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ARTICLE

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Humans rather than Eurasian lynx (*Lynx lynx*) shape ungulate browsing patterns in a temperate forest

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Abstract

The recolonization of human-dominated landscapes by large carnivores has been followed with considerable scientific interest; however, little is known about their interactive effect on ungulate foraging behavior. This study compared the risks imposed by humans and lynx on ungulate foraging behavior by examining the effects of browsing intensity (at two spatial scales), diet quality, and tree species selection. We hypothesized that: (1) in areas with high risk imposed by humans and lynx browsing intensity would be reduced; (2) risk effects would interact with habitat visibility at a fine scale, resulting in contrasting browsing patterns in response to humans versus lynx risk; (3) ungulates compensate for the higher costs incurred in high-risk areas by switching to a higher diet quality, and (4) browse a higher proportion of more-preferred tree species. These hypotheses were tested by measuring browsing intensity along 48 transects located at different distances from human settlements within the hunted and nonhunted areas of the Bavarian Forest. Dung samples were collected and analyzed as a proxy of diet quality (C:N ratio, fiber). The spatial patterns of browsing intensity, diet quality, and tree species selection were then linked to lynx risk, hunting intensity, recreation intensity, and distance to human settlements. Our results showed that (1) browsing intensity strongly decreased with increasing recreational activities, whereas it increased with lynx risk; (2) only in close proximity to human settlements tree browsing was higher in dense habitats and (3) a higher diet quality was obtained. (4) We found a stronger avoidance of the less preferred tree species in high-hunting intensity areas. In conclusion, our results indicate that the risk effects of human activities outweigh those of a natural large carnivore. Thus, highlighting the importance of taking those activities into account in predicting the impacts of large carnivores on ungulates and their plant-food choices.

Dries P. J. Kuijper and Marco Heurich contributed equally to this work as senior scientists.

KEYWORDS
ambush predator, browsing intensity, diet quality, diet selection, human activities, hunting, predation risk, recreation

INTRODUCTION

The "landscape of fear" concept, which describes the variation in perceived predation risk and its consequence for prey behavior and ecosystem functioning, is often applied as a framework in ecological studies (Brown et al., 1999; Brown & Kotler, 2004; Gaynor et al., 2019). Predation risk varies spatially or temporally (Creel et al., 2008; Kohl et al., 2018; Palmer et al., 2017; Tolon et al., 2009), with prey typically facing a trade-off between risk avoidance and food acquisition (Brown & Kotler, 2004; Lima & Dill, 1990; McArthur et al., 2014). In the case of ungulate prey species, their response to their large carnivore predators may include changing their spatial use and activity patterns (Bonnot et al., 2020; Kuijper et al., 2015; Latombe et al., 2014; Lima & Dill, 1990; Valeix et al., 2009), increasing their vigilance and/or group size (Brown, 1999; Delm, 1990; Périquet et al., 2010) or changing the composition of their diet (Churski et al., 2021). However, the extent to which these adopted behaviors in prey species trickle down to the plant level is unclear (Ford & Goheen, 2015).

Most knowledge on large carnivore–ungulate interactions has been obtained in studies conducted in large national parks in North America, where human influence is minimal (Kuijper et al., 2016). In Europe, where large carnivores were long ago extirpated from most human-dominated landscapes, programs supporting their natural recolonization or reintroduction (Chapron et al., 2014) have led to an increasing overlap between the habitats of humans and those of large carnivores. Consequently, human activities have come to play a key role in shaping the complex interactions of carnivores and their prey (Kuijper et al., 2016). For ungulate prey species in Europe, the dominant cause of mortality is hunting, conducted as a management effort to reduce human–wildlife conflicts or to prevent the spread of diseases (Apollonio et al., 2010). In addition to its lethal effects, hunting creates behavioral responses in ungulates (Lone et al., 2015, 2017; Proffitt et al., 2009). Besides, recreational activities such as (off-road) hiking, mountain-biking, and trail running are becoming increasingly popular in natural areas (Cordell, 2012; Manning et al., 2017; Vallecillo et al., 2019). All these human activities influence ungulate behavior including an increase in flight responses (Stankowich, 2008), shifting activity patterns (Bonnot et al., 2020), and changes in habitat selection (Dupke et al., 2017; Pelletier, 2014; Saïd et al., 2012) or spatiotemporal behavior (Coppes et al., 2017; Westekemper et al., 2018). Despite the impact of humans on large carnivore populations and ungulate behavior, few studies have been conducted in Europe on the compound effects of humans and large carnivores on their ungulate prey (Kuijper et al., 2016).

Among the factors that shape the behavioral responses of prey species are the spatial patterns of risk and perception of the areal cues that indicate an elevated risk (Gaynor et al., 2019). Since large carnivores such as lynx (*Lynx lynx*) and wolf (*Canis lupus*) tend to avoid areas of the landscape containing human settlements or hosting human activities (Carricondo-Sanchez et al., 2020; Filla et al., 2017; Sazatornil et al., 2016), ungulates may be trapped between the risk imposed by human activities in one part of the landscape and that imposed by large carnivores in another part of that same landscape (Lone et al., 2014). However, as "super predators" (Darimont et al., 2015), humans are likely to evoke behavioral responses in ungulates that are stronger than those induced by large carnivores (Bonnot et al., 2020; Ciuti et al., 2012; Proffitt et al., 2009). Moreover, risk effects are often context-dependent and linked to environmental factors (Kauffman et al., 2007; Kuijper et al., 2015), which can modify the risk associated with humans and large carnivores. Thus, for ungulate prey species, a choice must often be made between open areas, where hunting activities concentrate, and dense habitats, whereas ambush predators such as lynx pose a higher risk (Lone et al., 2014; Norum et al., 2015; Proffitt et al., 2009; Sih et al., 1998).

The antipredator responses of ungulates can affect their foraging behavior at different spatial scales (Brown & Kotler, 2004; Preisser et al., 2005). On a landscape scale, the spatial needs of large carnivores can influence the spatial distribution of their prey (e.g., Bubnicki et al., 2019; Thaker et al., 2011) such that browsing intensity is reduced in areas of the landscape where large carnivore activity is high (Kuijper et al., 2013). At finer spatial scales, prey behavior and browsing intensity may be affected by specific habitat features that limit visibility or possible escape options (Halofsky & Ripple, 2008; van Ginkel et al., 2019). These behavioral changes may result in a lower diet quality, which suggests that, among other factors, the ungulate diet is shaped by predation risk (Barnier et al., 2014; Christianson & Creel, 2010; Edwards, 1983; Hernández & Laundré, 2005; Mech, 1995; Stephens & Peterson, 1984). A similar conclusion regarding the relationship between food-plant quality and risk effects was reached in experimental studies of marsupials, whose food intake was higher in

risky, but higher-quality food patches (McArthur et al., 2012; Nersesian et al., 2011). Thus, in a heterogeneous landscape of food and fear, food quality and predation risk are intertwined (McArthur et al., 2014). In the case of ungulates, avoiding a higher predation risk could necessitate habitat shifts that result in a lower diet quality; conversely, the nutritional benefits of foraging in high-quality food patches may outweigh the costs associated with a higher predation risk (Schmidt & Kuijper, 2015). However, whether ungulates actively choose to compensate for the costs of antipredator behavior by increasing their diet quality, such as by selecting a higher proportion of more palatable food items, has rarely been tested (but see van Beeck Calkoen et al., 2021).

