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Perspective

Keep the wolf from the door: How to conserve wolves in Europe's human-dominated landscapes?

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ABSTRACT

The recolonization of wolves in European human-dominated landscapes poses a conservation challenge to protect this species and manage conflicts. The question of how humans can co-exist with large carnivores often triggers strong emotions. Here we provide an objective, science-based discussion on possible management approaches. Using existing knowledge on large carnivore management from Europe and other parts of the globe, we develop four potential wolf management scenarios; 1) population control, 2) protection and compensation, 3) fencing, 4) managing behaviour of wolf and man. For each scenario, we discuss its impact on wolf ecology, its prospects of reducing wolf-human conflicts and how it relates to current European legislation. Population control and fencing of local wolf populations are problematic because of their ecological impacts and conflicts with European legislation. In contrast, a no-interference approach does not have these problems but will likely increase human-wolf conflicts. Despite the large challenges in European, human-dominated landscapes, we argue that wolf management must focus on strengthening the separation between humans and wolves by influencing behaviour of wolves and humans on a fine spatio-temporal scale to prevent and reduce conflicts. As separation also demands a sufficiently large wild prey base, we urge restoring natural ungulate populations, to reduce human-wolf conflicts. Mutual avoidance provides the key to success, and is critical to avoid creating the conditions for reinstating wolf persecution as the default policy in Europe.

1. Introduction

In contrast to the global trend of range contractions (and loss of their ecosystem-level impacts) by most large carnivores over the last two centuries (Estes et al., 2011; Ripple et al., 2014), several large carnivore species in Europe and North America (US) show increasing population trends (Chapron et al., 2014; Mech, 2017). Surprisingly, these carnivores are expanding into landscapes dominated by humans or human impact (henceforth ‘human-dominated landscapes’). As large carnivores and humans have been at odds with each other since prehistorical times (Fritts et al., 2003), this growing co-occurrence of humans and large carnivores creates a new conservation challenge on how to protect these species (López-Bao et al., 2017) and manage emerging conflicts in these recolonized landscapes.

Despite the general avoidance of humans by large carnivores (Ordiz et al., 2011; Sazatornil et al., 2016; Filla et al., 2017), living close to humans may provide benefits in the form of human-derived resources (Newsome et al., 2015, Fig. 1). Wolves, particularly, have successfully recolonized human-dominated landscapes and increasingly occur close to humans in Europe (Chapron et al., 2014; Kuijper et al., 2016). For example, in Germany the first wolf breeding was recorded in 2000 after an absence of almost 100 years (Wagner et al., 2012). By 2016/2017 there were 73 wolf packs and 29 territorial pairs living in Germany, increasing annually by 30% (DBBW, 2018). Even in the most densely-populated countries like the Netherlands, wolves are observed increasingly often, with 10 known individuals in 2018, several of which appear to be settling (www.wolveninnederland.nl). These recolonized areas are within historical wolf range, but many aspects have changed

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Fig. 1. Human-dominated landscapes are often rich in potential food sources for wolves, easily leading to human-wolf conflicts. Densities of livestock are generally high and often difficult to protect against wolves in agricultural landscapes (a, sea coast Groningen, the Netherlands), in many nature reserves livestock is used as a management tool (b, Börkener Paradies, Germany), waste dumps provide rich food for wolves and other canids (c, Golden jackals, Croatia), which often contrasts sharply to relatively low, hard-to-catch prey densities in more natural areas (d, Red deer in the Białowieża forest, Poland).

during their absence, including shifts from extensive agricultural to intensive agricultural and urban landscapes (Fuchs et al., 2015). These changes coincide with a general increase of wild ungulate density (Apollonio et al., 2010) and livestock numbers (Thornton, 2010). Finally, increasing human population density and urbanization led to changed attitudes towards wolves (Williams et al., 2002; Dressel et al., 2015). Thus, wolves are recolonizing ecosystems with considerable variation in available prey species (both wild and domestic), and often with overriding human effects on ecosystem functioning (Kuijper et al., 2016).

Conservation of wolves in human-dominated landscapes quickly becomes complex as it generates conflict over livestock depredation, perceived competition with hunters and occasional killing of hunting dogs (Bisi et al., 2010; Dressel et al., 2015). Concerns about human safety are also an important issue. Although wolf attacks on humans are extremely rare compared to other risks humans face (Fritts et al., 2003), the fear of wolves is still a crucial factor undermining acceptance of wolf recovery (Penteriani et al., 2016). Moreover, despite being rare, wolf attacks on humans do occur, with at least 21 documented non-rabid attacks, including 4 lethal cases in Europe within the last 50 years (Linnell et al., 2002). As one of the most densely-populated regions globally, increasing wolf populations in Europe will likely lead to an increase in human-wolf encounters (McNay, 2002; Penteriani et al., 2016).

Spatial separation seems key to successful large carnivore conservation in human-dominated regions (Carter and Linnell, 2016; López-Bao et al., 2017), however, the question of how humans should live together with large carnivores triggers strong emotions. Recolonizing wolves (or other large carnivores) can have complex ecological and socio-economic impacts in human-dominated landscapes (Bruskotter, 2013). The social-economic impacts of wolves should not be downplayed, because anti-wolf sentiments may undermine support for wolf conservation (Redpath et al., 2013). These emotions can also blur an objective evaluation of management options. Even among conservation professionals there are opposing views on how to proceed with large carnivore conservation (Lute et al., 2018). However, there is broad consensus about the need for proactive solutions for successful conservation of large carnivores in human-dominated landscapes (Lute et al., 2018). Meaningful debate requires a science-based understanding of management options.

