REVIEW

Wild ungulate overabundance in Europe: contexts, causes, monitoring, and management recommendations

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ABSTRACT

1. High-density populations of large ungulates are now widespread. However, the perception of overabundance only appears when it produces a problem for humans, such as: a loss of plant diversity, damage to agricultural crops and forestry, ungulate-vehicle collisions, a nuisance to humans, disease transmission to livestock or changes in habitat for other species. The admissible level of density depends on the ecological and socio-economic context in which the population is located, and defining this level is important, in order to determine management strategies and actions.
2. We describe the main contexts in which ungulate overabundance occurs in Europe, record the causes of overabundance, and evaluate which set of indicators of ecological change is the most appropriate for monitoring and diagnosing overabundance in each scenario.
3. Our review of 318 published papers revealed six contexts of wild ungulate overabundance in Europe (protected areas, hunting areas, forestry, arable farming, livestock farming, and [peri]urban areas). In addition to population abundance, four sets of indicators of environmental change could be used to monitor overabundance within these contexts (impacts on habitats, impact on animal performance, increments in diseases and parasite loads, and increments in nuisance to humans).
4. Nine species of ungulate were found to be overabundant. Red deer *Cervus elaphus* was the species most likely to be overabundant in the contexts of protected areas (detailed in 27% of papers on that context) and hunting areas (38%); roe deer *Capreolus capreolus* in forestry (28%); wild boar *Sus scrofa* in arable farming (60%), livestock farming (29%), and (peri)urban areas (38%). Our evidence

shows that the diagnosis and monitoring of ungulate population overabundance via indicators of ecological change, and the management actions required to control these undesirable situations, are strongly context-dependent.

Keywords: conservation conflicts, Europe, indicators of ecological change, management challenges, ungulates, wildlife-human conflicts, wildlife-livestock interactions.

RESUMEN

1. Las poblaciones de ungulados con altas densidades están ahora muy extendidas. Sin embargo, la percepción de sobreabundancia poblacional solo aparece cuando dicha población produce un problema para los humanos, como: una pérdida de diversidad de plantas, daños a cultivos agrícolas y forestales, colisiones de vehículos ungulados, molestias para los humanos, transmisión de enfermedades al ganado o cambios en el hábitat para otras especies. El nivel de densidad admisible depende del contexto ecológico y socioeconómico en el que se encuentra la población, y es importante definir este nivel para determinar las estrategias y acciones de gestión.

2. Describimos los principales escenarios en los que aparecen situaciones de sobreabundancia de ungulados en Europa, registramos sus causas y evaluamos qué conjunto de indicadores de cambio ecológico es el más apropiado para monitorizar y diagnosticar la sobreabundancia en cada escenario.

3. Nuestra revisión de 318 artículos publicados reveló seis escenarios de sobreabundancia de ungulados silvestres en Europa (áreas protegidas, áreas de caza, silvicultura, agricultura, ganadería y áreas [peri] urbanas). Además de la abundancia de la población, se podrían utilizar cuatro conjuntos de indicadores para monitorizar la sobreabundancia (impactos en hábitats, impacto en el

rendimiento animal, incrementos en enfermedades y cargas parasitarias, e incrementos en molestias para los humanos).

4. Se encontraron ejemplos de nueve especies de ungulados sobreabundantes. El ciervo *Cervus elaphus* fue la especie más frecuentemente sobreabundante en las áreas protegidas (detalladas en el 27% de los trabajos centrados en ese escenario) y áreas de caza (38%); el corzo *Capreolus capreolus* lo es en silvicultura (28%); el jabalí *Sus scrofa* en la agricultura (60%), ganadería (29%) y áreas (peri)urbanas (38%). Mostramos que el diagnóstico y el monitoreo de la sobreabundancia poblacional de ungulados a través de indicadores de cambio ecológico, y las acciones de gestión necesarias para controlar estas situaciones indeseables, dependen en gran medida del escenario.

