Journal of Environmental Management 260 (2020) 110068

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: http://www.elsevier.com/locate/jenvman

Research article

Ungulate management in European national parks: Why a more integrated European policy is needed

Suzanne T.S. van Beeck Calkoen[a,b,*], Lisa Mühlbauer[c], Henrik Andrén[d], Marco Apollonio[e], Linas Balčiauskas[f], Elisa Belotti[g,h], Juan Carranza[i], Jamie Cottam[j], Flurin Filli[k], Tsegaye T. Gatiso[l], David Hetherington[m], Alexandros A. Karamanlidis[n,o], Miha Krofel[p], Hjalmar S. Kuehl[l], John D.C. Linnell[q], Jörg Müller[r,s], Janis Ozolins[t], Joseph Premier[a,b], Nathan Ranc[u,v], Krzysztof Schmidt[w], Diana Zlatanova[x], Mona Bachmann[l,y,z], Carlos Fonseca[aa], Ovidiu Ionescu[ab,ac], Madeleine Nyman[ad], Nikica Šprem[ae], Peter Sunde[af], Margo Tannik[ag], Marco Heurich[a,b]

[a] Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, Freyunger Straβe 2, 94481, Grafenau, Germany
[b] Chair of Wildlife Ecology and Management, Albert Ludwigs University Freiburg, Tennenbacher Straβe 4, 79106, Freiburg, Germany
[c] Department of Forestry, Hochschule Weihenstephan-Triesdorf, Hans-Carl-von-Carlowitz-Platz 3, 85354, Freising, Germany
[d] Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, 73091, Riddarhyttan, Sweden
[e] Department of Veterinary Medicine, University of Sassari, Via Vienna 2, 07100, Sassari, Italy
[f] Nature Research Centre, Akademijos 2, 08412, Vilnius, Lithuania
[g] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 1176, 16521, Prague, Czech Republic
[h] Department of Research and Nature Protection, Šumava National Park and PLA Administration, Sušická 399, 34192, Kašperské Hory, Czech Republic
[i] Ungulate Research Unit, Cátedra de Recursos Cinegéticos y Piscícolas (CRCP), Universidad de Córdoba, 14071, Córdoba, Spain
[j] Department of Environmental Sciences, Resource Ecology Group, Wageningen University, Droevendaalsesteeg 3a, 6708 PB, Wageningen, the Netherlands
[k] Swiss National Park, Chastè Planta-Wildenberg, 7530, Zernez, Switzerland
[l] Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany
[m] Cairngorms National Park Authority, 14 The Square, Grantown on Spey, PH26 3HG, UK
[n] ARCTUROS, Civil Society for the Protection and Management of Wildlife and the Natural Environment, Aetos, 53075, Florina, Greece
[o] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Universiteitstunet 3, 1433, Ås, Norway
[p] Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, 1000, Ljubljana, Slovenia
[q] Norwegian Institute for Nature Research, PO Box 5685 Torgard, 7485, Trondheim, Norway
[r] Department of Conservation and Research, Bavarian Forest National Park, Freyunger Straβe 2, 94481, Grafenau, Germany
[s] Chair of Zoology III, University of Würzburg, Am Hubland, 97074, Würzburg, Germany
[t] Latvian State Forest Research Institute SILAVA, Rigas iela 111, 2169, Salaspils, Latvia
[u] Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA, 02138, USA
[v] Department of Biodiversity and Molecular Ecology, Fondazione Edmund Mach, Via Edmund Mach 1, 38010, San Michele all'Adige, Italy
[w] Mammal Research Institute Polish Academy of Sciences, Stoczek 1, 17-230, Białowieża, Poland
[x] Department of Zoology and Anthropology, Faculty of Biology, Sofia University St. Kliment Ohridski, bul. Tsar Osvoboditel 15, 1164, Sofia, Bulgaria
[y] German Centre for Integrative Biodiversity Research, Deutscher Platz 5e, 04103, Leipzig, Germany
[z] Department of Geography, Faculty of Mathematics and Natural Sciences, Humboldt University, Unter den Linden 6, 10099, Berlin, Germany
[aa] Department of Biology & CESAM, University of Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal
[ab] Department of Silviculture, Faculty of Silviculture and Forest Engineering, Transilvania University, 1 Beethoven Lane, 500123, Braşov, Romania
[ac] Forest Research Institute (ICAS), Bulevardul Eroilor Number 128, Voluntari, Ilfov, 077190, Romania
[ad] Metsähallitus, Parks and Wildlife Finland, Lars Sonckin kaari 14, 02600, Espoo, Finland
[ae] Department of Fisheries, Beekeeping, Game Management and Special Zoology, Faculty of Agriculture, University of Zagreb, Svetošimunska cesta 25, 10000, Zagreb, Croatia
[af] Department of Bioscience, Aarhus University, Kalø, Grenåvej 14, 8410, Rønde, Denmark
[ag] The Environmental Board, Narva maantee 7a, 15172, Tallinn, Estonia

* Corresponding author. Hammerberg 9, 94566, Riedlhütte, Germany.
E-mail address: suzanne.vanbeeckcalkoen@ziggo.nl (S.T.S. van Beeck Calkoen).

https://doi.org/10.1016/j.jenvman.2020.110068
Received 15 January 2019; Received in revised form 9 November 2019; Accepted 2 January 2020

ARTICLE INFO

Keywords:
Wildlife management
European national parks
Naturalness
IUCN
Species composition
Human intervention

ABSTRACT

1. Primary objectives of national parks usually include both, the protection of natural processes and species conservation. When these objectives conflict, as occurs because of the cascading effects of large mammals (i.e., ungulates and large carnivores) on lower trophic levels, park managers have to decide upon the appropriate management while considering various local circumstances.

2. To analyse if ungulate management strategies are in accordance with the objectives defined for protected areas, we assessed the current status of ungulate management across European national parks using the naturalness concept and identified the variables that influence the management.

3. We collected data on ungulate management from 209 European national parks in 29 countries by means of a large-scale questionnaire survey. Ungulate management in the parks was compared by creating two naturalness scores. The first score reflects ungulate and large carnivore species compositions, and the second evaluates human intervention on ungulate populations. We then tested whether the two naturalness score categories are influenced by the management objectives, park size, years since establishment, percentage of government-owned land, and human impact on the environment (human influence index) using two generalized additive mixed models.

4. In 67.9% of the national parks, wildlife is regulated by culling (40.2%) or hunting (10.5%) or both (17.2%). Artificial feeding occurred in 81.3% of the national parks and only 28.5% of the national parks had a non-intervention zone covering at least 75% of the area. Furthermore, ungulate management differed greatly among the different countries, likely because of differences in hunting traditions and cultural and political backgrounds. Ungulate management was also influenced by park size, human impact on the landscape, and national park objectives, but after removing these variables from the full model the reduced models only showed a small change in the deviance explained. In areas with higher anthropogenic pressure, wildlife diversity tended to be lower and a higher number of domesticated species tended to be present. Human intervention (culling and artificial feeding) was lower in smaller national parks and when park objectives followed those set by the International Union for the Conservation of Nature (IUCN).

5. Our study shows that many European national parks do not fulfil the aims of protected area management as set by IUCN guidelines. In contrast to the USA and Canada, Europe currently has no common ungulate management policy within national parks. This lack of a common policy together with differences in species composition, hunting traditions, and cultural or political context has led to differences in ungulate management among European countries. To fulfil the aims and objectives of national parks and to develop ungulate management strategies further, we highlight the importance of creating a more integrated European ungulate management policy to meet the aims of national parks.

1. Introduction

Protected areas are a cornerstone of both national and international conservation strategies for preserving the functioning of natural ecosystems and to halt the loss of biodiversity (Dudley, 2008; Leroux et al., 2010). Their establishment has increased during the twentieth century because of concern over environmental degradation (Dudley, 2008; Watson et al., 2014). Despite this trend, species extinctions caused by human activities continue at an alarming rate (Convention on Biological Diversity, n.d.).

Most conservationists advocate greater attention to the protection of biodiversity and increased protected area coverage. However, biodiversity loss is likely to increase unless the effectiveness of protected area management is improved (Chape et al., 2005; Laurance et al., 2012). To increase its effectiveness, the underlying mechanisms causing biodiversity loss must be understood, management objectives should be clearly defined, and management practices should be tailored to the prevailing biological and social context within protected areas. Furthermore, appropriate governance systems and resources are required to be able to achieve conservation objectives (Chape et al., 2005). This goal is complicated by competing management objectives of the different stakeholders, which often results in complex management plans (Dupke et al., 2019; Leroux et al., 2010; Naughton-Treves et al., 2005; Watson et al., 2014). To overcome these complications and to ensure long-term nature conservation, the International Union for Conservation of Nature (IUCN) has developed standardized guidelines for six protected area categories, classifying protected areas for purposes of planning, setting regulations, and negotiating land and water uses (Ia Strict Natures Reserve, Ib Wilderness Area, II National Park, III Natural Monument or Feature, IV Habitat/Species Management Area, V Protected Landscape/Seascape, VI Protected Area with Sustainable Use of Natural Resources) (Dudley, 2008). Although the six categories are recognized as the global standard by the United Nations and many national governments, they are not consistently implemented and there is no consistent use of the terminology. For example, in the United Kingdom, several protected areas use the term national park, but more correctly fit the definition of Category V Protected Landscape, due to their cultural value and continuous human intervention (Department for Environment Food and Rural Affairs, 2016; National Parks UK, 2018). Hence, decisions on proper management practices not only depend on guidelines set by the IUCN, but also on the cultural and political context of the particular area, which determines the legislation (Theuerkauf and Rouys, 2008). Consequently, management practices of different areas within the same IUCN category can differ.