Here we provide a line of arguments to promote such an understanding regarding the conservation and management of wolves in human-dominated landscapes. We focus on those European countries where wolves have been absent for decades or centuries, but are now within their expanding range (see Chapron et al., 2014; Kuijper et al., 2016). We present and contrast four different wolf management scenarios, building on knowledge of wolf and large carnivore ecology and management from various parts of the world.

2. Different management scenarios to co-exist with wolves

Much knowledge on carnivore management is available from countries across the globe where modern societies co-exist with large carnivores. Here we present four commonly-used large carnivore management strategies as potential wolf management scenarios in Europe. Based on existing knowledge, for each scenario we explore its possible impact on wolf ecology and ecosystem effects and its effectiveness for reducing wolf-human conflicts. In the subsequent section we discuss how these options relate to European legislation.

2.1. Scenario I: management aimed at population control

Officially sanctioned (legal) large carnivore population control programs aimed at conflict prevention are widespread. Examples include, wolf population control outside National Parks in many states in the US to prevent livestock depredation (Fritts et al., 2003; Mech, 2017), or the control of dingoes (*Canis lupus dingo*) in Australia, particularly in regions with extensive sheep farming (Johnson et al., 2007). In fact, in many human-dominated landscapes there is some level of legal culling of carnivores to reduce human-carnivore conflict (Ordiz et al., 2013) or increasing discussion about re-introducing such control (Treves, 2009). Even within Europe, despite legal controversies, active government-driven population control occurs, such as in Norway, Sweden and Finland (e.g., Trouwborst et al., 2017a,b). In addition, illegal killing, and other human-induced mortality of large carnivores is widespread. In Italy, 15–20% of all wolves are killed illegally each year (Ciucci, 2015) and in Germany (DBBW, 2018) and western Poland (Nowak and Mysłajek, 2016) the majority of recorded wolf mortality was caused by motor-vehicle collisions, followed by poaching. Illegal killing can have a major impact on populations, both in terms of numbers and range. The Scandinavian wolf population, for example, has been estimated to be at only one quarter of what it would be without poaching, and poaching likewise appears responsible for the virtual absence of wolves in southern Sweden (Liberg et al., 2012), and the virtual extinction of wolves in southern Spain (López-Bao et al., 2018). Hence, human-related mortality is currently a dominant factor limiting wolf numbers in Europe. But what are the ecological and socio-economic consequences of management that actively aims to control the wolf population size?

2.1.1. Ecological impact

The main ecological consequence of population control is that it downgrades the functional role that wolves can play in ecosystems (Johnson et al., 2007; Ordiz et al., 2013; Oriol-Cotterill et al., 2015). A reduction in carnivore population size reduces the potential for numerical and behavioural (Soulé et al., 2003; Ordiz et al., 2013; Oriol-Cotterill et al., 2015) effects on prey populations and associated trophic cascades. Importantly, in social species such as wolves and dingoes, even a small reduction in the population can disrupt social stability (Fryxell et al., 2007; Wallach et al., 2010) and their impact on prey populations. Reduction of wolf pack size reduces hunting success (MacNulty et al., 2011), leading to the selection of easier-to-catch prey species, such as livestock (Imbert et al., 2016). Predator control programs can have other unexpected effects on predator behaviour. Control programs in Australia reduced dingo activity at dusk, improving alien invasive cats *Felis catus* hunting success through becoming more active at this time (Brook et al., 2012). Besides the loss of the potentially beneficial role of large carnivores regarding ecosystem functioning (Ripple et al., 2014), population control may also reduce genetic diversity (Liberg et al., 2012; Gómez-Sánchez et al., 2018). Moreover, small or isolated wolf populations have an increased chance of hybridization with dogs (Gómez-Sánchez et al., 2018). Inbreeding and hybridization are important threats for Europe's fragmented wolf populations, these may be vital additional factors preventing population recovery or long-term population viability (Liberg et al., 2012).

2.1.2. Socio-economic impact

The goal of population control programs is to reduce real and perceived human-wolf conflict. There is much evidence, however, suggesting that population control is often not effective in this regard, or may even be counterproductive (Treves et al., 2016). For example, effects on dingo abundance through control programs were inconsistent (Wallach et al., 2009). An important mechanism in this regard is the disruption of social stability in social carnivores. Heterogeneous control can, for example, induce source–sink dynamics, increasing immigration by individuals from surrounding, no-hunting areas, and effectively increase carnivore population growth rates (Knowlton et al., 1999; Stoner et al., 2006; Schmidt et al., 2017; Minnie et al., 2018). In addition, it is the young, dispersing, individuals that are most likely to move from unmanaged areas to areas where populations are controlled (Minnie et al., 2016). Such young wolves are the ones that typically appear closer to populated areas, and are more likely to attack livestock (Imbert et al., 2016).

The number of individuals dispersing towards managed areas is expected to increase during periods of population control, due to higher natality rates of wolves within surrounding areas that are not managed as a response to large-scale reductions in wolf density (Schmidt et al., 2017). Thus, spatially heterogeneous lethal management of carnivores may be counterproductive to the original management objectives (Gervasi et al., 2015; Minnie et al., 2018), and deliver mixed results (Eklund et al., 2017; Treves et al., 2016). Spatial heterogeneity in population control is particularly relevant for Europe, because the precise legal status of wolves varies (Trouwborst, 2018) between countries (Fig. 2), and wolf populations stretch across jurisdictional boundaries (Linnell and Boitani, 2012). In addition, wolf control programs can reduce survival, growth rates and densities of wolves inside neighbouring protected areas (Schmidt et al., 2017). A further challenge of lethal removal of large carnivores is that it diminishes their potentially beneficial effects on other human-wildlife conflicts. This includes the role of large carnivores in preventing (real or perceived) over-abundance of ungulate or mesopredator numbers (Ritchie et al., 2012), and their role in "managing" pathogen levels in populations of their prey (Packer et al., 2003). Hence, whereas population control may seem like a straightforward solution to solving human-wolf conflicts, in many cases it does not solve such conflicts (Harper et al., 2008; Bradley et al., 2015), and can even exacerbate human-wildlife conflict (Treves et al., 2016).