Palabras clave: conflictos de conservación, Europa, indicadores de cambio ecológico, desafíos de gestión, ungulados, conflictos entre la vida silvestre y humanos, interacciones entre la vida silvestre y el ganado.

INTRODUCTION

According to Caughley (1981), overabundance (or overpopulation) of a wildlife species in a given locality occurs when its population status: (1) affects human life or livelihood; (2) affects the fitness of the overabundant species; (3) reduces the density of other species with an economic or aesthetic value; or (4) causes dysfunctions in the ecosystem. Overabundance is a human value judgment that only gains an objective meaning when it is placed in a specific ecological and socio-economical context, i.e. when it is moved from a feeling to a quantified evaluation of: loss of plant or animal diversity, damage to arable or forestry crops, wildlife-vehicle collisions, nuisance to humans, disease transmission, or changes in the habitats of other species. After a low point that was estimated to occur around the turn of the 20th Century, populations of wild ungulates have increased and recolonised large areas during the last few decades in a multicontinental phenomenon (Putman et al. 2011a, Beguin et al. 2016). Locally, populations of ungulates in Europe have reached situations defined as overabundance in some areas, which has detrimental effects on biodiversity and ecosystem function (Apollonio et al. 2010, Valente et al. 2020).

The diagnosis of a population as overabundant requires a multidisciplinary approach (Côté et al. 2004). However, the admissible levels of population densities vary in relation to the ecological and socio-economical context where they are located (Putman et al. 2011b). Defining a population as overabundant or not also depends on the human perception of whoever makes the assessment, and this itself depends on the ecological and socio-economical context (König et al. 2020). Therefore, the criteria used to define a population as overabundant must be clearly set for each context, and should cover three perspectives: (1) biological (attributes of individuals and populations: e.g. body weight, productivity, antler size); (2) ecological (effects on the ecosystems: e.g. impact on plant or other animal species); and (3) socio-economical (wildlife-human conflicts, which can be direct, e.g. economic, nuisance, human health; or indirect, e.g. economic, relating to human health; Warren 2011, Salerno et al. 2020).

Definitions of overabundance show that the relevant indicators of overabundance are context-dependent, and that it is not possible to establish general density thresholds to be used as maximum admissible levels (Putman et al. 2011b). Therefore, the use of indicators of ecological change (IEC; Morellet et al. 2007, Garel et al. 2010) to monitor the population status of wild ungulates has been strongly recommended (Apollonio et al. 2017). This approach should allow managers to achieve their specific objectives better than by simply counting individuals in populations (see also Strickland et al. 2008), and has significant potential to be used as a practical and conceptual framework to diagnose and monitor situations of overabundance. The pioneering studies used as indicators population abundance, individuals' performance and habitat impact (see Morellet et al. 2007). However, other sets of indicators may be needed to complete the characterisation of overall population status, such as the prevalence of infectious diseases, parasitic loads, and indicators of damage to crops and nuisance to humans; these should be included within IEC (e.g. Gortázar et al. 2006, 2007, 2011, Duarte et al. 2015). The set of IEC should be as wide as possible in order to involve the key indicators that determine or limit the permissible levels of population density in each context. However, most of these indicators are evaluated within the human dimension (Conover 2001), requiring the use of surveys of members of the public to obtain their opinions and to set the admissible levels (VerCauteren et al. 2018). In this sense, it is necessary to consider the views of different stakeholders (hunters, foresters, farmers, shepherds; Martin et al. 2020), including those who are not directly involved in the conflicts (animal welfare, environmentalists, urban citizens), to diagnose and manage overabundance situations (Martínez-Jauregui et al. 2020, Valente et al. 2020).

We review the main contexts of wild ungulate overabundance that currently exist in Europe, in relation to causes and management options, adopting the framework of IEC to monitor these scenarios and to diagnose overabundance situations. We present some key processes arising from high densities of ungulates that may be critical for a reassessment of ungulate management, and highlight some of the gaps in knowledge. Our aim is to provide wildlife managers and policymakers with a modern perspective of monitoring ungulate populations that could be used to minimise the impact of situations of overabundance. Our methods can be used to support the redirection of current management plans concerning wild ungulates in Europe. Therefore, this review offers new information and insights, giving a global and holistic perspective of the most important contexts and ungulate species involved in overabundance situations in Europe.

