. (2010); mean life expectancy in captivity is ~8 years
A_{XB}	Ingestion of resources by B per unit B for overwhelming total resources and average carrion in diet	20.15	20.15	$year^{-1}$	Based on individual food requirement of 1209 kg $year^{-1}$ (Nagy 2021; Treyer et al. 2012) and assumed average individual weight of 60 kg with 16% carrion in diet
C_{VB}	Conversion factor from consumed resource V to B	0.055	0.055	—	Based on Chinn et al. (2022), Gethöffer, Sodeikat, and Pohlmeyer (2007), Treyer et al. (2012), Sá, Moreno, and Carciofi (2020), see conversion coefficient calculations (Appendix S1)
M_B	Death rate of B in the absence of hunting or predators	0.08	0.08	$year^{-1}$	Based on Massei (1995): maximum age of 12 years
u_a	Average portion of D carrion scavenged by B	0.16	0.16	—	Ballari and Barrios-García (2014)
u	Maximum portion of D carrion scavenged by B	0.2	0.2	—	Unknown, tested during sensitivity analyses and estimated based on average 16% of Ballari and Barrios-García (2014)
B_u	Half-saturation density of carrion portion in the scavenging of B on D carrion	0.1	0.1	—	Unknown, tested during sensitivity analyses and estimated based on average 16% of Ballari and Barrios-García (2014)
C_{DB}	Conversion factor from consumed resource D to B	0.069	0.069	—	Based on Chinn et al. (2022), Gethöffer, Sodeikat, and Pohlmeyer (2007), Treyer et al. (2012), see conversion coefficient calculations (Appendix S1)

(Continues)

TABLE 1 | (Continued)

Symbol	Meaning	Initial value	Value after sensitivity analysis	Unit	Reference/notes
q	Exponential decay rate of natural death rate of deer and boar with increasing predator density	10	10	—	Unknown, tested during sensitivity analyses
T_D	Targeted population density for D by hunters	0–1	0–1	ton ha^{-1}	Varied to analyse effect of hunting regimes
H_D	Hunting rate of D above aimpopD at overwhelming D	0–1	0–1	year^{-1}	Varied to analyse effect of hunting regimes
L_D	Not harvested portion of hunted D	0–1	0–1	—	Varied to analyse effect of hunting regimes
T_B	Targeted population density for B by hunters	0–1	0–1	ton ha^{-1}	Varied to analyse effect of hunting regimes
H_B	Hunting rate of B above aimpopB at overwhelming B	0–1	0–1	year^{-1}	Varied to analyse effect of hunting regimes
L_B	Not harvested portion of hunted B	0–1	0–1	—	Varied to analyse effect of hunting regimes
M_S	Death rate of S	0.2	0.2	year^{-1}	Based on overall death rate as in Focardi et al. (2017)
C_{XS}	Conversion factor from consumed resource D or B to S	0.054	0.1	—	Mean animal based conversion factor
M_W	Death rate of W	0.07	0.2	year^{-1}	Based on Hannon and Ruth (2001); life expectancy in captivity is max. 14 years
r	Predation rate by W per unit W for overwhelming resources	96.6	96.6	year^{-1}	Based on individual food requirement of 1642.5 kg year^{-1} (Jędrzejewski et al. 2002) and average individual weight of 25 kg (Jędrzejewski et al. 2002) and corrected for unconsumed portion
v	Portion of predated resources by W not consumed by W	0.32	0.32	—	Based on Metz et al. (2011) and Wilmers, Crabtree, et al. (2003)
C_{XW}	Conversion factor from consumed resource to W	0.038	0.038	—	Based on Jędrzejewski et al. (2002), Sidorovich et al. (2007), see conversion coefficient calculations (Appendix S1)
A_{XS}	Ingestion of resources by S per unit S for overwhelming resources	20	20	year^{-1}	Unknown, tested during sensitivity analyses
C_{VS}	Conversion factor from consumed resource V to S	0.036	0.036	—	Mean plant based conversion factor

Note: See Appendix S1 for the conversion factor calculations.

functional response, where r is the maximum total predation rate per wolf unit. The wolves' total predation rate is divided over deer and boar based on their relative availability. We amplified this selection preference of wolf for the most abundant prey by squaring the deer and boar biomass densities, so that it was easier to simulate a system in which both deer and boar could co-occur despite the higher vegetation conversion factors of boar versus deer (Table 1). This way we assumed that wolves became more specialistic hunters for a single prey species when that species was abundant compared to the other species (Becker et al. 2008; Sand et al. 2016; Zabihi-Seissan, Prokopenko, and Vander Wal 2022).

$$D_{\text{pred}} = \frac{r(D+B)}{B_{XX}+D+B}\frac{D^2}{D^2+B^2}W \tag{2b}$$

$$B_{\text{pred}} = \frac{r(D+B)}{B_{XX}+D+B}\frac{B^2}{D^2+B^2}W \tag{3c}$$

Hunting of both deer (Equation 2c) and boar (Equation 3d) is zero when their biomass is equal or below the hunters' target biomass T. When their biomass is higher, then only the amount above this target biomass is hunted with a hunting efficiency rate H (to simulate the increasing difficulty to find animals to hunt when their density drops). This describes hunting regimes that are standard in European countries, where the hunting quota of animals are determined based on the yearly estimated population size and the target population size, but where quota are often not fully realised when these targets are strict (Dijkhuis et al. 2023).

$$D_{\text{hunt}} = \begin{cases} 0, & \text{if } D \leq T_D \\ \left(1-\frac{T_D}{D}\right)H_D(D-T_D), & \text{if } D > T_D \end{cases} \tag{2c}$$

$$B_{\text{hunt}} = \begin{cases} 0, & \text{if } B \leq T_B \\ \left(1-\frac{T_B}{B}\right)H_B(B-T_B), & \text{if } B > T_B \end{cases} \tag{3d}$$

Finally, the natural mortality of deer (Equation 2d), boar (Equation 3e), scavengers (Equation 4d) and wolves (Equation 5c) are modelled by multiplying a static death rate M with the total biomass units of the respective populations. For both deer and boar, this natural mortality decreases with an exponential decay rate of q multiplied by the wolves' predation pressure. We implemented this process to simulate that wolves more often target old and weak prey, thereby lowering the natural mortality rate of these prey animals (Becker et al. 2008; Kittle et al. 2017).

$$D_{\text{death}} = e^{-\frac{qWD^2}{D(D^2+B^2)}}M_D D \tag{2d}$$

$$B_{\text{death}} = e^{-\frac{qWB^2}{B(D^2+B^2)}}M_B B \tag{3e}$$

$$S_{\text{death}} = M_S S \tag{4d}$$

$$W_{\text{death}} = M_W W \tag{5c}$$

2.2 | Parameter Estimation and Sensitivity Analysis

We aimed to develop an ODE model that resembles the actual processes of a temperate ecosystem, which is a non-trivial task. Especially the estimation of parameter values is not straightforward, because (1) not all parameter values can be estimated directly from the literature and (2) even parameter values derived from the literature may cause non-realistic simulations, given the simplifications of a model compared to reality. We approached this problem with a three-step workflow. First, we searched the literature using keyword based on the explained meaning of the parameters (Table 1) to estimate the parameter values. Second, we built up the complexity our model step-by-step (first a model only with vegetation (by setting the initial values of all other states at zero), then vegetation + deer, then vegetation + boar, etc.; see R script via link in Data Accessibility Statement), to estimate the values of the other parameters and to finetune the parameters that we based on the literature. These values were estimated to avoid both chaotic time series and crashing populations, when these were unrealistic patterns for the simulated scenarios based on our expert knowledge. When we needed to update parameter values, we updated them such that it would strike a balance between changing as few parameters as possible with as small a deviation per parameter as possible (Table 1). Third, during each step of this workflow, we also performed sensitivity analyses on the parameters to check that the simulations were relatively robust to alterations of our estimated parameter values (see R script via link in Data Accessibility Statement). At each step of this workflow, we varied the parameters that were introduced at this step by a factor of 0.75, 0.875, 1, 1.125 and 1.25. Then we ran the simulations for all combinations of these parameter values at each step of our workflow (e.g., so $5^4 = 625$ simulations in a single step when 4 parameters were introduced). Then we examined the output of the simulations using: (1) timeseries line charts of the different states (e.g., V) with multiple lines and figure panels for the different parameter values of the sensitivity analysis and (2) 2D image plots of the end state of the different states (e.g., V) with two parameters that were varied during the sensitivity analysis along both the x- and y-axis of the image plots and the other varied parameter values separated over multiple figure panels. When the qualitative patterns of the simulations were highly dependent on the parameter value range that we chose during our sensitivity analyses, then we updated our estimated parameter values in the same way as in step two to make the simulations more robust. Finally, at the end of each step, we visualised phase planes of each combination of two states to verify if the initial state values influenced the end states (which was never the case, i.e., all models converged to a single stable state).

After this three-step workflow to estimate parameter values was complete, we let our simulation run with these same parameter values for four different scenarios: with and without both boar and wolf (i.e., wolf and boar, only wolf, only boar, neither), by iteratively setting the initial state value of boar and wolf at zero. For each of these four scenarios, we also varied two parameters of interest: (1) the hunters' target biomass for both the deer and population and (2) the fraction of carrion left by hunters. Finally, when our interpretations of the results were highly dependent on a single parameter value, we performed a sensitivity analysis for this parameter at this stage again to test the robustness of our conclusions.