In some regions in the US, the site-specific non-lethal removal of wolves in response to depredations has been the primary method of population control (Fritts et al., 1992). Highly restricted trapping, coupled with other management methods, has potential for reducing both livestock losses and the number of wolves that need to be killed (Fritts, 1982). Allowing some level of large carnivore removal (lethal or not) has been proposed to increase acceptance of large carnivores among people that have to coexist with them. This is, for example, an important reason for current legal killing of wolves in Sweden (Epstein, 2017; Trouwborst et al., 2017a). However, whether legal killing increases acceptance levels is a matter of intense debate (Treves, 2009; Chapron and Treves, 2016; Kaltenborn and Brainerd, 2016).

2.2. Scenario II: no interference: management aimed at protection, prevention and damage compensation

No interference would allow wolves to settle and expand freely, which is obviously beneficial for the species, and will maximize the potential for wolves in ecosystem functioning. Under this scenario, the lethal removal of wolves would only be considered in exceptional circumstances, such as the killing of an animal posing a public safety hazard. No interference is the default approach in several Western European countries where the wolf is returning after an absence of over 100 years (e.g. in the Netherlands, Belgium, Germany, Denmark).

2.2.1. Ecological impact

No interference would maximize the ecological role that wolves can play in ecosystem functioning. For wolves to have a significant ecosystem impact via density- or behaviourally mediated effects, an established wolf pack (i.e. a family group) in an area is the starting point (see e.g. Fryxell et al., 2007; Wallach et al., 2009, 2010; Imbert et al., 2016). Hence, areas that are large enough and provide sufficient prey to host a wolf pack would offer sites where these ecosystem roles are likely (Kuijper et al., 2016). As ecosystem impacts of large carnivores are more complex in multispecies carnivore-ungulate systems (e.g. Owen-Smith, 2019) the presence of wild but also domestic carnivore and prey species (e.g. dogs and livestock) will likely modify the ecosystem impacts wolves can exert (Montgomery et al., 2019). Yet, as human influences are omnipresent in European landscapes, the functional role of wolves will be affected in various ways (Kuijper et al., 2016). While there is still very limited evidence available (Kuijper et al., 2016), the studies that do originate from European human-dominated landscapes suggest that wolves can have ecosystem-level impacts but these are strongly shaped anthropogenically. For example, ungulate browsing pressure in the Polish Białowieża forest was lower in high wolf-use than low wolf-use areas, but this effect coincided with low and high human activities in these areas, respectively (e.g. Kuijper et al., 2015; Van Ginkel et al., 2018). Similarly, increased moose browsing intensity in more productive Swedish forest plantations was confounded with lower wolf-use and higher human activity (Van Beeck Calkoen et al., 2018). Therefore, it is difficult to assess and predict the magnitude of ecosystem effects of wolves in human-dominated landscapes (Mech, 2012). Their ecological effects may be clear, subtle, or too small to be detected, all depending on the combination of population sizes of wolves and prey, area size, and human activities.

2.2.2. Socio-economical impact

Under the no-interference scenario, human-wolf conflicts are likely to increase. Wolves will be attracted to human-dominated landscapes when these provide anthropogenic resource subsidies (Fig. 1). Young, dispersing individuals can quickly traverse large areas (Wabakken et al., 2007), preying on prey they encounter. Therefore they often kill more livestock than established packs (Imbert et al., 2016). The situation in Poland is interesting in this respect, as a large wolf population (c. 1.500 individuals - Diserens et al., 2017) occurs without large human-wolf conflict. Livestock depredation shows large regional differences. The proportion of livestock in wolves' diet varies from < 1% in western and central Poland (Nowak et al., 2011) to 15% in some areas in NE-Poland (Jędrzejewski et al., 2012). In eastern Poland, with c. 50% of the Polish wolf population (Diserens et al., 2017), livestock comprises up to 5% of the diet (Nowak et al., 2011). The reasons for these generally low proportions are likely two-fold. Firstly, the regions with lowest livestock predation are characterised by high wild ungulate and low livestock abundance. As the proportion of a prey species in the wolf diet increases with increasing proportions of that species in the community (Nowak et al., 2011; Jędrzejewski et al., 2012), this explains why wild ungulates are the most attractive prey. Secondly, since wolves persisted in Poland (see Diserens et al., 2017), in most regions people are used to their presence and have effective ways to protect their livestock (Nowak et al., 2005).