METHODS AND CONTEXTS OF OVERABUNDANCE

We searched for papers on ungulate overabundance in Europe (Appendix S1) and included 318 papers in the review (Appendix S2). Each paper was assigned to one of six main contexts. Each context was defined by the biological, socio-economical and management circumstances in which the population was set. In most of Europe, ungulates occupy large areas devoted to different socio-economic activities (as detailed below under the heading ‘Mixed contexts’). However, a primary activity in each area predominates, and this was used to define the different contexts. In this sense, the context is a simplified description of the place where a situation of overabundance occurs, together with the causes, consequences and human perception of this situation. Based on this definition, we consider six contexts of ungulate overabundance in Europe, as detailed below.

Protected areas

Protected areas are mainly devoted to conservation, so that in this context, hunting of ungulates is either limited to management culling or, in a minority of cases, prohibited (e.g. national parks; Table 1). Wildlife populations are regulated in 68% of European national parks (n=209): by culling in 40% of them, hunting in 11%, or by both actions in 17% (van Beeck Calkoen et al. 2020). The main species involved in this context is red deer, covered in 27% of the publications (Fig. 1). Ungulate overabundance in the context of protected areas results from the restriction of culling and, in most cases, from the absence of natural predators (Gogan et al. 2001). The conservation problems include, among others: wild boar predation of nests and other species of vertebrates; interspecific competition, often damaging rare or endangered ungulates in favour of more common and widespread ones (Giménez-Anaya et al. 2008, Ferretti et al. 2011, Lovari et al. 2014, Corlatti et al. 2019); overgrazing and browsing (Zamora et al. 2001); and the transmission of pathogens to endangered species (Gortázar et al. 2011). Under these circumstances in areas of special conservation, a number of consequences result from overabundance, such as damage to vegetation (Perea et al. 2014), that have the potential to cause a loss of biodiversity. An example of this context is the reintroduction of the Iberian ibex *Capra pyrenaica* (a flagship species) to protected areas in the Iberian Peninnsula, such as the Sierra de Guadarrama (see Refoyo et al. 2016) and the Gerês-Xurés International Park (Fonseca et al. 2017). Populations of the Iberian ibex are now expanding and reaching unsustainable levels of herbivory, with severe impact on woody species and on threatened plant species (e.g. Perea et al. 2015).

In the protected area context, some authors recommend the use of population control measures, such as fertility control (Bradford & Hobbs 2008) or more extensive culling (Gogan et al. 2001) to regulate ungulate populations. However, perceptions and attitudes towards lethal management differ among the different stakeholders (Fix et al. 2010, Demaris et al. 2012), and depend on the purpose of the hunting activity: e.g. to improve animal health, for recreation, to reduce damage to crops (Garrido et al. 2017). According to Martínez-Jauregui et al. (2020), the use of indirect measures to reduce the impact of ungulates and live trapping are better perceived by society than lethal measures. Only 50% of people agree with the idea of selling licences to interested hunters in order to reduce the impacts of ungulates, but part of society shows a positive willingness-to-pay for other solutions in protected areas (Martínez-Jauregui et al. 2020).

Hunting areas

The context of hunting areas is characterised by land where the main human activity is hunting, and where hunting is carried out under commercial interests (Table 1). In this context, the studies on red deer and wild boar stand out (represented in 38% and 33% of the papers, respectively), since they are the main species of big game (Fig. 1). Hunting management is an agrarian land use of great economic importance in Europe (Delibes-Mateos et al. 2009). In general, hunting areas occur under two different management regimes: managed estates (fenced or open) and unmanaged estates (open; Torres-Porras et al. 2014), with various possible situations present in both regimes. For instance, the practice of supplementary feeding can be implemented under both management regimes and has the potential to alter population dynamics, leading, in some localities, to overabundance situations. In fact, winter feeding of wild free-ranging ungulates in open hunting areas is widespread in Europe.