In this study, we investigated whether perceived risk effects created by humans and lynx influence ungulate foraging behavior. Specifically, we tested the changes in browsing intensity (analyzed at two spatial scales), diet quality, and food-item selection of ungulate foraging in a lynx/human predator system. We hypothesized that: (1) on the landscape scale, overall browsing intensity will be reduced in areas with a high perceived risk imposed by humans or lynx; (2) on a fine scale, the interaction of risk effects with habitat visibility will result in contrasting patterns, with the lowest browsing intensity occurring in association with low visibility in high lynx-risk areas and with high visibility in high human-risk areas; (3) to compensate for the higher costs of predation risk, whether that of lynx or of humans, within food patches with a higher perceived risk, ungulates will select a higher overall diet quality; and (4) therefore browse a higher proportion of more-preferred tree species.

METHODS

Study area

The study was conducted in the Bavarian Forest National Park (BFNP; 242 km^2, 49°3′19″N, 13°12′9″E) and the adjacent state forest enterprise Neureichenau (SFEN; 185 km^2), together referred to in this study as the Bavarian Forest. This mountainous area (300–1453 m above sea level) borders the Czech Republic and hosts a wide range of recreational activities enjoyed by ~1.3 million visitors each year (Arnberger et al., 2016). The main tree species within the Bavarian Forest are Norway spruce (*Picea abies*), silver fir (*Abies alba*) and, European beech (*Fagus sylvatica*), with rowan (*Sorbus aucuparia*), sycamore maple (*Acer pseudoplatanus*), and birch (*Betula pendula*, *Betula pubescens*; Bayerische Staatsforsten, 2018; Cailleret et al., 2014) also present in abundance. Lynx is the main predator species in the area, with 1–2 lynx/100 km^2 in the BFNP (Heurich et al., 2015; Palmero et al., 2021). In 2015, a wolf pair became established in the area and in 2017, the first wolf pack since 1846 was confirmed. At the time of the study, the wolf pack's territory was mostly situated on the Czech side of the BFNP and did not include our study location. The most common ungulate species in the study area are roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). Although precise estimates of roe deer and red deer densities are lacking, camera trapping rates from a total of 139 camera traps deployed in the BFNP (90 cameras) and the SFEN (49 cameras) for more than 12 months in 2018/2019 showed 4.5 to 2-fold higher trapping rates for red deer (BFNP: 7.2 events/100 days; SFEN: 5.3 events/100 days) compared to roe deer (BFNP: 1.6 events/100 days; SFEN: 2.6 events/100 days), for the BFNP and SFEN respectively (Henrich et al., 2021).

Within the buffer zone of the BFNP, ungulate management in the form of hunting is conducted every year during predefined hunting seasons to reduce the impacts on forest regeneration and to mitigate conflicts with adjacent privately owned commercial forests and agricultural areas. Red deer populations are controlled mainly within the park's winter enclosures (accounting for ~66% of the total number of red deer shot per year) but also from hunting blinds (~33% of shot red deer). Within the BFNP, an average of 117 red deer were shot each year between 2000 and 2018 (Bavarian Forest National Park, unpublished data), or 0.43 red deer/km^2 during the 2018/2019 hunting season (Henrich et al., 2021), and an average of 93 roe deer between 2000 and 2012 (Bavarian Forest National Park, unpublished data). With the reestablishment of lynx in the BFNP in the 1980s, by 2012 roe deer populations no longer required human control. Available evidence suggests that current roe deer mortality rates are likely similar to those prior to the reestablishment of lynx and the cessation of roe deer management (Heurich et al., 2012). Within the adjacent SFEN, red deer, roe deer, and wild boar are hunted each year, mostly from hunting blinds (accounting for 80% of the animals shot), followed by drive hunts (15%) and stalking (5%; Bayerische Staatsforsten, n.d.). There is no culling within the SFEN's winter enclosures. During the 2016/2017 hunting season, 179 red deer and 335 roe deer were shot, and during the 2018/2019 hunting season 0.53 red deer/km^2 (Henrich et al., 2021). Similar to the BFNP, all hunting in the SFEN takes place during predefined hunting seasons (Bayerischen Jagdverband, n.d.).

Study design

Transect placement

The impact of the perceived risk effects of lynx and humans on ungulate foraging behavior was studied along

48,100-m-long transects (Figure 1). All transects were located within young regeneration stands, where trees smaller than the ungulate browsing line (<230 cm; Nichols et al., 2015) covered at least 60% of the transects and where the majority of trees were accessible to both roe deer and red deer (i.e., average tree height ~100 cm). Half of the transects were set within the BFNP and half in the adjacent SFEN (all hunted). Four transects inside the BFNP were situated within wildlife management zones, resulting in 20 transects in nonhunted areas and 28 transects in hunted areas. Because large carnivores avoid areas of high human activity and change their activity patterns in response to them (Filla et al., 2017; Ordiz et al., 2011; Rogala et al., 2011; Theuerkauf et al., 2003; Wam et al., 2012), the transects were placed at different distances from human settlements (Table 1). Furthermore, all transects were located at least 50 m away from roads (primary roads, forest roads, and walking paths), to minimize their disturbance on predator and prey behaviors (Kaartinen et al., 2005; Whittington et al., 2011; Zimmermann et al., 2014). Even though, especially for red deer, annual home ranges are generally large within our study area, they show a great overlap between different individuals (Henrich et al., 2021). To reduce the probability of the same individual deer visiting different transects, while accounting for all the above-described prerequisites, the transects were separated from each other by a minimum distance of 500 m.

Quantifying browsing intensity, diet quality, and tree species selection

Field measurements along each transect were conducted during the hunting season between 19 October 2017 and 17 November 2017. The 100-m-long transects consisted of 10 equally spaced plots of 5 × 1 m. For each tree within a plot, its height and species were recorded; however, since four tree species (European beech, rowan, Norway spruce, and silver fir) comprised >95% of all trees recorded, only these species were analyzed further. Browsing was measured by recording both the browsing of the current year's apical shoot (apical browsing: yes/no) and the proportion (number) of the top 10 lateral shoots browsed (lateral browsing), following Kuijper et al. (2013). Browsing intensity was determined based on the total number of shoots browsed (lateral and apical) compared to the total number of available shoots measured per tree (maximum: 11). The tree density of each plot was calculated by dividing the total number of trees within a plot by the plot area. The influence of habitat structure on the perceived predation risk, for example, predator detection, prey escape, and ambush opportunities for predators, was taken into account by measuring the average habitat visibility (Podgórski et al., 2008). Thus, the distance from the middle of the plot to the closest object (rocks, fallen trees, bushes, or standing trees) obstructing the view along a straight line was measured at a height of 125 and 160 cm (corresponding to the average heights of roe and red deer) for every 45° using a Bushnell Scout DX1000 ARC rangefinder.

As a proxy of diet quality, fresh dung pellet groups (intact surface without fungus) of roe deer and red deer found within a 150-m buffer along the transects were collected and analyzed for their carbon (C)/nitrogen (N) ratio, acid detergent fiber (ADF)/neutral detergent fiber (NDF) ratio, and their lignin content. The pellet groups were frozen at −25°C and shipped on dry ice to our laboratory for chemical analyses. Their C and N contents were determined in an EA 1110 Elemental Analyzer using the Dumas method (Dumas, 1831), and their ADF, NDF, and lignin contents using the procedure developed by Van Soest and Wine (1968).