Management of national parks and other protected areas is further complicated by different opinions on the primary objectives because of concerns over the impact of wildlife on lower trophic levels and cascading effects on vegetation (Côté et al., 2004; Demarais et al., 2012), animal population declines due to human–wildlife conflicts (Woodroffe and Ginsberg, 1998) and the spread of diseases (Gortázar et al., 2007; Putman et al., 2011). Within the primary objectives of national parks, the protection of biodiversity and natural processes are emphasized (Dudley, 2008). Other objectives defined are, among other things, to maintain viable and ecologically functional populations, to take the needs of indigenous people and local communities into account and to contribute to local economies through tourism (Dudley, 2008). However, management intervention and other human influences are only allowed at a level that will not cause significant biological or ecological degradation (Dudley, 2008). As a result, ungulate populations within national parks should ideally be regulated by food availability, interspecific competition and predation by large carnivores (Sinclair, 1998).

The persecution of large carnivores in the past (Ripple et al., 2014) has led to their disappearance in many parts of Europe and North America. In the last decades, large carnivores are successfully recovering in large parts of Europe (Chapron et al., 2014). However, most of the continent supports low carnivore densities, and the proportion of their geographical range covered by European national parks is small, as they require extensive areas of habitat to maintain viable populations (Soulé et al., 2003; Woodroffe and Ginsberg, 1998). Furthermore, large carnivores within European protected areas (Rauset et al., 2016) or at their edges are prone to legal hunting and poaching, which will consequently reduce their densities and affects their functional role (Kowalczyk et al., 2015; Müller et al., 2014; Woodroffe and Ginsberg, 1998). In protected areas where large carnivores are absent or occur in low densities and in protected areas located within highly productive environments, ungulate populations can be high (Hansen and DeFries, 2007; Melis et al., 2009). Populations of large ungulates occurring at high densities can severely affect plant communities through extensive browsing and consequently change vegetation structure and impact natural processes and subsequently local biodiversity (Apollonio et al., 2017; Demarais et al., 2012; Fuller and Gill, 2001; Gill, 1992; Kuijper et al., 2009). These direct and indirect impacts have triggered much debate about appropriate management of large ungulates (Demarais et al., 2012). Human intervention in the form of culling or artificial feeding to reduce the pressure on the natural vegetation, to compensate for lost wintering grounds or food shortage are often considered necessary (Conover, 2001; Möst et al., 2015; Putman and Staines, 2004). In Europe, hunting is currently the main cause of mortality for ungulate populations. Thus, park authorities have to balance the objectives of national parks to protect biodiversity and to keep human interference to a minimum to determine appropriate management practices.

The naturalness concept has proven to be a valid management tool for quantifying the intactness or integrity of ecosystems (Anderson, 1991; Cole et al., 2008; Steinhoff, 2012; Winter 2012; Winter et al., 2010). Although a commonly accepted definition of naturalness is lacking, it has been proposed that naturalness is a non-binary variable that can be described relative to ecosystem structure and human activity (Anderson, 1991; Günther and Heurich, 2013; Leroux et al., 2010; Winter 2012; Winter et al., 2010) or that naturalness or a natural system is a self-regulating ecosystem that should be free of any human influence (Anderson, 1991; Cole et al., 2008). The naturalness concept has been used descriptively to provide a conceptual framework for the evaluation of ecosystems (Anderson, 1991) or quantitatively in terms of defined naturalness indicators (Winter 2012). Such naturalness indicators have to be able to detect differences between variables measured in the field and a reference system, which in general should represent the most natural state (Winter 2012). Some studies associate this with the state before human colonization, or subject to limited human intervention (i.e. Pleistocene, early Holocene) (Anderson, 1991; Winter et al., 2010). The assessment of how natural a system is provides a relevant framework for ecosystem maintenance and restoration (Winter 2012). However, the feasibility of using the naturalness concept solely to define natural ecosystem integrity has been questioned (Porter and Underwood, 1999; Winter et al., 2010). First, because completely natural ecosystems no longer exist, due to the global effects of human activities (Cole et al., 2008; Winter 2012). Second, because management decisions should not only focus on the desired state of naturalness but also describe which natural processes should be preserved (Cole et al., 2008; Theuerkauf and Rouys, 2008). In previous studies the naturalness concept was applied to describe the current status of (forest) ecosystems using a reference system (for an overview, see Anderson, 1991) to influence forestry management practices or to enable legislation and management policy for the preservation of protected areas (Cole et al., 2008; Steinhoff, 2012; Winter 2012; Winter et al., 2010). In contrast, we used the naturalness concept as a tool to rank ungulate management in terms of the natural state (species composition) and the processes influencing the natural state (assessment of human impact on the system). So far, only one study has focused on the relationship between ungulate management and the naturalness concept, where a red deer management naturalness index was calculated for twenty national parks using five pre-defined naturalness indicators (Günther and Heurich, 2013). Our study aims at filling this gap by assessing the current status of ungulate management, evaluating the diversity of ungulate management within European national parks using the naturalness concept and to analyse which variables influence the naturalness of ungulate management. We believe that a better understanding of ungulates and their management in Europe is necessary to develop ungulate management strategies in accordance with the objectives defined for protected areas.

2. Methods

We collected data on management objectives and practices within national parks across Europe by means of an electronic questionnaire survey. The survey (Fig. 1) was sent to experts in wildlife management in each European country, who subsequently distributed it to local wildlife management authorities. Each participating national park submitted one completed questionnaire for our analyses. Similar to Winter et al. (2010), we focused on national parks as these represent the areas in Europe with the maximum level of naturalness; IUCN Category Ia (strict nature reserve) and Ib (wilderness area) areas are uncommon in Europe due to land-use history and high human population density (Cole et al., 2008; Winter et al., 2010). Furthermore, we considered all areas called national parks, whether or not they are officially defined as IUCN category II to include the full range of management approaches possible within European national parks. The survey consisted of 36 open-ended, closed and mixed questions that provided general information about the national park and its objectives, ungulate management and social aspects of the management (see Appendix; Table S1). Data were collected from May 2015 to May 2016. First, to evaluate the diversity of ungulate management within European national parks, two ungulate management indicators were identified and for each of the two indicators a

Fig. 1. Location of all national parks that participated in the study.

naturalness score was calculated for each national park (2.1). Second, several variables which could potentially influence these naturalness scores were identified (2.2) and their influence tested.

2.1. Ungulate management naturalness indicators

We evaluated the naturalness of ungulate management within European national parks by considering species composition and human intervention.

I. Species composition: To analyse the self-regulation potential of the park's ecosystem, we recorded which ungulate and large carnivore species were present within each national park and whether they are native to the area.
II. Human intervention: We also recorded to what extent ungulate populations are controlled by human intervention and artificial feeding.

For each of these two components a naturalness score of 0 (least natural) to 100 (most natural) was calculated for each national park.

2.1.1. Species composition

For each national park, a naturalness score was calculated for ungulate, large carnivore species and for domesticated species; these scores were then combined into the species composition naturalness score for each park.

First, for each ungulate and large carnivore species present within a national park a naturalness score was calculated as follows: ungulates and large carnivores were given a score of 0 (least natural) if they were not present or were present but not native; a score of 0.5 × 100/(total number of species native to the national park) if they were transient but native; and a score of 1 × 100/(total number of species native to the national park) if they were present and native or temporarily resident for reproduction and native. The maximum score a national park could receive is 100 (most natural) and the ratios used accounted for the different maximum numbers of native species in the national parks. Second, for each national park the individual species scores were summed resulting in one ungulate and one large carnivore naturalness score. To account for the possible negative impacts of ungulate and large carnivore species that increase their native ranges or are artificially introduced (Keller et al., 2011), we considered whether the species is native to each national park based on the ecological baseline of Pyšek (1995). According to Pyšek (1995), a species is native to an area when its occurrence is independent of human activities, and is considered native if it settled or was introduced by humans before the beginning of the Neolithic period and is still present. We recognize that some ungulate and large carnivore species present during the Holocene and Pleistocene have gone extinct and consequently we focused on the ungulate and large carnivore species that currently still exist. We obtained information on the fossil records from the Holocene and Pleistocene from scientific literature (Appendix; Table S2).

The naturalness score for free-ranging domesticated species (maximally 8 species, namely boar, cow, sheep, goat, horse, donkey, dog and reindeer) was assigned based on the number of species present. Due to the anticipated negative effect of the domesticated species (Mack et al., 2000; Taylor et al., 2001), a score of 100 (most natural) was attributed to the national park where no domesticated species were present within the area. Specifically, a score of 100, 70, 60, 50, 40, 30, 20, 10, and 0 was given for 0, 1, 2, 3, 4, 5, 6, 7, and 8 species. The uneven distribution of the scores considered the anticipated negative effect of domesticated species on naturalness (Mack et al., 2000; Taylor et al., 2001). A combined species composition naturalness score for ungulates, large carnivores and domesticated species in each national park was calculated by summing the three individual scores and dividing by three. A summary of the naturalness score calculations for ungulates, large carnivores and domesticated species can also be found in Table S3 in the appendix.

2.1.2. Human intervention

Human intervention is often considered necessary to maintain stable populations and to reduce pressure on natural vegetation (Conover, 2001; Möst et al., 2015; Putman and Staines, 2004). For each national park, a naturalness score was calculated for two human activities with the focus on ungulate management that could influence ungulate population numbers and ecosystem functioning, namely ungulate population control (Conover, 2001; Geisser and Reyer, 2004) and artificial feeding (Miranda et al., 2015; Putman and Staines, 2004). These scores were then summed to produce the human intervention naturalness score for each national park. A summary of the naturalness score calculations for human intervention can be found in Table S3 in the appendix.

2.1.2.1. Ungulate population control. The naturalness score for ungulate population control, through culling and commercial hunting, was assessed based on the motivation of ungulate removal, the method used for legal ungulate control, number of months of legal ungulate population control, and estimated extent of poaching.

Ungulate removal by means of culling is a common management practice used to maintain ungulate populations at a level that keeps wildlife damage to the vegetation at acceptable levels, reduces the spread of diseases, maximizes environmental benefits for other species and maintains stable populations (Conover, 2001; Geisser and Reyer, 2004). On the other hand, hunting may also take place for commercial use of animal products, trophy hunting and meat consumption. In this study, the difference between the culling of ungulates and commercial hunting is defined by their different objectives as explained above and is irrespective of the performing hunting body. National parks received a score of 0, 33, 66, 100 for commercial hunting, commercial hunting and culling, culling and no ungulate removal respectively.