The situation in Poland differs from many regions in Western Europe (e.g. Netherlands, Germany, Denmark), where livestock is very abundant, wild ungulates are less abundant or diverse (Fig. 1) and wolves were historically extirpated. Here, farmers are not used to actively protecting their livestock against predation, and societal awareness regarding wolf presence was lost with their extinction (over) 100 years ago. Hence, under no interference management and expected expanding wolf populations in these regions, re-establishment of livestock protection methods is urgently needed, exploring the range of options for non-lethal management of predation on livestock (see Du Plessis et al., 2018). Despite the general lack of proper scientific testing, evidence suggests that non-lethal methods may be more effective than lethal methods (Treves et al., 2016), especially if applied proactively and on large spatial scales (Stone et al., 2017). Proven effective ways to protect livestock in restricted areas are the use of guard dogs, fladry and night enclosures for livestock (Du Plessis et al., 2018; Treves et al., 2016; Gehring et al., 2011; Linnell and Cretois, 2018). Proper livestock protection methods need to be combined with equitable compensation schemes (Linnell and Cretois, 2018), and also with preparing society at large for the return of the wolf. Compensation offers short-term relief but might not be an enduring solution, possibly subsidizing further increases in wolf populations, and exacerbating the problem (Fritts et al., 2003; Mech, 1995). Therefore wolf management in the US aims at a zonation of areas with none and with some level of population control (Mech, 1995). Such zonation is, however, problematic in large parts of Europe due to international and European Union (EU) legislation (see under '3. Legal viability of the four management scenarios'). Instead, Linnell and Cretois (2018) recommended that compensation funds mainly need to be directed towards financing livestock protection measures, rather than losses. In combination with supporting a high availability and diversity of wild ungulate species, it seems to provide an effective long term conservation measure to reduce livestock predation (Meriggi and Lovari, 1996; Meriggi et al., 1996; Fritts et al., 2003).

2.3. Scenario III: fencing: management aimed at separating wolves from humans

Fencing is a common management tool for large carnivores, providing the strictest separation between humans and carnivores. Australia, New Zealand and southern Africa have embraced fencing to separate biodiversity from its threats either by "fencing-out" (i.e. fencing to keep carnivores out of areas) or by "fencing-in" (i.e. fencing to keep carnivores within areas) to better protect them or protect endangered native species against their impact and/or prevent human-carnivore conflicts. There are clear benefits of fencing as regards mitigating human-wildlife conflicts, but it also entails ecological and economic costs (Hayward and Kerley, 2009).

2.3.1. Ecological impact

Fencing for wildlife conservation is a double-edged sword. On the one hand, fencing is controversial for creating artificial barriers constraining natural behaviour and population dynamics not only of the large carnivore but of many more species in and out of the fenced area. In the already fragmented European landscape, fencing would increase fragmentation with undesired impacts on ecosystems. Impacts of fencing-in on carnivore populations and behaviour have been well studied in South Africa, where fencing is a common conservation management tool (for an overview see Hayward and Kerley, 2009). A key problem with fencing-in, is that it leads to fragmented and isolated populations, limiting gene flow. Therefore a strategic managed meta-population plan is required to maintain genetic diversity and improve the long-term conservation of the species (Miller et al., 2015).

On the other hand, fencing can lead to better protection of large carnivores because strict separation between carnivores and humans prevents negative human influences on carnivores. Packer et al. (2013) demonstrate that lion populations in fenced reserves in Africa were closer to the carrying capacity than unfenced populations. In fenced areas, lion population size was determined by density-dependent factors, while in unfenced areas humans were the main factor limiting lion numbers. As a result, the long-term annual budget (not counting fence installation itself) for lion protection was > 4 times higher in unfenced areas, while attaining only half the potential densities (Packer et al., 2013). Hence, physical protection between humans and lions by fencing was highly effective for lion conservation. However, others strongly contest this claim by stating that in total many more lions are conserved per dollar invested in unfenced ecosystems without the ecological and economic costs of fencing (Creel et al., 2013). Fencing populations in small, intensively managed reserves, combined with a strategic meta-population plan, might for some species, especially dangerous and damage causing ones (such as lions in Africa) be the only option to ensure persistence of the species (Bauer et al., 2015).

Fencing may also affect the functional role of large carnivores by affecting predator-prey dynamics. For example, African wild dogs (*Lycaon pictus*), coursing predators (like wolves), profit from fences which facilitate killing prey (Davies-Mostert et al., 2013): movement towards the fences at the start of each hunt suggested that African wild dogs actively used the fences. While this may be beneficial for the large carnivore, it will also strengthen their top-down effects on prey populations (Bull et al., 2018) which could limit the ability of small reserves to support such predators (Davies-Mostert et al., 2013). A recent simulation study on wolf introductions in human-dominated landscapes suggests that fencing could lead to viable wolf populations within fenced areas (requiring additional meta-population management) but the trophic interactions in the ecosystem depended on the wolf density that was achieved in the area (Bull et al., 2018).

2.3.2. Socio-economic impact

As large-scale fencing can provide hard boundaries between areas with and without wolves (although varying permeability could be achieved by less favourable conditions surrounding the area or via metapopulation management, Bull et al., 2018), it can largely prevent human-wildlife conflict. However, fences are very costly on the scale needed for wolves, with home ranges for one wolf pack between 116 and 310 km^2 (Jędrzejewski et al., 2007). Despite these high costs, (partial) fences have been erected in large conservation areas: the Kruger National Park (19,485 km^2), Kgalagadi Transboundary Frontier Park (36,000 km^2, Packer et al., 2013), or the well-known 5614 km dingo fence in Australia (Bauer, 1964). Is fencing on this scale a realistic option for European landscapes? A key issue in Europe is the many, relatively small and fragmented nature reserves, individually offering insufficient habitat for wolves. These should thus not be fenced. Moreover, wolves recolonizing Western Europe occupy both natural and human-dominated areas (including urban areas, see e.g. Fechter and Storch, 2014). Also in Central Europe, wolves increasingly settle in habitats considered suboptimal (with a high proportion of urban areas) when their preferred more natural habitats are occupied (Nowak et al., 2017). Fencing in these landscapes is problematic, as roads, agricultural areas, and villages are included in the wolf's home ranges. In addition, in some European countries private land is freely accessible for public (the 'right to roam' principle in e.g. Germany, Scotland and Sweden), further complicating fencing. Thus, fencing-in these mixed natural and urban areas is not practical.

