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RESEARCH ARTICLE

Numerical top-down effects on red deer (*Cervus elaphus*) are mainly shaped by humans rather than large carnivores across Europe

Suzanne T. S. van Beeck Calkoen[1,2] | Dries P. J. Kuijper[3] | Marco Apollonio[4] | Lena Blondel[5] | Carsten F. Dormann[5] | Ilse Storch[2] | Marco Heurich[1,2,6]

[1]Department of Visitor Management and National Park Monitoring, Bavarian Forest National Park, Grafenau, Germany; [2]Chair of Wildlife Ecology and Management, Albert Ludwigs University Freiburg, Freiburg, Germany; [3]Mammal Research Institute Polish Academy of Sciences, Białowieża, Poland; [4]Department of Veterinary Medicine, University of Sassari, Sassari, Italy; [5]Biometry and Environmental System Analysis, Albert Ludwigs University Freiburg, Freiburg, Germany and [6]Faculty of Applied Ecology, Agricultural Sciences and Biotechnology, Inland Norway University of Applied Sciences, Koppang, Norway

Correspondence
Suzanne T. S. van Beeck Calkoen
Email: suzanne.van_beeck_calkoen@tu-dresden.de

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Abstract

1. Terrestrial ecosystems are shaped by interacting top-down and bottom-up processes, with the magnitude of top-down control by large carnivores largely depending on environmental productivity. While carnivore-induced numerical effects on ungulate prey populations have been demonstrated in large, relatively undisturbed ecosystems, whether large carnivores can play a similar role in more human-dominated systems is a clear knowledge gap. As humans influence both predator and prey in a variety of ways, the ecological impacts of large carnivores can be largely modified. We quantified the interactive effects of human activities and large carnivore presence on red deer (*Cervus elaphus*) population density and how their impacts interacted and varied with environmental productivity.
2. Data on red deer density were collected based on a literature survey encompassing 492 study sites across 28 European countries. Variation in density across study sites was analysed using a generalized additive model in which productivity, carnivore presence (grey wolf, European lynx, Brown bear), human activities (hunting, intensity of human land-use activity), site protection status and climatic variables served as predictors.
3. The results showed that a reduction in deer density only occurred when wolf, lynx and bear co-occurred within the same site. In the absence of large carnivores, red deer density varied along a productivity gradient without a clear pattern. Although a linear relationship with productivity in the presence of all three large carnivore species was found, this was not statistically significant. Moreover, hunting by humans had a stronger effect than the presence of all large carnivores in reducing red deer density and red deer density increased with increasing intensity of human land use, with stronger large carnivore

effects (all three carnivore species present) at sites with low human land-use activities.

4. *Synthesis and applications*. This study provides evidence for the dominant role played by humans (i.e. hunting, land-use activities) relative to large carnivores in reducing red deer density across European human-dominated landscapes. These findings suggest that when we would like large carnivores to exert numeric effects, we should focus on minimizing human impacts to allow the ecological impacts of large carnivores on ecosystem functioning.

KEYWORDS

Cervus elaphus, environmental productivity, human land-use activities, hunting by humans, large carnivores, numerical effects, top-down control

1 | INTRODUCTION

Large carnivores can play a key role in food web dynamics and can be an important factor limiting prey populations (Estes et al., 2011; Ripple et al., 2014), by both directly causing prey mortality and indirectly influencing prey survival or fecundity through behaviourally mediated effects (Creel & Christianson, 2008; Preisser et al., 2005). These carnivore-induced numerical effects have been demonstrated to affect ungulate prey density in large, relatively undisturbed ecosystems (Ripple et al., 2014). Whether and to what extent large carnivores in more human-dominated systems can play a similar role as observed in those more undisturbed systems is less clear (Kuijper et al., 2016).

