

## Article

# Spatial Distribution of Hunting and Its Potential Effect on Browsing Impact of Roe Deer (*Capreolus capreolus*) on Forest Vegetation

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**Abstract:** Increasing numbers of wild ungulates in human-dominated landscapes in Europe could lead to negative effects, such as damages to forests through browsing. To prevent those effects and, thus, mitigate wildlife-based conflicts while ensuring viable ungulate populations, sustainable management is required. Roe deer, as the most abundant cervid species in Europe, is primarily managed via hunting to decrease population densities through harvesting. Besides direct mortality, non-lethal effects of hunting activities further affect the spatial habitat selection for this species. Accordingly, the spatial distribution of hunting locations might influence game impact on forest vegetation. To examine these relationships in more detail, we linked the spatial distribution of hunting locations for roe deer with forest damage through browsing in 20 regions in Upper Austria. Consistent with our hypothesis, an avoidance of forests by hunters was found in regions with <20% forest cover and intolerable browsing impact. When hunters in certain regions, however, used forests according to their availability, game impact on forest vegetation was tolerable. Although forest damage by ungulates depends on numerous factors, we conclude that careful consideration of hunting locations might be an additional approach to reduce browsing intensity by roe deer, at least in regions with low forest cover.

**Keywords:** anthropogenic predation risk; Central European landscapes; game impact; hunting locations; habitat use; landscape of fear (LOF); ungulate management



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## 1. Introduction

In most parts of Europe, abundances of wild ungulates are increasing [1]. This is especially true for roe deer (*Capreolus capreolus*) populations [2]. Due to its adaptiveness, e.g., niche breadth concerning habitat use [3] or diet [4], roe deer became the most abundant cervid species on this continent [5,6]. Game impact on vegetation through foraging by roe deer might rise simultaneously, based on this species' high population densities [7]. In this context, roe deer are especially known for their browsing impact on forest restoration [8], where the animals bite off shoots and young branches of trees, leading to reduced or aberrant growth or even the deaths of trees. Consequently, forests can degrade regarding their functional economic, ecological, or socio-cultural roles [9]. As a result, contrasting perspectives about wildlife management generate conflicts between stakeholders (e.g.,

landowners, hunters, and recreational users), which we refer to henceforth as wildlife-based conflicts. Coordinated management of wild ungulates and their habitats is, therefore, a necessity in human-dominated landscapes across Europe to effectively prevent such conflicts [7,10,11]. Regarding this management, hunting is used to regulate population numbers through harvesting [1], and influence habitat selection of wild ungulates [12–14].

When choosing suitable habitats, animals have to consider multiple aspects, such as resource quality and availability, shelter, and potential threats [15]. Regarding the latter, predator–prey interactions consist of direct predation along with modification of prey’s behavioural response to the anticipation or risk of possible attacks [5,16]. As hunters have replaced large carnivores as apex predators in many regions all over the world [17,18], herbivores are sensitive to hunting activities [5]. Thus, hunting plays an important role in ungulate management, species’ habitat selection, and the prevention of wildlife-based conflicts. In this context, effects of hunting can act directly as well as indirectly on ungulate species. Direct effects of hunting are achieved through reducing population numbers through harvesting [1,19]. Indirect effects are often associated with adjustments of behavioural patterns of prey species [20]. Several studies concerning large mammals [21], such as white-tailed deer (*Odocoileus virginianus*) in Oklahoma, USA [14,18], wild boar (*Sus scrofa*) in Sweden [12], mouflon (*Ovis gmelini*) in France [22], or red deer (*Cervus elaphus*) in Austria [23], have highlighted that ungulates respond to those indirect effects and adapt their spatio-temporal behaviour to avoid potential contact with humans. Accordingly, Büttner [24] found that regions in Germany with intensive hunting were avoided by roe deer. Moreover, Padié et al. [13] recently verified that habitat selection of roe deer is driven by hunting pressure in France. In hunted roe deer populations, anthropogenic predation risk should, therefore, lead to adjustments in habitat selection. What remains to be investigated, however, is the connection between those adjustments and game impact on forest vegetation. Mols et al. [25] have highlighted that human activities (e.g., hunting) create behaviourally mediated cascading effects that can influence vegetation growth within nature reserves in the Netherlands. Detailed knowledge regarding these effects in partially forested areas, which are typical of Central European landscapes, is, however, still limited, and further investigations are needed. Thus, we conducted a case study in Upper Austria, an Austrian province located in Central Europe, to examine correlations between spatial distribution of hunting and browsing impact on forest vegetation.