Whereas fences are often used to keep animals inside areas, fencing is also used to exclude animals from conflict-prone areas. A well-known example is the c. 37,500 ha New Forest in the UK where ungulates freely roam while the various villages are fenced to avoid human-wildlife conflicts (Putman, 2012). Fencing enclaves of human-occupied zones within larger wildlife-dominated ecosystems has also been recommended for reducing conflicts between wolves and ranchers in livestock-production areas around Yellowstone National Park (Stone et al., 2008). This fencing-out scenario probably fits well with the highly fragmented European landscapes with hot-spots of intensive livestock farming. Here, non-lethal high-voltage electric fences could be used to prevent livestock predation by carnivores, as commonly done in, e.g., Sweden and Germany (e.g., Linnell and Cretois, 2018). This prevents wolves from entering pastures with livestock, but proper construction and maintenance is crucial for the effectiveness of these fences (Du Plessis et al., 2018; Frank and Eklund, 2017; Linnell and Cretois, 2018). Hence, fencing-out highly-conflict prone areas within the (future) wolf range may work. Subsidies for fencing-out livestock areas within larger wolf areas would not only help reducing livestock predation, but also improve the societal attitude towards wolf presence at local scales (Karlsson and Sjostrom, 2011). In human-dominated landscapes, fencing-out may be a suitable scenario for wolf conservation while minimizing human-wildlife conflicts. Fencing-out could also facilitate management for other species such as European bison (*Bison bonasus*), promoting restoration of wild ungulate prey species.

2.4. Scenario IV: soft boundaries: reducing human-wolf conflicts by managing behaviour of wolves and humans

An alternative approach to reduce human-wolf interactions is to manage the behaviour of both species, behaviourally separating wolves and humans. This may be particularly important for the parts of Europe where wolves are recolonizing areas densely populated with societies that are not well prepared for the presence of wolves. In fact, European wolves are increasingly seen near human settlements across Europe (Huber et al., 2016) and frequently these wolves show relatively little fear towards humans, suggesting we might be witnessing a process of habituation among European wolves (Newsome et al., 2017). Therefore, instilling fear for humans in wolves through non-lethal means could be a potential management tool to ensure fine-scale separation between wolves and humans (while not hampering recolonization as such) to prevent wolf-human conflicts. This could be done by means of aversive conditioning (see below) or the use of repellents and deterrents that discourage wolves from approaching human habitats. The restoration of a high abundance of wild prey as an alternative to anthropogenic food sources is likely a crucial factor to increase the effectiveness of such methods. We use the term 'soft boundaries' for this scenario to refer to methods that aim to keep wolves and humans separated by changing their behaviour. Importantly, an effective separation of space use of both species depends at least as much on changes in human behaviour (especially avoidance of wolves) in areas inhabited by wolves.

2.4.1. Ecological impact

Management primarily aimed at changing wolf and human behaviour, and separating humans and wolves in space and time, arguably impacts less the wolf's role in ecosystem functioning than lethal population control and hard fences. Management measures specifically targeted at wolves are unlikely to affect other wildlife. Moreover, the main effect of this management is that wolves avoid areas with high human or livestock density and will concentrate in the more natural parts of the landscape. This would concentrate their impact on ecosystem functioning in areas away from human-dominated areas. Such human-induced changes in wolf space use, resulting in a diminished impact of wolves on the ecosystem close to human settlements, have already been observed in areas with strong gradients of human use (Hebblewhite et al., 2005; Van Ginkel et al., 2018). A consequence of this management could be that the prey of wolves would move and concentrate more near human settlements ("human shield effect", e.g. Hebblewhite et al., 2005), where increased impact by this prey on lower trophic levels may be ecologically undesirable. In such areas, current tools to mitigate impacts of ungulates may need to be intensified (e.g., population control through hunting).

2.4.2. Socio-economic impact

Keeping wolves away from human settlements and livestock areas would strongly reduce human-wolf conflicts. The big question is: can we create strong enough stimuli that lead to long-lasting avoidance of humans and human habitats? While this is a common strategy in the management of some taxa (e.g. birds, Atkins et al., 2017), it is still rather unclear if it can be used effectively to solve human-carnivore conflicts (Fritts et al., 2003; Eklund et al., 2017; Linnell and Cretois, 2018). A range of methods has been tested on different carnivore species, including the use of repellents and deterrents (physical, chemical and acoustic stimuli or devices), e.g., to keep dingoes away from humans (Appleby et al., 2017a), the use of aversive conditioning techniques such as shock-collars (Hawley et al., 2009; Rossler et al., 2012) and treating bait with an emetic compound (Smith et al., 2000). However, most of these methods have shown mixed results (see Smith et al., 2000; Eklund et al., 2017; Du Plessis et al., 2018 for reviews). Several of these lead to an immediate response of some large carnivores (e.g. bears reacting to projectile repellents), but many work for only a limited time, as predators quickly habituate to the deterrent (Darrow and Shivik, 2009). However, as Eklund et al. (2017) recently stressed, very few of these methods have been tested in well-replicated, case-control designs for long-enough periods to truly check their effectiveness. There is thus an urgent need for managers and scientists to jointly invest in evidence-based testing of non-lethal interventions at large spatial and time scales (Treves et al., 2016; Eklund et al., 2017).