In fenced managed hunting estates, the main management measures are perimetric fences, supplementary feeding (Putman & Staines 2004) and, less frequently, the addition of individual ungulates to relieve inbreeding (Mysterud 2010). The increasing manipulative management of wild ungulates in hunting areas has several implications. In the first place, it results in an increase in density and aggregation, and consequently in an increase in transmission rates of pathogens, some of which have the capacity to regulate population dynamics (Fernandez-Morán et al. 1997, Oleaga et al. 2008, Barasona et al. 2016). Furthermore, the increase in ungulate density has an impact on the environment (Côté et al. 2004, Carpio et al. 2015, Lecomte et al. 2016), and may result in reductions in body condition or performance (Kie 1998). The resulting reduced antler size (Torres-Porras et al. 2009) may constrain the economic interests in hunting areas. In open managed hunting estates (the most common hunting area regime in Europe; Putman & Apollonio 2014), the most common management measure is winter feeding, which is associated with maintaining high densities of animals for hunting, and improving the quality of trophies (Milner et al. 2014).

Forestry

The forestry context occurs in areas where the main land-use is for forest, which is most common in northern and central Europe (San-Miguel-Ayaz et al. 2016). In this context, the main species involved in overabundance situations according to the scientific literature were the roe deer *Capreolus capreolus* and red deer *Cervus elaphus* (represented in 28% and 27%, respectively, of the papers published that related to the forestry context; see Fig. 1). In many countries, the disconnection of different management agencies responsible for forestry and for wildlife has been a source of conflicts (Reimoser 2003). The main conflict resulting from the overabundance of ungulates in the forestry context is damage to trees, which depends on the sylvicultural system (Table 1; Reimoser & Gossow 1996, Caudullo et al. 2003). In addition to poor silvicultural practices, for instance clear cutting in narrow strips (Reimoser & Gossow 1996) and the regeneration of uneven-aged stands (Caudullo et al. 2003), wildlife management measures such as supplementary feeding for hunting interests may influence this conflict (Putman & Staines 2004).

Supplementary feeding may lead to increased damage around feeders, or to nutritional imbalance (due to the unsuitable composition of supplementary feeds) that can result in increased browsing on vegetation (van Beest et al. 2010a, 2010b, Felton et al. 2017). Moreover, a substantial increase in damage to other wild species is found around feeding stations, as in the case of nest depredation, either directly by the fed species (Oja et al. 2015), or by predators favoured by the change in vegetation density (Selva et al. 2014). However, one of the primary goals of winter feeding of ungulates in Europe has become the prevention of environmental damage, particularly damage to commercial and native forests (Putman & Staines 2004). Despite this, Milner et al. (2014) and Putman and Staines (2004) found limited evidence of the effectiveness of diversionary feeding to protect forestry and natural habitats, and any positive effects were often undermined by increases in the ungulate population density. Additional factors determining the browsing, bark-stripping and fraying impact of ungulates are related to forest properties, forest structure, disturbance and site features (Gerhardt et al. 2013).

A detailed account of impacts of ungulates in forestry can be found in Reimoser and Putman (2011) and Putman et al. (2011b). Under some conditions, the ungulates can act as permanent stressors of the forest (Côté et al. 2004). Due to the complexity of the problem, previous authors have used the term ‘management challenges’ (Beguin et al.

2016) and suggested the need for adaptive management plans to handle wild populations in this context (Arnold et al. 2018). Management plans should include silvicultural measures, population control and spatial planning (see also Hothorn & Müller 2010).