Upper Austria has seen an increase in roe deer abundance consistent with the European trend [7]. As such, harvest data indicate an increase in abundance by more than 100% over the past 40 years. While in 1983, 36,602 roe deer were harvested in Upper Austria, that number increased to 79,132 in 2020 [26]. Although harvest data do not necessarily represent roe deer abundance, they serve as a proxy to infer population trends. According to the positive population trend in Upper Austria, game impact on forest vegetation is currently high [27]. Additionally, with a human population density of 124 residents per km<sup>2</sup> in 2022 [26], Upper Austria can be described as a human-dominated landscape in Central Europe. At the same time, the spatial distribution of land use is structured in small mosaics. About half of the province’s area is used for agricultural purposes, while 42% is forested. The remaining 8% contains settlements, industrial areas, and other land uses. In 2016, the average size of an agricultural farm was 33 ha [28]. By having such a small-structured mosaic-like landscape, Upper Austria provides a wide range of suitable habitats for roe deer, as this species mainly utilises forest-edge habitats [29] between forests and agricultural land [30]. Hunting in Upper Austria represents the main management tool to mitigate wildlife-based conflicts regarding roe deer through reducing the density of this species (see [31] for details). However, current hunting practices often fail in this context, as impact of browsing on forests is still a major problem [27].

Hunters can select locations for hunting based on the available habitats for roe deer or avoid certain habitat types beyond their availability. This selection is assumed to affect habitat use by roe deer and, hence, the impact of this species on forest vegetation. Thus, the spatial distribution of hunting activities might also influence the success in

preventing damages to forests. Considering the human-dominated landscape, the mosaic-like distribution of roe deer habitats, and hunting practices, Upper Austria serves as an ideal case study for examining effects of hunting distribution on the game impact on forest vegetation in a Central European context. As browsing impact by roe deer is a major problem in forests [32] but not in agricultural fields of Austria, we concentrate exclusively on forests within this study. To examine effects of hunting distribution on game impact, we focus on two dependent research questions. Firstly, are hunting locations concerning roe deer randomly distributed within selected regions of Upper Austria? In this study, a hunting location is defined as the precise location where a hunter harvested roe deer. Secondly, if hunting locations are not randomly distributed, is the distribution of these locations affecting game impact on forest vegetation? To answer these questions, we link georeferenced hunting locations with game impact and land use, using information gathered from hunters, remote sensing, and the Upper Austrian Government. Regarding our research questions, we hypothesise that (i) hunting is not evenly spread within the study regions, as roe deer mainly prefer forest edges as suitable habitats. Furthermore, we anticipate that a concentration of hunting activities in forests will lead to reduced roe deer abundance in forests, as density is directly reduced and individuals are assumed to avoid areas with high predation risks. Thus, we also hypothesise that (ii) regions with more intensive forest-based hunting will have a lower game impact on forest vegetation. Ultimately, the aim of this case study is to reveal whether the selection of hunting locations can be a valuable component of a sustainable roe deer management strategy to mitigate wildlife-based conflicts in Central European landscapes.