Further, the naturalness score assigned to each of the different ungulate population control methods was based on the duration of the disturbance (in days) and the related predation pressure. According to some studies, permanent ungulate population control pressure (regular, repeated single hunts/battues) was the main cause for an increase in home range size for ungulates (Keuling et al., 2008; Maillard and Fournier, 2014), while ungulate behaviour was less influenced when exposed to less intensive control pressure (Keuling et al., 2008; Scillitani et al., 2010). In this study, control pressure is expected to be lower with drive hunts as more animals can be killed in a shorter time span. In contrast, single hunting methods, such as hunting from blind seats or stalking are considered to be more intensive as ungulates will be exposed to hunting pressure for a longer time compared to drive hunts in order to remove the same number of animals. Population control using trapping facilities enables managers to catch large groups and whole social units effectively, with concentration of hunting pressure on small areas and time spans (Heurich et al., 2011). Consequently, naturalness scores for control methods were assigned as follows: scores of 100, 75, 50, 25, and 0 for no hunting, trapping, drive hunting, shooting from a blind/single shootings/stalking, and baiting, respectively, which considered the intensity of the hunting pressure. The score regarding the number of months ungulate population control (0–12 months) took place decreased for each month of hunting according to the following formula: $100 - (100/12 \times n)$, where 100 represents the maximum score, 12 the maximum number of months and n the number of months hunting took place. Poaching (illegal hunting) can reduce species densities and can change species behaviour and spatial patterns (Haller, 2016; Liberg et al., 2012). The extent of poaching estimated by park managers was assigned scores of 100, 75, 50, 25, and 0 for no poaching, little poaching, moderate poaching, high poaching and very high poaching, respectively. These three scores were summed and divided by three to obtain the ungulate population control naturalness score for each national park.

2.1.2.2. Artificial feeding. The naturalness score for artificial feeding considered the type of food provided and the time of the year when feeding took place. High-caloric value supplements such as corn and concentrated feed were considered to be the least natural, silage was considered as moderate and hay feeding was assessed as the most natural as it resembles natural feed, does not contain additional artificial products and is therefore less suitable for rapid weight gains (Ouellet et al., 2001). Consequently, the type of food was assigned scores of 100, 66, 33, and 0 for no feeding, hay, silage, and concentrated/corn, respectively.

According to the questionnaires, the national parks provided no other artificial food types. Furthermore, the rationale of artificial feeding is to maintain or increase population densities, body weights, improve reproductive performance and fertility or to reduce levels of damage to agriculture and forestry (Putman and Staines, 2004). However, artificial feeding would be most natural if it resembled natural conditions. In Mediterranean ecosystems, food shortage for ungulates is most severe during late summer and early autumn (Bugalho and Milne, 2003). In autumn, food supplementation is likely to affect the distribution of females and the mating system in some ungulate species (Carranza et al., 1995; Pérez-González et al., 2010). As a result, for the national parks within the Mediterranean biogeographical region, scores of 100, 66, 33, and 0 were assigned for no feeding, winter, spring/-autumn, and summer, respectively. In other European ecosystems, food availability is generally highest during summer and lowest during winter (Muhly et al., 2013). For these ecosystems, the time of year of feeding was assigned scores of 100, 66, 33, and 0 for no feeding, summer, spring/autumn, and winter, respectively. For each national park, the scores for the type of food provided and the season feeding took place were averaged to obtain the artificial feeding naturalness score for each national park.

2.2. Variables potentially influencing ungulate management practices

Based on a literature review and the conducted survey, five variables potentially influencing ungulate management were considered, namely park size, years since park establishment, percentage of government-owned land, naturalness scores of the objectives, and human influence index. Further, to account for differences in species composition, wildlife conservation histories, differences in the political/cultural situation and biogeographical regions, we included country and biogeographical region as random variables in our analyses.

2.2.1. Park size

The size of a protected area is an important variable that can influence ecosystem dynamics (Green and Paine, 1997; Woodroffe and Ginsberg, 1998). Conservation theory advocates that protected areas should be large enough to minimize species extinction risk and maximize the representation of ecological communities as larger protected areas are better buffered against outside pressures (Green and Paine, 1997). Even though it is difficult to assess whether a national park is too small for the species assemblages and their inherent dynamics, we assumed that smaller parks generally contain less wildlife, especially large carnivores, and are more influenced by processes from the outside (i.e., edge effects). This could negatively influence natural ecosystem dynamics (Woodroffe and Ginsberg, 1998) which may lead to human intervention aimed at i.e. reducing the pressure on the natural vegetation (Conover, 2001; Möst et al., 2015; Putman and Staines, 2004). As a result, we hypothesized that species composition scores would be lower in smaller parks. In addition, we hypothesized that human intervention, i.e. artificial feeding and ungulate population control, would more likely occur in smaller national parks to counteract the effects from surrounding areas and low large carnivore densities.

2.2.2. Years since establishment

Effective management strategies in protected areas are crucial for the conservation and functioning of natural ecosystems (Hebblewhite et al., 2005; Watson et al., 2014). In Europe, where national parks are typically established in cultural landscapes, it might take years to modify the use of natural resources in accordance with the primary objective of the national park's category. For example, in the newly established national parks in Germany, a transition period of 30 years is given to achieve the protection of natural dynamics and processes for at least 75% of the area as required by the IUCN (Nationale Naturlandschaften, 2008). In addition, management can change over time as a result of changes in governance, changes in the interaction of people with nature, and development of naturalness concepts (Dudley, 2008). Consequently, we hypothesized that as administrations develop their skills and improve management based on experience, naturalness scores for species composition and human intervention will generally increase over time.

2.2.3. Government-owned land

Most European national parks are predominantly owned by the government (Protected Planet, 2014), which generally ensures a similar mission and management focus among the national parks of one country. Within government-owned national parks, small land parcels, such as those around human settlements, may be privately owned. In such cases, park managers have to consider the rights of private owners, which results in more complex management plans. To test whether governance affects the naturalness of wildlife management within European national parks, we included the percentage of government-owned land as an independent variable in the species composition and human intervention models. We hypothesized that when a larger part of the land is government owned, and therefore a larger percentage of the park has a common management approach, the human intervention and species composition naturalness scores will be higher.

2.2.4. Naturalness score of management objectives

Management objectives are crucial for conservation efficiency (Ivancevich, 1974). However, managers face challenges in keeping to the IUCN Category II objectives because of differences in the cultural, political and ecological contexts in each area, which can result in differences in management among national parks. To test whether the naturalness of ungulate management was influenced by the objectives set by park managers, we included a naturalness score for management objectives as an explanatory variable. For each national park, an overall management objectives naturalness score was calculated based on several IUCN national park objectives and their ranking of importance by park managers. We hypothesized a positive correlation between the naturalness score of the management objectives and the naturalness scores for both species composition and human intervention.

According to the IUCN, one of the most important objectives of national parks is to protect large-scale ecological processes along with species and ecosystem characteristics (Dudley, 2008). Consequently, national parks scored highest (100) when the protection of species populations and the protection of natural processes were prioritized, whereas those that did not consider these objectives scored lowest (0), with intermediate scores of 25 (subordinate objective), 50 (neutral), or 75 (important objective), accordingly. Furthermore, the promotion of education and recreation is also a primary IUCN objective, but it should be at a level that will not cause significant biological and ecological degradation of the natural resources (Dudley, 2008). For example, visitor numbers can be limited or core zones where access is denied can be created (Dudley, 2008). (Eco)tourism can generate income for the park, contribute to local communities (Dudley, 2008) and help in the conservation of nature and wildlife (Ballantyne et al., 2009), but if human disturbances are high, animal behaviour and ecosystem processes can be affected (for an overview, see Green and Giese, 2004; Manor and Saltz, 2005). Visitor numbers tend to be high, but visitors are concentrated on trails. By contrast, researcher numbers are lower, but researchers tend to deviate from trails, which increases disturbance. As a result, national parks scored highest (100) when (eco)tourism and research objectives were regarded as neutral, lowest (25) when the objectives were regarded as very important or when there were no such objectives, and intermediate (75) when the objectives were regarded as subordinate or important. The last management objective considered was hunting, which could be sustainable in that it controls damages caused by wildlife (Geisser and Reyer, 2004) or it is used for commercial use of animal products, trophy hunting and meat consumption. Both types of hunting can affect wildlife behaviour and spatial distribution (Keuling et al., 2008; Maillard and Fournier, 2014). Consequently, national parks scored lowest (0) for the objectives "damage prevention" and "hunting" when managers considered them very important and highest (100) when managers had no such objectives, with intermediate scores of 25 (important objective), 50 (neutral), and 75 (subordinate objective). A summary of the naturalness score calculations for the management objectives can be found in Table S3 in the appendix.

2.2.5. Human influence index

Habitat loss as a result of an increase in human population is the greatest threat for a wide range of species (Brooks et al., 2002; Wilcove et al., 1998). In addition, human land-use practices, infrastructure and activities such as hunting can directly influence both ungulate and predator densities or indirectly influence their habitat selection and foraging behaviour (Kuijper et al., 2016; Rogala et al., 2011). To assess whether anthropogenic impacts on the landscape influence ungulate management, we calculated the human influence index as developed by the Wildlife Conservation Society for each national park. The human influence index is a data set based on human population pressure (population density), human land use and infrastructure (built-up areas, night-time lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers), which is mapped globally in 1 × 1 km grid cells (Wildlife Conservation Society - WCS and Center for International Earth Science Information Network - CIESIN - Columbia University, 2005). First, we acquired a shapefile containing all European protected areas from the European Environment Agency (European Environment Agency, 2017) and selected only the polygons from participating national parks. We then obtained one human influence index value per national park by calculating the mean of the human influence values found within the national park plus a 5-km buffer using the extract function from the raster package (Hijmans, 2016) in R 3.4.1 (R. Core Team, 2017). The 5-km buffers around the national park borders were included using the gBuffer function from the rgeos package (Bivand et al., 2016) because protected area management is strongly influenced by edge effects and human activity at the borders. We expected that in areas where anthropogenic influences were higher, more management interventions would be necessary to compensate negative impacts from outside the park, and vice versa. In other words, we hypothesized that the human influence index of a national park would be negatively correlated to the naturalness scores for species composition and human intervention.