The role of large carnivores for ecosystem structure and functioning is contingent on the specific conditions of the studied ecosystem (see Hoeks et al., 2020). The strength of top-down control of large carnivores on herbivore populations depends largely on environmental productivity. Herbivore populations are predicted to be increasingly top-down controlled by large carnivores with increasing environmental productivity (Oksanen et al., 1981). Besides these large (continental or biome scale) patterns, variation in productivity that occurs on finer spatiotemporal scales has been found to modify the strength of large carnivore top-down effects on herbivore prey populations in opposite direction (Jędrzejewska et al., 1997; Melis et al., 2009). Comparing systems within the range of roe deer across Europe, Melis et al. (2009) found that the effects of large carnivores were relatively weak in highly productive environments but increased markedly in regions with low vegetation productivity and harsh winters. Even at a finer scale, in the Białowieża primeval forest (Poland), changes in productivity between years (i.e. higher plant production during mild years) affected the strength of carnivore top-down effects. Here, the strongest limitation in ungulate numbers by large carnivores was observed during periods with lowest mean annual temperatures based on a more than 100-year period (Jedrzejewska & Jedrzejewski, 2005). Both these large-scale (i.e. global and continental) and fine-scale (i.e. temporal variation within a system) relations with environmental productivity illustrate the importance of bottom-up effects in modifying carnivore top-down impacts on prey populations.

Besides large carnivores, humans often have profound ecosystem impacts that can far exceed the influence of large carnivores (Darimont et al., 2015). In the Anthropocene, humans should therefore be seen as an integral part of food web dynamics as they strongly influence the density, distribution and behaviour of both large carnivores and their prey species. In this way, they are expected to largely modify the ecological impacts of large carnivores (as reviewed in Kuijper et al., 2016). The greatest direct impact on ungulate populations is hunting as a widespread tool to control ungulate numbers and mitigate human–wildlife conflicts (Apollonio et al., 2010). In fact, even in most national parks in Europe hunting occurs and only a few areas can be found where no human intervention takes place (van Beeck Calkoen et al., 2020). Conversely, other human activities can positively influence ungulate density, such as supplementary feeding or increased food availability through agricultural practices (Mysterud et al., 2002). For example, meadows, agriculture and forestry practices can alter ecosystem productivity, food quality and habitat suitability for ungulates (Haberl et al., 2007; Muhly et al., 2013) and can thus modify the effects of large carnivores. These strong direct and indirect impacts of humans on ungulate populations (and on large carnivores) begets the question to what extent large carnivores can still impose measurable top-down effects on their ungulate prey in human-dominated landscapes (Kuijper et al., 2016; Muhly et al., 2013).

In Europe, grey wolves (*Canis lupus*), Eurasian lynx (*Lynx lynx*) and brown bear (*Ursus arctos*) are currently recolonizing their historical ranges, largely as a result of strict legal protection (Chapron et al., 2014). The return of large carnivores into these novel human-dominated landscapes creates unique opportunities to examine the relative role of human and carnivore impacts on prey populations and the interplay with bottom-up processes. During earlier efforts to quantify large-carnivore top-down impacts on a European scale for roe deer (Melis et al., 2009), wild boar (Melis et al., 2006) or cervid densities (Ripple & Beschta, 2012), the relative importance of carnivore- versus human-induced population impacts and the context dependency on productivity have not been sufficiently taken into account. Moreover, some studies (Ripple & Beschta, 2012) did not cover Western and Central Europe where wolf numbers have been rapidly increasing during last decades and human impacts are predicted to be most pronounced

(Kuijper et al., 2016). This illustrates the urgent need to quantify the potential for numerical top-down effects of ungulate prey species by large carnivores within the context of omnipresent human impacts.

In this study, we analysed the interactive numeric effects of large carnivores and humans on red deer density across sites differing in environmental productivity. We compiled data on red deer density from 492 study sites across 28 European countries and analysed how large carnivores, humans and productivity affected red deer density. We predicted that:

1. Large carnivore presence reduces red deer density, with a combination of multiple large carnivore species more strongly reducing red deer density.
2. The strength of large carnivore top-down control depends on productivity, with red deer density decreasingly limited by large carnivores as productivity increases, whereas red deer density linearly increases with environmental productivity at sites devoid of large carnivores.
3. Hunting by humans reduces red deer density, whereas density increases with an increase in human land-use activity.
4. The strength of large carnivore control depends on human land use intensity with red deer density in less human-dominated environments being more limited by large carnivores.

2 | MATERIALS AND METHODS

2.1 | Literature search

Data on red deer density or population estimates were collected through an extensive literature search using Web of Science and Google Scholar. For a detailed description of the literature search and for an overview of the literature included, see Appendix S1. Given the rapid and recent increase in red deer density, only population estimates from studies published after 2000 were included. Articles featuring population density or both red deer population size and study site were retained. In addition, whether hunting by humans on red deer populations occurred in the area was recorded; when available, geographic coordinates were included. If geographic coordinates were not stated, the name of the study site was searched in Open Street Map (www.openstreetmap.org) and its coordinates then recorded in decimal degrees.