2.3 | Numerical Simulations

We performed the numerical simulations in *R 4.3.1* (R Core Team 2023) with the *deSolve* package to solve the ODE model (Soetaert, Petzoldt, and Setzer 2010), the *data. table* package to process the data (Dowle and Srinivasan 2023), and the *ggplot2* package to visualise (Wickham 2016). We used *lsoda* as the ODE solving algorithm (Petzold 1983), which switches automatically between stiff and non-stiff methods. As such, this algorithm adaptively changes the time step size during integration to e.g., avoid overshooting. We let the simulations of all our different scenarios run for 250 time-steps (years), because this was long enough to stabilise the different states from its initial values and still short enough to visually investigate the evolution of the states over time.

3 | Results

3.1 | Effect of Wild Boar on Scavenger Dynamics

In the scenarios with a population target of 0, i.e., more hunting, all deer and boar became extinct (Appendix S2: Figures S2.1– S2.2), so, to assess the effect of boar on scavenger dynamics, we focused on the scenarios with a high or medium hunting target (Figure 2). When boar is present but wolf absent, we observed that the overall scavenger biomass was the lowest (Figure 2). In this scenario, there is more competition for vegetation resources between boar, deer and scavengers (Appendix S2: Figures S2.1–S2.3). Deer biomass is higher in the absence of boar (Appendix S2: Figure S2.1),

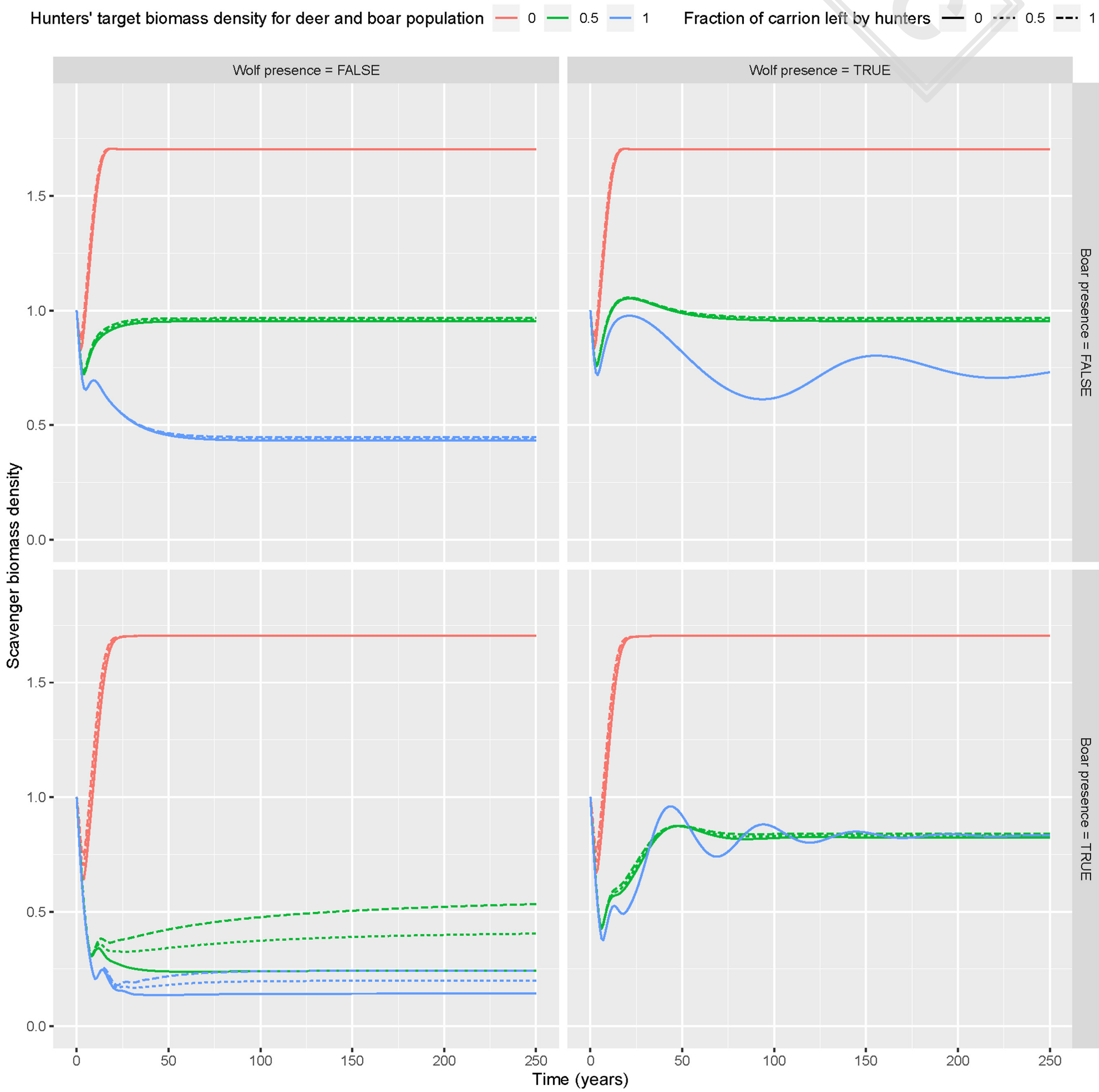

FIGURE 2 | Scavenger biomass density ODE model simulations (y-axis) over time (x-axis), with boar (horizontal panels) and wolf present/absent (vertical panels), for different hunting target values (line colours) and fractions of carrion left by hunters (line types).

but in the presence of boar, there is more biomass of deer and boar combined (Appendix S2: Figures S2.1 and S2.2). This means that competition for vegetation resources would drive scavenger biomass, rather than competition for carrion. This becomes also apparent from the lower vegetation biomass in the scenario with boar and without wolves (Appendix S2: Figure S2.3).

The importance of vegetation resources in determining scavenger biomass could be heavily influenced by the parameter value we used for the conversion factor of vegetation for scavengers C_{VS}. We assessed the importance of this parameter value with a sensitivity analysis. When C_{VS} was 30% higher, the same qualitative time series patterns of scavenger biomass occurred for all scenarios, with only the absolute scavenger biomass values becoming higher by a factor of 1–1.25 (Appendix S3: Figures S3.2 and S3.3). Similarly, we found the same patterns, but with lower absolute biomass values by a factor of 0.5–1, when C_{VS} was 30% lower (Appendix S3: Figures S3.1 and S3.2). That means that our results are robust to varying values of the conversion factor of vegetation for scavengers. Thus, the observation that vegetation resources, rather than carrion, are limiting scavenger biomass is robust. Our simulations showed that the effect of boar on scavenger biomass is negative in the absence of wolf but neutral in the presence of wolf (Figure 2).

3.2 | Effect Re-Establishing Wolf on Scavenger Dynamics

Our simulations showed a general positive trend in scavenger biomass in the presence of wolf (Figure 2). In the absence of boar, we found that wolf could only maintain their presence when the hunting target was high (so when there was little hunting) (Appendix S2: Figure S2.4). In the presence of boar, wolf could maintain their presence with both high and medium hunting targets (Appendix S2: Figure S2.4). In the scenarios where wolf could maintain their presence, we observed more fluctuations in the scavenger biomass around a stable equilibrium (Figure 2), which followed fluctuations in population dynamics of deer and boar (Appendix S2: Figures S2.1 and S2.2). This again is due to general predator prey dynamics, since the fluctuations in biomass of deer and boar followed the fluctuations of wolf biomass and vice versa (Appendix S2: Figures S2.1– S2.4).

3.3 | Effect of Human Hunting Strategies on Scavenger Dynamics

The hunting target had, via the populations of deer and boar (Appendix S2: Figures S2.1 and S2.2), a huge effect on scavenger biomass in general (Figure 2). The lower the biomass of deer and boar, the higher the biomass of scavengers, resulting from decreasing competition for vegetation resources. We observed that more hunting resulted in less deer and boar (Appendix S2: Figures S2.1 and S2.2), which subsequently resulted in higher biomass of scavengers (Figure 2).

In the presence of both boar and wolf, medium and high hunting targets caused the same scavenger biomass (Figure 2). The higher the hunting target, the more the wolf took over from humans in killing deer and boar. This often resulted in deer and boar populations below the hunting target in this scenario, meaning that there was no human hunting needed in this scenario to maintain deer and boar population targets (Appendix S2: Figures S2.1 and S2.2). This, in turn, resulted in the same scavenger biomass (Figure 2), although population dynamics fluctuated more when the wolf dominated the hunting.

We found that the fraction of carrion left behind by hunters was only important for scavenger biomass when wolf was absent but boar present (Figure 2). The more carrion that was left behind by hunters, the higher the scavenger biomass (Figure 2). The reason that the extra growth scavengers gained from carrion was only important in this scenario is again due to competition for vegetation resources between scavengers, deer and boar. The vegetation resources were more limited in this scenario than in the three others (Appendix S2: Figure S2.3), and therefore higher fractions of carrion left behind by hunters, actually also resulted in lower populations of deer and boar in this scenario due to competition for vegetation resources with scavengers (Appendix S2: Figures S2.1 and S2.2).