To test if ungulate selection toward different tree species varied between areas differing in (perceived) risk of lynx predation or human activities (hypothesis 4), tree species were divided into "preferred" and "less preferred" groups. To define these groups, the Jacobs selectivity index (Jacobs, 1974) was calculated for each tree species measured within each 100-m-long transect, based on the total number of shoots browsed relative to its availability. The index is calculated as: $D = (r - p)/(r + p - 2rp)$, where r is the proportion of a particular species browsed relative to all browsed trees within a transect and p is the proportion of that species relative to all trees within that transect (Jacobs, 1974; Kauhala & Auttila, 2010). Absolute avoidance of a tree species is indicated by $D = -1$, the selection of a tree species in proportion to its availability by $D = 0$ and an absolute preference for a tree species by $D = 1$. Consequently, tree species with a Jacobs index >0 were categorized as more preferred, and those with an index of <0 as less preferred.

Explanatory variables

Human and lynx risk factors

The effects of lynx or human activities on ungulate browsing intensity, diet quality, and tree species selection were assessed using a lynx habitat suitability map, created as a proxy for lynx risk, and (raster) datasets on hunting intensity, recreation intensity, and distance to human settlements (together referred to as human activities), all of which potentially influence ungulate foraging behavior. All spatial analyses were conducted in R (R Core Team, 2020) using the packages rgeos (Bivand & Rundel, 2020), raster (Hijmans, 2020), and dismo (Hijmans et al., 2020).

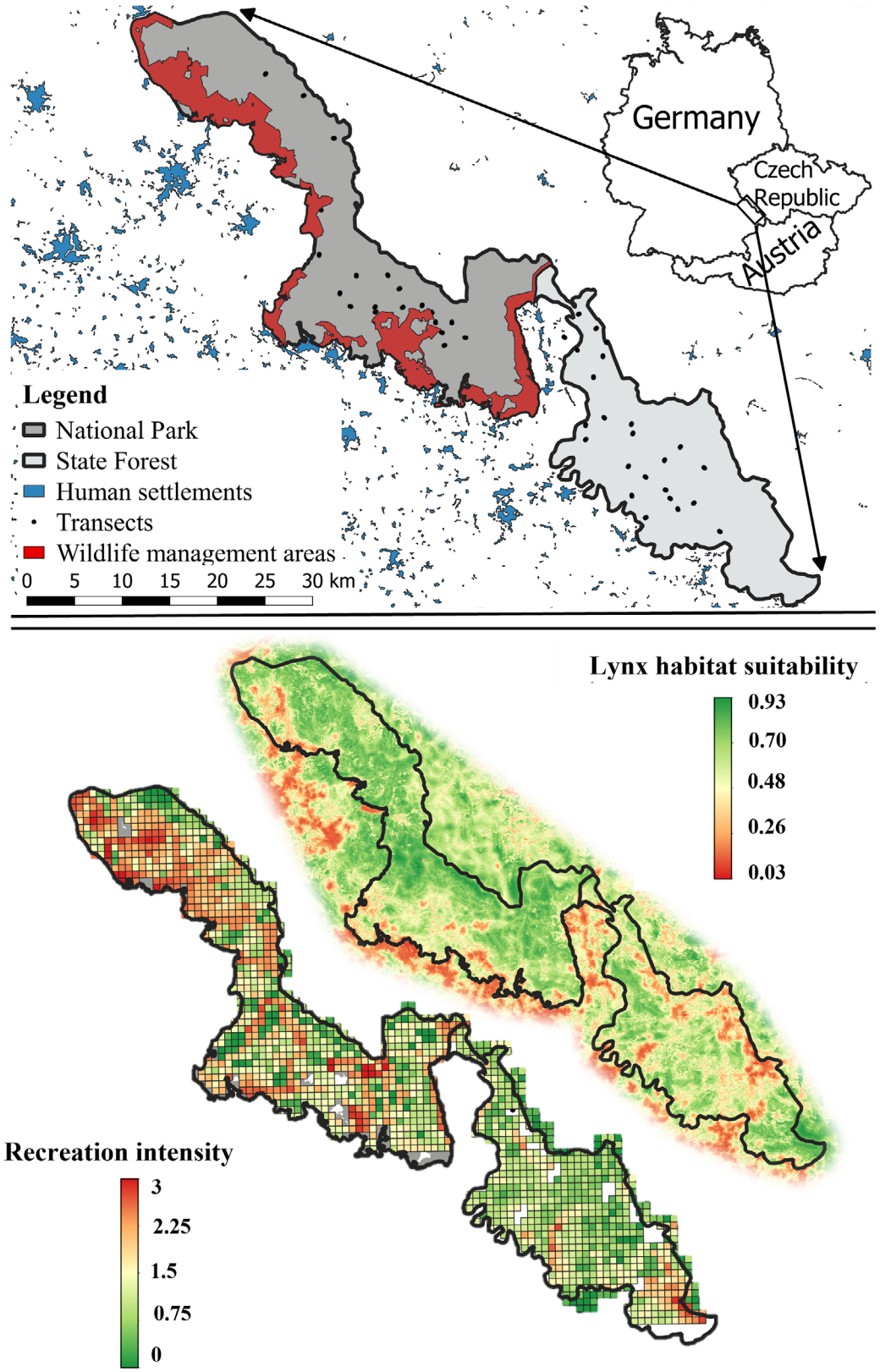


FIGURE 1 Top: transects within the Bavarian Forest. The black dots represent the 48 transects placed within the Bavarian Forest National Park (BFNP; dark gray; $n = 24$) and the adjacent state forest (SFEN: light gray; $n = 24$). The red zones within the BFNP represent wildlife management areas where red deer are hunted; in other parts of the BFNP hunting is prohibited. In the SFEN, hunting of roe deer and red deer is not restricted to specific areas and hence occurs across the entire area. The blue areas represent surrounding human settlements (>3000 m^2 built-up area). Bottom: Lynx risk and recreational intensity in the study area. Lynx habitat suitability values reflect the relative rate of lynx occurrence where higher suitability values correspond to a higher perceived predation risk for ungulates. For recreation intensity, higher values represent a stronger and more regular recreation activity

TABLE 1 Characteristics of the studied locations in hunted and nonhunted areas within the Bavarian Forest

Variable	Nonhunted	Hunted
No. transects measured	20	28
No. trees measured	2230	3546
Trees with at least one apical/lateral shoot browsed (%)	51.3	42.4
Trees with apical shoot browsing (%)	18.2	12.3
Average proportion of browsing per tree	0.23	0.16
Browsing intensity (%, no. browsed/no. total)		
European beech	76.3	63.9
	1022/1340	1059/1658
Rowan	100	88.5
	26/26	392/443
Silver fir	39.2	18.4
	20/51	19/103
Norway spruce	9.5	2.4
	77/813	32/1342
Lynx risk (0–1)	0.71 ± 0.09	0.65 ± 0.1
Hunting intensity (avg. distance to closest 10 cull locations, in m)	1095–4422	329–3440
Recreation intensity (0–3)	1.5 ± 0.6	1 ± 0.7
Distance to human settlements (m)	392–3799	246–3660
Avg. habitat visibility (m)	11.5 ± 6	15.1 ± 7.4
Avg. tree density (no. trees/m^2)	4.7 ± 2.5	6.8 ± 5.4
Avg. tree height (cm)	90 ± 46	93 ± 48
Solar radiation (kWh/m^2)	10,368–24,034	9671–21,968