2.2.6. Biogeographical region

Decisions on proper management practices depend on the ecological, cultural and political context of the area where the national park is located. Besides the size of the national park, which is important within the ecological context, the biogeographical region also potentially influences ecosystem dynamics. Biogeographical regions are spatial units of various scales that bear distinctive flora and fauna assemblages as a result of differences in evolutionary history, climate and physical and/or ecological barriers (Dapporto et al., 2016; European Environment Agency, 2016; Huggett, 2011). These assemblages live in conjunction with the abiotic factors present within these regions, which results in area-specific interactions (Bryant et al., 1991; Fortin et al., 2005; Kuijper et al., 2013; Lima and Dill, 1990; Ripple et al., 2001). By contrast, abiotic factors such as soil, sunlight, temperature, rain and available nutrients are variables that influence vegetation structures and consequently determine which wildlife species occur in the region. Therefore, we expected that national parks in different biogeographical regions will have different natural conditions. We accounted for differences in natural conditions by adding the biogeographical region as a random variable in our models. The following 8 biogeographical regions were included: Alpine, Arctic, Atlantic, Boreal, Continental, Mediterranean, Pannonian and Steppe Region (European Environment Agency, 2016).

2.2.7. Country

The occurrence and densities of both ungulates and their predators differ between areas, resulting in area-specific species interactions, impacts and problems, which in turn leads to differences in ungulate management between areas. On the other hand, recent and historic ungulate management can affect both ungulate and large carnivore densities, their interactions and impacts and problems. In addition, countries have different legal and administrative frameworks within which ungulate management is carried out (Putman, 2010), which reflect differences in political and socioeconomic history, but are also influenced by cultural traditions. Humans had already settled and influenced the landscape through agriculture and hunting long before national parks were established. Ungulate management practices are likely influenced by hunting history and its place within cultural tradition, hunting rights ownership, hunting methods applied and proportion of people engaged in hunting activities, all of which may differ among countries (Putman, 2010). To account for these differences in species composition, wildlife conservation histories and differences in the political/cultural situation, we added country as a random variable in our analyses.

2.3. Statistical analyses

All statistical analyses were performed using R 3.4.1 (R. Core Team, 2017). First, we tested if there is less human intervention taking place in national parks with a more natural species composition, using a linear model from the stats package (R. Core Team, 2017). Second, we tested how the naturalness scores of species composition and human intervention were influenced by the above-mentioned variables, using generalized additive mixed models from the mgcv package (Wood, 2011). National parks with a marine focus or situated on islands where no large mammal species were present, were excluded from the analysis. Two different models were constructed with species composition and human intervention as response variables. The years since establishment (y), park size (ha), percentage of government-owned land, objective score, and human influence index were used as explanatory variables in both models. In addition, the variables country and biogeographical region were included as random effects. All independent variables were included as smooth terms, spline functions of a single explanatory variable, in the gam model because of their flexible characteristics that allow the best fitting of response variables. Further, we tested the change in model deviance after removing single smooth terms from the full model. This was repeated for all smooth variables separately. To avoid a correction in smooth term correlations in the reduced models, all reduced models used the same smoothing parameters as the full model using the mgcv package (Wood, 2011).

3. Results

3.1. General characteristics of national parks

Of the 335 national parks from 31 countries across Europe contacted, managers of 209 national parks from 29 countries responded (Fig. 1; Table 1). Although all of these parks identified themselves as a national park, only 87.5% correspond to IUCN category II and consequently are managed following the IUCN guidelines. Of the national parks in the study, 88.5% were established between 1951 and 2016, of which most were established between 1991 and 2000 (23.4%; Table 1). The national parks represented 8 of the 11 biogeographical regions of Europe, with

Table 1
Characteristics of the national parks analysed.

	IUCN category							
	1a	1b	II	III	IV	V	VI	None
Number of national parks	1	1	183	1	1	16	3	3
Percentage	*0.5*	*0.5*	*87.5*	*0.5*	*0.5*	*7.7*	*1.4*	*1.4*

	Year of establishment							
	1909–1950	1951–1960	1961–1970	1971–1980	1981–1990	1991–2000	2001–2010	2011–2016
Number of national parks	24	26	10	15	39	49	37	9
Percentage	*11.5*	*12.4*	*4.8*	*7.2*	*18.7*	*23.4*	*17.7*	*4.3*

	Biogeographical region							
	Alpine	Arctic	Atlantic	Boreal	Continental	Mediterranean	Pannonian	Steppe
Number of national parks	56	1	30	60	38	16	6	2
Percentage	*26.8*	*0.5*	*14.3*	*28.7*	*18.2*	*7.6*	*2.9*	*1*

	Number of domesticated species present								
	0	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Number of national parks	*113*	*46*	*16*	*12*	*7*	*11*	*3*	*1*	*0*
Percentage	*54.1*	*22.0*	*7.7*	*5.7*	*3.3*	*5.3*	*1.4*	*0.5*	*0.0*

	Human intervention						
	Ungulate population control					Artificial feeding	
	Culling	Commerical hunting	Commercial hunting/Culling	None	Unknown	Yes	No
Number of national parks	84	22	36	64	3	170	39
Percentage	*40.2*	*10.5*	*17.2*	*30.6*	*1.5*	*81.3*	*18.7*

	Non-intervention zone relative to national park size (%)				
	<25%	25–50%	50–75%	75–100%	NA
Number of national parks	84	12	10	59	42
Percentage	*40.6*	*5.8*	*4.8*	*28.5*	*20.3*

most in the Alpine (26.8%) and Boreal (28.7%) regions (Table 1). Furthermore, the majority of the national parks had 0 (54.1%) or 1 (22.0%) domesticated species present (Table 1). In 67.9% of the national parks, ungulate population were regulated by culling (40.2%) or hunting (10.5%) or both (17.2%). Artificial feeding occurred in 81.3% of the national parks. Many of the national parks (40.6%) had a non-intervention zone covering up to 25% of the park area, and only 28.5% had a non-intervention zone that covered 75–100% of the park area (Table 1).

We determined the species composition and human intervention scores for each national park (Appendix: Table S3 and Table S4). The average species composition scores varied between countries (Fig. 2A), as did the human intervention scores (Fig. 2B). Slovakia and Finland showed the highest naturalness scores, while The Netherlands, United Kingdom, Ireland and Spain showed the lowest naturalness scores for species composition. The average human intervention naturalness scores were highest (less human intervention; most natural) in Switzerland, Finland, Romania, Italy and Ireland and lowest (highest human intervention; least natural) in Hungary, Slovakia, Latvia and Lithuania. The total naturalness score of each country was calculated as the average of the species composition and human intervention scores (Fig. 2C) and was highest in Finland, Switzerland and Romania.

3.2. Naturalness of ungulate management

First, we found no correlation between the human intervention naturalness score and the species composition naturalness score (0.063 ± 0.068, t = 0.923, df = 175, P = 0.357). Furthermore, our generalized additive mixed model of species composition explained 67.0% of the deviance (n = 177, adjusted R^2 = 0.614). The naturalness score of species composition tended to decrease as the human influence index increased (Fig. 3, F = 3.043, P = 0.083). Further, we found no effect of park size, the number of years since park establishment, the percentage of government-owned land and the naturalness score of the

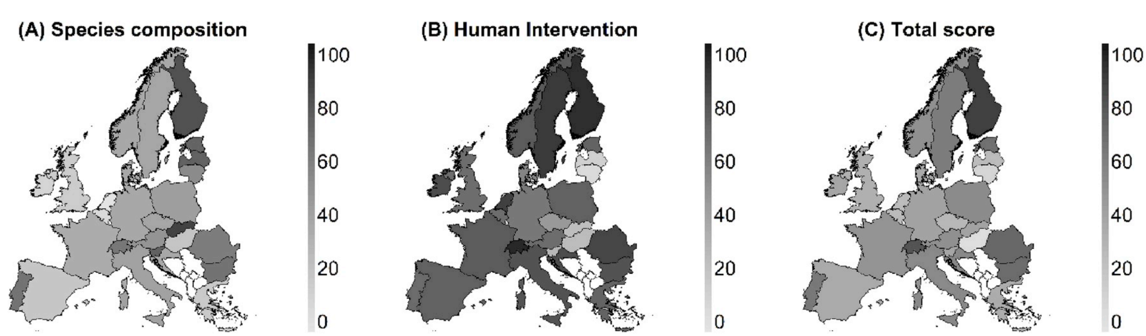

Fig. 2. (A) Species composition naturalness score, (B) human intervention naturalness score and (C) total naturalness score. For each country, the average naturalness score was calculated where a score of 0 represents the least natural conditions and a score of 100 the most natural. The total naturalness score of each country was calculated as the average of the species composition and human intervention scores.