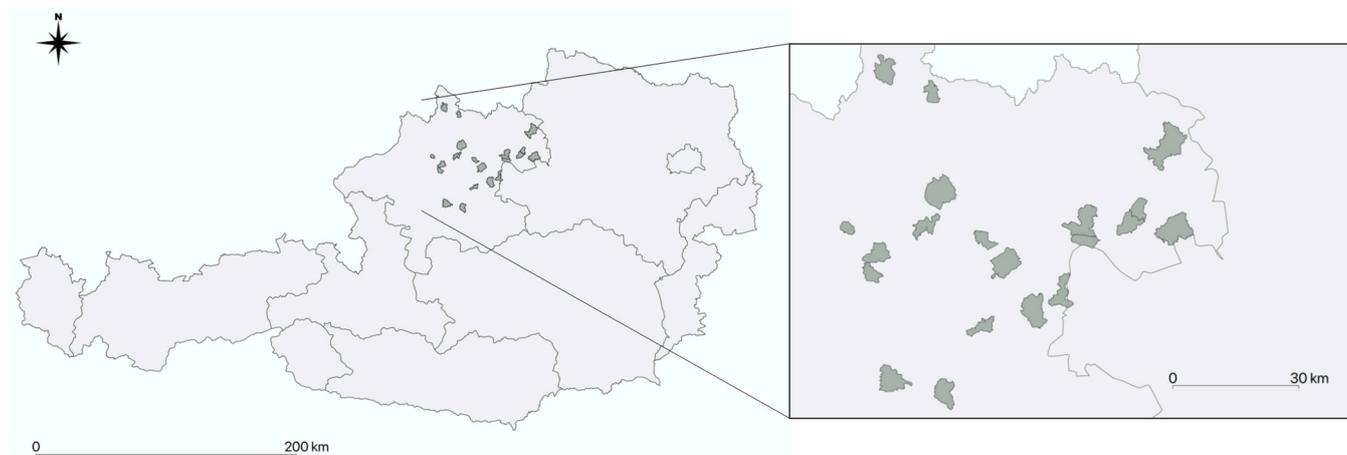
## 2. Materials and Methods

### 2.1. Study Regions

We chose 20 study regions, each representing a hunting ground, located in the Austrian province of Upper Austria (Figure 1) at elevations between 270 m and 769 m above sea level. Consisting of small forest patches and agricultural land, the mosaic landscapes of all regions can be described as suitable habitats for roe deer [33]. Accordingly, roe deer is the most abundant wild ungulate species in all regions. Based on estimations and annual counts conducted by hunters, there are, on average, 15 living individuals per 100 ha in spring within each region (survey conducted by the University of Natural Resources and Life Sciences, Vienna in 2014, unpubl. data). Roe deer is mainly regulated by recreational hunters, based on harvest quota given by local authorities. According to hunting protocols, these quota are annually achieved through hide hunting (70%), stalking (20%), and drive hunting (10%). Hunting season for roe deer starts on 1 May and lasts until 31 December, differentiated into sex and age classes (fawns and females older than one year: 16 August–31 December; one-year old-females: 1 May–31 December; one-year-old males: 1 May–30 September; males between two and five years: 1 June–30 September; five-year-old males and older (antler weight < 300 g): 1 June–30 September; five-year-old males and older (antler weight > 300 g): 1 August–30 September). Thus, there is one long hunting season, which does not consist of distinct short seasons. Further information regarding hunting management in Austria can be found in Trouwborst and Hackländer [34].

Study regions were chosen based on a set of criteria including forest percentage, game impact, and willingness of hunters to cooperate. At the beginning of this study, representatives of each study region were invited to a joint workshop to discuss the details of the project (e.g., data acquisition). Throughout the study, there was a regular exchange between practitioners and scientists to ensure standardised data collection. All hunters active in the study regions participated voluntarily. All study regions had a size of more than 1000 ha, except one with about 700 ha. Regions were specifically targeted to differ in browsing impact on forest vegetation and percentage of forest cover. Based on remote sensing, forest cover was included in the selection to consider the potential effects of landscape characteristics. Twelve regions had <20% forest cover (group A), whereas the other eight had 30–50% forest cover (group B). Half of the regions within each group had

a tolerable game impact on forest vegetation, and the other half had an intolerable game impact (the methodology of game impact is described in the next paragraph).