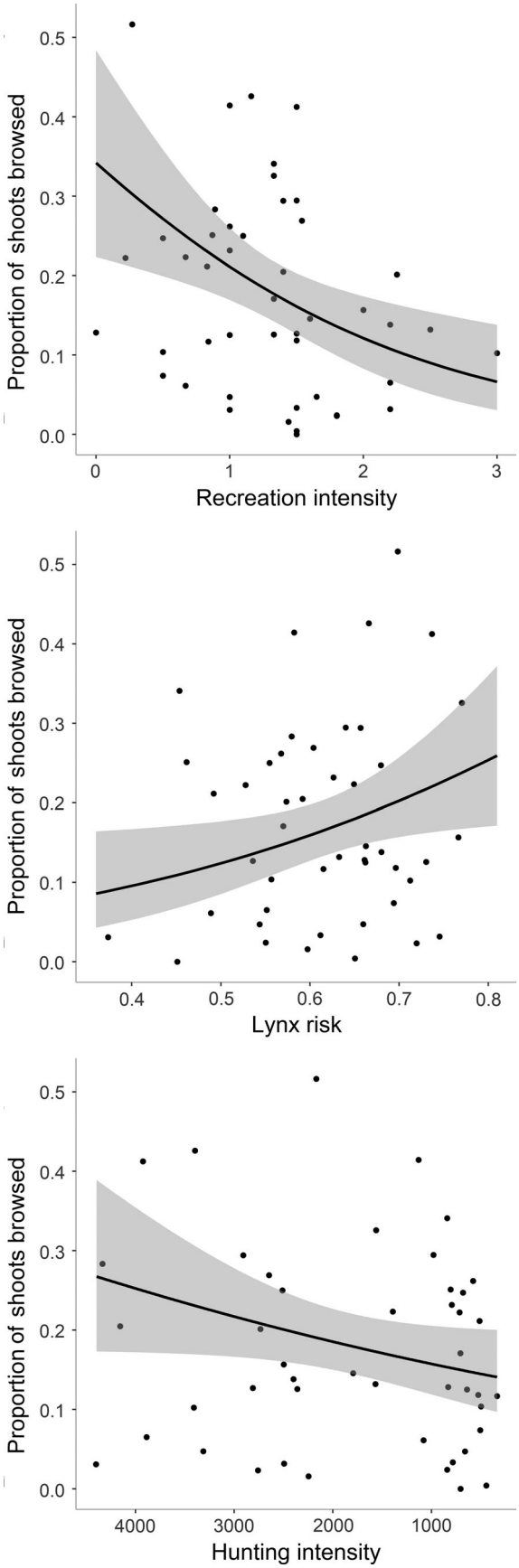
Note: The four tree species comprised >95% of all trees measured. Lynx risk represented the average lynx habitat suitability values ranging from 0 to 1 where higher values correspond to higher predation risk; hunting intensity was based on the average distance to the closest 10 cull locations, with smaller distances representing a higher hunting intensity. For recreation intensity, the median value of all expert assessments (0–3) with the median absolute deviation is presented, with higher values representing strong/typical recreation activity.

Habitat suitability for lynx was mapped at a 30-m spatial resolution using the Maxent algorithm (Phillips et al., 2006) based on a total of 3679 lynx locations collected through GPS telemetry (2005–2012) from nine lynx individuals (four females and five males). As lynx activity is lowest during the day and highest at night, with peaks at twilight, in accordance with the hunting behavior of these animals (Heurich et al., 2014), only the nighttime positions of lynx were used to map the lynx risk. Based on previous studies of lynx habitat use and habitat suitability modeling, 15 environmental predictor variables were selected for inclusion (Filla et al., 2017; Magg et al., 2015; Oeser et al., 2019; Schadt et al., 2002). Habitat suitability for 2017 (i.e., the year of field sampling) was predicted using remotely sensed environmental variables calculated for the same year. As the habitat suitability values predicted by Maxent (ranging from 0 to 1) reflect the relative rate of lynx occurrence (Merow et al., 2013), higher suitability values correspond to a higher predation risk for ungulates (Figure 1). Lynx habitat suitability values were extracted for each plot within a transect and using the locations where dung samples were collected (referred to in the following as areas of lynx risk). A detailed description of our modeling approach is provided in Appendix S1.

The influence of human hunting on red deer and roe deer foraging behavior was assessed using a hunting intensity variable derived from hunting data for the period between April 2016 and March 2018. For each transect plot and dung sample location, the average distance to the closest 10 cull locations was calculated. For the SFEN, the coordinates and the culled species were recorded whereas within the BFNP data were available only for the number of red deer individuals shot within a district encompassed by the wildlife management area (average size of 59 ha), such that the center point of each district was used.

An overview of recreation intensity in the study area was obtained by preparing maps with a grid of 500 × 500 m covering both the BFNP and the SFEN. For each grid cell, recreation intensity was rated based on direct enquiries of rangers, foresters, and hunters (see Rösner et al., 2014 for details) and using the following scoring system within a range 0–3: 0 = almost no activities, 1 = low activity, that is, use of very small paths or occasional (illegal) off-trail walking; 2 = medium activity, that is, moderate use of hiking routes and trails and 3 = intense and regular activities, including large parking places and forest roads. For each grid cell, the mean value of the assessments was calculated (Figure 1) and then extracted for each plot on the transect and to each dung sample location.

The average distance of each transect to human settlements was also calculated. Single features of buildings in the study area were downloaded from OpenStreetMap (Haklay & Weber, 2008) and then aggregated within ArcGIS 10.5.1. Areas of human settlements were defined by filtering the data for artificial surfaces >3000 m^2, with a maximum of 100 m between buildings in order to include all human settlements surrounding the area. The minimum distance of each



plot within a transect and each dung sample location to the human settlements were then determined.

Statistical analyses

Ungulate browsing intensity

At the landscape scale, we tested if the proportion of browsed shoots between transects was more strongly influenced by lynx risk or by human activities (hypothesis 1). This was assessed by determining the number of shoots browsed versus the total number of shoots available for all trees in a transect and then relating the resulting proportion (dependent variable) to the average predicted lynx risk, hunting intensity, recreation intensity, and distance to human settlements within that transect (explanatory variables). To test this, a generalized linear model (GLM) with a β-binomial family (link = "logit") was used (glmmTMB package: Brooks et al., 2017).

At the fine scale, we examined whether browsing on a single tree was differentially altered by the interaction of the perceived risk effects imposed by lynx and humans with habitat visibility (hypothesis 2) by fitting a GLMM with a β-binomial family (link = "logit") (glmmTMB package; Brooks et al., 2017) in which the proportion of shoots browsed for each tree individual was the response variable. Four interactions with habitat visibility (at roe deer and red deer height) were tested: (1) lynx risk, (2) hunting intensity, (3) recreation intensity, and (4) distance to human settlements. The variables tree height, tree density, elevation, and solar radiation (as a measure of light availability as a possible confounding factor affecting chemical composition; Molvar et al., 1993; Modrý et al., 2004) were also added to the model. All variables were mean-centered and scaled. A categorical variable differentiating between the four tree species (European beech, rowan, Norway spruce, and silver fir) was added as an independent variable. Potential differences between transects and plots were accounted for by the inclusion of both as nested random intercepts.

FIGURE 2 Plots of the generalized linear model predicting browsing intensity at the landscape scale (the proportion of shoots browsed within a transect) (*y*-axis) as a function of recreation intensity, lynx risk (i.e., relative rate of lynx occurrence), and hunting intensity. Hunting intensity is measured as the average distance to the closest 10 cull sites, with smaller distances representing a higher hunting intensity. The shaded areas indicate the 95% confidence intervals

Diet quality and tree species selection

A potential association between perceived lynx and human risk and changes in diet quality (C:N ratio, NDF, ADF, and lignin; hypothesis 3) was tested using four linear mixed-effects models (lmer package: Bates et al., 2016; nlme package: Pinheiro et al., 2020) created with the respective component as the response variable. Within each model, four interactions with ungulate species (i.e., red deer or roe deer) were added: (1) lynx risk, (2) hunting intensity, (3) recreation intensity, and (4) distance to human settlements. All these variables were mean-centered and scaled and transect number was added as a random intercept to account for the different number of dung samples found along each transect.