3.4 | Main Resource for Scavengers

To assess the main resource for scavengers under different scenarios, we first checked the importance of vegetation versus carrion for the growth of scavenger biomass. Overall, we found that vegetation resources caused way more growth of scavenger biomass compared to carrion (Figure 3). The only exception was when boar was present but wolf absent. Here, the scenarios with high and medium hunting targets resulted in more competition for vegetation resources and simultaneously for more deer and boar biomass that became available as carrion (Figure 3; Appendix S3: Figure S3.5). For that reason, carrion became more important in these scenarios (Figure 3). The sensitivity analysis of the conversion factor of vegetation resources for scavengers indicated that competition for vegetation resources was still a dominant process, rather than the availability of carrion in general, in determining the biomass of scavengers (Appendix S3: Figures S3.1–S3.3).

When wolf was present but boar absent, the available carrion comes either from hunting or from predation (Appendix S2: Figure S2.5). The lower the hunting target, the more carrion was relatively obtained from hunting (Appendix S2: Figure S2.5). In the presence of boar, the fraction of carrion left behind by hunters matters in the case of medium hunting target (Appendix S2: Figure S2.5). In this scenario, we observed that higher fractions of carrion left behind by hunters, the larger the fraction of carrion that is originated from hunting.

In the presence of boar, we found that there was always more boar carrion than deer carrion available (Figure 4). This is because, in general, boar biomass was always higher than deer biomass in our simulations (Appendix S2: Figures S2.1 and S2.2). With a medium hunting target and in the absence of wolf, deer was not outcompeted by boar and scavengers (Appendix S2: Figures S2.1–S2.4). Also, deer was not outcompeted in the

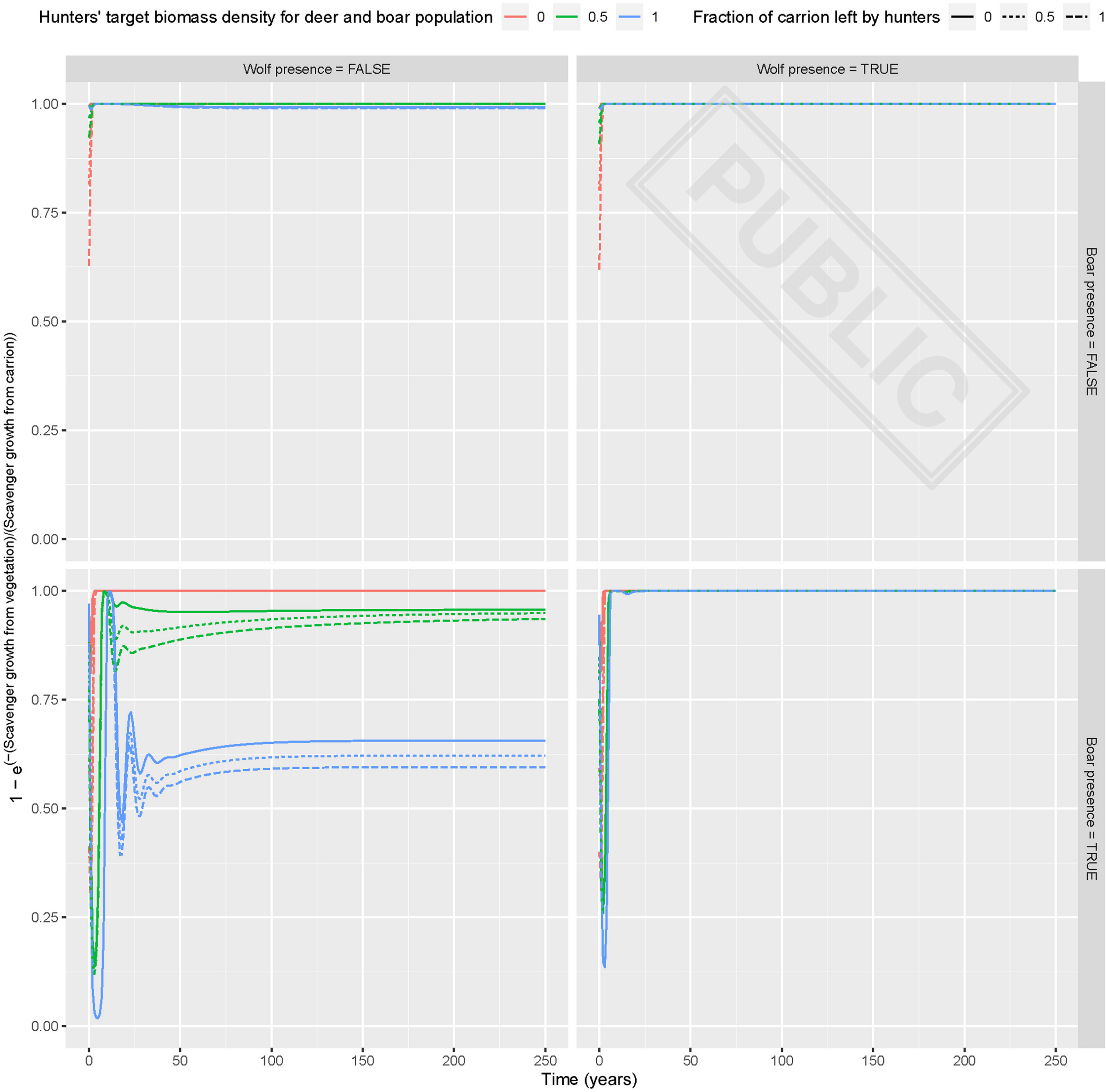

FIGURE 3 | Scavenger growth from vegetation versus scavenger growth from carrion ODE model simulations (y-axis, transformed from [0, ∞] to [0, 1] range) over time (x-axis), with boar (horizontal panels) and wolf present/absent (vertical panels), for different hunting target values (line colours) and fractions of carrion left by hunters (line types).

presence of wolf, but only when the hunting target was zero (Appendix S2: Figure S2.1). Only in the scenarios with medium hunting target, the fraction of carrion left behind by hunters influenced the fraction of deer versus boar carrion (Figure 4).

4 | Discussion

In this study, we examined how different human hunting strategies, combined with the presence or absence of boar and wolf, influenced the dynamics of scavenger biomass in a system with only facultative scavengers. We did not aim to create fully realistic scenarios of specific existing natural systems, but intended to create a mathematical model to improve our theoretical understanding of all the interacting processes that are involved. Given the nature of a simulation study, we made many assumptions to simplify reality to obtain generalisable conclusions. These assumptions included that the wolves' diet was exclusively based on deer and boar predation, that there was only one shared vegetation resource for all populations, that wild boar did not scavenge on conspecifics, no scavenging by wolves, no human prosecution of wolves, and that the populations are limited by food (instead of space). Regardless of these assumptions, we found some patterns that provided new insights into the population dynamics of facultative scavengers when wolves and/or boar are re-establishing under different human hunting strategies.

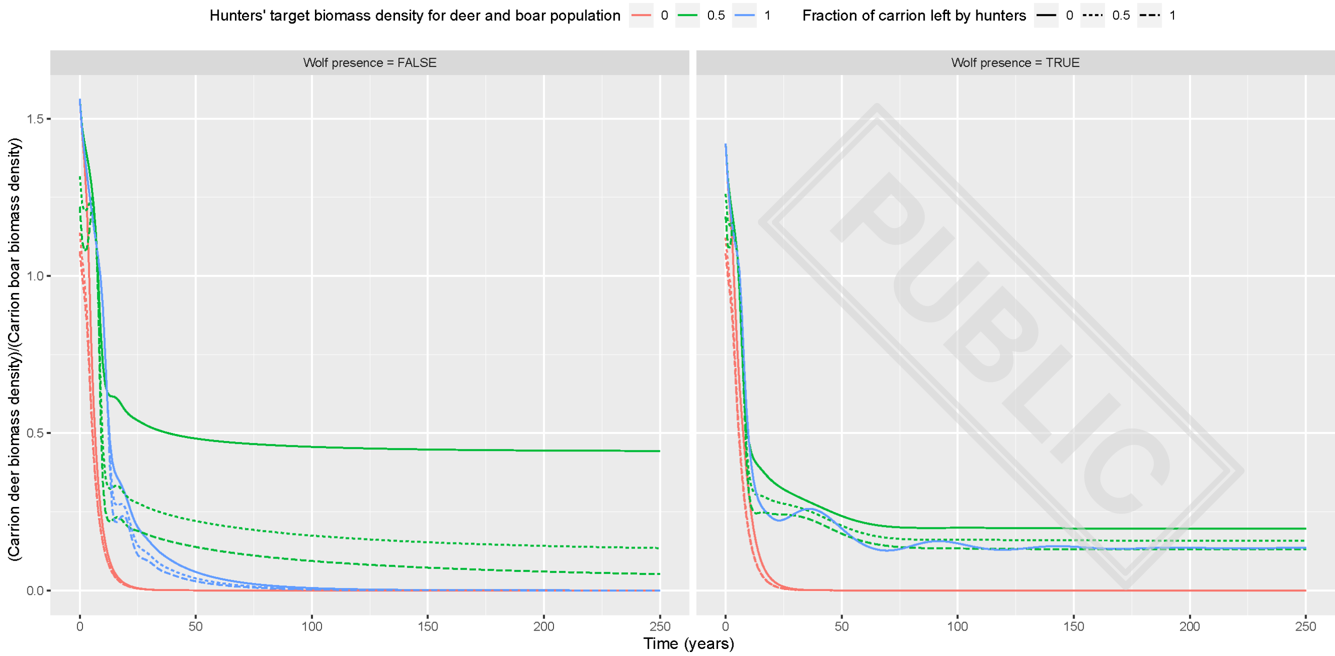

FIGURE 4 | Deer carrion versus boar carrion biomass density ODE model simulations (y-axis) over time (x-axis), with wolf present/absent (panels), for different hunting target values (line colours) and fractions of carrion left by hunters (line types).