Arable farming

The arable farming context is characterised by areas where the main land-use is for growing agricultural crops, and, therefore, one of the most common problems is damage to crops by wild ungulates (see Table 1), especially by the wild boar *Sus scrofa* that is represented in 60% of the papers on this context (Fig. 1; see also Schley et al. 2003, Calenge et al. 2004, Herrero et al. 2006, Schley et al. 2008), roe deer (15%), red deer 13%; Trdan & Vidrih 2008, Bleier et al. 2012, 2017), and also fallow deer *Dama dama* (9%), which is known for its capacity to reach high densities (Menichetti et al. 2019). Various circumstances have allowed the expansion of populations of wild ungulates (Morelle et al. 2016), including changes in land use (Acevedo et al. 2011) that potentially lead to situations in which the preferred habitats of wild ungulates are closer to arable farming areas (Delibes-Mateos et al. 2009). Moreover, some kinds of agricultural practice have promoted the conflict, such as the increasing cultivation of maize *Zea mays* and rapeseed *Brassica napus* which has substantially favoured increasing wild boar density in Central Europe (Keuling et al. 2009, Kopji & Panek 2016, Bobek et al. 2017). In relation to this issue, a refuge effect may be provided by protected areas close to arable fields; this setting may generate conflicts when ungulates move to refuge areas to avoid being hunted (Amici et al. 2012) and therefore minimise the risk of predation by humans (Tolon et al. 2009). In these contexts, measures to reduce crop damage could include: increasing hunting effort and disturbance in damaged areas to modify the 'landscape of fear' perceived by ungulates (Cromsigt et al. 2013); allowing temporary hunting in protected areas (Giménez-Anaya et al. 2016); or providing diversionary supplemental food to distract ungulates from arable crops (Geisser & Reyer 2004). Calenge et al. (2004) showed that diversionary feeding practices significantly reduced wild boar damage, suggesting that food availability had a major influence on the likelihood and extent of damage caused to crops. However, diversionary feeding can increase ungulates' reproductive output, carrying capacity and hence population size (González-Crespo et al. 2018, Cappa et al. 2019).

In arable farming areas, preventive measures to avoid crop damage have not always had positive outcomes, as they need a careful setting and a constant maintenance; this is the case with electric fences (Geisser & Reyer 2004), fences with a metal mesh (Rosell et al. 2019), and measures to frighten and deter ungulates that are either chemical or biological (Santilli et al. 2004, Schlageter & Haag-Wackernagel 2012), or acoustic or bioacoustic (Gilsdorf et al. 2004). Moreover, the effect of some of these measures has proved to be inconsistent (Geisser & Reyer 2004). For example, Frackowiak et al. (2013) showed that diversionary feeding via planting protective strips of maize does not reduce damage to crops and, in addition, increases wild boar reproduction rates; therefore, their recommendation is that it should be discontinued. However, Calenge et al. (2004) showed that diversionary feeding by spreading of maize is an efficient tool to reduce the level of damage to crops. According to Geisser and Reyer (2004), only some consequences of hunting (such as management, population regulation or creating a 'landscape of fear') reduce wild boar damage in arable farming areas.

Livestock farming

The livestock farming context occurs in land areas dedicated to animal husbandry, mainly in extensive systems, where livestock-wildlife interactions are currently frequent (see Table 1). The main species involved in this context are wild boar and red deer, each represented in 29% of the publications (Fig. 1). The situation is that the numbers of livestock raised outdoors have been significantly reduced over the last twenty years in Europe (Food and Agriculture Organisation of the United Nations; available at: http://faostat.fao.org/). However, the remaining extensively farmed livestock is now at a higher risk of contact with wild ungulates (e.g. Triguero-Ocaña et al. 2019) and, under limiting conditions (summers in the Mediterranean and winters in northern Europe), food shortages for ungulates may occur (Putman & Staines 2004, Vicente et al. 2007). The reduction of free-ranging livestock has altered land use in a way that favours natural vegetation and produces more suitable conditions for recolonisation by wild ungulates (San Miguel et al. 2010, Acevedo et al. 2011, Austrheim et al. 2011). Thus, farmed livestock and wild ungulates now share more resources than they did some decades ago, when human activities effectively segregated livestock from ungulates (Delibes-Mateos et al. 2009). Currently, livestock areas are frequented by wild ungulates, and farming and hunting activities are widely overlapping (Berentsen et al. 2014, Carrasco-Garcia et al. 2016, Gilbert et al. 2018).