To test whether the selection toward different tree species changed under varying levels of perceived lynx and human risk (hypothesis 4), tree species were divided into "preferred" and "less preferred" groups (determined using the Jacobs selectivity index). For each of these groups, a linear mixed model with a β-binomial family (link = "logit") was created (glmmTMB package: Brooks et al., 2017). The proportion of shoots browsed, calculated for each tree species per transect, was added as the response variable. Similar to the browsing intensity at the landscape scale, lynx risk, hunting intensity, recreation intensity, and distance to human settlements were added as explanatory variables within each of the models. All variables were mean-centered and scaled and transect number was added as a random intercept. Last, a zero-inflated structure from the "glmmTMB" package (Brooks et al., 2017) was added within the less preferred species model to account for the high number of zero counts.

All statistical analyses were conducted in R 3.5.1 (R Core Team, 2020). Residual diagnostics were performed using the DHARMa package (Hartig, 2020). None of the variables included in the models were highly correlated ($r \geq 0.7$; Dormann et al., 2013).

RESULTS

Browsing intensity (measured on 5776 trees) and tree density were generally higher in nonhunted than in hunted areas and differed considerably between tree species, with the highest browsing on rowan and the lowest on Norway spruce (Table 1).

Ungulate browsing intensity under human and lynx risk effects

Browsing intensity at the landscape scale decreased with increasing recreation intensity (−0.411 ± 0.138,

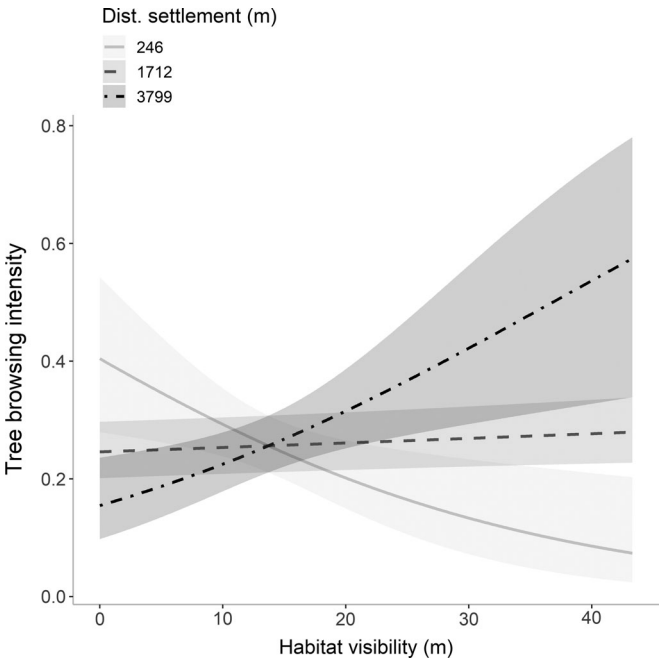
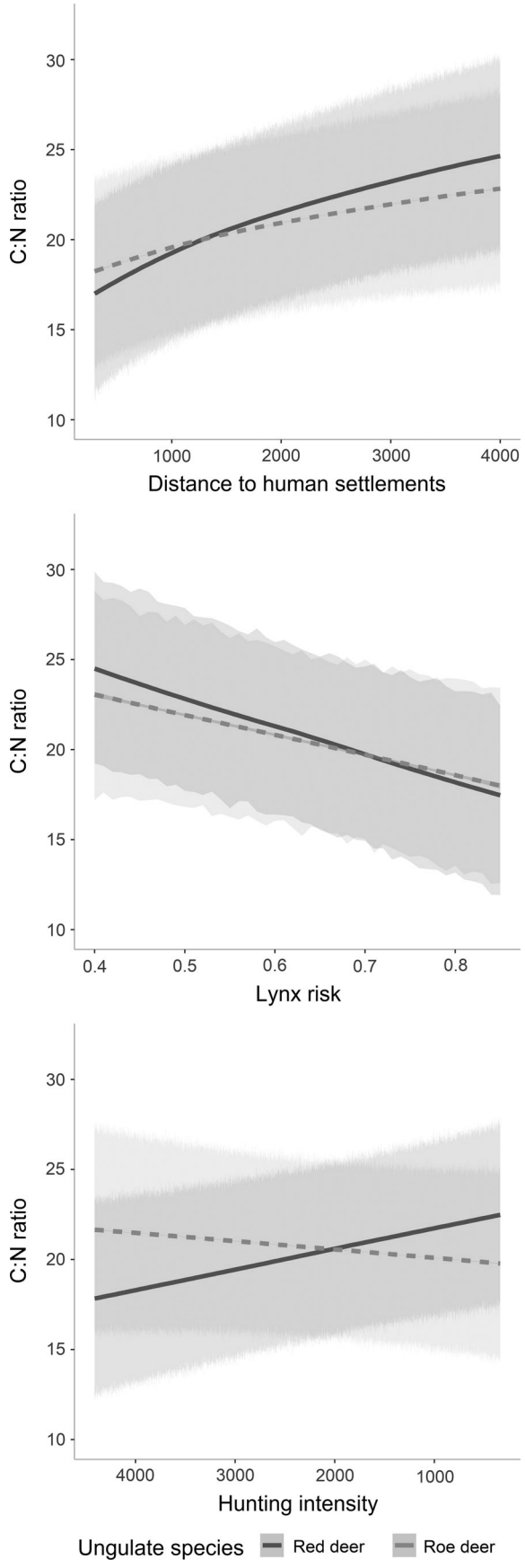


FIGURE 3 Plot of the generalized linear mixed modes predicting tree browsing intensity (proportion of shoots browsed per tree) (*y*-axis) for the interaction between roe and red deer habitat visibility and distance to human settlements (Dist. settlement, m). For the latter, the minimum (246), mean (1712), and maximum (3799) distances to human settlements are plotted, with the shaded areas indicating the 95% confidence intervals

TABLE 2 Outputs of the generalized linear mixed-effect model predicting browsing intensity on individual trees

Model parameter	Estimate ± SE	*z*	*p*
Intercept	−1.068 ± 0.122	−8.79	<0.001
Habitat visibility : lynx risk	−0.046 ± 0.049	−0.95	0.344
Habitat visibility : hunting intensity	0.053 ± 0.068	0.78	0.436
Habitat visibility : recreation intensity	0.001 ± 0.072	0.02	0.988
Habitat visibility : distance to human settlements	**0.165 ± 0.061**	**2.70**	**0.007**
Solar radiation	0.119 ± 0.120	0.99	0.320
Elevation	−0.201 ± 0.125	−1.60	0.109
Tree density	0.066 ± 0.074	0.89	0.371
Tree height	**−0.451 ± 0.026**	**−17.48**	**<0.001**
Norway spruce	**−3.953 ± 0.119**	**−33.35**	**<0.001**
Rowan	**1.554 ± 0.097**	**15.98**	**<0.001**
Silver fir	**−2.181 ± 0.192**	**−11.33**	**<0.001**

Note: Significant variables are indicated in bold ($p < 0.05$).



