


Challenges and science-based implications for modern management and conservation of European ungulate populations

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Abstract Wildlife management systems face growing challenges to cope with increasingly complex interactions between wildlife populations, the environment and human activities. In this position statement, we address the most important issues characterising current ungulate conservation and management in Europe. We present some key points arising from ecological research

that may be critical for a reassessment of ungulate management in the future.

Keywords Ecosystem · Population sustainability · Science-based management · Wildlife management · Adaptive management

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Wildlife management systems face growing challenges to cope with the increasingly multifaceted interactions between wildlife populations, the environment and human activities. Dense ungulate populations, such as those occurring in many parts of Europe, have impacts on agriculture and forestry production. In addition, landscape fragmentation, due to the development of infrastructure, is leading to an increase in ungulate-traffic collisions and the synurbization of many species, while a few species and subspecies are still endangered (Apollonio et al. 2010). Simultaneously, populations of large carnivores—the ungulates' natural limiting factor—are returning and stabilising in some areas of Europe (Chapron et al. 2014).

In such a context, ungulates should not be managed in isolation, but as important “ecosystem engineers” (Smit and Putman 2011) and to do so means that they need to be considered as an integral part of both ecosystems and ecosystem management. It is thus necessary to develop a holistic approach that enables the widespread presence of ungulates to be considered as an opportunity and a renewable resource rather than a nuisance, and to manage ungulate species and populations in the face of a changing environment and human society.

In this position statement, we address some of the most important issues characterising current ungulate management and conservation in Europe. We present some key points arising from ecological research that may be critical for a reassessment of ungulate management in the future and highlight some of the knowledge gaps. The goal of this statement is to provide wildlife managers and policymakers with a modern perspective of the position of ungulates in the ecosystem. We believe it should be used to support the redirection of current management plans and goals to ensure the viability and endurance of sustainable ungulate populations. We propose ten management and conservation measures to help achieve this.

The role of ungulates in forest ecosystems

The impacts of ungulate herbivory on forest vegetation are crucial for shaping the age and species composition and spatial structure of forests. This includes the formation of open areas, which play an important role in maintaining the heterogeneity of habitats required to support a diversity of fauna and flora, as well as impacts on tree regeneration (Kuijper 2011; Clasen et al. 2015). The maintenance of sustainable wild, native ungulate populations is thus an important mechanism in both the conservation and restoration of forest ecosystems. However, many interacting factors affect forest composition besides browsing, and successful germination, survival and growth of seedlings are also influenced by seed predation, competition within and between tree species and weather conditions (Kuijper et al. 2010; Nopp-Mayr et al. 2012, Cailleret et al. 2014, Leonardsson et al. 2015). Effective and scientifically sound management of well-integrated ungulate-forest

ecosystems should be based on inferences from well-designed research and monitoring. These should include the long-term assessment of ecosystem effects across the full spectrum of ungulate densities and environmental productivity. Such knowledge could be used to develop indices and indicators to evaluate and predict browsing effects across a range of temporal and spatial scales.

Multi-ungulate communities and competition

A trend towards restoring or creating more complex multi-ungulate communities has been occurring in many regions of Europe over recent decades (Apollonio et al. 2010). Natural processes such as the expansion of native ungulate species are involved, as well as translocation of non-native ones (Dolman and Wäber 2008; Ferretti and Lovari 2014). This has markedly increased the number of locally coexisting species in some communities (Bartoš et al. 2002). Ecological theory predicts that as interspecific competition increases, species increasingly specialize on the resources they use most efficiently (Namgail et al. 2009; Anderwald et al. 2016). Consequently, an overlap of diet and realized ecological niches between species may foster niche contraction, leading to a decline in population density and fitness of less competitive species (Forsyth and Hickling 1998; Ferretti et al. 2015). Interactions between herbivores, including feeding behaviour, dietary plasticity and diet selectivity, therefore need to be studied to generate reliable predictions of the grazing and browsing pressures in multi-ungulate ecosystems. Such information is also important in understanding the influences of alien ungulate species on native taxa, as well as promoting sustainable game use and the conservation of biological diversity.