2.2 | Variables potentially influencing red deer density

Red deer density estimates found in the literature search were related to factors shown to affect ungulate density; indices of net primary productivity (NPP) as a proxy of food availability (Melis et al., 2009; Oksanen et al., 1981), large carnivore presence (Jedrzejewska & Jedrzejewski, 2005; Ripple et al., 2014) and hunting by humans as a management tool (Hothorn & Müller, 2010) that can both suppress red deer population density, a human influence index as a proxy for human land-use activities that can affect both ungulate density as well as the functional role of large carnivores (see Kuijper et al., 2019) and the protection status of the study site that relates to the naturalness and amount of human intervention in the area (see van Beeck Calkoen et al., 2020). The percentage of tree cover, summer drought (PDSI) and winter severity (NDSI) was also included as predictors, as these are critical factors affecting ungulate survival (i.e. Borowik et al., 2013; Forchhammer et al., 1998).

TABLE 1 Characteristics of variables explaining red deer density across Europe.

Variable	Definition	Years	Spatial resolution (m)	Temporal resolution	Range[a]
Net primary productivity (NPP)	Average NPP	2000–2020	500 × 500	8-day	0.1–1.0 kg C/m^2/year
Large carnivore presence	Permanent bear, lynx and/or wolf presence	Prior to 2011	—	—	All predators (n = 26); Lynx (n = 30); Wolf (n = 55); Wolf/Lynx (n = 29); Bear (n = 11), None (n = 341)
Hunting by humans	Hunting presence of humans on red deer populations	—	—	—	0 (n = 34)/1 (n = 458)
Human influence index (HII)	Average HII	1995–2004	1000 – 1000	Average Year	8.4–48.0
Site protection status	Allocated IUCN Category (I–VI) or Unprotected	—	—	—	Unprotected (n = 81), Less strict (n = 221), Strict (n = 190)
Tree cover density	Avg. percentage of tree cover	2000, 2005, 2010, 2015	30 × 30	Average Year	1.2–69.5
Palmer drought severity index (PDSI)	Avg. summer PDSI (21.06–21.09)	2000–2020	~ 5000 × 5000 *(1/24th degree)*	Monthly	−1.5–0.7
Normalized difference snow index (NDSI)	Sum of daily winter NDSI values (21.12–21.03)	2000–2020	500 × 500	1-day	98–61,225

[a]Considering presence points only.

For an overview of the used variables, see Table 1. Since red deer movement can cover large areas (Henrich et al., 2021; i.e. Szemethy et al., 1999), all variables (except for the binary data representing carnivore presence and hunting) were calculated for each study site with an additional 10-km radius around the centre (about 314 km^2; following Melis et al., 2009). To check the sensitivity of our results, we also applied a 5-km buffer and tested the effect of variable resolution by transforming all variables to the coarser resolution. These analyses showed qualitatively similar results (see Appendix S2: Tables S2 and S3). For a detailed description of the variables, see Appendix S1.

2.3 | Statistical analysis

A generalized additive model was used to analyse the effect of top-down versus bottom-up variables on red deer population density (mgcv package; Wood, 2011) within R 4.0.5 (R Core Team, 2021). Red deer density was the dependent variable, which was log-transformed to meet normality and homoscedasticity assumptions. Within our model, the effects of NPP, human influence index, tree cover density, summer drought and NDSI were represented by thin-plate regression splines ($k=9$), while large carnivore presence and protection status of a site were added as categorical variables (Table 1). Problems with dispersion and heteroscedasticity arose due to the small number of sites where bears were present; lynx–bear ($n=3$), wolf–bear ($n=3$) and bear only ($n=5$). Instead, bear presence was represented by a factor including all three categories above ('Bear', $n=11$) and a second factor that included all large carnivores ('All predators', $n=26$; Table 1). To test the interactive effects of NPP and human land-use activities with large carnivore presence, spline functions were estimated for each level of large carnivore presence, resulting in centred smooth terms (Wood, 2011). In total, data from 492 study sites across 28 European countries were included in the analyses (Figure 1). Exploratory analyses and model diagnostics were performed using the DHARMa (Hartig, 2020) and mgcv package (Wood, 2011) and can be found within Appendix S3. In addition, we tested the stability of our model by randomly deleting 10% of our data, which showed qualitatively similar results (Appendix S3: Table S7). Last, we tested the change in model deviance after removing single terms from the full model. 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). The results are presented in Table S9 within Appendix S3.