In livestock farming areas, the main conflict results from pathogen transmission, e.g. the (re)emergence of disease in livestock (e.g., chronic wasting disease), and shared diseases such as classical swine fever, African swine fever and animal tuberculosis (Frölich et al. 2002, Gortázar et al. 2015, Guinat et al. 2017, Vicente et al. 2019). Gortázar et al. (2015) describe a series of preventive measures, such as translocation, barriers, deterrents, husbandry, removal of harvested animals, arthropod vector control, population control and vaccination of wildlife, that can be used, in relation to the target pathogen, to reduce the risk of transmission at the wildlife-livestock interface. Sanitary problems in this context are directly related to aggregation of individual ungulates (Miller et al. 2003, Barasona et al. 2017), which has been favoured by increasing wildlife densities, intensive management (fences and feeding), changes in livestock breeding systems, and by the reduction of the human presence in pastures (Corner et al. 2006, Gortázar et al. 2007, Barasona et al. 2013). Therefore, many of the management measures suitable for livestock farming are aimed at reducing the risk of contact between livestock and wild ungulates by, for example, reducing the density of wild populations (Boadella et al. 2012), using exclusion fences (Barasona et al. 2013), implementing pasture management (Hutchings & Harris 1997), and translocation of livestock (Gortázar et al. 2015).

Peri-urban and urban areas

Peri-urban and urban areas are characterised by built-up areas connected by roads and highways, as well as green areas composed of a mosaic of patches of various types, such as gardens, squares, road verges, playgrounds, allotments, orchards, parks, and cemeteries (Ciach & Fröhlich 2019). In this context, the main overabundant ungulate species are the wild boar and roe deer (the subject of 38% and 28% of the papers, respectively; see Fig. 1). Ungulates may be attracted to (peri)urban areas (Table 1) because of improved habitat (Fernández et al. 2006, Kilpatrick et al. 2011), the lack of predators, or increased opportunities for feeding (Cahill et al. 2012, Castillo-Contreras et al. 2018, Conejero et al. 2019). Other causes are the expansion of urban areas into the countryside (Amendolia et al. 2019), with rivers and roads acting as the main movement corridors (Stillfried et al. 2017b), and hunting restrictions (Sterwart 2011), since hunting is often forbidden in urban areas (Storm et al. 2007). Under these circumstances, populations of ungulates have suffered a process of habituation (Geist 2011, Cahill et al. 2012) with an absence or decrease in the ‘landscape of fear’ (Stillfried et al. 2017a), resulting in a process of semi-domestication (Mysterud 2010). In this context, the overabundance of ungulates causes a series of conflicts, grouped mainly into: ungulate-vehicle collisions (Zuberogoitia et al. 2014), nuisance to humans (Duarte et al. 2015) and transmission of zoonotic disease (Gortázar et al. 2006, Rizzoli et al. 2014, Vourc’h et al. 2016).

Due to the recent increase in human-ungulate conflicts, there is a need for urban wildlife management (Putman et al. 2014, Honda et al. 2018, Martin et al. 2020; König et al. 2020) with the objectives to control animal movement and reduce population size in order to avoid conflicts (Reidinger & Miller 2013, Putman et al. 2014). One difficulty is the use of lethal methods in the case of urban ungulates, since urban residents often disagree with culling animals for aesthetic and security reasons (Stewart 2011, Honda et al. 2018). In some cases, for example in the city of Berlin, Germany, the municipality allows wild boar culling within the urban area (Stillfried et al. 2017b). Excluding deer from urban areas with fencing is unrealistic (Heltai 2013), although fencing may be effective for roads and highways (Bruinderink & Hazebroek 1996, Stull et al. 2011). Therefore, other management alternatives should be used, including capture and translocation (Grund 2011, Massei & Cowan 2014) or fertility control and contraception, although the effectiveness of fertility control is strongly questionable: more than 50% of fertile females must be maintained infertile to obtain meaningful reductions in ungulate numbers (Hobbs et al. 2000), and this is difficult to achieve. So, Raiho et al. (2015) suggest that fertility control is incapable of rapidly reducing deer abundance, and that it should be combined with other methods, e.g. culling, to control population growth.