$z = -2.986$, $p = 0.003$) and increased with lynx risk (0.264 ± 0.118, $z = 2.231$, $p = 0.026$; Figure 2). Furthermore, browsing intensity tended to decrease with increasing hunting intensity (i.e., smaller distance to cull sites; 0.245 ± 0.130, $z = 1.881$, $p = 0.060$; Figure 2), whereas no effect of distance to human settlements (0.090 ± 0.126, $z = 0.711$, $p = 0.477$) on browsing intensity at the landscape scale was found.

At the fine scale, tree browsing intensity was influenced by the interaction between habitat visibility and distance to human settlements (0.165 ± 0.061, $z = 2.70$, $p = 0.007$), where in areas in close proximity to human settlements tree browsing intensity was higher in areas with less visibility (Figure 3). Tree browsing intensity decreased with tree height (-0.451 ± 0.026, $z = -17.48$, $p \leq 0.001$) and differed between tree species. At the species level, tree browsing intensity was higher on rowan than on European beech (1.554 ± 0.097, $z = 15.98$, $p < 0.001$) and lower on Norway spruce (-3.953 ± 0.119, $z = -33.35$, $p < 0.001$) and silver fir (-2.181 ± 0.192, $z = -11.33$, $p < 0.001$). Tree browsing was neither influenced by the interactions between habitat visibility and lynx risk, nor by visibility and hunting intensity, or by visibility and recreation intensity. There was also no significant association between tree browsing intensity and either solar radiation or tree density (Table 2).

Diet quality and tree species selection under human and lynx risk

Diet quality decreased (reflected by an increase in the C:N ratio in deer pellets; 2.239 ± 0.972, $t = 2.304$, $p = 0.032$) with increasing distance to human settlements, but tended to increase (reflected by a decrease in the C:N ratio; -1.431 ± 0.718, $t = -1.993$, $p = 0.059$) with increasing lynx risk (Figure 4). Hunting intensity and recreation intensity were not related to the C:N ratio (hunting intensity: -1.429 ± 0.910, $t = -1.570$, $p = 0.131$; recreation intensity: 0.509 ± 0.750, $t = -0.679$, $p = 0.505$). However, C:N ratio tended to differ between ungulate species in relation to hunting intensity (species × hunting intensity interaction: 2.004 ± 1.014, $t = 1.976$, $p = 0.061$). Although the difference between species was not statistically significant, the C:N ratio tended to increase (i.e., decrease in diet quality) for red deer with hunting intensity (i.e., smaller distance to cull

FIGURE 4 Plots of the linear mixed model predicting the C:N ratio (*y*-axis) as a function of distance to human settlements (m), lynx risk, and hunting intensity. Hunting intensity is measured as the average distance to the closest 10 cull sites, with smaller distances representing a higher hunting intensity. The shaded areas indicate the 95% confidence intervals

TABLE 3 Model output results of the generalized linear effect models predicting the influence of perceived lynx and human risk on the browsing intensity for preferred and less preferred tree species

	Preferred tree species			Less preferred tree species		
Model parameter	**Estimate ± SE**	***z***	***p***	**Estimate ± SE**	***z***	***p***
Intercept	−0.470 ± 0.111	−4.222	<0.001	−3.521 ± 0.392	−8.972	<0.001
Lynx risk	0.041 ± 0.117	0.350	0.727	0.026 ± 0.169	0.151	0.880
Hunting intensity	0.161 ± 0.130	1.243	0.214	**0.464 ± 0.201**	**2.309**	**0.021**
Recreation intensity	0.009 ± 0.128	0.067	0.947	−0.204 ± 0.191	−1.066	0.287
Distance to human settlements	−0.060 ± 0.117	−0.511	0.609	−0.093 ± 0.210	−0.440	0.660

Note: Based on the Jacobs selectivity index, rowan and European beech were defined as preferred tree species, and Norway spruce and silver fir as less preferred tree species. Significant variables are indicated in bold ($p < 0.05$).

sites), whereas that of roe deer tended to decrease (i.e., increase in diet quality) with hunting intensity (i.e., smaller distance to cull sites; Figure 4). Whereas differences between species were found in overall diet quality with higher ADF content for roe deer compared to red deer (3.977 ± 1.823, $t = 2.181$, $p = 0.041$) and the lignin content tended to be higher for roe deer (2.182 ± 1.254, $t = 1.740$, $p = 0.097$), neither lynx nor human risk had an effect on the ADF, NDF, and lignin content (Appendix S2: Table S1).

Based on the average Jacobs selectivity index values, European beech and rowan were the preferred tree species, whereas silver fir and Norway spruce were less preferred (Appendix S2: Figure S1). None of the lynx or human risk variables influenced the browsing intensity for the preferred species (Table 3). For the less preferred tree species, browsing intensity increased with decreasing hunting intensity (i.e., greater distance to cull sites; 0.464 ± 0.201, $z = 2.309$, $p = 0.021$), whereas no effect of lynx risk, recreation intensity, or distance to human settlements was found (Table 3).

DISCUSSION

Both humans and large carnivores play an important role in structuring forest ecosystems, as they influence the abundance and behavior of ungulates and thereby the abundance and diversity of forest plants as well. Our results showed that browsing intensity at the landscape scale decreased with increasing intensity of recreational activities and tended to decrease with hunting intensity, whereas it increased with increasing lynx risk. Furthermore, tree browsing intensity was higher in denser habitats, and additionally, a higher diet quality was obtained in close proximity to human settlements. Last, we found a stronger avoidance of the less preferred tree species in areas with higher hunting intensity, whereas no difference was observed on the preferred tree species. As the increasing browsing intensity in relation to lynx risk indicates that deer do not avoid parts of the landscape with higher (perceived) lynx predation risk, our results indicate that the perceived risk effects of human activities seem to outweigh those of a natural large carnivore in affecting foraging behavior of red and roe deer. These results highlight the importance of taking those activities into account in predicting the impacts of large carnivores on ungulates and their plant-food choices.

Browsing intensity under lynx and human risk effects

Recreational activities may influence ungulate behavior by increasing flight distances, vigilance behavior, and spatial avoidance (Jayakody et al., 2008; Papouchis et al., 2001; Stankowich, 2008). Although these responses likely alter foraging patterns, direct links between the effects of recreation and ungulate browsing (as shown in this study) have rarely been explored. Our results showed a strong reduction in browsing intensity with increasing recreation intensity at the landscape scale, suggesting a general avoidance of areas with greater recreational activity. A previous study conducted within our study area showed that, in places frequently visited by humans, roe deer often seek refuge in closed habitats, presumably to avoid human encounters (Dupke et al., 2017). In refute of our second hypothesis, there was no evidence of an interactive effect of habitat visibility and recreation intensity at the plot scale, thus indicating that within areas of higher recreation intensity, ungulates do not increase their browsing in denser habitats. Behavioral decisions are governed by immediate stimuli and thus likely vary at finer temporal scales (Ensing et al., 2014; Fortin et al., 2002). This was also the conclusion reached by Dupke et al. (2017), who found that, in areas frequently visited by humans, ungulates exhibited hiding behavior

during the day but mostly selected human-related habitats (settlements, roads, cultivated meadows) at night. Despite the temporal change in spatial use by ungulates in relation to human activity within our study area, no measurable differences in browsing intensity could be observed. It should be noted that within the study area, recreation intensity was measured on a coarse scale (500 × 500 m), as more fine-scale recreational data were unavailable. Recreation intensity is strongly governed by the number of hiking trails, and numerous studies have shown that roads strongly influence ungulate behavior (Borowski et al., 2021; Jerina, 2012; Muhly et al., 2011), such that the small-scale effects of recreation might have been observable only in closer proximity to trails and roads. In conclusion, recreational activity was associated with a strong avoidance response at the landscape scale but not with a more fine-scale variation in browsing intensity, which suggests that ungulates generally avoid areas with high recreation intensity.