3 | RESULTS

Red deer density varied by over three orders of magnitude, between 0.03 and 44.6 individuals per 100 ha. Based on our analysis, 34% of the variance could be attributed to the included model predictors ($n=492$, adjusted $R^2=0.34$). Red deer density varied depending on large carnivore presence ($F_{5,448}=2.18$, $p=0.056$), as it was negatively associated with the presence of all three large carnivore species and tended to be higher at sites where lynx was the only large carnivore present (Appendix S2: Table S4; Figure 2). By contrast, no effect of wolf presence on red deer density was found, neither when it was present as the sole carnivore nor when it occurred in combination with lynx. Also the presence of bear in combination with lynx or wolf did not reduce red deer density (Appendix S2: Table S4). In the absence of large carnivore species, red deer density varied, albeit without a clear pattern, with NPP ($F_{6,448}=3.0$, $p=0.005$). By contrast, in the presence of all three large carnivores, red deer density linearly increased with NPP, but this was not significant (Table 2; Figure 3). In addition, no relation between red deer density and NPP was found for sites with either wolf, lynx, bear or a combination (Table 2). In contrast, red deer density was significantly higher at the 34 hunting-free sites (7% of all sites included) than at the sites where hunting took place ($F_{1,448}=23.1$, $p<0.001$; Figure 2). Moreover, at sites harbouring all three large carnivore species, red deer density increased linearly with the human influence index ($F_{1,448}=4.8$, $p=0.029$). A similar but nonsignificant relationship was found in areas without large carnivores ($F_{2.1,448}=2.6$, $p=0.080$; Figure 4). There was also no relation between red deer density and

FIGURE 1 Distribution of collected red deer population density as determined in a literature review (white dots, $n=492$), shown together with the current distribution of red deer in Europe (grey shaded, after Lovari et al., 2018).

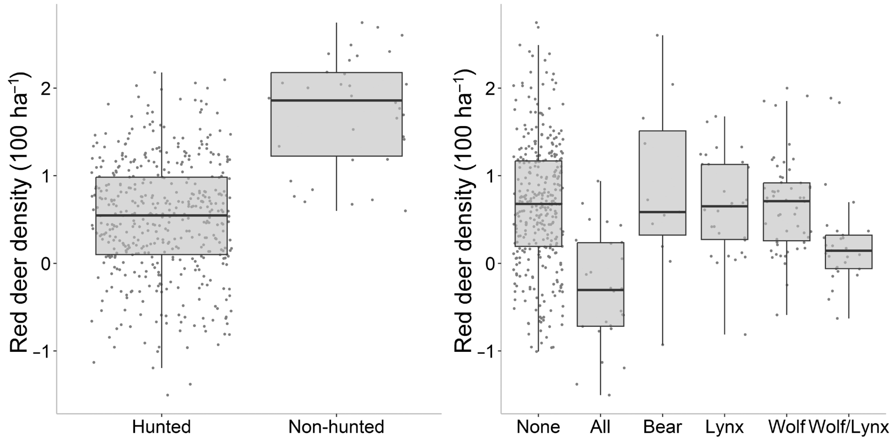

FIGURE 2 Plot of the generalized additive model predicting the effects of hunting and large carnivore presence on red deer density (*y*-axis; log-scale) across Europe. For each of these partial residuals are added (grey dots).

TABLE 2 Summary of the results of the generalized additive model predicting the (interactive) effects of multiple variables on red deer density across Europe.

Approximate significance of parametric coefficients		df	*F*-value	*p*-value
Hunting		**1**	**23.1**	**<0.001**
Predator presence		**5**	**2.18**	**0.056**
Site protection status		**2**	**5.32**	**0.005**
Approximate significance of smooth terms	**Edf**	**Res df**	***F*-value**	***p*-value**
HII × No predators	*2.11*	*2.71*	*2.59*	*0.080*
HII × All predators	**1.00**	**1.00**	**4.67**	**0.029**
HII × Bear	1.18	1.32	1.82	0.129
HII × Lynx only	1.63	2.03	0.60	0.538
HII × Wolf only	1.00	1.00	0.01	0.937
HII × Wolf/Lynx	1.00	1.00	0.80	0.373
NPP × No predators	**6.05**	**7.22**	**2.95**	**0.005**
NPP × All predators	1.00	1.00	2.52	0.113
NPP × Bear	1.44	1.75	0.32	0.770
NPP × Lynx only	2.56	3.12	1.57	0.191
NPP × Wolf only	3.99	4.78	1.51	0.131
NPP × Wolf/Lynx	1.00	1.00	0.00	0.966
Tree canopy cover	**2.48**	**3.16**	**4.40**	**0.004**
NDSI	**4.09**	**5.03**	**10.7**	**<0.001**
Palmer drought index	**4.45**	**5.47**	**4.01**	**0.001**