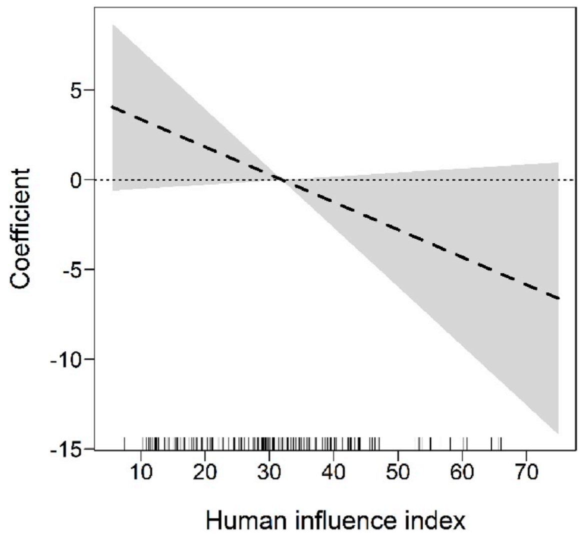

Fig. 3. Plot of the generalized additive mixed model predicting the difference in the naturalness score of species composition in European national parks (y-axis) influenced by the human influence index.

management objectives on the species composition naturalness score (Table 2). The model deviance decreased the most after removing country from the full model. In other words, the amount of unexplained variation is highest for the reduced model with country removed in comparison to the other reduced models. After country, the deviance decreased the most after removing the biogeographical region, but was relatively unaffected by the inclusion of percentage of government-owned land, the number of years since establishment, the human influence index, park size and the objective score (Table 2; Appendix Fig. S1).

Our generalized additive mixed model of human intervention explained 76.8% of the deviance (n = 177, adjusted $R^2 = 0.722$). The human intervention naturalness score decreased with park size (Fig. 4A, F = 6.069, P = 0.002). Whereas the human intervention naturalness score increased with the objective score (Fig. 4B, F = 4.662, P = <0.001), although only very low or very high objective scores influenced the naturalness score. Furthermore, the percentage of government-owned land, the human influence index and the number of years since park establishment did not influence the human intervention naturalness score (Table 3). Finally, the deviance decreased the most after removing country from the full model, followed by the objective score, park size, government-owned land, the human influence index, the number of years since establishment and the biogeographical region (Table 3; Appendix Fig. S1).

Table 2
Summary of the results of generalized additive mixed models predicting the influence of the selected explanatory variables on the naturalness scores of species composition in the national parks. Significant variables are highlighted in bold and variables showing a trend are underlined. "edf" = estimated degrees of freedom; "Res df" = residual degrees of freedom. Delta (Δ) deviance explained represents the difference in percentage of deviance explained by the full model – the percentage deviance explained by the reduced models.

Approximate significance of smooth terms	Δdeviance explained (%)	edf	Res df	F-value	P-value
Country	**11.2**	**11.114**	**21.000**	**7.013**	**0.001**
Biogeographical region	**8.1**	**6.168**	**7.000**	**25.010**	**<0.001**
Government-owned land (%)	1.0	2.861	3.501	0.874	0.428
Years since establishment	0.7	2.385	2.952	0.849	0.533
Human influence index	0.6	1.000	1.000	3.043	0.083
Park size (ha)	0.4	1.000	1.000	1.432	0.233
Objective score	0.0	1.000	1.000	0.000	0.995

4. Discussion

Our study provides new insights on the current status of the naturalness of ungulate management in European national parks and identifies the explanatory variables that influence the naturalness of ungulate management. Our results prove that the cultural and political context of the country more strongly influences ungulate management in European national parks compared to the other variables tested. Park size, the human influence index and the percentage of government-owned land also influenced ungulate management, although only explained a small part of the deviance. In contrast to our hypothesis, the management objectives set by a given park and the years since park establishment did not influence ungulate management in European national parks.

4.1. The naturalness concept as a useful management tool

Most studies that included the naturalness concept focused on the naturalness of forest ecosystems (Gibbons et al., 2008; Liira and Sepp, 2009; Paillet et al., 2008; Winter 2012) and only one considered the naturalness concept in relation to ungulate management (Günther and Heurich, 2013). Our study is the first to attempt to evaluate and quantify wildlife management strategies in most of the national parks in Europe. Consequently, the main naturalness variables considered in our study (i.e. years since establishment, park size, percentage of government-owned land, objective score, and human influence index) have not been considered in other studies.

Our large-scale electronic survey covered all of Europe. The inherent risk of electronic surveys is their subjectivity and differences in question interpretation. To maximize the response rate, we limited our survey to 36 questions, which respondents should have been able to answer within 15 min, but may have resulted in a loss of detail. For example, an estimate of the number of animals shot per area unit, the livestock units, the animal densities present, or the mass of artificial food per unit area might have provided a better understanding of the management practices. However, these exact numbers are often not readily available to national park managers. Further, the number of animals poached per species would give a better estimation of the extent of poaching, but this number is elusive since it is an illegal activity. Still, we believe problems of subjectivity, question interpretability and loss of detail were minimized through cooperation with local wildlife specialists. As they distributed questionnaires to the national park authorities, the answers are not the opinion of a single person, but the official statement of the park. Further, due to their expertise and ecological backgrounds these wildlife specialists were highly capable of judging whether the data provided by the national park authorities were in accordance with local circumstances. Consequently, we believe the method provides a relevant characterization of the most important drivers of ungulate management, the challenges involved, and the variables influencing current ungulate management in European national parks.

4.2. Variables influencing ungulate management

Managers need to fully understand the strengths and weaknesses of their management of protected areas to maximize the potential to conserve natural ecosystem functioning (Kilgo et al., 1998). This entails understanding which variables influence management. Within this study, variables potentially influencing the naturalness of ungulate management were considered based on a literature review and the conducted survey. Unfortunately, we had to exclude the size of the non-intervention zone from our analyses because this specific question was often left unanswered. We speculate that this may be due to the lack

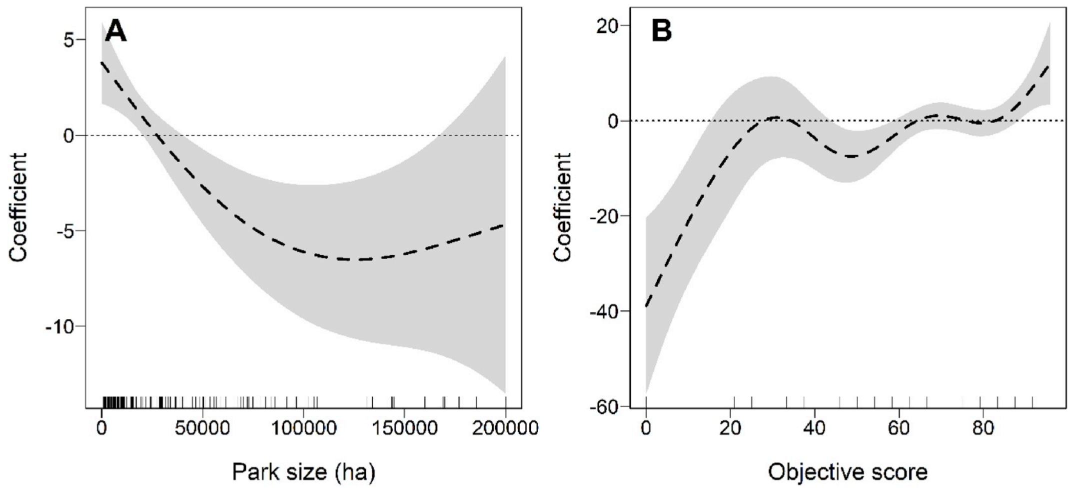

Fig. 4. Plots of generalized additive mixed models predicting the naturalness score of human intervention in European national parks (y-axis) influenced by (A) park size and (B) objective score.

Table 3
Summary of the results of generalized additive mixed models predicting the influence of the selected explanatory variables on the naturalness scores of human intervention in the national parks. Significant variables are highlighted in bold and variables showing a trend are underlined. "edf" = estimated degrees of freedom; "Res df" = residual degrees of freedom. Delta (Δ) deviance explained represents the difference in percentage of deviance explained by the full model – the percentage deviance explained by the reduced models.

Approximate significance of smooth terms	Δdeviance explained (%)	edf	Res df	F-value	P-value
Country	**31.3**	**18.130**	**21.000**	**9.626**	**<0.001**
Objective score	**5.1**	**5.883**	**6.942**	**4.662**	**<0.001**
Park size (ha)	**2.2**	**1.949**	**2.400**	**6.069**	**0.002**
Government-owned land (%)	0.2	1.310	1.541	0.400	0.482
Human influence index	0.1	1.321	1.572	0.278	0.582
Years since establishment	0.1	1.000	1.000	1.329	0.251
Biogeographical region	0.0	0.000	8.000	0.000	0.982

of such zones in several national parks or to uncertainty. As an alternative, we considered national park size in our statistical models, but included the size of the non-intervention zone relative to the size of the national park in descriptive analyses. Only 28.5% of the 165 national parks that answered the question had a non-intervention zone covering 75–100% of the national park area. The IUCN highlights that for all protected areas, the primary management objective of a park should apply to at least 75% of the protected area (Dudley, 2008). Consequently, this result shows that despite the main objective of national parks to protect biodiversity and support environmental processes, national parks have set only a relatively small area aside for the preservation of natural processes without intervention.

Regarding the number of years since park establishment we have to note that we do not have information on the initial conditions of each national park. Some parks might have experienced major developments, but others might have changed little over time. For example, forestry was important before the establishment of the Bavarian Forest National Park, and a transition period was necessary for people to recognize the importance of nature protection and the concept of pristine nature and to gradually increase the size of the non-intervention zone within the national park. The concept of "let nature be nature" was especially challenged after the first bark beetle attack and windthrows of August 1983, but this set the course for further management actions (Nationalparkverwaltung Bayerischer Wald, n.d.). By contrast, the Swiss National Park was established with the aim of developing a "complete nature reserve", where all human activities are prohibited and the forest is left unmanaged (Kupper, 2013).

No correlation was found between the human intervention score and the species composition score. In other words, in national parks with higher wildlife diversity and lower numbers of domesticated species present, human intervention in the form of ungulate population control and artificial feeding took place to the same degree. In addition, we found that wildlife regulation took place in the form of culling (40.2%), commercial hunting (10.5%) or both (17.2%). Artificial feeding occurred in 81.3% of the national parks. This shows that, independent of species composition and whether a top-down naturally-regulated system was present, human intervention measures are considered a necessary tool for restoring or maintaining ecological integrity in accordance with IUCN category II objectives or that other objectives or traditions, like hunting or livestock farming, were pursued.