A key conclusion of our simulations is that carrion was not the most important resource in determining the biomass growth of facultative scavengers (Figure 3). These facultative scavengers are flexible in their diet and behaviour and can therefore adapt to local circumstances (Díaz-Ruiz et al. 2013; Rooney and Montgomery 2013; Papakosta et al. 2014; Jain et al. 2022). As a result, carrion is not equally consumed among and within ecosystems and different local scavenger guilds, which results in high variability of the carrion decomposition process in general (Newsome et al. 2021; Wenting, Rinzema, and van Langevelde 2022; Wenting et al. 2024; Vandersteen et al. 2023). This implies that carrion is an ephemeral resource for facultative scavengers, which supplements their diet and behaviour but does not necessarily determine it (Wilson and Wolkovich 2011; Barton et al. 2013), which is in line with our results. Moreover, the presence of wolves also has indirect effects by changing intraguild dynamics between large and small prey species (Ripple and Beschta 2004; Jędrzejewski et al. 2012), ultimately changing dynamics among facultative scavenger guilds (Wikenros et al. 2013) and vegetation resources (Jędrzejewski et al. 2012; Kuijper et al. 2013).

Due to the direct competition for vegetation resources in our model by deer and boar with scavengers, we assumed that the competitive release hypothesis (Ketterson and Nolan Jr 1976; Le Bagousse-Pinguet, Gross, and Straile 2012) applies to our study system. As such, a lower population of one group often positively impacts the populations of other groups (Berg et al. 2019; Van Moorter et al. 2021). This has been demonstrated for the European ecosystems where wolves are present (Chapman et al. 2011), which is reflected in our results (Appendix S2: Figures S2.1–S2.4).

The presence of wolf had an overall positive effect on the scavenger population and could take over the role of human hunting in controlling ungulate populations under some conditions (Figure 2). In our model, wolf was fully dependent on predation on deer and boar. It can supplement its diet with other resources, including livestock (Janeiro-Otero et al. 2020) and carrion (Petroelje et al. 2019; Wirsing and Newsome 2021). Carrion consumption by wolves is extensively documented in some ecosystems (Mateo-Tomás et al. 2015). In temperate ecosystems, on which our simulations were based, it has only been proven in areas where wolves were re-established for multiple years, or where they were never extinct (Jędrzejewski et al. 2002; Selva 2004; Selva and Fortuna 2007). In other areas, where wolves recently re-established, evidence is only anecdotical or absent. Thus, it is unknown whether recently re-established wolves scavenge substantially or change their scavenging habits over time. Based on this, we decided to simplify the model by only focusing on scavenging by facultative scavengers and hence not to include scavenging behaviour of wolves.

Depending on the local circumstances, including the presence of large carnivores (that can induce fear), facultative scavengers establish a specific way of scavenging behaviour (Selva et al. 2005; Pereira, Owen-Smith, and Moleón 2014; Kane et al. 2017). For example, the willingness of species to forage in open areas decreases with increasing predation pressure (Allen et al. 2015), in line with the ecology of fear (Haswell et al. 2018, 2020; Gaynor et al. 2021; Ramirez et al. 2024). This, in turn, might reduce the potential effects of habitat type on scavenging behaviour in general, meaning that scavengers might forage more in open landscapes instead of forests only, and vice versa (Wenting et al. 2024). We suppose that facultative scavengers, due to their adaptable nature, eventually adapt their scavenging habits when large carnivores re-establish. However, the question is about the speed at which they will adapt their behaviour. This might cause some iterations in scavenger dynamics when wolves re-establish, until scavengers have adapted their behaviour to the wolves' presence. However, the ultimate consequences are unclear and hard to predict, especially in human-dominated landscapes (Hebblewhite et al. 2005; Dorresteijn et al. 2015).

Boar outcompeted deer in the scenarios with low hunting pressure and without wolves (Appendix S2: Figures S2.1 and S2.2). This is because we assumed boar to be more efficient in exploiting vegetation resources than deer, i.e., boar had a higher conversion factor of vegetation resources than deer (Table 1), mainly due to their higher reproductive rate (Appendix S1). For simplicity, we used only one vegetation resource for all species. Consequently, boar and deer competed directly for exactly the same resource. This is not realistic due to niche differentiation among those boar and deer species (Gebert and Verheyden-Tixier 2001; Ballari and Barrios-García 2014; Mikulka et al. 2018; Spitzer et al. 2020). The same applies to facultative scavengers; although they are predominantly omnivores, e.g., Red fox and European badger, that contain plant-based resources in their diet, the vegetation they consume do not fully overlap with deer and boar (Castañeda et al. 2022; Jain et al. 2022). We assume this simplification to be the main limitation of our model for interpreting our results. However, although in reality the resources of all the species do not fully overlap, it is still reasonable that they do show some overlap. The absolute values of our results do not have any predictive power for reality, but the patterns that we modelled still do, which is exemplified by our sensitivity analyses on the vegetation conversion coefficients by scavengers (Appendix S3: Figures S3.1–S3.3). Therefore, our result that carrion might not be the main resource that determines the biomass growth of facultative scavengers is still valid.

We found that the presence of boar on scavenger biomass was negative when wolf was absent but neutral when wolf was present (Figure 2). However, scavenger biomass does not automatically reflect the functionality of the scavenger community and the potential effects that scavengers can have on ecological processes. Nonetheless, the simulations are in line with the alleged unique role of boars in carrion decomposition (Wenting, Rinzema, and van Langevelde 2022; Wenting et al. 2024). Also, based on our simulations, we expect that the co-occurrence of both boar and wolf stimulates fundamental ecological processes – e.g., nutrient cycling and restoring biodiversity – the most.

Our simulations with and without boar's presence can be seen as an example of human influences that extend beyond hunting. Both boar and wolf are involved in human-wildlife conflicts (Massei et al. 2015; Storie and Bell 2017; Kuijper et al. 2019; König et al. 2020). Wolf is, unlike boar, strictly protected by law in the EU, meaning that their presence needs to be tolerated (Trouwborst and Fleurke 2019). Boars are not tolerated everywhere, or their populations are extensively controlled (Thurfjell, Spong, and Ericsson 2013; Massei et al. 2015). Our simulations imply, however, that the coexistence of both boar and wolf would positively influence the scavenger dynamics in general by increasing the overall scavenger biomass densities. Consequently, the co-existence of both species would, eventually, enhance the overall ecosystem functioning. We consider this as the most noticeable conclusion of our study.

When the hunting target was low, wolf could replace the effects of human hunting by keeping the populations of deer and boar below the hunting target (Appendix S2: Figures S2.1 and S2.2). That implies that human hunting in general should be reconsidered and adapted to re-establishing wolf populations. This has not only ecological benefits, as our model implies (Figure 2), but would also reduce human-wildlife conflicts since it has been widely documented that established wolves prefer wild prey over livestock (Meriggi and Lovari 1996; Sidorovich, Tikhomirova, and Jędrzejewska 2003; Ferretti et al. 2019).

In conclusion, our model indicates that population dynamics of facultative scavengers are not mainly driven by the availability of carrion but rather by the presence of and competition for vegetation and other resources. The co-occurrence of boar and wolf can have positive effects on scavengers' population dynamics. Their population dynamics showed more fluctuations as human hunting, to control deer and boar densities, was taken over by wolves. Although this is in line with well-documented natural predator–prey interactions (Wangersky and Cunningham 1957; Mougi and Iwasa 2010), it highlights the importance of changing the human hunting strategy in accordance with wolves' re-establishment.

Author Contributions

Elke Wenting: conceptualization (lead), formal analysis (equal), methodology (equal), software (supporting), visualization (equal), writing – original draft (equal), writing – review and editing (equal). **Jasper A. J. Eikelboom:** conceptualization (supporting), formal analysis (equal), methodology (equal), software (lead), visualization (equal), writing – original draft (equal), writing – review and editing (equal). **Henk Siepel:** conceptualization (supporting), methodology (supporting), writing – original draft (supporting). **Femke Broekhuis:** conceptualization (supporting), writing – original draft (supporting). **Frank van Langevelde:** conceptualization (supporting), methodology (supporting), writing – original draft (supporting).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The complete R script of the ODE model, including all sensitivity analyses to produce the manuscript figures, is available via: https://doi.org/10.4121/a5a040e7-de45-4d60-9ac4-eec4e826aa85.