Note: HII refers to the human influence index, and × indicates a statistical interaction. Significant variables ($p<0.05$) are highlighted in bold and variables showing a trend ($p<0.1$) are italicized.
Abbreviations: edf, estimated degrees of freedom; NDSI, normalized difference snow index; NPP, net primary productivity; Res df, residual degrees of freedom.

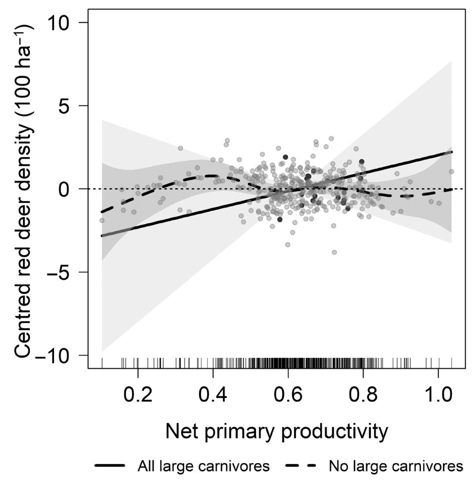

FIGURE 3 Plot of the generalized additive model predicting the effects of net primary productivity on red deer density (*y*-axis; log-scale) across Europe. Smooth functions were fit for sites with no large carnivores present (partial residuals; grey dots) and sites where all three carnivore species were present (partial residuals; black dots).

the human influence index at sites with different combinations of large carnivores (Table 2). Other factors related to environmental productivity, including winter severity, tree canopy cover and summer drought, influenced red deer density at a continental scale (Table 2). Specifically, red deer density was higher at sites with higher winter severity (NDSI), a higher forest cover and a higher Palmer drought severity index (i.e. wetter study sites; Table 2; Appendix S2: Figure S1). Finally, red deer density differed across sites and varied depending on the protection status of the site ($F_{2,448}=5.3$, $p=0.005$) with lower red deer density in non-protected compared to less strictly protected areas (Appendix S2: Table S4), but there was no difference between strictly protected and less strictly protected areas (Appendix S2: Table S4).

4 | DISCUSSION

Within this study, covering the entire distributional range of red deer across Europe, we found that the potential impact of large carnivores in reducing red deer density was only visible when multiple large carnivore species (wolf, lynx, bear) occurred. Furthermore, we found that red deer density, in the absence of large carnivores, did not increase with primary productivity and no significant effect of productivity could be observed at sites with large carnivores

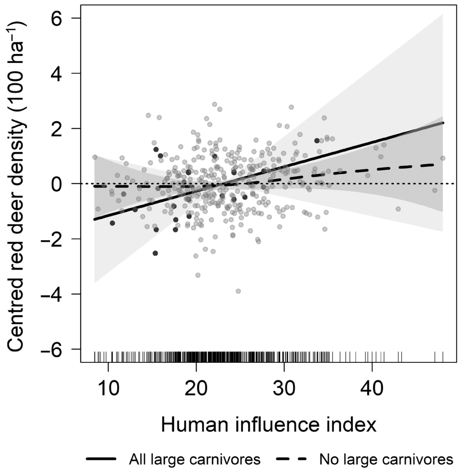

FIGURE 4 Plot of the generalized additive model predicting the effects of human influence index on red deer density (*y*-axis; log-scale) across Europe. Smooth functions were fit for sites with no large carnivores present (partial residuals; grey dots) and sites where all three carnivore species were present (partial residuals; black dots).

present. Instead, humans by means of hunting and land-use activities played a dominant role relative to large carnivores in influencing red deer density across human-dominated landscapes.