Interspecific competition can amplify negative effects of environmental changes on important aspects of foraging and social behaviour of native ungulates (Mason et al. 2014). These in turn may decrease their reproductive performance and offspring survival, which are major determinants of population trends. Moreover, environmental changes may also amplify (or release) the potential for competition between native species. Therefore, extreme care should be taken when (re)introductions of ungulates are planned, particularly within the geographic range of threatened taxa (Lovari et al. 2014). Given the potential of non-native species to out-compete native ones, the introduction of non-native ungulates should be avoided.

Large carnivores, human hunting and disturbance

Ungulates show close relationships with predators, which shape their population dynamics and affect their evolutionary ecology (Jędrzejewska and Jędrzejewski 2005). These

relationships may be particularly influenced by climatic anomalies and limiting ecological conditions (Wilmers et al. 2007; Melis et al. 2009). Predators are known to exert both direct (density mediated) and indirect (risk mediated) effects on prey (Creel and Christianson 2008). The risks associated with predators' presence affect ecosystems through trophic, scale-dependent interactions (trophic cascades), emphasizing inseparable links between predators, herbivores and vegetation (Kuijper et al. 2013; Ripple et al. 2014, 2016). Prey species have evolved behavioural and physiological adaptations to the risks associated with predators (Creel et al. 2007; Boonstra 2013; Kuijper et al. 2014; Wikenros et al. 2015). Herbivores may respond to predation risk by shifting foraging sites. This can create spatial variation in grazing and browsing pressure, with the potential to influence vegetation composition and dynamics (Creel et al. 2005; Hernández and Laundré 2005). On the other hand, human activities contribute to a broad spectrum of disturbances that may also affect ungulates both directly and indirectly (Hayward et al. 2015; Lone et al. 2015). In the case of hunting, which represents by far the most important mortality cause of wild ungulates in Europe, the risk experienced by animals varies depending on season and hunting method (Grignolio et al. 2011; Cromsigt et al. 2013). Therefore, human-induced risks may differ from and even exceed those of natural predators.

Populations of ungulates under natural predation pressure in concert with a hunting harvest may decline, as most ungulates (with the notable exception of wild boar) cannot compensate for such additive mortality by increased fecundity or reduced age at first reproduction (Vucetich et al. 2005). This problem is more pronounced at high latitudes, where productivity is low (Melis et al. 2009) and will lead to reduced predator carrying capacity (Hayward et al. 2007). Therefore, the link between natural predation, human hunting, ungulate responses and ecosystem effects should be closely assessed in wildlife and habitat management systems, to ensure the long-term viability and persistence of both ungulates and their predators (Jędrzejewski et al. 2011).

Population dynamics

Climatic changes can contribute to the decline of some ungulates, especially of arctic or alpine species (Vors and Boyce 2009) and those at the southern limit of their distributional ranges (Grayson and Delpech 2005), while others benefit from warming and are expanding their ranges northwards (Elmhagen et al. 2015; Vetter et al. 2015). Management systems therefore need to account for possible mismatches between population phenology, life histories and changing resource availability. This is particularly true for thermally sensitive species that cannot cope with high temperatures (van Beest and Milner 2013).

Individual variation in animal-habitat relationships is increasingly appreciated. Individual characteristics in terms of their behavioural phenotype (i.e. animal personality) may influence juvenile survival, natal dispersal and the resource acquisition-risk avoidance trade-off (Bonnot et al. 2015). Because these individual differences have important repercussions for population dynamics, they also have potential knock-on effects on population management.

Migrations

Migration is an adaptation to seasonal variation in limiting resources and is commonly assumed to positively affect reproductive performance of migrants (Rolandsen et al. 2017). Many ungulate populations are partially migratory, which means that only a proportion of the population migrates, while the remainder stays resident on the same range year-round (Cagnacci et al. 2011; Mysterud et al. 2011). Migration is likely triggered by forage maturation in spring (Bischof et al. 2012) and is related to snow fall and the onset of the hunting season in autumn (Rivrud et al. 2016).