Mixed contexts

The reality is much more complex than the simplified contexts described above, and in many areas, there is a mixture of interests because more than one use of the contexts coexist. For example, many protected areas such as national parks (e.g. Doñana National Park in southern Spain) maintain traditional livestock (Triguero et al. 2019). In other cases, hunting is a commercial activity in some protected areas, or protected areas are surrounded by hunting areas (Pedrotti 2017). Even clearer examples are the mixed forestry and hunting areas in the Nordic countries, and mixed arable farming and hunting areas in the Mediterranean countries (Felton et al. 2017, Cerri et al. 2018). Therefore, the management in each of these situations is complex and requires an individualised approach.

INDICATORS OF ECOLOGICAL CHANGE

The IEC are based on the concept of density-dependence, which allows the monitoring of populations of ungulates (Morellet et al. 2007, Maublanc et al. 2016). In this sense, all the parameters that respond to changes in relative density can be viewed as candidate indicators (Garel et al. 2010). The maximum permissible level of density in each context depends on the circumstances and the ecological and socio-economical impact that ungulate populations generate, and the threshold density is perceived in that context (Putman et al. 2011b, 2011c). Thus, a different set of indicators may be required to give a warning of overabundance in each context. Based on this definition, and on previous studies (Gortázar et al. 2006, 2007, Morellet et al. 2007, Putman 2011c, Hothorn et al. 2012), four sets of IEC are distinguished (Table 2), as detailed below.

Impact on habitat: these indicators are especially useful in those contexts where the intention is to protect the ecosystem (protected areas) or vegetation (forestry and arable farming areas). The most commonly used indicators are based on the intensity of browsing and on the regeneration rate of the most palatable species (e.g. Frerker et al. 2013, Perea et al. 2015), on meristem removal and defoliation (Rhodes et al. 2018), on levels of debarking (Iijima & Nagaike 2015), or on the use of remote sensing to assess changes in the structure and composition of vegetation over time (Villamuelas et al. 2016).

Impact on animal performance: this set of indicators is especially useful in the context of hunting areas (Table 2), where the main objective is to produce high-quality game animals and large trophies (Coltman et al. 2003, Garel et al. 2007, Mysterud 2011). This set includes reproduction, mortality, phenotypic quality and body condition indices, which are density-dependent factors and are useful for describing the overall performance of individual ungulates (Bowyer et al. 2014, Santos et al. 2018).

Increment in the prevalence of shared and zoonotic diseases and parasite loads: these indicators are especially relevant for the livestock farming and (peri)urban area contexts (Table 2), due to the importance there of shared and zoonotic diseases, respectively. For example, high densities of wild ungulates in hunting areas near to livestock farming or urban areas have been associated with higher rates of animal tuberculosis (La Hue et al. 2016) or outbreaks of zoonotic disease (Mackenstedt et al. 2015, Tomassone et al. 2018). Epidemiological surveillance is needed, and should be integrated with population data to monitor this set of indicators.

Increment in nuisance to humans: this set of indicators could be useful in (peri)urban areas (Table 2). It includes aspects directly related to human discomfort, such as ungulate-vehicle collisions; damage to gardens, parks, and sport grounds; and aggressive encounters between humans and ungulates (Schley et al. 2008, Hothorn et al. 2012, Duarte et al. 2015, Stillfried et al. 2017b). Urban and larger forested areas are associated with higher numbers of ungulate-vehicle collisions than other contexts (Seiler et al. 2004). Numbers of collisions and numbers of news items regarding incidents involving wildlife are the most commonly used indicators (Wiggers 2011, Hothorn et al. 2012).