Open Research Badges

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.4121/a5a040e7-de45-4d60-9ac4-eec4e826aa8.

References

Allen, B. L., L. R. Allen, H. Andrén, et al. 2017. "Can We Save Large Carnivores Without Losing Large Carnivore Science?" *Food Webs* 12: 64–75. https://doi.org/10.1016/j.fooweb.2017.02.008.

Allen, M. L., L. M. Elbroch, C. C. Wilmers, and H. U. Wittmer. 2015. "The Comparative Effects of Large Carnivores on the Acquisition of Carrion by Scavengers." *American Naturalist* 185: 822–833. https://doi.org/10.1086/681004.

Ansorge, H., G. Kluth, and S. Hahne. 2006. "Feeding Ecology of Wolves *Canis lupus* Returning to Germany." *Acta Theriologica* 51: 99–106. https://doi.org/10.1007/BF03192661.

Ballari, S. A., and M. N. Barrios-García. 2014. "A Review of Wild Boar *Sus scrofa* Diet and Factors Affecting Food Selection in Native and Introduced Ranges." *Mammal Review* 44: 124–134. https://doi.org/10.1111/mam.12015.

Barja, I., Á. Navarro-Castilla, L. Ortiz-Jiménez, et al. 2023. "Wild Ungulates Constitute the Basis of the Diet of the Iberian Wolf in a Recently Recolonized Area: Wild Boar and Roe Deer as Key Species for Its Conservation." *Animals* 13: 3364. https://doi.org/10.3390/ani13213364.

Bar-On, Y. M., R. Phillips, and R. Milo. 2018. "The Biomass Distribution on Earth." *Proceedings of the National Academy of Sciences of the United States of America* 115: 6506–6511. https://doi.org/10.1073/pnas.1711842115.

Barrios-Garcia, M. N., M. Gonzalez-Polo, D. Simberloff, and A. T. Classen. 2023. "Wild Boar Rooting Impacts Soil Function Differently in Different Plant Community Types." *Biological Invasions* 25: 583–592. https://doi.org/10.1007/s10530-014-0818-7.

Barton, P. S., S. A. Cunningham, D. B. Lindenmayer, and A. D. Manning. 2013. "The Role of Carrion in Maintaining Biodiversity and Ecological Processes in Terrestrial Ecosystems." *Oecologia* 171: 761–772. https://doi.org/10.1007/s00442-012-2460-3.

Baruzzi, C., and M. Krofel. 2017. "Friends or Foes? Importance of Wild Ungulates as Ecosystem Engineers for Amphibian Communities." *North-Western Journal of Zoology* 13: 320–325.

Beasley, J. C., Z. H. Olson, N. Selva, and T. L. DeVault. 2019. "Ecological Functions of Vertebrate Scavenging." In *Carrion Ecology and Management*, edited by P. P. Olea, P. Mateo-Tomás, and J. A. Sánchez-Zapata, 125–157. Cham: Springer.

Becker, M. S., R. A. Garrott, P. J. White, C. N. Gower, E. J. Bergman, and R. Jaffe. 2008. "Wolf Prey Selection in an Elk-Bison System: Choice or Circumstance?" *Terrestrial Ecology* 3: 305–337. https://doi.org/10.1016/S1936-7961(08)00216-9.

Berg, J. E., M. Hebblewhite, C. C. St. Clair, and E. H. Merrill. 2019. "Prevalence and Mechanisms of Partial Migration in Ungulates." *Frontiers in Ecology and Evolution* 7: 325. https://doi.org/10.3389/fevo.2019.00325.

Boczulak, H., N. P. Boucher, A. Ladle, M. S. Boyce, and J. T. Fisher. 2023. "Industrial Development Alters Wolf Spatial Distribution Mediated by Prey Availability." *Ecology and Evolution* 13: e10224. https://doi.org/10.1002/ece3.10224.

Boonman-Berson, S., C. Driessen, and E. Turnhout. 2019. "Managing Wild Minds: From Control by Numbers to a Multinatural Approach in Wild Boar Management in the Veluwe, The Netherlands." *Transactions of the Institute of British Geographers* 44: 2–15. https://doi.org/10.1111/tran.12269.

Castañeda, I., T. S. Doherty, P. A. Fleming, A. M. Stobo-Wilson, J. C. Woinarski, and T. M. Newsome. 2022. "Variation in Red Fox *Vulpes vulpes* Diet in Five Continents." *Mammal Review* 52: 328–342. https://doi.org/10.1111/mam.12292.

Chapman, B. B., C. Brönmark, J. Å. Nilsson, and L. A. Hansson. 2011. "The Ecology and Evolution of Partial Migration." *Oikos* 120: 1764–1775. https://doi.org/10.1111/j.1600-0706.2011.20131.x.

Chapron, G., P. Kaczensky, J. D. C. Linnell, et al. 2014. "Recovery of Large Carnivores in Europe's Modern Human-Dominated Landscapes." *Science* 346: 1517–1519. https://doi.org/10.1126/science.1257553.

Chinn, S. M., P. E. Schlichting, T. J. Smyser, C. F. Bowden, and J. C. Beasley. 2022. "Factors Influencing Pregnancy, Litter Size, and Reproductive Parameters of Invasive Wild Pigs." *Journal of Wildlife Management* 86: e22304. https://doi.org/10.1002/jwmg.22304.

DeVault, T. L., O. E. Rhodes Jr., and J. A. Shivik. 2003. "Scavenging by Vertebrates: Behavioral, Ecological, and Evolutionary Perspectives on an Important Energy Transfer Pathway in Terrestrial Ecosystems." *Oikos* 102: 225–234. https://doi.org/10.1034/j.1600-0706.2003.12378.x.

Díaz-Ruiz, F., M. Delibes-Mateos, J. L. García-Moreno, J. María López-Martín, C. Ferreira, and P. Ferreras. 2013. "Biogeographical Patterns in the Diet of an Opportunistic Predator: The Red Fox *Vulpes vulpes* in the Iberian Peninsula." *Mammal Review* 43: 59–70. https://doi.org/10.1111/j.1365-2907.2011.00206.x.

Dijkhuis, L. R., P. A. Jansen, J. den Ouden, et al. 2023. "Estimating Red Deer Population Size Using Vantage Point Counts at Baited Sites." *Journal of Wildlife Management* 87: e22489. https://doi.org/10.1002/jwmg.22489.

Dorresteijn, I., J. Schultner, D. G. Nimmo, et al. 2015. "Incorporating Anthropogenic Effects Into Trophic Ecology: Predator–Prey Interactions in a Human-Dominated Landscape." *Proceedings of the Royal Society B: Biological Sciences* 282: 20151602. https://doi.org/10.1098/rspb.2015.1602.

Dowle, M., and A. Srinivasan. 2023. "_data.table: Extension of 'data.frame'_. R package version 1.14.8." https://CRAN.R-project.org/package=data.table.

Ferretti, F., S. Lovari, V. Mancino, L. Burrini, and M. Rossa. 2019. "Food Habits of Wolves and Selection of Wild Ungulates in a Prey-Rich Mediterranean Coastal Area." *Mammalian Biology* 99: 119–127. https://doi.org/10.1016/j.mambio.2019.10.008.

Flajšman, K., K. Jerina, and B. Pokorny. 2017. "Age-Related Effects of Body Mass on Fertility and Litter Size in Roe Deer." *PLoS One* 12: e0175579. https://doi.org/10.1007/s13364-017-0348-7.

Focardi, S., J. M. Gaillard, F. Ronchi, and S. Rossi. 2008. "Survival of Wild Boars in a Variable Environment: Unexpected Life-History Variation in an Unusual Ungulate." *Journal of Mammalogy* 89: 1113–1123. https://doi.org/10.1644/07-MAMM-A-164.1.

Focardi, S., M. Materassi, G. Innocenti, and D. Berzi. 2017. "Kleptoparasitism and Scavenging Can Stabilize Ecosystem Dynamics." *American Naturalist* 190: 398–409. https://doi.org/10.1086/692798.

Ford, A. T., and J. R. Goheen. 2015. "Trophic Cascades by Large Carnivores: A Case for Strong Inference and Mechanism." *Trends in Ecology & Evolution* 30: 725–735. https://doi.org/10.1016/j.tree.2015.09.012.

Found, R. 2016. "Managing Large Herbivores in Protected Areas." *Global Journal of Ecology* 1: 001–011. https://doi.org/10.17352/gje.000001.

Galaverni, M., R. Caniglia, E. Fabbri, P. Milanesi, and E. Randi. 2016. "One, No One, Or One Hundred Thousand: How Many Wolves Are There Currently in Italy?" *Mammal Research* 61: 13–24. https://doi.org/10.1007/s13364-015-0247-8.

Gantchoff, M. G., D. E. Beyer, J. D. Erb, et al. 2022. "Distribution Model Transferability for a Wide-Ranging Species, the Gray Wolf." *Scientific Reports* 12: 1–11. https://doi.org/10.1038/s41598-022-16121-6.