Hunting intensity also tended to decrease browsing intensity on the landscape scale. This result is in line with other reports of a reduction in browsing pressure following population reductions through hunting (Gaston et al., 2008; Hothorn & Müller, 2010). An overall reduction in browsing when hunting actions reduce overall population size is not surprising, but besides these direct (lethal) effects of hunting the strength of indirect (nonlethal) effects of hunting are rather unexplored (Cromsigt et al., 2013; but see Möst et al., 2015). In fact, common methods of hunting (e.g., hunting blinds) have been designed to prevent strong behavioral effects on ungulates that reduce subsequent hunting efficiency. In this study, as a proxy for hunting intensity, the average distance to the 10 closest cull sites was calculated as a finer-scale measurement than allowed by a large-scale binary variable (hunting/nonhunting). For example, a transect situated in a predefined hunting-free area is likely perceived as risky if the distance to successful hunts is small. Although this proxy of hunting intensity was used to better capture the spatial variation in (perceived) risk, it was based only on successful hunting events and excluded the activities of hunters that did not result in a kill but which may have been perceived by ungulates as risk. However, hunting activities are presumably higher in areas with more successful hunts. Despite the uncertainties in quantifying the activities with the strongest risk effects, the identified landscape-scale patterns suggest that spatial patterns in hunting intensity result in long-term effects whose impact at the tree level is measurable.

Despite the greater exposure in more open areas and thus the higher risk of being hunted (Lone et al., 2014; Proffitt et al., 2009), there was no reduction in tree browsing intensity in areas characterized by a higher habitat visibility and a greater hunting intensity. Thus, at a finer scale, deer browsing seems to be unaffected by differences in visibility at different levels of human-induced risk related to hunting. Within the study area, ungulates face contrasting risk effects of lynx and humans, such that the avoidance of one could increase the risk of the other. Under these conditions, ungulates may respond by changing not only their spatial movement patterns but also their temporal activity to minimize the predation risk (Bonnot et al., 2020; Lone et al., 2017). It is also possible that ungulates change their spatial movements only at the onset of or during the hunting season (Little et al., 2014; Lone et al., 2015; Tolon et al., 2009) by restricting their browsing activity to dense areas. As our browsing measurements included all current year (<1 year) browsing events, differences in browsing specifically related to visibility during the hunting season could not be distinguished. Instead, we found that in close proximity to human settlements ungulates browsed in denser habitats, whereas further away from human settlements more open areas were preferred. This observation supported our second hypothesis that, under high human risk, ungulates perceive open areas as riskier. As the meadows surrounding the settlements likely provide large amounts of high-quality food, and human activities within and surrounding the settlements are temporally predictable (high activity during the day, low activity at night), rather than exhibiting an overall avoidance of areas close to human settlements ungulates shift their browsing in these areas to denser habitats, as also reported by Dupke et al. (2017).

Contradicting hypotheses 1 and 2, browsing increased with increasing lynx risk on the landscape scale, and no reduction in tree browsing intensity was observed in high lynx risk areas characterized by a lower visibility. This indicates that we did not find evidence for red deer and roe deer avoiding areas with supposed higher risk for lynx predation, neither by avoiding parts of the landscape with a higher presence of lynx nor by avoiding low visibility habitats which are preferentially used by hunting lynx (Podgórski et al., 2008). Prey species living in a landscape of fear are assumed to adjust their spatial behaviors in response to the perceived predation risk (Laundre et al., 2010). However, optimal foraging seems to be hierarchical and context-dependent (Senft et al., 1987). For example, a previous study in the Bavarian Forest reported small-scale behavioral responses that included increased vigilance by roe deer under a pulsed heightening of risk created using the olfactory cues of lynx (Eccard et al., 2015) but did not lead to an avoidance of habitats with a higher lynx predation risk (Dupke et al., 2017). Instead, large-scale temporal variations in roe deer habitat selection were primarily governed by food resources

(Dupke et al., 2017) as was also previously suggested (Ratikainen et al., 2007; Samelius et al., 2013). This could explain why ungulate browsing in our study increased with the perceived risk imposed by lynx. While ungulates generally prefer to feed in areas with open canopy cover (i.e., forest gaps or harvested stands; Kuijper et al., 2009) where young regeneration is available, the low visibility in these areas increases lynx hunting success (Podgórski et al., 2008). Consequently, it was hypothesized that tree browsing intensity would be lower in dense habitats with increased lynx risk. However, on a fine scale, no differences in tree browsing intensity were found with lynx risk. This apparent lack of avoidance of risky places, does not exclude that ungulates actively avoid their predator at temporal timescales (Gaynor et al., 2019), that is, react to "risky times" rather than "risky places." Several recent studies illustrate that the landscape of fear that is perceived by prey species often is a highly dynamic process that strongly depends on actual predator presence (Kohl et al., 2018; Rossa et al., 2021). Moreover, reactions to predators can occur on even finer spatial scales, for example, by reaction to olfactory cues indicating (recent) predator presence. Predator's scent is found to be an important cue determining prey behavior where several studies found that both roe deer and red deer responded to olfactory cues of lynx by increasing their vigilance (Eccard et al., 2015) or reducing their visitation duration (van Beeck Calkoen et al., 2021; Wikenros et al., 2015) which consequently led to a reduction in browsing intensity (van Beeck Calkoen et al., 2021).

Thus, within the study area, differences in browsing intensity were stronger related to the perceived risk associated with human activities (i.e., recreation activities, hunting intensity, and human settlements) rather than to the perceived predation risk of lynx based on their habitat suitability. This conclusion is in line with other studies in which the effects of humans were shown to outweigh those of large carnivores (Ciuti et al., 2012; Muhly et al., 2011; Proffitt et al., 2009). Our results accordingly indicate that, despite a high abundance of lynx in the study area (Palmero et al., 2021), the risk posed by this large ambush predator, unlike that posed by human activities, did not cascade down to measurable differences in browsing intensity.

Diet quality and tree species selection under different levels of risk

Herbivore species are typically classified along a browser–grazer continuum (Hofmann, 1989; Spitzer et al., 2020). Where red deer are generally classified as intermediate feeders that forage on a wide range of woody and nonwoody vegetation (Gebert & Verheyden-Tixier, 2001; Krojerová-Prokešová et al., 2010; Latham et al., 1999; Storms et al., 2008), roe deer are more selective browsers that feed on more concentrated food sources (Latham et al., 1999; Storms et al., 2008; Tixier & Duncan, 1996). Overall differences in diet composition between roe deer and red deer are best explained by the proportion of grasses in their diets, with varying seasonal shifts to woody browse (Redjadj et al., 2014; Spitzer et al., 2020). Even though differences in feeding niches between red deer and roe deer are observed, with additional strong seasonal variations in diet composition, these differences do not necessarily need to result in different browsing pressures on woody plant species. This is demonstrated by our previous study conducted in the same study area, in which, neither species was disproportionately responsible for the browsing on two palatable tree species (silver fir and rowan) (van Beeck Calkoen et al., 2019). However, Redjadj et al. (2014) showed that from September to mid-November, diet quality could differ between ungulate species, which overlaps with the time of our pellet group collection (19 October–17 November) and could explain the higher ADF and lignin content found within roe deer pellets compared to red deer. Even though coniferous trees played an important role in the diet quality in both roe deer and red deer, the decrease in diet quality (i.e., related to an increase in lignin and cellulose content) could be explained by the stronger increase of coniferous intake by roe deer compared to red deer at the time of our measurements as was also observed in Redjadj et al. (2014).