4.2.1. *Species composition*

The naturalness of the species composition in a national park can be improved directly by expansion of the natural range of species, e.g. recolonization of grey wolves (*Canis lupus*) in Europe (Chapron et al., 2014) and active reintroduction of species, e.g. Eurasian lynx (*Lynx lynx*; Kaczensky et al., 2012) and Alpine ibex (*Capra ibex*; Stüwe and Nievergelt, 1991). National park managers could create suitable habitats for natural recolonization and authorize/implement the latter process. In contrast to our hypotheses, we found no positive correlation between species composition and years since establishment, objective score and the percentage of state-owned land, which suggests that national park authorities play a limited role in influencing the naturalness of the species composition. National park authorities may be restricted in organizing active reintroductions, due to the lack of financial support or stakeholder attitudes. Large carnivore reintroductions have often led to local resistance due to fear for human safety, killing of livestock or the potential competition with hunters (Linnell et al., 2002; Treves and Karanth, 2003). In parallel, damage to crops and increased browsing pressure outside national parks shape human-wildlife conflicts with respect to herbivore reintroduction (Balčiauskas et al., 2016; Jenny and Filli, 2014).

In accordance with our hypothesis, the naturalness score for species composition tended to be lower when the human influence index was higher, which indicates that greater anthropogenic pressure leads to lower wildlife diversity and higher numbers of domesticated species.

Large carnivore and herbivore movements tend to be lower in areas with a higher human influence because of barriers in the form of habitat change and fragmentation on the one hand, and enhanced resources in the form of crops and artificial feeding on the other hand. Both mechanisms likely affect animal densities and species composition within an area (Tucker et al., 2018).

Finally, in contrast to our hypothesis, we found no influence of park size on the naturalness scores of species composition. Smaller national parks face more edge effects and as a direct consequence of the national park objectives, human influences are expected to be generally higher outside national parks. As a result of this interaction, we expected that in accordance with Woodroffe and Ginsberg (1998), species are more likely to disappear from smaller national parks with higher anthropogenic influences. Although our study indicated that human influences did indeed negatively affect species composition, smaller national parks did not have a significant lower naturalness of species composition. Consequently, the anthropogenic effects within and surrounding the national parks negatively influenced the species composition more than parks size did. In this study, five very large national parks (>200,000 ha) were excluded from the analyses, as these were much bigger in comparison to all other European national parks and had a strong influence (leverage) on the results. The model results for species composition with these five large parks included are summarized in the Appendix Table S5. When these large parks were included, we found that park size negatively influenced the species composition naturalness score ($F = 2.714$, $P = 0.005$). These large national parks had either no ungulate or large carnivore species present that were native to the area. This might be explained by the location of these national parks (e.g. covering high mountain ranges, river delta) and the large carnivore management measures (including hunting) present.

4.2.2. Human intervention

In accordance with our hypotheses, we found that the naturalness score for the objectives was positively correlated with the naturalness of human intervention. This result implies that when national parks are managed in accordance with the primary objectives defined by IUCN Category II, which stress the protection of species and natural processes, less human intervention in the form of ungulate regulation and artificial feeding should occur. Furthermore, we found no support for our hypotheses that less human intervention occurred in older national parks or when a greater part of the park is owned by the government. This indicates that as long as national parks are managed according to IUCN objectives, the private or governmental body owning the area and the years since park establishment are of lesser importance. This result also suggests that older parks have not necessarily developed towards more effective management strategies to reduce human intervention.

In contrast to our hypothesis, the human intervention naturalness score decreased with park size, where naturalness scores were highest for national parks <2,000ha. After including the five large parks in the analyses, the same result was found ($F = 2.441$, $P = 0.071$, Appendix Table S6). It might be easier to implement a non-intervention zone in smaller national parks because stakeholders (foresters, hunters) can, e.g. hunt ungulates outside the national parks. In larger parks with no or low densities of predators, higher ungulate densities can persist and it is generally assumed that their numbers must be controlled. However, large non-intervention zones are important for the protection of natural processes as large carnivores are more likely to reach ecologically functional densities in such areas. Lastly, in contrast to the naturalness of species composition, the degree of anthropogenic influences did not influence the naturalness of human intervention. This result suggests that the ungulate population control by humans is less important because the number of species present in the area is already influenced by the degree of anthropogenic influences.

4.3. Variation in the cultural/political context among countries explains diversity of ungulate management practices

Our results show that in comparison to the other variables, country explained the largest part of the deviance for both the species composition naturalness and the human intervention naturalness scores. The different countries reflect differences in legal and administrative frameworks and are also influenced by their political and socioeconomic histories and cultural traditions, such as hunting and agricultural practices. The fact that the variable country explained a larger part of the unexplained variation mirrors the extreme variability in ungulate management systems adopted by different countries in Europe (Apollonio et al., 2010) and highlights the importance of the cultural/political context in influencing ungulate management.

In contrast to the USA where all national parks are managed by the federal National Park Service following the same management policies (US Department of the Interior National Park Service, 2001), European national parks have no responsible central authority for managing protected areas, and therefore there is no institutionalized cooperation in managing ungulates in national parks among European countries. The only conservation system at the EU level is the Natura 2000 network, which ensures the long-term survival of valuable and threatened species and habitats, listed under the Birds Directive and the Habitats Directive (Sundseth, 2014). The directives provide a legislative framework for the 28 member states and have been instrumental in protecting vulnerable habitat types and species (Sundseth, 2014). Although, these directives shape the governance of protected areas, their main focus is on the protection of endangered or endemic species and the designation of special areas for conservation (Paavola, 2004).

Another encumbrance to park management is the lack of a European-wide legal definition of protected areas. Most European national parks are managed by a central or local nature conservation authority of the respective country to which the park authorities report (Baskin et al., 2004; Klemm and Shine, 1996). For example, in France, national park management strategies are set by a board representing governmental agencies, local authorities and NGOs (Klemm and Shine, 1996). In Germany, each federal state (Bundesland) is responsible for designating protected areas and creating legislative plans within the federal framework (Kemkes, 2008). In Italy, the Ministry of Environment manages all national parks. In Romania, the National Forest Administration (ROMSILVA), which consists of county departments, forest districts and park administrations implements state forest legislation (Ioras and Abrudan, 2006).

5. Conclusions

The results of our study reveal the usefulness of the naturalness score as a tool to assess the current status of ungulate management and the diversity of the management, and to determine which variables influence the naturalness of ungulate management. Our study shows that despite IUCN categorization of protected areas and the standardized guidelines set for protected area management, ungulate management greatly varied among European countries and that most European national parks do not fulfil the aims of protected area management as stated by the IUCN. To fulfil the aims of protected areas, the legal, institutional and managerial frameworks must be defined and sufficient resources must be provided (Getzner et al., 2012). To be able to develop ungulate management strategies further, and to set-up and integrate these frameworks, we highlight the importance of achieving a more integrated European management policy, which is in accordance with IUCN guidelines and helps to enforce international guidelines for national park management. A more integrated ungulate management framework is needed that provides a common definition of national parks with clearly specified laws, regulations and policies, an integrated adaptive management system that considers all ecosystem processes, local traditions and socio-political contexts, and a network of national park authorities that facilitates the exchange of knowledge and the development of the management system.

Author contribution

Suzanne T.S. van Beeck Calkoen; Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft, Visualization, Project administration. Lisa Mühlbauer; Conseptualization, Methodology, Resources. Henrik Andrén; Resources, Validation, Writing – Review&Editing. Marco Apollonio; Resources, Validation, Writing – Review&Editing. Linas Balčiauskas; Resources, Validation, Writing – Review&Editing. Elisa Belotti; Resources, Validation, Writing – Review&Editing. Juan Carranza; Resources, Validation, Writing – Review&Editing. Jamie Cottam; Resources, Writing – Review&Editing. Flurin Filli; Resources, Validation, Writing – Review&Editing. Tsegaye T. Gatiso; Validation, Writing – Review&Editing. David Hetherington; Resources, Validation, Writing – Review&Editing. Alexandros A. Karamanlidis; Resources, Validation, Writing – Review&Editing. Miha Krofel; Resources, Validation, Writing – Review&Editing. Hjalmar S. Kuehl; Validation, Writing – Review&Editing. John D.C. Linnell; Resources, Validation, Writing – Review&Editing. Jörg Müller; Validation, Writing – Review&Editing. Janis Ozolins; Resources, Validation, Writing – Review&Editing. Joseph Premier; Validation, Writing – Review&Editing. Nathan Ranc; Resources, Validation, Writing – Review&Editing. Krzysztof Schmid; Resources, Validation, Writing – Review&Editing. Diana Zlatanova; Resources, Validation, Writing – Review&Editing. Mona Bachmann; Validation, Writing – Review&Editing. Carlos Fonseca; Resources, Validation. Ovidiu lonescu; Resources, Validation. Madeleine Nyman; Resources, Validation. Nikica Šprem; Resources, Validation. Peter Sunde; Resources, Validation. Margo Tannik; Resources, Validation. Marco Heurich; Conseptualization, Methodology, Writing – Review&Editing, Supervision, Project administration.

Acknowledgements

We thank the staff of all European national parks for kindly responding to our questionnaire survey and we would like to thank all others involved for their help in the data collection. Further, we would like to thank University of Aveiro, Portugal and FCT/MEC for the financial support to CESAM RU (UID/AMB/50017) through national funds and co-financed by the FEDER, within the PT2020 Partnership Agreement as well as the Instituto da Conservação da Natureza e das Florestas (ICNF) for the data supply. In addition, we thank Dr Tomasz Pucek (Ministry of Environment, Poland) for help in obliging the administration of Polish National Parks to participate in the survey and Prof. Dr. Carsten Dormann for kindly answering our emails and providing insights. Last, we thank K. A. Brune for linguistic revision of the manuscript. S.T.S. van Beeck Calkoen was financially supported by the Gregor Louisoder Umweltstiftung and the Deutscher Akademischer Austauchdienst (DAAD).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2020.110068.