It seems impossible to separate wolves from humans in any landscape where wolves must rely on livestock or other anthropogenic food sources due to low wild prey availability, as in some regions in SW Europe (Lagos and Bárcena, 2018; Vos, 2000). The proportion of livestock in the diet of wolves is strongly determined by the availability of wild relative to domestic prey (Meriggi and Lovari, 1996; Meriggi et al., 1996; Imbert et al., 2016; Nelson et al., 2016). Ungulate management traditionally aims at lowering densities below ecological carrying capacity to reduce conflicts with forestry or agriculture. In mountainous regions of Central Europe (e.g. Germany, Austria, Czech Republic) the traditional system of red deer management consists of winter enclosures where the majority of animals are kept and supplementary fed in winter to prevent browsing damage in forests (Rivrud et al., 2016). In this way traditional ungulate management often lowers wild prey availability or creates (seasonal) fluctuations in the prey base. To increase the effectiveness of aversive conditioning techniques, ensuring high enough year-round abundance of wild prey is crucial (see also Fritts et al., 2003).

In reinforcing behavioural boundaries between wolves and humans, it is perhaps even more important to change the behaviour of humans in wolf areas. A recent study in developed countries demonstrated that human behaviour triggered large carnivore attacks in half of the recorded cases (Penteriani et al., 2016). Examples of risk-enhancing human behaviours included leaving children unattended in wolf habitat, walking with unleashed dogs, outdoor activities at night, approaching wounded animals, getting too close (< 100 m) to bold carnivores, and feeding of wolves (Penteriani et al., 2016). Similarly, a large number of cases of livestock predation reflect humans failing to adjust their livestock management practices (Nowak et al., 2005; Wagner et al., 2012; Imbert et al., 2016). Resource subsidies, whether intentional or unintentional (e.g. livestock, leaving waste food), play a major role in the habituation of wolves (Newsome et al., 2015) and in wolf-human conflicts (Linnell et al., 2002). The reduction of food subsidies should thus be particularly prioritized in terms of changing behaviour of humans and wolves. Hence, rather than investing in expensive fencing or controversial culling programs, authorities should perhaps invest more in the development of evidence-based programs focused on changing human behaviours in the light of the ongoing carnivore recovery.

3. Legal viability of the four management scenarios

National legislation and local regulations on wildlife conservation and management may vary and are subject to frequent changes, however, two international legal instruments impose stable minimum standards across Europe, thus providing boundaries which national and local authorities must respect in policies and actions. The first is the 1979 Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), binding to most European states. The second is the 1992 EU Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive), binding only for the 28 EU Member States. Both the Convention and the Directive include various lists of species, each list corresponding to a particular set of legal obligations. The rules that are applicable to wolves vary from country to country (Fig. 2). In many countries where wolves are making a comeback, the strictest rules apply. Prominent among these is the Habitats Directive's Annex IV regime, which requires member states to prohibit the killing of wolves, and to effectively prevent their illegal killing. Similar prohibitions apply to capturing and disturbing of wolves, and the destruction of their breeding sites and resting places. Exceptions may be granted only when several strict conditions are met, namely that (i) the exception (e.g., killing, disturbing) is for one of the purposes defined in the Directive; (ii) that satisfactory alternatives to the intended action are absent; and (iii) that the exception will not affect the achievement or maintenance of a favourable conservation status. Regarding the first condition, the Directive defines the following purposes:

(a) in the interest of protecting wild fauna and flora and conserving wild habitats;
(b) to prevent serious damage, in particular to crops, livestock, forests, fisheries and water and other types of property;
(c) in the interest of public health and public safety, or for other imperative reasons of overriding public interest, including those of a social or economic nature …;
(d) for the purpose of research and education, of repopulating and re-introducing these species …;
(e) to allow, under strictly supervised conditions, on a selective basis and to a limited extent, the taking or keeping of certain specimens … in limited numbers specified by the competent national authorities.

Broadly similar strict protection requirements follow from the Bern Convention's Appendix II regime. The regimes of Habitats Directive Annex V and Bern Convention Appendix III are comparatively flexible, and allow for exploitation as long as conservation status is not impaired. Where the Directive's Annex II applies, member states must designate and conserve the most suitable wolf areas as part of the Natura 2000 protected site network.

The compatibility of the four management scenarios we developed with the Bern Convention and Habitats Directive (Table 1) will depend on the circumstances of each situation, but some general conclusions can nevertheless be drawn. Population control, the designation of wolf exclusion or low-density zones, and the large-scale deployment of fences (other than the local fencing-out of livestock pastures) pose particular legal difficulties (Table 1). Conversely, aversive conditioning, deterrents, and other tailor-made and non-lethal measures are easier to reconcile with the Habitats Directive and the Bern Convention (Table 1).

4. Synthesis

The recovery of wolves in Europe is often celebrated as a conservation success of both species and ecosystem restoration (Mech, 2012; Chapron et al., 2014). Conversely, it poses the major challenge of conserving wolves in human-dominated landscapes without losing public support. While wolves in human-dominated landscapes under certain conditions exert ecosystem-level impacts and could contribute to mitigating pre-existing human-wildlife conflicts (Kuijper et al., 2016), their presence will also have other socio-economic impacts. We argue that these impacts, together with emotional arguments (including perceived fear), should be taken seriously because attitudes towards wolf conservation in Europe are unstable and sensitive to how conflicts are resolved (Williams et al., 2002; Dressel et al., 2015; Kaltenborn and Brainerd, 2016). When attacks involving human victims occur, the public support towards large carnivore conservation can rapidly change (Appleby et al., 2017b). Therefore we urge policy makers to adopt a pro-active rather than a passive approach regarding wolves and conflicts. Whereas many countries currently being recolonized by wolves have management plans, what is often missing are practical ‘in field’ measures including sufficient well trained staff and effective financial resources to mitigate conflicts.