4.1 | Large carnivore impacts on red deer density across Europe

With the current return of large carnivores in Europe, there is an ongoing debate whether the effects of large carnivores in human-dominated landscapes can be large enough to impact their ungulate prey populations. Our study showed a lower red deer density at sites where all three large carnivores (wolf, lynx, bear) were present compared to sites where large carnivores were absent (in line with our prediction 1). Due to the small number of sites with bear, bear presence was represented in the categorical variable that included all large carnivores and a second variable describing the sites was only bear occurred or in combination with wolf or lynx. Consequently, the effect of bear as sole carnivore could not be disentangled from the combined effect of bear with wolf or lynx. However, our results also showed that in sites where only wolf or lynx (or a combination of both) occurred, red deer density was not significantly reduced. This indicates that neither large carnivore species alone or in combination with one other species is associated generally with a lower red deer density and only overall lower red deer density occurred when all three large carnivore species were present. This is in accordance with Melis et al. (2009) who showed that large carnivores can have additive effects and their combined effects on prey population sizes are stronger when multiple large carnivores are present. An underlying reason is that differences in selection of different age classes among large carnivore species create different impacts on cervid population sizes (Gaillard et al., 2000). Whereas wolves prey upon both fawns and adult red deer (Śmietana, 2005), red deer fawns are especially vulnerable to lynx predation (Heurich et al., 2016) and are also targeted by bear (Linnell et al., 1995). Besides, interactions between large carnivore species can alter their impact on prey populations. For example, bear can profit from the presence of other large carnivores, which provide increased scavenging opportunities, forcing wolves to kill more frequently (Elbroch et al., 2015; Krofel et al., 2012). However, other studies found that, in some areas, the presence of single or combinations of two large carnivore species are able to reduce red deer density (see e.g. Gazzola et al., 2005; Jędrzejewski et al., 2012). One potential reason for the slight variation in red deer density in relation to the presence of either one or more carnivore species is the variation that exists in carnivore density across sites. As large carnivores have been expanding and showing increasing numbers in Europe during the last decades (Chapron et al., 2014), the time since recolonization also adds to this variation. We are aware of these shortcomings of our large-scale, European-wide approach that aimed at finding general patterns in red deer density in relation to large carnivore presence. As reliable information on large carnivore density is unknown in many areas throughout Europe, we could not test for this on a European scale. We argue that this is an important topic to be addressed in future studies by including only a subset of areas with reliable estimates of carnivore density and including the time since large carnivore species have recolonized each area allowing them to exert their ecological impacts on prey species.

Furthermore, at sites with no large carnivores present, red deer density significantly varied with NPP, albeit without a clear pattern. In contrast, there was a trend of red deer density to linearly increase with productivity at sites with all three large carnivores present suggesting a stronger reduction of deer density at sites of lower productivity (prediction 2), but this was not statistically significant. In addition, no effect of wolf nor lynx was found, neither as the sole carnivore nor in combination. In comparison, both Jędrzejewska et al. (1997) and Melis et al. (2009) found significantly larger effects of large carnivores in regions and periods with low vegetation productivity and harsh winters, showing that the percentage of predation is inversely density dependent (see Messier, 1995). Besides a lack of effect of large carnivores on deer density at sites with lower productivity, we found, in contrast to Melis et al. (2009), an increase, rather than a decrease in red deer density with increasing winter severity (measured as snow cover duration). In their study, Melis et al. (2009) focused on roe deer density, which compared to red deer are more sensitive to adverse environmental conditions, such as high snow cover, due to its small body size, meagre fat reserves and its being an income breeder (Apollonio et al., 2020). All of this increases the energetic costs of movement, reduces forage availability and may result in a higher predator hunting success (Grøtan et al., 2005; Holand et al., 1998). Additionally, although not directly tested in this study, supplementary winter feeding is a common practice throughout Europe where red deer are fed in nearly all countries within Europe (Gill, 1990; as cited in Putman & Staines, 2004). Though, within this study, the increasing deer numbers with winter severity can likely be

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explained by the fact that at five of the nine study sites with summed daily NDSI values >45,000 (i.e. higher number of days with snow cover) hunting was not allowed, which led to a high red deer density.