Recently, a decrease in the migration rate of several species has been observed (Harris et al. 2009; Cole et al. 2015). Climate change, anthropogenic pressure and possibly changes in predator-prey dynamics have all been indicated as potential drivers of this decline. The loss of migratory behaviour in ungulates could have significant consequences for the ecosystems encompassed by their seasonal ranges and affect population dynamics. Impairment of migration (e.g. by anthropogenic landscape effects) could contribute to population declines. Migration behaviour differs among populations within species in relation to individual traits and environmental factors (Cagnacci et al. 2011). The plasticity in migration patterns needs to be considered in population management. Furthermore, because a large fraction of populations may cross administrative boundaries during migration, appropriate management practices should be implemented across large geographic scales to reflect migratory processes. A new approach to ungulate management should be developed that accounts for the dynamic and variable character of migration (either to maintain migration or adapt to the change of movement patterns).

Supplementary feeding

Supplementary feeding can enhance survival, reproduction and population growth under adverse conditions (Milner et al. 2014; Putman and Staines 2004). However, there is limited evidence of the effectiveness of diversionary feeding to protect crops, forest regeneration and natural habitats, with any positive effects often being undermined by increases in

ungulate density. The feeding of wild ungulates often has unintended effects, which are typically complex (Milner et al. 2014). These may involve changes to vegetation composition and structure with consequent cascading effects on other trophic levels (Mathisen and Skarpe 2011), as well as exacerbating within- and between-species disease persistence and transmission risks (Sorensen et al. 2014), browsing damage and competition between ungulate species (Felton et al. 2017). We urge managers to consider both the costs and benefits of supplementary and diversionary feeding before deciding whether to feed ungulates or not.

Genetic composition of ungulates

Various management practices (selective harvesting, translocation, captive-breeding, fencing, introduction of non-native species) lead to changes in the gene pool of ungulates within populations (Randi 2005; Linnell and Zachos 2011; Niedziałkowska et al. 2012; Fernández-García et al. 2014). Consequences of such changes may include a decline in genetic variability, an increase in inbreeding, a decrease in population viability and the loss of local adaptations (Zachos et al. 2007; Zachos and Hartl 2011; Galarza et al. 2015). There is an urgent need for research to quantify these risks and identify solutions, as well as to develop policies and regulations to manage these emerging threats. Genotyping methods could be implemented as valuable tools to monitor genetic changes in ungulate populations, maintenance of their original genetic structure and to perform more precise censuses, particularly in the case of rare or endangered species (Giglio et al. 2016).

Ungulate management databases

An important goal of a vision for European ungulate management is to increase the scientific basis of wildlife management, rather than to rely only on opinion/experience-based management systems. To achieve this, consistent long-term monitoring and systematically collected data are essential. Tools for the remote capture, digital storing and processing of large-scale data related to ungulate management (e.g. observations, harvest, mortality and recruitment rates) have become available and are commonly used in several European countries (Ueno et al. 2014; Zaragozí et al. 2015; Helle et al. 2016; Bubnicki et al. 2016). As accurate spatial data accumulates, it will provide valuable information for e.g. preventing forest or agricultural damage and/or implementing mitigation measures to reduce ungulate-traffic collisions. In addition to ensuring effective and adaptive management, remotely accessible spatial databases are an important asset for scientific research concerning the interactions of ungulates with the environment and human activities, both within countries and at a

pan-European scale. Therefore, the engagement of hunters in game research and field work or as contributors of databases should be encouraged. Such initiatives should be promoted across national borders to develop a pan-European approach to ungulate management.