An important message from our discussion of different wolf management scenarios is that the various management actions to varying degrees affect the ecological functioning of wolves (and their ecosystem effects) and address socio-economic conflicts (Table 2). Some of the discussed management scenarios are in clear conflict with current European legislation, or have other objections. This applies in particular to population control, despite the latter often being advocated by opponents of wolves' recovery. Population control is legally problematic in countries where strict European protection regimes apply (Linnell et al., 2017; Epstein, 2017; Trouwborst et al., 2017b; Trouwborst and Fleurke, 2019), thus, in most countries experiencing wolf recolonization. There is little scope for large-scale control

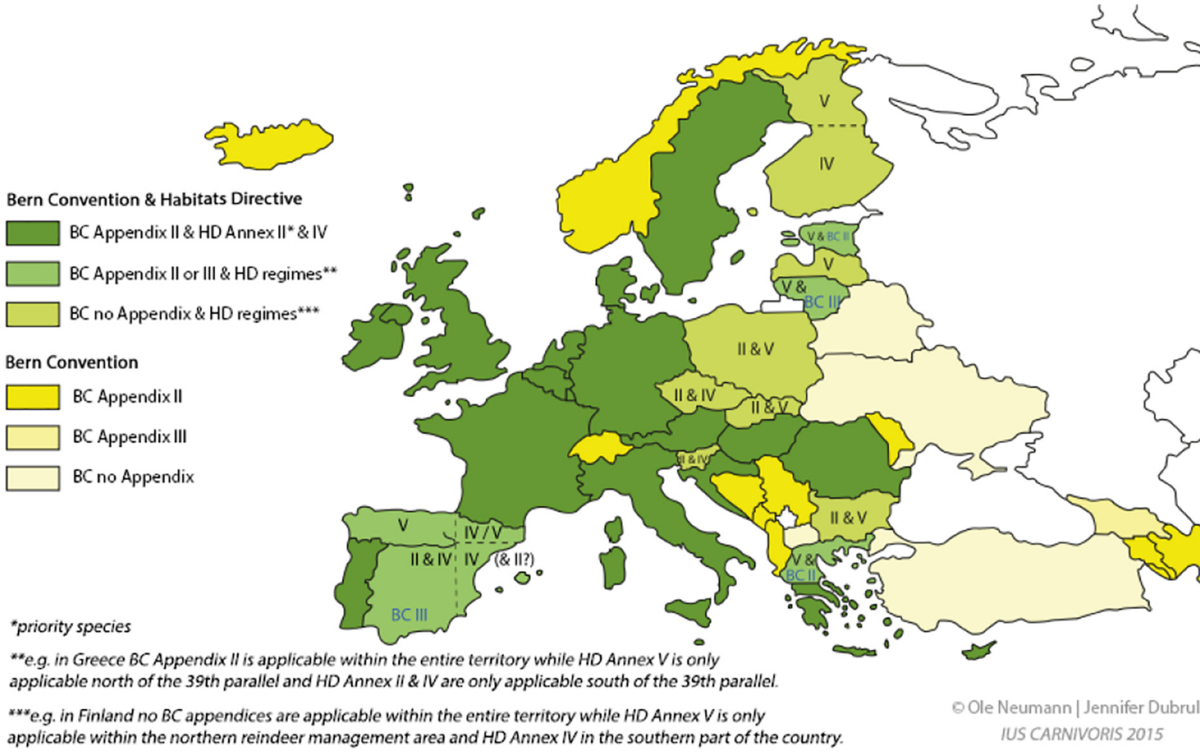


Fig. 2. An overview of the legal status of wolves under the Bern Convention (BC) and the Habitats Directive (HD) in Europe. The exact legal regimes (with a particular set of legal obligations) that are applicable to wolves vary from country to country (map from "Ius Carnivoris: Law and large carnivores in Europe" with permission from authors). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

programs aimed at reducing or controlling wolf numbers in countries where wolves have not reached a favourable conservation status (Trouwborst et al., 2017a; Trouwborst and Fleurke, 2019). Furthermore, as most European wolf populations are transboundary (Chapron et al., 2014), population control in one country can influence the conservation status of the same wolf population in a neighbouring country (e.g. Kutal et al., 2016; Schmidt et al., 2017). In addition, both European and national protection regimes may vary between countries. This may lead to spatial heterogeneity in control programs, known to be especially counterproductive, given predicted increased immigration by wolves from surrounding areas, and accelerated wolf population growth rates (Knowlton et al., 1999; Stoner et al., 2006; Kutal et al., 2016; Schmidt et al., 2017; Minnie et al., 2018). This would thus fail to solve local human-wolf conflicts (Harper et al., 2008; Bradley et al., 2015), and may even exacerbate them (Treves et al., 2016).

Fencing, a common large carnivore management tool in other parts of the world, is challenging in Europe. The lack of large blocks of wild lands (as opposed to the US, see Mech, 2017) in the highly fragmented and multi-use European landscapes makes fencing impractical at the scale needed to maintain a healthy wolf population. Moreover, large-scale fencing has negative impacts on other wildlife by increased ecological fragmentation. This conflicts with current policies to increase

Table 1
Legal aspects of four discussed management scenarios to conserve wolves and manage conflicts in human-dominated landscapes. For each scenario is indicated its compatibility with the various regimes that may be applicable with regard to wolves under the overarching legal frameworks of the EU Habitats Directive (HD) and the Bern Convention (BC). For more detailed analysis we refer readers to the literature indicated in the third column (illustrations by T. Samojlik).