References

Anderson, J.E., 1991. A conceptual framework for evaluating and quantifying naturalness. Conserv. Biol. 5, 347–352.

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

Apollonio, M., Belkin, V.V., Borkowski, J., Borodin, O.I., Borowik, T., Cagnacci, F., Danilkin, A.A., Danilov, P.I., Faybich, A., Ferretti, F., Gaillard, J.M., Hayward, M., Heshtaut, P., Heurich, M., Hurynovich, A., Kashtalyan, A., Kerley, G.I.H., Kjellander, P., Kowalczyk, R., Kozorez, A., Matveytchuk, S., Milner, J.M., Mysterud, A., Ozoliņš, J., Panchenko, D.V., Peters, W., Podgórski, T., Pokorny, B., Rolandsen, C.M., Ruusila, V., Schmidt, K., Sipko, T.P., Veeroja, R., Velihurau, P., Yanuta, G., 2017. Challenges and science-based implications for modern management and conservation of European ungulate populations. Mamm. Res. 62, 209–217. https://doi.org/10.1007/s13364-017-0321-5.

Balčiauskas, L., Kazlauskas, M., Balčiauskienė, L., 2016. European bison: changes in species acceptance following plans for translocation. Eur. J. Wildl. Res. 63, 4. https://doi.org/10.1007/s10344-016-1066-1.

Ballantyne, R., Packer, J., Hughes, K., 2009. Tourists' support for conservation messages and sustainable management practices in wildlife tourism experiences. Tour. Manag. 30, 658–664. https://doi.org/10.1016/j.tourman.2008.11.003.

Baskin, L., Ball, J.P., Danell, K., 2004. Moose escape behaviour in areas of high hunting pressure. Alces 40, 10.

Bivand, R., Rundel, C., Pebesma, E., Stuetz, R., Hufthammer, K.O., 2016. rgeos: interface to geometry engine-open source (GEOS). http://CRAN.R-project.org/package=rgeos. R package version 0.3-4.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv. Biol. 16, 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., du Toit, J.T., 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annu. Rev. Ecol. Systemat. 22, 431–446. https://doi.org/10.1146/annurev.es.22.110191.002243.

Bugalho, M.N., Milne, J.A., 2003. The composition of the diet of red deer (Cervus elaphus) in a Mediterranean environment: a case of summer nutritional constraint? Forest Ecology and Management, Forest Dynamics and Ungulate Herbivory : From Leaf to Landscape 181, 23–29. https://doi.org/10.1016/S0378-1127(03)00125-7.

Carranza, J., Garcia-Muñoz, A.J., de Dios Vargas, J., 1995. Experimental shifting from harem defence to territoriality in rutting red deer. Anim. Behav. 49, 551–554. https://doi.org/10.1006/anbe.1995.0077.

Chape, S., Harrison, J., Spalding, M., Lysenko, I., 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philos. Trans. R. Soc. Biol. Sci. 360, 443–455. https://doi.org/10.1098/rstb.2004.1592.

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519. https://doi.org/10.1126/science.1257553.

Cole, D.N., Yung, L., Zavaleta, E.S., Aplet, G.H., Chapin, F.S., Graber, D.M., Higgs, E.S., Hobbs, R.J., Landres, P.B., Millar, C.I., Parsons, D.J., Randall, J.M., Stephenson, N.L., Tonnessen, K.A., White, P.S., Woodley, S., 2008. Naturalness and beyond: protected area stewardship in an era of global environmental change. George Wright Forum 25, 36–56.

Conover, M.R., 2001. Effect of hunting and trapping on wildlife damage. Wildl. Soc. Bull. 29, 521–532 (1973-2006).

Convention on Biological Diversity, n.d. History of the Convention [WWW Document]. URL https://www.cbd.int/history/(accessed 11.3.2018).

Côté, S.D., Rooney, T.P., Tremblay, J.-P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Systemat. 35, 113–147. https://doi.org/10.1146/annurev.ecolsys.35.021103.105725.

Dapporto, L., Ciolli, G., Dennis, R.L.H., Fox, R., Schreeve, T.G., 2016. Biogeographic regions: what are they and what can they tell us? URL. https://methodsblog.com/2016/08/11/biogeographic-regions/.

Demarais, S., Cornicelli, L., Kahn, R., Merrill, E., Miller, C., Peek, J.M., Porter, W.F., Sargeant, G.A., 2012. Ungulate management in national parks of the United States and Canada. The Wildlife Society Technical Review 12.

Department for Environment Food and Rural Affairs, 2016. National parks: 8-point plan for england (2016 to 2020) [WWW Document]. GOV.UK. https://www.gov.uk/government/publications/national-parks-8-point-plan-for-england-2016-to-2020. (Accessed 11 March 2018).

Dudley, N., 2008. Guidelines for Applying Protected Area Management Categories. IUCN. https://doi.org/10.2305/IUCN.CH.2008.PAPS.2.en.

Dupke, C., Dormann, C.F., Heurich, M., 2019. Does public participation shift German national park priorities away from nature conservation? Environ. Conserv. 46, 84–91. https://doi.org/10.1017/S0376892918000310.

European Environment Agency, 2016. Biogeographical regions [WWW Document]. Data. https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3. (Accessed 11 July 2018).

European Environment Agency, 2017. Nationally designated areas (CDDA) [WWW Document]. European environment agency. https://www.eea.europa.eu/data-and-maps/data/nationally-designated-areas-national-cdda-12. (Accessed 11 July 2018).

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

Fuller, R.J., Gill, R.M.A., 2001. Ecological impacts of increasing numbers of deer in British woodland. Forestry 74, 193–199. https://doi.org/10.1093/forestry/74.3.193.

Geisser, H., Reyer, H.-U., 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J. Wildl. Manag. 68, 939–946.

Getzner, M., Jungmeier, M., Pfleger, B., 2012. Evaluating Management Effectiveness of National Parks as a Contribution to Good Governance and Social Learning. Protected Area Management. https://doi.org/10.5772/50092.

Gibbons, P., Briggs, S.V., Ayers, D.A., Doyle, S., Seddon, J., McElhinny, C., Jones, N., Sims, R., Doody, J.S., 2008. Rapidly quantifying reference conditions in modified landscapes. Biol. Conserv. 141, 2483–2493. https://doi.org/10.1016/j.biocon.2008.07.009.

Gill, R.M.A., 1992. A review of damage by mammals in North temperate forests: 1. Deer. Forestry 65, 145–169. https://doi.org/10.1093/forestry/65.2.145.

Gortázar, C., Ferroglio, E., Höfle, U., Frölich, K., Vicente, J., 2007. Diseases shared between wildlife and livestock: a European perspective. Eur. J. Wildl. Res. 53, 241. https://doi.org/10.1007/s10344-007-0098-y.

Green, R., Giese, M., 2004. In: Negative Effects of Wildlife Tourism on Wildlife. Wildlife Tourism: Impacts, Management and Planning, vol. 106. CRC for Sustainable Tourism and Common Ground Publishing, Altona, pp. 81–97.

Green, M.J., Paine, J., 1997. State of the world's protected areas at the end of the twentieth century. In: Unpublished Paper Presented at Protected Areas in the 21st Century: from Islands to Networks. World Commission on Protected Areas, Albany, WA, Australia.

Günther, S., Heurich, M., 2013. Assessment of the naturalness of the red deer management in central European national parks. Allg. Forst Jagdztg. 184, 1–16.

Haller, H., 2016. 6. Zwischenbilanz: auswirkungen der Wilderei auf einzelne Wildtierarten. In: Wilderei Im Rätischen Dreiländereck. Grenzüberschreitende Recherchen Mit Einer Spurensuche Bis Nach Tibet. Nat.park-Forsch. Schweiz 105/1, Bern.

Hansen, A.J., DeFries, R., 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecol. Appl. 17, 974–988.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144.

Heurich, M., Baierl, F., Günther, S., Sinner, K.F., 2011. Management and conservation of large mammals in the bavarian forest national park. Silva Gabreta 17, 1–18.

Hijmans, R.J., 2016. raster: geographic data analysis and modeling. R package ver 2, 5–8.

Huggett, R., 2011. Biogeographical regions. eLS. https://doi.org/10.1002/9780470015902.a0003231.pub2.

Ioras, F., Abrudan, I.V., 2006. The Romanian forestry sector: privatisation facts. Int. For. Rev. 8, 361–367.

Ivancevich, J.M., 1974. Changes in performance in a management by objectives program. Adm. Sci. Q. 19, 563–574. https://doi.org/10.2307/2391811.

Jenny, H., Filli, F., 2014. 9. Wildforschung erarbeitet Grundlagen für Schutz und Jagd. In: Wissen Schaffen. 100 Jahre Forschung Im Schweizerischen Nationalpark. Haupt Verlag Bern.

Kaczensky, P., Chapron, G., von Arx, M., Huber, D., Andrén, H., Linnell, J., 2012. Status, management and distribution of large carnivores – bear, lynx, wolf & wolverine – in Europe. Istituto di Ecologia Applicata, and IUCN/SSC Large Carnivore Initiative for Europe.

Keller, R.P., Geist, J., Jeschke, J.M., Kühn, I., 2011. Invasive species in Europe: ecology, status, and policy. Environ. Sci. Eur. 23, 23. https://doi.org/10.1186/2190-4715-23-23.

Kemkes, W., 2008. Quality criteria and standards for German national parks: developing a procedure to evaluate management effectiveness. Europarc Deutschland. http://www.europarc-deutschland.de/wp-content/uploads/2012/08/2008_Quality_criteria_and_standards_for_German_national_parks.pdf.

Keuling, O., Stier, N., Roth, M., 2008. How does hunting influence activity and spatial usage in wild boar Sus scrofa L.? Eur. J. Wildl. Res. 54, 729. https://doi.org/10.1007/s10344-008-0204-9.

Kilgo, J.C., Labisky, R.F., Fritzen, D.E., 1998. Influences of hunting on the behavior of white-tailed deer: implications for conservation of the Florida panther. Conserv. Biol. 12, 1359–1364.