Hunting and disease management

It has become increasingly apparent that hunting has wider ranging effects than solely reducing densities of ungulates (Setsaas et al. 2007; Mysterud 2014; Festa-Bianchet 2017). Selective removal of individuals may change aspects of social organization and dispersal rates (Milner et al. 2007; Allendorf and Hard 2009; Averbeck et al. 2010; Borg et al. 2015; Leclerc et al. 2017), while hunting disturbance can induce escape movements and temporary home range displacement (Kamei et al. 2010; Grignolio et al. 2011; Thurfjell et al. 2013; Jarnemo and Wikenros 2014). In the case of wild boar, repeated hunting disturbance may affect social structure, leading to an increase in fission-fusion dynamics in the population, potentially facilitating the spread of diseases (Iacolina et al. 2009; Scillitani et al. 2010; Saïd et al. 2012). To reduce the risk of diseases spreading into and between ungulate populations, it may be beneficial to minimize hunting disturbance in disease-prone areas. For example, less intensive hunting methods such as single hunts do not cause long-distance movements of animals, leading to lower disturbance than drive hunts. However, the suitability of hunting methods must also be judged in the light of their efficiency to manage ungulate density, and in many cases, driven hunts may be a more effective way to achieve this goal.

Conservation of endangered species: the European bison as a model

Particular attention should be paid to the conservation and management of endangered ungulates. The iconic European bison plays a flagship role in nature conservation and rewilding programmes in several countries of Europe and serves as a powerful model for the conservation of other European ungulates (Kerley et al. 2012; van de Vlasakker 2014). Effective conservation of the bison requires a refining of conservation targets and the development of sound science-based management, built on strong partnerships between scientists and managers. Conservation should counteract actual and potential threats to the bison and result in the wider restoration of the species. One of the first steps in a new approach to bison management should be the identification of suitable habitats and a reduction of human intervention (specifically supplementary feeding and culling). Large-scale farm abandonment in Eastern Europe creates favourable opportunities

for bison restoration in optimal, open habitats (Kerley et al. 2012). However, reintroductions of bison to post-Soviet countries also require improved protection regimes to avoid uncontrolled hunting and poaching.

Proposed management and conservation measures to ensure the viability and long-term persistence of sustainable ungulate populations

1. Effective management of ungulates should not be undertaken in isolation from the ecosystem. Long-term research and monitoring of performance indicators of habitat productivity and ecosystem responses are required across the full gradient of ungulate densities.
2. Re-establishment of native ungulate populations should be considered as an important component of the conservation and restoration of ecosystems. However, great caution should be undertaken when translocation, captive-breeding and fencing are considered as elements of the ungulate management system. Measures to avoid hybridization between species and subspecies should be implemented, and the introduction of non-native ungulate species should be avoided.
3. Knowledge of foraging selectivity and interactions between herbivores should be applied to optimise feeding pressure in ecosystems where the manipulation of species composition and densities is used as a management tool. This should enhance conservation of biological diversity and efficiency of game use.
4. Close attention should be paid to the link between predation and ungulate responses, both in wildlife and habitat management. Consideration of the variable effects of predation in wildlife management is crucial to ensure long-term viability and persistence of both ungulates and predators. As human harvesting effects may differ from those of predators, human hunting should not automatically be considered as an adequate substitute.
5. The timing of life history events (phenology) and its individual variability, as well as changes in resource availability due to climate and anthropogenic changes, need to be considered in ungulate management systems.
6. Plasticity in migration patterns should be considered in management strategies. A new approach to ungulate management should be developed to account for the dynamic and variable characteristics of migration, either to maintain migration or to adapt to changes in movement patterns. Ideally, population management units should reflect the annual spatial requirements of the different species.
7. Supplementary and diversionary feeding can have complex, indirect and unintended effects. Therefore, careful analysis of disease and conservation risks, as well as

economic issues, should be taken into account when considering feeding. Many feeding programmes should be reviewed accordingly.