Finally, our study was based on available red deer density estimates in peer-reviewed and grey literature. These densities were derived with a large variation in methods (12 different methods were recorded), including aerial counts, drive census, harvest numbers etc., which are known to have varying levels of precision. In most cases, the exact method used per area for estimating red deer numbers could not be obtained from the literature from 310 of the 492 study sites. This did not allow us to consider the method of density estimation in our models as was done by Melis et al. (2009) for roe deer. We acknowledge that the method and scale at which red deer density are estimated can influence density estimates (Keiter et al., 2017). Consequently, to check the validity of our results, we randomly increased or decreased our density estimates by 60% (Ahrestani et al., 2013; Murphy et al., 2022) and obtained qualitatively similar results (Appendix S3: Table S8). Consequently, we argue that the four orders of magnitude of differences in red deer density recorded within our large-scale study covering 492 study sites across Europe (i.e. between 0.03 and 44.6 individuals per 100 ha) is unlikely explained by the substantial yet much smaller differences observed between different methods of density estimation.

4.2 | Human impacts on red deer density across Europe

In support of our third prediction, our study revealed that hunting by humans creates strong top-down effects on red deer density. This result is in line with other studies showing that hunting by humans is often the predominant cause of mortality for wild ungulates in Europe (Apollonio et al., 2010), resulting from active ungulate management with the aim of reducing browsing damage in forests and agricultural lands (Hothorn & Müller, 2010). In our study, information on differences between areas in actual hunting intensity and hunting method was not available from the literature and consequently its influence on red deer density or in combination with large carnivore presence could not be tested. We could only add hunting as a binary variable, with hunting reported for 93% (458/492) of the study sites. This shows that almost all red deer populations occurring in European areas are confronted with active (hunting) management. This finding is in line with a previous study, which found that ungulate populations are even regulated in the majority of European national parks (67.9% of 209 national parks; van Beeck Calkoen et al., 2020). These human effects were likely also reflected in our results on area protectiveness, which showed a lower red deer density in non-protected areas than in less strictly protected areas, whereas no difference in red deer density was found between less strictly and strictly protected areas. Besides a certain degree of hunting by humans occurring in the majority of strictly protected areas, an area may be strictly protected for reasons other than its ecological importance (Joppa & Pfaff, 2009), or it may be too small to maintain viable populations (such as when large carnivores commonly occur outside the area) (Rodrigues et al., 2004; Watson et al., 2014). Both the occurrence of hunting and the locality could explain the lack of a significant difference in red deer density between strictly protected and less strictly protected areas.

Additionally, we found that red deer density increased with human land-use activities at sites regardless of the presence or absence of large carnivores (although not statistically significant for sites where large carnivores were absent). The human influence index is a measure of human land-use activities that include infrastructure, built-up areas and land-use and thus serves as a proxy for the effects of human activities on the resource landscape. Human land-use activities can support increases in ungulate population density, by positively contributing to forage biomass and productivity through, that is, forage crop production, forestry and an increase in pasture land (Haberl et al., 2007; Muhly et al., 2013). This has raised concerns over the cascading impact of ungulates on the vegetation (Côté et al., 2004; Demarais et al., 2012) and the spread of diseases (Gortázar et al., 2007) such that strong hunting pressure is often considered necessary.

4.3 | Implications for the functional role of large carnivores in human-dominated landscapes

Human activities can in a variety of ways modify, and often reduce, the ecological role that large carnivores play (Kuijper et al., 2016). Also, in our study, we found that red deer density was more strongly limited by large carnivores at sites with lower human land-use activities, in line with our fourth prediction. Within Europe, large carnivores increasingly occur in human-dominated landscapes (Chapron et al., 2014), leading to perceived competition for game between hunters and large carnivores, increased depredation of livestock and concerns regarding human safety (Khorozyan & Heurich, 2022; Kuijper et al., 2019). Although most large carnivore species are now legally protected, multiple European studies have documented the extent of human-caused mortality in different large carnivore species, with poaching and vehicular collisions accounting for up to 46% of the total mortality (Andrén et al., 2006; Heurich et al., 2018; Liberg et al., 2012; Sunde et al., 2021). In Yellowstone National Park (USA), however, where density-dependent intraspecific aggression is the major driver of wolf mortality (Cubaynes et al., 2014), studies have found that the numerical responses of wolves were shown to reduce ungulate prey populations (White & Garrott, 2005). Even though we could not directly test differences in large carnivore density with varying degrees of human activities within this study, the reductions in large carnivore populations by human-caused mortality observed in different areas across Europe can strongly influence the ecological impacts of large carnivores on ecosystem functioning (see Kuijper et al., 2019).

In a recent study, Cretois et al. (2021) showed that the human footprint is a poor predictors of species distribution within Europe.