MANAGEMENT IMPLICATIONS AND FUTURE PERSPECTIVES

In order to improve the management of ungulate populations, Apollonio et al. (2017) proposed implementing an adaptive management approach. This approach depends on each of the situations (contexts) of overabundance. Therefore, the starting point must be monitoring populations through different IEC, with special emphasis on the set of indicators that makes it possible to establish an alarm threshold (Morellet et al. 2007, Putman et al. 2011b). Therefore, we propose sets of IEC for each context, with priority ratings given to each set based on the permissible levels of ungulate density. However, more studies are needed to evaluate how the sets of indicators complement and relate to each other, since certain management actions (e.g. supplementary feeding, hunting, and fencing) may interfere with the relationships among the indicators and between them and ungulate population density. Management measures are also context-dependent, since they are focused on handling different conflicts in different contexts. Therefore, only through a more complete understanding of ecosystem dynamics will we be able to propose in detail effective measures to manage problems resulting from the overabundance of wild ungulates in all six common contexts in Europe.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Description of the methodology used for literature search in the systematic review.

Appendix S2. The 318 references used in this review of ungulate overabundance.

Figure legend

Fig. 1. Composition of the literature on ungulate overabundance for each of six contexts and nine species. N indicates the number of papers relating to each context. For details of data sources and searching procedure, see Appendices S1 and S2.

Graphical Abstract text

We describe six contexts of wild ungulate overabundance in Europe (protected areas, hunting areas, forestry, arable farming, livestock farming, and [peri]urban areas).

Protected areas are mainly devoted to conservation, where hunting of ungulates is either limited to management culling or, in a minority of cases, prohibited.

Hunting areas is characterised by land where the main human activity is hunting, and where hunting is carried out under commercial interests.

Forestry context occurs in areas where the main land-use is for forest, very common in northern and central Europe

Arable farming context is characterised by areas where the main land-use is for growing agricultural crops.

Livestock farming context occurs in land areas dedicated to animal husbandry, mainly in extensive systems, where livestock-wildlife interactions are currently frequent.

Peri-urban and urban areas are characterised by built-up areas connected by roads and highways, as well as green areas composed of a mosaic of patches of various types.

Table 1. Summary showing the main situations, causes and management measures to mitigate the overabundance of ungulates in each of the main six contexts described for Europe.

Context	Situations	Causes	Management measures
Protected areas	Conservation conflicts	- Banned hunting - Overgrazing and browsing - Competition - Lack of large predators	- Population control - Fertility control - Protection of key resources
Hunting areas	Effects on individual performance	- Supplementary feeding - Fences - Translocations	- Selective hunting - Supplementary feeding - Sustainable management
Forestry	Damage to trees (bark-stripping, browsing, fraying)	- Poor management (e.g. silvicultural techniques) - Supplementary feeding - Lack of large predators	- Population control - Changed silvicultural measures - Improved spatial planning
Arable crops	Damage to crops	- Refuge effects - Easy availability of food	- Culling - Diversionary feeding - Electric or metal fences - Frighten and deter ungulates
Livestock farming	Wildlife-livestock interactions and transmission of pathogens	- Shared resources, mainly in periods of food shortage	- Pasture management - Spatial segregation of key resources: food and/or water - Segregation of main activities: livestock and game - Exclusion fences
(Peri)urban	Human-wildlife conflicts (ungulate-vehicle collisions, disease transmission, nuisance)	- Hunting restrictions - Food accessibility - Spread of urban areas into the countryside - Lack of predation and hunting	- Fertility control - Live-capture relocation - Fencing

Table 2. Sets of indicators of ecological change and their potential level of impact in each context, defined as: low, medium or high. Those indicators with high impact in a given context are considered to be the most relevant for diagnosing and monitoring ungulate overabundance situations.

Context	Impacts on habitats	Impact on animal performance	Increments in diseases and parasite loads	Increments in nuisance to humans
Protected areas	high	medium	medium	low
Hunting areas	medium	high	medium	low
Forestry	high	low	low	low
Arable farming	high	low	low	medium
Livestock farming	low	low	high	medium
(Peri)urban	low	low	high	high