Diet quality correlates positively with the dietary nitrogen content but it decreases with an increase in fiber, especially the indigestible lignin content (Redjadj et al., 2014). In our study, the C:N ratio tended to decrease with increasing lynx risk suggesting a higher diet quality for both ungulate species in areas of high lynx risk, and additionally a higher diet quality closer to human settlements was observed. Our first finding contradicts those of other studies showing a shift in ungulate habitats from grassy meadows to safer forest locations offering a lower-quality diet in response to a higher wolf predation risk and that an increase in browsing corresponds with lower diet quality (Christianson & Creel, 2010; Creel et al., 2005; Creel & Christianson, 2009). A higher-quality diet despite a higher large-carnivore risk could be explained as follows. Ungulates base their foraging decisions on the trade-off between food acquisition and fear avoidance (Brown et al., 1999) and hence will either tolerate higher levels of risk in habitats with a high food quality or more strongly select for high-quality food in more risky areas to compensate for the higher costs of predation (McArthur et al., 2012, 2014; Nersesian et al., 2011). As diet composition generally

correlates with diet quality (Redjadj et al., 2014), our results regarding tree species selection do not support the conclusion that a higher diet quality in high lynx risk areas reflects a shift toward more preferred (and likely higher quality) tree species. This can be explained by the fact that, besides tree species, grasses and shrubs form an important part of the ungulate diet (Barančeková et al., 2010; Krojerová-Prokešová et al., 2010). Within our study area, Dupke et al. (2017) found that forage availability had a predominant role over lynx predation risk in determining roe deer habitat selection, as roe deer highly selected habitats with high risk of lynx predation (e.g., unmanaged meadows, clearcuts). As especially grasses correlate with high-quality diet in terms of nitrogen fraction (Redjadj et al., 2014), this could explain the high-quality diet we found in high lynx risk areas. In addition, meadows surrounding human settlements are highly attractive to deer because, as in our study area, they contain higher-quality food than in surrounding forests (Dupke et al., 2017; Riesch et al., 2019). We estimated diet quality from fecal samples collected along the transects inside the forest, but based on home ranges, estimated from telemetry data obtained in our study area and the mean residence time, the pellet samples collected represented a deer diet from an area with a maximum distance from the sample locations of 444 m for roe deer and 800 m for red deer. Thus, for the transects close to human settlements (minimum distance 246 m), meadows are within range. While tree browsing close to human settlements was mostly in denser habitats, likely chosen to minimize human encounters, no differences in the proportion of more or less preferred tree species browsed in relation to distance to human settlements were found. Consequently, the determined differences in diet quality cannot be explained by differences in tree species browsing but more likely reflected a higher proportion of grasses.

Furthermore, differences in C:N ratio between red deer and roe deer tended to occur in relation to hunting intensity. Where the C:N ratios increased (i.e., decrease in diet quality) for red deer with hunting intensity (i.e., smaller distance to cull sites), C:N ratios for roe deer decreased (i.e., increase in diet quality) with increasing hunting intensity. Thus, under high risk of hunting, red deer were found to select a lower diet quality, whereas roe deer selected a higher diet quality. Despite the fact that both red deer and roe deer are hunted, the tendency for a different response to hunting could potentially be explained by differences in the hunting pressure and hunting method between both species. Between April 2016 and March 2018, a total of 335 roe deer and 300 red deer were shot within our study area. Within the Bavarian Forest, Henrich et al. (2021) found camera trapping rates for red deer to be approximately 2–4.5 times higher compared to roe deer. Although these numbers cannot be directly converted to densities (Hofmeester et al., 2019), these results suggest higher red deer densities within our study area. Thus, the relative number of roe deer shot is higher than that of red deer, and consequently, roe deer are likely to perceive a higher hunting pressure in general and react differently compared to red deer along gradients in hunting intensity in our study area. We excluded the number of red deer culled inside winter enclosures, because these are unlikely to result in fear effects related to hunting because of the completely different method. Furthermore, we found that hunting intensity influenced the proportion of less preferred tree species browsed. Where the proportion of less preferred tree species browsed decreased with hunting intensity (i.e., smaller distance to cull sites), no differences in browsing intensity on the more-preferred tree species were observed. Thus, instead of a stronger selection for the more-preferred tree species, ungulates were found to avoid the less preferred tree species more in high-hunting intensity areas.

Finally, roe deer and red deer were shown to preferentially browse on European beech and rowan rather than on the coniferous species silver fir and Norway spruce. These results contrast with those of a large-scale browsing survey conducted in the Bavarian Forest National Park, where 0.3% of Norway spruce was browsed followed by European beech (6%), silver fir (11%), and rowan (32%; Möst et al., 2015). Other studies also identified silver fir and rowan as highly attractive food sources (Edenius & Ericsson, 2015; Motta, 2003; Senn & Suter, 2003). However, whereas deciduous trees are mainly browsed during the growing season, browsing on coniferous trees increases in winter (Barančeková et al., 2010; Krojerová-Prokešová et al., 2010; Odermatt, 2014). Our fieldwork was conducted during the hunting season in autumn, as the effects of hunting on diet quality selection would be most pronounced. Consequently, browsing during the preceding spring and summer was mainly surveyed, when deciduous rather than coniferous species would have been extensively browsed. This could explain the proportionally lower browsing levels of silver fir compared to other tree species in comparison with the abovementioned large-scale browsing survey. To test if the classification of tree species into preferred and less preferred species affected our results, we conducted the same analyses with rowan and silver fir as preferred species versus Norway spruce and European beech as less preferred tree species a posteriori. Again, we found a stronger avoidance of the less preferred tree species in areas with higher hunting intensity, whereas no differences were observed on the preferred tree species (Appendix S2: Table S2). This confirms our results that ungulates were found to

avoid the less preferred tree species more in high-hunting intensity areas.

In summary, even though differences in diet quality and tree species selection could suggest a stronger selection under higher levels of perceived lynx risk or human risk (close to human settlements and with hunting intensity), alternative food resources are likely to play an important role as well. Ungulate food choice follows a complex trade-off in which, besides perceived risk, plant availability, nutrient composition, handling time, and specific physiological traits, such as metabolic requirements and digestive capacity, strongly influence diet quality (Bergman et al., 2001; Månsson et al., 2007; Owen-Smith & Novellie, 1982; Senft et al., 1987). Our study suggests that ungulate diet quality and food selection are not influenced solely by risk effects but more likely by a complex mixture of environmental and/or physiological processes that remain to be individually elucidated.

CONCLUSION

This study showed that predictions of the effects of large carnivores on herbivore foraging behavior in human-dominated landscapes must also consider the increasingly large impact of human activities. This study is the first to simultaneously test the risk effects of human activities and lynx predation on ungulate browsing intensity, diet quality, and tree species selectivity. Our results indicate that the perceived risk effects of human activities outweigh those of lynx (representative of a large carnivore) in shaping ungulate browsing in the Bavarian Forest. They also support the need for a reduction of human activities within more strictly protected areas such as national parks, as their growing number of visitors and the intensity of human activities contradict their primary objective, which is to maintain the biological and ecological processes that thrive within their boundaries. Further studies of the ecosystem impact of large carnivores in diverse human-dominated landscapes are needed to ensure the protection of national parks and forested areas while allowing their continued hosting of human activities.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (van Beeck Calkoen et al., 2021) are available from Zenodo: 10.5281/zenodo.5636412.

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