Gaynor, K. M., M. J. Cherry, S. L. Gilbert, et al. 2021. "An Applied Ecology of Fear Framework: Linking Theory to Conservation Practice." *Animal Conservation* 24: 308–321. https://doi.org/10.1111/acv.12629.

Gebert, C., and H. Verheyden-Tixier. 2001. "Variations of Diet Composition of Red Deer (*Cervus elaphus* L.) in Europe." *Mammal Review* 31: 189–201. https://doi.org/10.1111/j.1365-2907.2001.00090.x.

Gethöffer, F., G. Sodeikat, and K. Pohlmeyer. 2007. "Reproductive Parameters of Wild Boar (*Sus scrofa*) in Three Different Parts of Germany." *European Journal of Wildlife Research* 53: 287–297. https://doi.org/10.1007/s10344-007-0097-z.

Gordon, I. J. 2009. "What Is the Future for Wild, Large Herbivores in Human-Modified Agricultural Landscapes?" *Wildlife Biology* 15: 1–9. https://doi.org/10.2981/06-087.

Greenspoon, L., E. Krieger, R. Sender, et al. 2023. "The Global Biomass of Wild Mammals." *Proceedings of the National Academy of Sciences* 120: e2204892120. https://doi.org/10.1073/pnas.2204892120.

Hannon, B., and M. Ruth. 2001. "Reestablishment of Wolves." In *Dynamic Modeling. Modeling Dynamic Systems*. New York, NY: Springer. https://doi.org/10.1007/978-1-4613-0211-7_20.

Haswell, P. M., K. A. Jones, J. Kusak, and M. W. Hayward. 2018. "Fear, Foraging and Olfaction: How Mesopredators Avoid Costly Interactions With Apex Predators." *Oecologia* 187: 573–583. https://doi.org/10.1007/s00442-018-4133-3.

Haswell, P. M., J. Kusak, and M. W. Hayward. 2017. "Large Carnivore Impacts are Context-Dependent." *Food Webs* 12: 3–13. https://doi.org/10.1016/j.fooweb.2016.02.005.

Haswell, P. M., J. Kusak, K. A. Jones, and M. W. Hayward. 2020. "Fear of the Dark? A Mesopredator Mitigates Large Carnivore Risk Through Nocturnality, but Humans Moderate the Interaction." *Behavioral Ecology and Sociobiology* 74: 1–9. https://doi.org/10.1007/s00265-020-02831-2.

Hebblewhite, M., C. A. White, C. G. Nietvelt, et al. 2005. "Human Activity Mediates a Trophic Cascade Caused by Wolves." *Ecology* 86: 2135–2144. https://doi.org/10.1890/04-1269.

Ho, C., J. M. Marzluff, D. R. Stahler, et al. 2023. "Scavengers Use Natural and Anthropogenic Resources Connecting Protected Areas With Surrounding Lands." *Frontiers in Bird Science* 2: 1119507. https://doi.org/10.3389/fbirs.2023.1119507.

Holling, C. S. 1966. "The Functional Response of Invertebrate Predators to Prey Density." *Memoirs of the Entomological Society of Canada* 98: 5–86.

Jain, V., T. Bugnyar, S. J. Cunningham, M. Gallego-Abenza, M. C. Loretto, and P. Sumasgutner. 2022. "The Spatial and Temporal Exploitation of Anthropogenic Food Sources by Common Ravens (*Corvus corax*) in the Alps." *Movement Ecology* 10: 1–15. https://doi.org/10.1186/s40462-022-00335-4.

Janeiro-Otero, A., T. M. Newsome, L. M. Van Eeden, W. J. Ripple, and C. F. Dormann. 2020. "Grey Wolf (*Canis lupus*) Predation on Livestock in Relation to Prey Availability." *Biological Conservation* 243: 108433. https://doi.org/10.1016/j.biocon.2020.108433.

Jędrzejewski, W., M. Niedziałkowska, M. W. Hayward, et al. 2012. "Prey Choice and Diet of Wolves Related to Ungulate Communities and Wolf Subpopulations in Poland." *Journal of Mammalogy* 93: 1480–1492. https://doi.org/10.1644/10-MAMM-A-132.1.

Jędrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jędrzejewska, and R. Kowalczyk. 2007. "Territory Size of Wolves *Canis lupus*: Linking Local (Białowieża Primeval Forest, Poland) and Holarctic-Scale Patterns." *Ecography* 30: 66–76. https://doi.org/10.1111/j.0906-7590.2007.04826.x.

Jędrzejewski, W., K. Schmidt, J. Theuerkauf, et al. 2002. "Kill Rates and Predation by Wolves on Ungulate Populations in Białowieża Primeval Forest (Poland)." *Ecology* 83: 1341–1356. https://doi.org/10.1890/0012-9658(2002)083[1341:KRAPBW]2.0.CO;2.

Kane, A., K. Healy, T. Guillerme, G. D. Ruxton, and A. L. Jackson. 2017. "A Recipe for Scavenging in Vertebrates–the Natural History of a Behaviour." *Ecography* 40: 324–334. https://doi.org/10.1111/ecog.02817.

Ketterson, E. D., and V. Nolan Jr. 1976. "Geographic Variation and Its Climatic Correlates in the Sex Ratio of Eastern-Wintering Dark-Eyed Juncos (*Junco hyemalis hyemalis*)." *Ecology* 57: 679–693. https://doi.org/10.2307/1936182.

Kittle, A. M., M. Anderson, T. Avgar, et al. 2017. "Landscape-Level Wolf Space Use is Correlated With Prey Abundance, Ease of Mobility, and the Distribution of Prey Habitat." *Ecosphere* 8: e01783. https://doi.org/10.1002/ecs2.1783.

Klauder, K. J., B. L. Borg, K. J. Sivy, and L. R. Prugh. 2021. "Gifts of an Enemy: Scavenging Dynamics in the Presence of Wolves (*Canis lupus*)." *Journal of Mammalogy* 102: 558–573. https://doi.org/10.1093/jmammal/gyab020.

König, H. J., C. Kiffner, S. Kramer-Schadt, C. Fürst, O. Keuling, and A. T. Ford. 2020. "Human–Wildlife Coexistence in a Changing World." *Conservation Biology* 34: 786–794. https://doi.org/10.1111/cobi.13513.

Kuijper, D. P., C. De Kleine, M. Churski, P. Van Hooft, J. Bubnicki, and B. Jędrzejewska. 2013. "Landscape of Fear in Europe: Wolves Affect Spatial Patterns of Ungulate Browsing in Białowieża Primeval Forest, Poland." *Ecography* 36: 1263–1275. https://doi.org/10.1111/j.1600-0587.2013.00266.x.

Kuijper, D. P. J., M. Churski, A. Trouwborst, 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. J., T. A. Diserens, E. Say-Sallaz, et al. 2024. "Wolves Recolonize Novel Ecosystems Leading to Novel Interactions." *Journal of Applied Ecology* 61: 906–921. https://doi.org/10.1111/1365-2664.14602.

Lanszki, J., M. Márkus, D. Újváry, Á. Szabó, and L. Szemethy. 2012. "Diet of Wolves *Canis lupus* Returning to Hungary." *Acta Theriologica* 57: 189–193. https://doi.org/10.1007/s13364-011-0063-8.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. "Wolves, Elk, and Bison: Reestablishing the "Landscape of Fear" in Yellowstone National Park, USA." *Canadian Journal of Zoology* 79: 1401–1409. https://doi.org/10.1139/z01-094.

Le Bagousse-Pinguet, Y., E. M. Gross, and D. Straile. 2012. "Release From Competition and Protection Determine the Outcome of Plant Interactions Along a Grazing Gradient." *Oikos* 121: 95–101. https://doi.org/10.1111/j.1600-0706.2011.19778.x.

Lesmerises, F., C. Dussault, and M. H. St-Laurent. 2012. "Wolf Habitat Selection Is Shaped by Human Activities in a Highly Managed Boreal Forest." *Forest Ecology and Management* 276: 125–131. https://doi.org/10.1016/j.foreco.2012.03.025.

Levi, T., and C. C. Wilmers. 2012. "Wolves–Coyotes–Foxes: A Cascade Among Carnivores." *Ecology* 93: 921–929. https://doi.org/10.1890/11-0165.1.

Libois, R., V. Schockert, C. Lambinet, et al. 2019. "Trophic Niche of Three Carnivores in Southern Belgium: Raccoon (*Procyon lotor*), European Badger (*Meles meles*) and Stone Marten (*Martes foina*)."

Marshall, K. N., D. J. Cooper, and N. T. Hobbs. 2014. "Interactions Among Herbivory, Climate, Topography and Plant Age Shape Riparian Willow Dynamics in Northern Yellowstone National Park, USA." *Journal of Ecology* 102: 667–677. https://doi.org/10.1111/1365-2745.12225.

Massei, G. 1995. "Feeding Ecology, Home Range and Habitat Use by the Wild Boar in a Mediterranean Coastal Area (Central Italy)." Doctoral dissertation, University of Aberdeen.

Massei, G., J. Kindberg, A. Licoppe, et al. 2015. "Wild Boar Populations Up, Numbers of Hunters Down? A Review of Trends and Implications for Europe." *Pest Management Science* 71: 492–500. https://doi.org/10.1002/ps.3965.