Klemm, C. de, Shine, C., 1996. Legal Measures for the Conservation of Natural Areas. Council of Europe.

Kowalczyk, R., Górny, M., Schmidt, K., 2015. Edge effect and influence of economic growth on Eurasian lynx mortality in the Białowieża Primeval Forest, Poland. Mamm. Res. 60, 3–8. https://doi.org/10.1007/s13364-014-0203-z.

Kuijper, D.P.J., Cromsigt, J.P.G.M., Churski, M., Adam, B., Jędrzejewska, B., Jędrzejewski, W., 2009. Do ungulates preferentially feed in forest gaps in European temperate forest? For. Ecol. Manag. 258, 1528–1535. https://doi.org/10.1016/j.foreco.2009.07.010.

Kuijper, D.P.J., De Kleine, C., Churski, M., Van Hooft, P., Bubnicki, J., Jędrzejewska, B., 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography 36, 1263–1275.

Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K., Cromsigt, J.P.G.M., 2016. Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proc. R. Soc. B 283, 20161625. https://doi.org/10.1098/rspb.2016.1625.

Kupper, P., 2013. The Swiss National Park: A Model of Nature Conservation for Scientific Research. Arcadia Collection: National Parks in Time and Space 5271.

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Arias-G, J.C., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C.A., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O'Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K.E., Sukumar, R., Surbeck, M., Tobler, M., Tscharntke, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Verea, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D. D., Wright, P., Xiankai, L., Yonzon, P., Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294. https://doi.org/10.1038/nature11318.

Leroux, S.J., Krawchuk, M.A., Schmiegelow, F., Cumming, S.G., Lisgo, K., Anderson, L.G., Petkova, M., 2010. Global protected areas and IUCN designations: do the categories match the conditions? Biol. Conserv. 143, 609–616. https://doi.org/10.1016/j.biocon.2009.11.018.

Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T., Sand, H., 2012. Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. Proc. R. Soc. B 279, 910–915. https://doi.org/10.1098/rspb.2011.1275.

Liira, J., Sepp, T., 2009. Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Ann. Bot. Fenn. 46, 308–325.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68, 619–640. https://doi.org/10.1139/z90-092.

Linnell, J., Andersen, R., Andersone, Z., Balciauskas, L., Blanco, J., Boitani, L., Brainerd, S., Breitenmoser, U., Kojola, I., Liberg, O., Loe, J., Okarma, H., Pedersen, H., Sand, H., Solberg, E., Valdmann, H., Wabakken, P., 2002. The Fear of Wolves: A Review of Wolf Attacks on Humans. Rocky Mountain Wolf Recovery Annual Reports.

Mack, R.N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10, 689–710.

Maillard, D., Fournier, P., 2014. Effects of shooting with hounds on size of resting range of Wild boar (Sus scrofa L.) groups in mediterranean habitat. J. Mt. Ecol. 3.

Manor, R., Saltz, D., 2005. Effects of human disturbance on use of space and flight distance of mountain gazelles. J. Wildl. Manag. 69, 1683–1690.

Melis, C., Jędrzejewska, B., Apollonio, M., Bartoń, K.A., Jędrzejewski, W., Linnell, J.D., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., 2009. Predation has a greater impact in less productive environments: variation in roe deer, Capreolus capreolus, population density across Europe. Glob. Ecol. Biogeogr. 18, 724–734.

Miranda, M., Cristóbal, I., Díaz, L., Sicilia, M., Molina-Alcaide, E., Bartolomé, J., Fierro, Y., Cassinello, J., 2015. Ecological effects of game management: does supplemental feeding affect herbivory pressure on native vegetation? Wildl. Res. 42, 353–361. https://doi.org/10.1071/WR15025.

Möst, L., Hothorn, T., Müller, J., Heurich, M., 2015. Creating a landscape of management: unintended effects on the variation of browsing pressure in a national park. For. Ecol. Manag. 338, 46–56. https://doi.org/10.1016/j.foreco.2014.11.015.

Muhly, T.B., Hebblewhite, M., Paton, D., Pitt, J.A., Boyce, M.S., Musiani, M., 2013. Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. PLoS One 8, e64311. https://doi.org/10.1371/journal.pone.0064311.

Müller, J., Wölfl, M., Wölfl, S., Müller, D.W.H., Hothorn, T., Heurich, M., 2014. Protected areas shape the spatial distribution of a European lynx population more than 20 years after reintroduction. Biol. Conserv. 177, 210–217. https://doi.org/10.1016/j.biocon.2014.07.007.

National Parks UK, 2018. National parks [WWW Document]. https://nationalparks.uk/. (Accessed 11 January 2018).

Nationalparkverwaltung Bayerischer Wald, n.d. Homepage des Nationalparks Bayerischer Wald [WWW Document]. URL https://www.nationalpark-bayerischer-wald.bayern.de/(accessed 11.7.2018).

Nationale Naturlandschaften, 2008. Nationalparks in Deutschland. Nationale Naturlandschaften [WWW Document]. http://www.nationale-naturlandschaften.de/wissensbeitraege/nationalparks-in-deutschland/. (Accessed 11 March 2018).

Naughton-Treves, L., Holland, M.B., Brandon, K., 2005. The role of protected areas in conserving biodiversity and sustaining local livelihoods. Annu. Rev. Environ. Resour. 30, 219–252. https://doi.org/10.1146/annurev.energy.30.050504.164507.

Ouellet, J.-P., Crête, M., Maltais, J., Pelletier, C., Huot, J., 2001. Emergency feeding of white-tailed deer: test of three feeds. J. Wildl. Manag. 65, 129–136. https://doi.org/10.2307/3803285.
Paavola, J., 2004. Protected areas governance and justice: theory and the European Union's Habitats Directive. Environ. Sci. 1, 59–77.
Paillet, Y., Archaux, F., Breton, V., Brun, J.-J., 2008. A quantitative assessment of the ecological value of sycamore maple habitats in the French Alps. Ann. For. Sci. 65 https://doi.org/10.1051/forest:2008058, 713–713.
Pérez-González, J., Barbosa, A.M., Carranza, J., Torres-Porras, J., 2010. Relative effect of food supplementation and natural resources on female red deer distribution in a mediterranean ecosystem. J. Wildl. Manag. 74, 1701–1708. https://doi.org/10.2193/2009-130.
Porter, W.F., Underwood, H.B., 1999. Of elephants and blind men: deer management in the US National Parks. Ecol. Appl. 9, 3–9.
Protected Planet, 2014. Protected area coverage per country/territory by UN Environment Regions [WWW Document]. https://www.protectedplanet.net/c/unep-regions.
Putman, R.J., 2010. A review of the various legal and administrative systems governing management of large herbivores in Europe. Ungulate management in Europe: problems and practices 54–79.
Putman, R.J., Staines, B.W., 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mamm Rev. 34, 285–306.
Putman, R., Apollonio, M., Andersen, R., 2011. Ungulate Management in Europe: Problems and Practices. Cambridge University Press.
Pyšek, P., 1995. On the terminology used in plant invasion studies. In: Plant Invasions: General Aspects and Special Problems. Academic Publishing, pp. 71–81.
R. Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2017.
Rauset, G.R., Andrén, H., Swenson, J.E., Samelius, G., Segerström, P., Zedrosser, A., Persson, J., 2016. National parks in northern Sweden as refuges for illegal killing of large carnivores. Conservation Letters 9, 334–341.
Ripple, W.J., Larsen, E.J., Renkin, R.A., Smith, D.W., 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biol. Conserv. 102, 227–234. https://doi.org/10.1016/S0006-3207(01)00107-0.
Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world's largest carnivores. Science 343, 1241484. https://doi.org/10.1126/science.1241484.
Rogala, J.K., Hebblewhite, M., Whittington, J., White, C.A., Coleshill, J., Musiani, M., 2011. Human activity differentially redistributes large mammals in the Canadian Rockies National Parks. Ecol. Soc. 16.
Scillitani, L., Monaco, A., Toso, S., 2010. Do intensive drive hunts affect wild boar (Sus scrofa) spatial behaviour in Italy? Some evidences and management implications. Eur. J. Wildl. Res. 56, 307–318.
Sinclair, A.R.E., 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildl. Soc. Bull. 399–409.
Soulé, M.E., Estes, J.A., Berger, J., Del Rio, C.M., 2003. Ecological effectiveness: conservation goals for interactive species. Conserv. Biol. 17, 1238–1250.
Steinhoff, G., 2012. Naturalness and biodiversity: why natural conditions should be maintained within protected areas. Wm. & Mary Envtl. L. & Pol'y Rev. 37, 77.
Stüwe, M., Nievergelt, B., 1991. Recovery of alpine ibex from near extinction: the result of effective protection, captive breeding, and reintroductions. Appl. Anim. Behav. Sci. 29, 379–387.
Sundseth, K., 2014. The EU Birds and Habitats Directives- European Commission.
Taylor, L.H., Latham, S.M., Mark, E.J., 2001. Risk factors for human disease emergence. Philos. Trans. R. Soc. Lond. B Biol. Sci. 356, 983–989.
Theuerkauf, J., Rouys, S., 2008. Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. For. Ecol. Manag. 256, 1325–1332.
Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv. Biol. 17, 1491–1499.
Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S. C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359, 466–469.
US Department of the Interior National Park Service, 2001. Management Policies: the Guide to Managing the National Park System.
Watson, J.E., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515, 67.
Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. Bioscience 48, 607–615.
Wildlife Conservation Society - WCS, Center for International Earth Science Information Network - CIESIN - Columbia University, 2005. Last of the Wild Project. Global Human Footprint Dataset (Geographic), 2005 (LWP-2), Version 2.
Winter, S., 2012. Forest naturalness assessment as a component of biodiversity monitoring and conservation management. Forestry 85, 293–304.
Winter, S., Fischer, H.S., Fischer, A., 2010. Relative quantitative reference approach for naturalness assessments of forests. For. Ecol. Manag. 259, 1624–1632.
Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B 73, 3–36.
Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science 280, 2126–2128.