8. Citizen science is a powerful source of data for wildlife management. Online, remotely accessible databases with spatial and temporal information on ungulate harvests, distribution and abundances should be developed and implemented to provide data on interactions of ungulates with the environment and human activities at national and pan-European scales. Data persistence, standardization and accessibility (including linguistic accessibility) should be promoted.
9. Wildlife management should recognise the impacts of hunting beyond simply reducing population densities. Hunting may lead to changes in both behaviour and social organization of ungulates and affect movements over short and long distances. These could potentially play important roles in the transmission of parasites and diseases. Management practices that cause disturbance and increase contact rates within and between populations and/or species should therefore be considered in the light of the risk of infectious disease transmission.
10. The effective management and conservation of ungulates (particularly endangered species) requires a redefinition of goals and the development of strong partnerships between scientists, managers and conservationists to ensure science-based management strategies are established. Identification and protection of suitable habitats, designation of “wildlife migration corridors”, control of poaching, “re-naturalization” of populations, understanding and preventing the risks of inbreeding and disease transmission, and accounting for climate change are all formidable challenges for ungulate management that warrant joint efforts beyond national borders.

Critical issues for the management of ungulates in Belarus and other post-Soviet countries with similar management models

Management of ungulates as a renewable resource would benefit from being based on the achievements of modern ecological science. In Belarus, as well as in some other countries of the former Soviet Union, the approaches and principles, upon which management is based, have remained unchanged for the past 50 years.

Currently, ungulate management in Belarus is based on two indices:

1. A static assessment of “optimal population size” of a given species in a particular area, determined by habitat quality estimated from vegetation surveys.

2. Population size, obtained by conducting censuses.

The achievements of modern ecology together with examples of successful adaptive management of wildlife populations in some European countries allow us to conclude that these principles are based on outdated theories due to the following:

1. Each terrestrial ecosystem provides resources and living conditions for many animal species. It is, however, not possible to reliably determine the desired ungulate population size by assessing habitat quality using vegetation surveys alone.

Habitat quality and carrying capacity are dynamic entities with no scientifically justified or comprehensive method of evaluation. Evaluation attempts based on vegetation abundance and species composition should be linked to the knowledge of population performance to become more reliable and hence should only serve as testable hypotheses (Van Horne 1983; Hobbs and Hanley 1990; Hall et al. 1997; Johnson 2007).

2. Despite the existence of a large number of direct and indirect census methods for ungulates, their reliability and accuracy are often unknown and most likely low. Ungulates are notoriously difficult to count (Morellet et al. 2007; Bonenfant et al. 2009).
3. Most census methods are based not on direct animal counts, but rather on abundance indices (such as dung counts or number of animal tracks on a transect), which are then transformed into estimates of animal numbers. Due to the unknown relationship between abundance indices and true population size, abundance indices should not be directly converted to population densities or numbers. Indices may provide a useful indicator of whether a population is increasing, decreasing or stable within a given area, but should nonetheless be used with caution because of their high reliance on detection probability which is variable. The use of abundance indices should be preceded by extensive replication and validation against independent measures of population density (Anderson 2001; Anderson 2003; Witmer 2005).

In order to improve the management of ungulate populations, we propose implementing an adaptive management approach instead of relying upon the existing model. Adaptive management corresponds to an organized and systematic trial-and-error (learning by doing) process and was offered by the international scientific community in the face of uncertainty and constant variability of factors affecting wildlife populations. Adaptive management

explicitly defines our understanding of ecological systems as a hypothesis, and management interventions can be seen as tests of predictions arising from this hypothesis. Adaptive management requires that the outcomes of interventions are monitored with a set of population (e.g. body mass, antler quality, jaw length, reproduction performance, health status of individuals) and environmental (e.g. browsing index, vegetation composition, damages in agriculture) indices, which are used to continually revise the hypothesis. Based on this, explicit management aims should be formulated prior to any action (e.g. changing population size) in relation to ethical or economic considerations (Lancia et al. 1996).

We welcome the accession of the Republic of Belarus to the “Convention on the Conservation of European Wildlife and Natural Habitats” in 2013. We also encourage all countries that have not yet implemented the “European Charter for Hunting and Biodiversity” adopted by the Standing Committee of the Convention in 2007 to do so. The charter recommends and provides the legal basis for implementing the principles of adaptive management practices in the management of wildlife resources.

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