Mateo-Tomás, P., P. P. Olea, M. Moleón, et al. 2015. "From Regional to Global Patterns in Vertebrate Scavenger Communities Subsidized by Big Game Hunting." *Diversity and Distributions* 21: 913–924. https://doi.org/10.1111/ddi.12330.

Mattioli, L., C. Capitani, A. Gazzola, M. Scandura, and M. Apollonio. 2011. "Prey Selection and Dietary Response by Wolves in a High-Density Multi-Species Ungulate Community." *European Journal of Wildlife Research* 57: 909–922. https://doi.org/10.1007/s10344-011-0503-4.

Mech, L. D., and L. Boitani, eds. 2019. *Wolves: Behavior, Ecology, and Conservation*. Chicago, IL: University of Chicago Press.

Meriggi, A., and S. Lovari. 1996. "A Review of Wolf Predation in Southern Europe: Does the Wolf Prefer Wild Prey to Livestock?" *Journal of Applied Ecology* 33: 1561–1571. https://doi.org/10.2307/2404794.

Metz, M. C., J. A. Vucetich, D. W. Smith, D. R. Stahler, and R. O. Peterson. 2011. "Effect of Sociality and Season on Gray Wolf (*Canis lupus*) Foraging Behavior: Implications for Estimating Summer Kill Rate." *PLoS One* 6: e17332. https://doi.org/10.1371/journal.pone.0017332.

Mikulka, O., J. Zeman, J. Drimaj, et al. 2018. "The Importance of Natural Food in Wild Boar (*Sus scrofa*) Diet During Autumn and Winter." *Folia Zoologica* 67: 165–172. https://doi.org/10.25225/fozo.v67.i3-4.a3.2018.

Moleón, M., J. A. Sánchez-Zapata, N. Selva, J. A. Donázar, and N. Owen-Smith. 2014. "Inter-Specific Interactions Linking Predation and Scavenging in Terrestrial Vertebrate Assemblages." *Biological Reviews* 89: 1042–1054. https://doi.org/10.1111/brv.12097.

Moleón, M., N. Selva, M. M. Quaggiotto, D. M. Bailey, A. Cortés-Avizanda, and T. L. DeVault. 2019. "Carrion Availability in Space and Time." In *Carrion Ecology and Management*, 23–44. Cham: Springer International. https://doi.org/10.1007/978-3-030-16501-7_2.

Moore, G. H., R. P. Littlejohn, and G. M. Cowie. 1988. "Liveweights, Growth Rates, and Mortality of Farmed Red Deer at Invermay." *New Zealand Journal of Agricultural Research* 31: 293–300. https://doi.org/10.1080/00288233.1988.10423418.

Mori, E., L. Benatti, S. Lovari, and F. Ferretti. 2017. "What Does the Wild Boar Mean to the Wolf?" *European Journal of Wildlife Research* 63: 1–5. https://doi.org/10.1007/s10344-016-1060-7.

Mougi, A., and Y. Iwasa. 2010. "Evolution Towards Oscillation or Stability in a Predator–Prey System." *Proceedings of the Royal Society B: Biological Sciences* 277: 3163–3171. https://doi.org/10.1098/rspb.2010.0691.

Muhly, T. B., M. Hebblewhite, D. Paton, J. A. Pitt, M. S. Boyce, and M. Musiani. 2013. "Humans Strengthen Bottom-Up Effects and Weaken Trophic Cascades in a Terrestrial Food Web." *PLoS One* 8: e64311. https://doi.org/10.1371/journal.pone.0064311.

Müller, D. W., J. M. Gaillard, L. Bingaman Lackey, J. M. Hatt, and M. Clauss. 2010. "Comparing Life Expectancy of Three Deer Species Between Captive and Wild Populations." *European Journal of Wildlife Research* 56: 205–208. https://doi.org/10.1007/s10344-009-0342-8.

Mulley, R. 2002. "The Feed Requirements of Adult Red Deer." *NZGA: Research and Practice Series* 9: 51–55.

Nagy, K. 2021. "Food Requirements of Wild Animals: Predictive Equations for Free-Living Mammals, Reptiles, and Birds." *Nutrition Abstracts and Reviews* 71: 21R–31R.

Newsome, T., R. Cairncross, C. X. Cunningham, et al. 2023. "Scavenging With Invasive Species." *Biological Reviews* 99: 562–581. https://doi.org/10.1111/brv.13035.

Newsome, T. M., B. Barton, J. C. Buck, et al. 2021. "Monitoring the Dead as an Ecosystem Indicator." *Ecology and Evolution* 11: 5844–5856. https://doi.org/10.1002/ece3.7542.

Nores, C., L. Llaneza, and Á. Álvarez. 2008. "Wild Boar *Sus scrofa* Mortality by Hunting and Wolf *Canis lupus* Predation: An Example in Northern Spain." *Wildlife Biology* 14: 44–51. https://doi.org/10.2981/0909-6396(2008)14[44:WBSSMB]2.0.CO;2.

Nowak, S., R. W. Mysłajek, M. Szewczyk, P. Tomczak, T. Borowik, and B. Jędrzejewska. 2017. "Sedentary But Not Dispersing Wolves *Canis lupus* Recolonizing Western Poland (2001–2016) Conform to the Predictions of a Habitat Suitability Model." *Diversity and Distributions* 23: 1353–1364. https://doi.org/10.1111/ddi.12621.

O'Malley, C., L. M. Elbroch, P. E. Lendrum, and H. Quigley. 2018. "Motion-Triggered Video Cameras Reveal Spatial and Temporal Patterns of Red Fox Foraging on Carrion Provided by Mountain Lions." *PeerJ* 6: e5324. https://doi.org/10.7717/peerj.5324.

Papakosta, M., K. Kitikidou, D. Bakaloudis, and C. Vlachos. 2014. "Dietary Variation of the Stone Marten (*Martes foina*): A Meta-Analysis Approach." *Wildlife Biology in Practice* 10: 85–101. https://doi.org/10.2461/wbp.2014.10.11.

Pereira, L. M., N. Owen-Smith, and M. Moleón. 2014. "Facultative Predation and Scavenging by Mammalian Carnivores: Seasonal, Regional and Intra-Guild Comparisons." *Mammal Review* 44, no. 1: 44–55. https://doi.org/10.1111/mam.12005.

Petroelje, T. R., J. L. Belant, D. E. Beyer Jr., and N. J. Svoboda. 2019. "Subsidies From Anthropogenic Resources Alter Diet, Activity, and Ranging Behavior of an Apex Predator (*Canis lupus*)." *Scientific Reports* 9: 13438. https://doi.org/10.1038/s41598-019-49879-3.

Petzold, L. 1983. "Automatic Selection of Methods for Solving Stiff and Nonstiff Systems of Ordinary Differential Equations." *SIAM Journal on Scientific and Statistical Computing* 4: 136–148. https://doi.org/10.1137/0904010.

Planillo, A., M. Wenzler-Meya, I. Reinhardt, et al. 2023. "Understanding Habitat Selection of Range-Expanding Populations of Large Carnivores: 20 Years of Grey Wolves (*Canis lupus*) Recolonizing Germany." *Diversity and Distributions* 30: 71–86. https://doi.org/10.1111/ddi.13789.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing. https://www.R-project.org/.

Ramirez, J. I., D. P. Kuijper, J. Olofsson, et al. 2024. "Applied Ecology of Fear: A Meta-Analysis on the Potential of Facilitating Human-Wildlife Coexistence Through Nonlethal Tools." *Ecological Solutions and Evidence* 5: e12322. https://doi.org/10.1002/2688-8319.12322.

Reinhardt, I., G. Kluth, C. Nowak, et al. 2019. "Military Training Areas Facilitate the Recolonization of Wolves in Germany." *Conservation Letters* 12: e12635. https://doi.org/10.1111/conl.12635.

Ripple, W. J., and R. L. Beschta. 2004. "Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems?" *Bioscience* 54: 755–766. https://doi.org/10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2.

Ripple, W. J., and R. L. Beschta. 2012. "Trophic Cascades in Yellowstone: The First 15 Years After Wolf Reintroduction." *Biological Conservation* 145: 205–213. https://doi.org/10.1016/j.biocon2011.11.005.

Ripple, W. J., R. L. Beschta, J. K. Fortin, and C. T. Robbins. 2015. "Wolves Trigger a Trophic Cascade to Berries as Alternative Food for Grizzly Bears." *Journal of Animal Ecology* 84: 652–654. https://doi.org/10.1111/1365-2656.12339.

Rooney, E., and W. I. Montgomery. 2013. "Diet Diversity of the Common Buzzard (*Buteo buteo*) in a Vole-Less Environment." *Bird Study* 60: 147–155. https://doi.org/10.1080/00063657.2013.772085.

Sá, A. G. A., Y. M. F. Moreno, and B. A. M. Carciofi. 2020. "Food Processing for the Improvement of Plant Proteins Digestibility." *Critical Reviews in Food Science and Nutrition* 60: 3367–3386. https://doi.org/10.1080/10408398.2019.1688249.