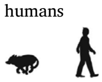
Scenario	Compatibility	Sources
I. Population control 	Typically difficult to reconcile with HD Annex II and IV regimes and BC Appendix II regime. More scope where different regimes apply. Precise scope will depend on circumstances, in particular the conservation status of the wolf population(s) involved.	Linnell et al., 2017 Trouwborst et al., 2017b Epstein, 2017 Trouwborst, 2018 Epstein et al., 2019 Trouwborst and Fleurke, 2019
II. Protection & compensation 	Compatible with all HD and BC regimes.	Trouwborst, 2010
III. Hard fences 	Difficult to reconcile with HD and BC, especially when applied on a large scale – with a view both to effects on wolves and broader ecology.	Trouwborst et al., 2016
IV. Managing behaviour of wolves and humans 	Compatible with all HD and BC regimes, provided it does not impair conservation status and certain other conditions are met.	Trouwborst, 2010 Trouwborst and Fleurke, 2019

Table 2
Summary of ecological, socio-economical impacts of four discussed management scenario's to conserve wolves and manage conflicts in human-dominated landscapes (illustrations by T. Samojlik).

Scenario	Ecological	Social/Societal
I. Population control 	− Induces source-sink dynamics in populations and downgrades functional role of wolf	+/− Can decrease human-wolf conflicts; but not effective when surrounded by unmanaged populations
II. Protection & compensation 	+ Maximizes population development and functional role of wolf	− Increases human-wolf conflicts; compensation and education required
III. Fencing 	+/− Negative impact on wolf population dynamics & general ecosystem impacts but may maximize functional role of wolf	+ Eliminates human-wolf conflict; but costly in large areas. Restricts the accessibility of nature by humans.
IV. Managing behaviour of wolves and humans 	+ Negligible impact on population dynamics, reduces functional role of wolf close to humans but maximizes role far from humans	+ Can decrease human-wolf conflicts (but context-dependent); install natural boundary between human & wolf; more testing of methods required

connectivity (e.g., the Pan European Ecological Network), and conservation legislation (Trouwborst et al., 2016). However, fences are effective to exclude wolves from highly conflict-prone areas, as the use of electric fencing at a small scale to protect livestock illustrates (Reinhardt et al., 2012; Eklund et al., 2017). Conflict-prone areas are mainly those with high livestock densities but lacking current livestock protection methods, such as large parts of Belgium and the Netherlands, parts of Germany, France, Italy and Denmark. Areas with free ranging livestock, such as cows and sheep on alpine meadows without shepherds, or semi-wild reindeer in Scandinavia, will (or currently do) also experience conflict (Linnell and Cretois, 2018). Livestock husbandry developed during the period without the threat of wolf predation, is vulnerable to conflict when wolves re-appear. Local communities involved are generally reluctant, and face practical difficulties to change their ways of livestock keeping. A clear warning is the example of > 160 sheep killed in 2018 by non-resident wolves in the Netherlands. This demands a proactive approach to potential conflict, preparing local communities for this risk, and fencing out wolves at a local scale may help.

Least contentious, from a legal and ecological perspective, is strict protection and no interference, but a growth in wolf numbers is likely to augment human-wolf conflicts. Hence, the focus needs to be on re-establishing methods to prevent livestock predation (e.g. electric fences, guard dogs, night enclosures for livestock) in combination with effective compensation schemes. The focus on using the non-lethal measures to reduce livestock predation (Eklund et al., 2017; Stone et al., 2017), must be supplemented with strategies to ensure availability of wild prey (Meriggi et al., 1996; Meriggi and Lovari, 1996; Linnell and Cretois, 2018). The increasing number of rewilding projects across Europe offers promising opportunities for restoration of natural habitats and prey communities. We strongly recommend restoring natural ungulate populations to support viable wolf populations, while reducing livestock depredation and other human-wolf conflict.

The increasing risk of negative human-wolf encounters coinciding with growing wolf populations in densely-populated regions (Penteriani et al., 2016) must also be addressed. The increased frequency of wolves occurring in densely-populated areas across Europe, suggests that wolves are increasingly losing fear of humans (Huber et al., 2016). We argue that it is very important to maintain or augment the separation between wolf and man in space and/or time to reduce the likelihood of attacks on people. An underexplored tool is to reinstill fear (sensu Cromsigt et al., 2013) for humans in wolves by means of aversive conditioning or via the use of repellents and deterrents that discourage wolves from approaching human habitats. This approach has many unknowns relating to the effectiveness of different methods (Linnell and Cretois, 2018), and these demand urgent research. Again, the effectiveness of such methods likely depends on sufficient wild prey for wolves. Just as important in this respect, is the maintenance of some respect of wolves by humans. We would not wish to broadcast a message that wolves pose a serious human safety risk, but rather to advocate proper behaviour by humans in wolf habitat (Penteriani et al., 2016), and mutual avoidance appears to be the key to success. The challenge is to provide the general public with a well-balanced view on wolves that persuades it of the ecological value of having wolves returning, that they pose a very negligible human safety risk, but also emphasising that wolves are large predators that demand respect. So a key aspect is educating people that recovering large carnivore populations are natural and welcome, and that we need to relearn (lifting baselines) how to live with them (Roman et al., 2015).

To conclude, despite the large challenges, we argue that wolf management needs to be aimed at strengthening the separation between humans and wolves on fine spatio-temporal scales to avoid conflicts. Too often we focus only on reactive approaches (killing, compensation) rather than focusing on the root of the problem. Influencing behaviour of wolves and perceptions of humans, while ensuring an adequate wild prey base, has the best prospects of a win:win situation for humans and wolves. We should be wiser this time and avoid creating the conditions for reinstating wolf persecution as the default policy in Europe.

Competing interests

The authors have no competing interests to declare.

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