In comparison, our study showed that human activities (i.e. hunting, land-use activities) are the main drivers of red deer population density observed across Europe. This indicates that, not red deer distribution but rather their abundance is affected by human activities. In most areas, the presence of only wolf, wolf and lynx or a combination with bear presence did not suffice to exert numeric effects on red deer density. A reduction in deer density was only found when all species of large carnivores (wolf, lynx, bear) were present or in the least human-impacted areas with lowest human influence index. Important to emphasize is that we found a large variation between areas indicating that even the presence of a single carnivore species under certain conditions may lead to significant reductions in red deer density. This indicates that there is a high level of context dependency in the impacts of large carnivores on prey populations. This context dependency has already been illustrated in several studies from more natural, less human-disturbed areas, but is expected to be even more pronounced in more human-dominated landscapes (see Haswell et al., 2017). In these systems, humans will modify large carnivore impacts in a variety of ways (see Kuijper et al., 2016). Rather than studying whether large carnivores exert ecosystem impacts in human-dominated landscapes, we argue that understanding under what conditions they can exert their impact, hence to focus on this context dependency, would be a highly recommended direction for future studies.

4.4 | Management implications

A better understanding of the context dependency of large carnivore impacts would also facilitate steps how to restore the ecological role of large carnivores. Looking at the results of the current study already highlights that the overruling human impacts may prevent large carnivores to exert their impact on prey species. A lack or limited extent of numeric effects found in our study does not rule out that large carnivores can influence ecosystem functioning in human-dominated landscapes. As large carnivores, with special reference to wolves, are quickly increasing in Europe and their number is far from being stabilized, their impact on their prey may therefore become greater in the next decades and can potentially change predator–prey relationships. Besides these density-mediated impacts on ungulate prey species, several studies have demonstrated the importance of the behaviourally mediated effects on ungulate prey species and mesocarnivores induced by the presence and patterns of space use of large carnivores, which also occur in human-dominated landscapes of Europe (Bubnicki et al., 2019; Diserens et al., 2021; Kuijper et al., 2014; Sunde et al., 2022; van Beeck Calkoen et al., 2021; Wikenros et al., 2017).

While our study and also other studies found that humans often outweigh the effects of large carnivores on ungulate prey populations in highly human-dominated landscapes (i.e. see Kuijper et al., 2019), we also showed that large carnivores can exert numeric effects on prey populations under certain conditions. As human influences are omnipresent in Europe and their impact outweighs the impact of large carnivores, the functional role of large carnivores in affecting prey population size is strongly overruled by humans. These findings suggest that when we would like large carnivores to exert numeric effects, we should focus on minimizing human impacts to allow the ecological impacts of large carnivores on ecosystem functioning.

AUTHOR CONTRIBUTIONS

Suzanne T. S. van Beeck Calkoen, Marco Apollonio and Marco Heurich conceived the ideas and designed methodology. Lena Blondel conducted the literature search. Suzanne T. S. van Beeck Calkoen conducted the spatial analyses and applied the statistical methods to analyse the data. Validation of the research outputs was conducted by Carsten F. Dormann, Dries P. J. Kuijper, Ilse Storch and Marco Heurich. Suzanne T. S. van Beeck Calkoen prepared the initial draft, which was reviewed by Dries P. J. Kuijper, Marco Apollonio, Carsten F. Dormann, Ilse Storch and Marco Heurich. Supervision of the project was conducted by Marco Heurich. Management and coordination responsibility for the research activity planning and execution was performed by Suzanne T. S. van Beeck Calkoen. Marco Heurich and Suzanne T. S. van Beeck Calkoen were both responsible for the acquisition of the financial support for the project leading to this publication. All authors gave their final approval.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.0cfxpnw7w (van Beeck Calkoen et al., 2023). In addition, data are available at Github (github.com/SuzannevBC/RedDeer_density_Europe).

ORCID

Suzanne T. S. van Beeck Calkoen https://orcid.org/0000-0002-2574-9056
Dries P. J. Kuijper https://orcid.org/0000-0002-0324-5893
Marco Apollonio https://orcid.org/0000-0002-8953-9138
Carsten F. Dormann https://orcid.org/0000-0002-9835-1794
Ilse Storch https://orcid.org/0000-0002-3252-2036
Marco Heurich https://orcid.org/0000-0003-0051-2930

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Material and methods.

Appendix S2: Results.

Appendix S3: Premodelling exploratory analyses.

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