Sand, H., A. Eklund, B. Zimmermann, C. Wikenros, and P. Wabakken. 2016. "Prey Selection of Scandinavian Wolves: Single Large or Several Small?" *PLoS One* 11: e0168062. https://doi.org/10.1371/journal.pone.0168062.

Sand, H., J. A. Vucetich, B. Zimmermann, et al. 2012. "Assessing the Influence of Prey–Predator Ratio, Prey Age Structure and Packs Size on Wolf Kill Rates." *Oikos* 121: 1454–1463. https://doi.org/10.1111/j.1600-0706.2012.20082.x.

Sandom, C. J., J. Hughes, and D. W. Macdonald. 2013. "Rewilding the Scottish Highlands: Do Wild Boar, *Sus scrofa*, Use a Suitable Foraging Strategy to Be Effective Ecosystem Engineers?" *Restoration Ecology* 21: 336–343. https://doi.org/10.1111/j.1526-100X.2012.00903.x.

Selva, N. 2004. "The Role of Scavenging in the Predator Community of Białowieża Primeval Forest." Ph.D. dissertation, Polish Academy of Sciences. Warsaw, Poland.

Selva, N., and M. A. Fortuna. 2007. "The Nested Structure of a Scavenger Community." *Proceedings of the Royal Society B: Biological Sciences* 274: 1101–1108. https://doi.org/10.1098/rspb.2006.0232.

Selva, N., B. Jędrzejewska, W. Jędrzejewski, and A. Wajrak. 2005. "Factors Affecting Carcass Use by a Guild of Scavengers in European Temperate Woodland." *Canadian Journal of Zoology* 83: 1590–1601. https://doi.org/10.1139/z05-158.

Sidorovich, V. E., V. P. Stolyarov, N. N. Vorobei, N. V. Ivanova, and B. Jędrzejewska. 2007. "Litter Size, Sex Ratio, and Age Structure of Gray Wolves, *Canis lupus*, in Relation to Population Fluctuations in Northern Belarus." *Canadian Journal of Zoology* 85: 295–300. https://doi.org/10.1139/Z07-001.

Sidorovich, V. E., L. L. Tikhomirova, and B. Jędrzejewska. 2003. "Wolf *Canis lupus* Numbers, Diet and Damage to Livestock in Relation to Hunting and Ungulate Abundance in Northeastern Belarus During 1990–2000." *Wildlife Biology* 9: 103–111. https://doi.org/10.2981/wlb.2003.032.

Skalski, G. T., and J. F. Gilliam. 2001. "Functional Responses With Predator Interference: Viable Alternatives to the Holling Type II Model." *Ecology* 82: 3083–3092. https://doi.org/10.1890/0012-9658(2001)082[3083:FRWPIV]2.0.CO;2.

Smietana, W., and A. Klimek. 1993. "Diet of Wolves in the Bieszczady Mountains, Poland." *Acta Theriologica* 38: 245–251.

Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. "Solving Differential Equations in R: Package deSolve." *Journal of Statistical Software* 33: 1–25. https://doi.org/10.18637/jss.v033.i09.

Špinkytė-Bačkaitienė, R., and K. Pėtelis. 2012. "Diet Composition of Wolves (*Canis lupus* L.) in Lithuania." *Acta Biologica Universitatis Daugavpiliensis* 12: 100–105.

Spitzer, R., A. Felton, M. Landman, N. J. Singh, F. Widemo, and J. P. Cromsigt. 2020. "Fifty Years of European Ungulate Dietary Studies: A Synthesis." *Oikos* 129: 1668–1680. https://doi.org/10.1111/oik.07435.

Stahler, D., B. Heinrich, and D. Smith. 2002. "Common Ravens, *Corvus corax*, Preferentially Associate With Grey Wolves, *Canis lupus*, as a Foraging Strategy in Winter." *Animal Behaviour* 64: 283–290. https://doi.org/10.1006/anbe.2002.3047.

Storie, J. T., and S. Bell. 2017. "Wildlife Management Conflicts in Rural Communities: A Case-Study of Wild Boar (*Sus scrofa*) Management in Ērgļu Novads, Latvia." *Sociologia Ruralis* 57: 64–86. https://doi.org/10.1111/soru.12122.

Thurfjell, H., G. Spong, and G. Ericsson. 2013. "Effects of Hunting on Wild Boar *Sus scrofa* Behaviour." *Wildlife Biology* 19: 87–93. https://doi.org/10.2981/12-027.

Treyer, D., P. Linderoth, T. Liebl, M. Pegel, U. Weiler, and R. Claus. 2012. "Influence of Sex, Age and Season on Body Weight, Energy Intake and Endocrine Parameter in Wild Living Wild Boars in Southern Germany." *European Journal of Wildlife Research* 58: 373–378. https://doi.org/10.1007/s10344-011-0557-3.

Trouwborst, A., and F. M. Fleurke. 2019. "Killing Wolves Legally: Exploring the Scope for Lethal Wolf Management Under European Nature Conservation Law." *Journal of International Wildlife Law & Policy* 22: 231–273. https://doi.org/10.1080/13880292.2019.1686223.

Turchin, P., and G. O. Batzli. 2001. "Availability of Food and the Population Dynamics of Arvicoline Rodents." *Ecology* 82: 1521–1534. https://doi.org/10.1890/0012-9658(2001)082[1521:AOFATP]2.0.CO;2.

van Moorter, B., N. J. Singh, C. M. Rolandsen, et al. 2021. "Seasonal Release From Competition Explains Partial Migration in European Moose." *Oikos* 130: 1548–1561.

Vandersteen, J., C. Fust, M. S. Crowther, et al. 2023. "Carcass Use by Mesoscavengers Drives Seasonal Shifts in Australian Alpine Scavenging Dynamics." *Wildlife Research* 50: 1031–1045. https://doi.org/10.1071/WR22100.

Vucetich, J. A., L. M. Vucetich, and R. O. Peterson. 2012. "The Causes and Consequences of Partial Prey Consumption by Wolves Preying on Moose." *Behavioral Ecology and Sociobiology* 66: 295–303. https://doi.org/10.1007/s00265-011-1277-0.

Walker, L. E., J. M. Marzluff, M. C. Metz, et al. 2018. "Population Responses of Common Ravens to Reintroduced Grey Wolves." *Ecology and Evolution* 8: 11158–11168. https://doi.org/10.1002/ece3.4583.

Wangersky, P. J., and W. J. Cunningham. 1957. "Time Lag in Prey-Predator Population Models." *Ecology* 38: 136–139. https://doi.org/10.2307/1932137.

Wenting, E., P. A. Jansen, M. J. Laugeman, and F. van Langevelde. 2023. "Leakage of Nutrients Into the Soil Due to Carrion Decomposition Can Enhance Plant Growth." *Journal of Soil Science and Plant Nutrition* 23: 6874–6879. https://doi.org/10.1007/s42729-023-01430-0.

Wenting, E., P. A. Jansen, L. Pattipeilohy, P. van Lunteren, H. Siepel, and F. van Langevelde. 2024. "Influence of Tree Cover on Carcass Detection and Consumption by Facultative Vertebrate Scavengers." *Ecology and Evolution* 14: e10935. https://doi.org/10.1002/ece3.10935.

Wenting, E., S. C. Rinzema, and F. van Langevelde. 2022. "Functional Differences in Scavenger Communities and the Speed of Carcass Decomposition." *Ecology and Evolution* 12: e8576. https://doi.org/10.1002/ece3.8576.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer-Verlag.

Wikenros, C., H. Sand, P. Ahlqvist, and O. Liberg. 2013. "Biomass Flow and Scavengers Use of Carcasses After Re-Colonization of an Apex Predator." *PLoS One* 8: e77373.

Wikenros, C., S. Ståhlberg, and H. Sand. 2014. "Feeding Under High Risk of Intraguild Predation: Vigilance Patterns of Two Medium-Sized Generalist Predators." *Journal of Mammalogy* 95: 862–870. https://doi.org/10.1644/13-MAMM-A-125.

Williams, S. T., K. S. Williams, B. P. Lewis, and R. A. Hill. 2017. "Population Dynamics and Threats to an Apex Predator Outside Protected Areas: Implications for Carnivore Management." *Royal Society Open Science* 4: 161090. https://doi.org/10.1098/rsos.161090.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003. "Trophic Facilitation by Introduced Top Predators: Grey Wolf Subsidies to Scavengers in Yellowstone National Park." *Journal of Animal Ecology* 72: 909–916. https://doi.org/10.1046/j.1365-2656.2003.00766.x.

Wilson, E. E., and E. M. Wolkovich. 2011. "Scavenging: How Carnivores and Carrion Structure Communities." *Trends in Ecology & Evolution* 26: 129–135. https://doi.org/10.1016/j.tree.2010.12.011.

Wirsing, A. J., and T. M. Newsome. 2021. "Scavenging Effects of Large Canids." *Integrative and Comparative Biology* 61: 117–131. https://doi.org/10.1093/icb/icab012.

Zabihi-Seissan, S., C. M. Prokopenko, and E. Vander Wal. 2022. "Wolf Spatial Behavior Promotes Encounters and Kills of Abundant Prey." *Oecologia* 200: 11–22. https://doi.org/10.1007/s00442-022-05218-4.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.