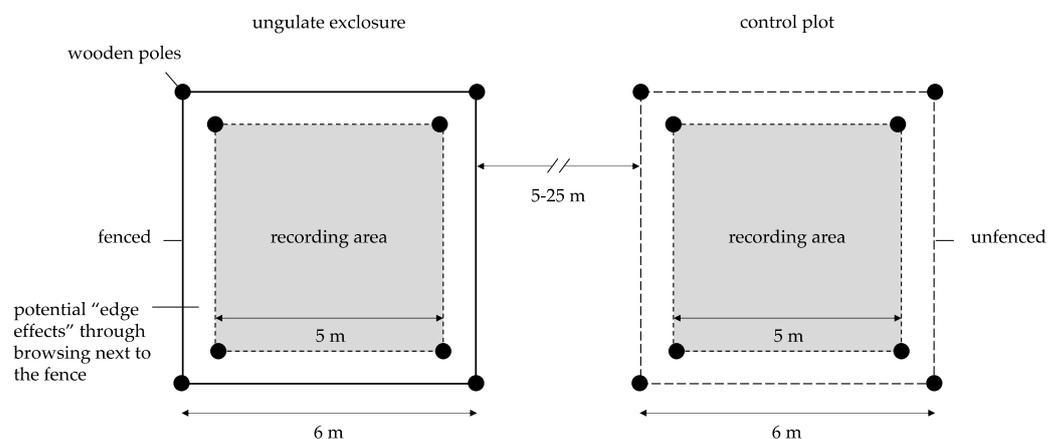
**Figure 1.** Study regions (dark-grey areas,  $n = 20$ ), located in Central Europe in Austrian province of Upper Austria. Lines represent borders between provinces.

## 2.2. Game Impact

Game impact was determined via surveys of the governmental evaluation of ungulate impact on forests via browsing over several years (1995–2015). Specifically, forested areas in each region are assessed annually by hunters, landowners, and local authorities. Depending on natural forest community and forest function, the forest authority sets concrete targets for forest regeneration (e.g., tree species composition, minimum density of trees per species). If the target was not achievable due to the impact of roe deer (browsing, fraying), the impact was described as intolerable. According to legal requirements in Upper Austria, ungulate exclosures and unfenced control plots (Figure 2) are used for measuring the impact of roe deer on forest regeneration (see [35] for a comparable approach). At least one exclosure per 100 ha forest must be established within each hunting ground. The total number of exclosures per hunting ground must be at least three and at most 20. In regions where roe deer is the most abundant wild ungulate species, exclosures are constructed with a fence that is at least 1.5 m tall and encloses an area of  $6 \times 6$  m. Due to the structure of the fences, smaller mammals such as mice and lagomorphs were able to enter the exclosures. For each exclosure, an unfenced control plot (reference area) existed in close proximity (5–25 m) with comparable site and stand conditions. Plant data was recorded inside a central  $5 \times 5$  m square within each exclosure (to exclude areas that might be browsed through the fence) and compared to the corresponding control plot. In particular, the composition of regenerating tree species and the total number and height per species were surveyed for each exclosure/control pair. Application of bait or the removal of young trees was prohibited next to exclosures and control plots to prevent biases in these surveys.

In addition to exclosure/control pairs, longitudinal transects are used in Upper Austria to measure game impact on forest vegetation. Those transects were unfenced and variable in length and included approximately 80 to 100 individual trees with heights between 30 to 150 cm. Once the majority of the trees reached a height of 150 cm, a new transect was established. Per hunting ground, there were at least three transects, each containing at least 50 trees of the respective target tree species (e.g., silver fir (*Abies alba*), Norway spruce (*Picea abies*), or deciduous trees, such as oak species (*Quercus* sp.), European beech (*Fagus sylvatica*), or maple species (*Acer* sp.)). For each target species, the browsing intensity on the transect was surveyed through counting the number of trees (with a height between 30 to 150 cm) of which the leading shoot was browsed the previous year. Browsing impact of the respective year in which the survey is conducted was not considered as not all transects can be monitored at the same time. Transects surveyed earlier in the year were exposed to

browsing for a shorter time than transects surveyed later in the year. To counteract this bias, only the previous year was considered. The final classification (tolerable vs. intolerable) was made separately for each transect and depended on the targets defined by the forest authority. Guideline values regarding game impact on longitudinal transects are available in the Appendix A.



**Figure 2.** Ungulate enclosure and unfenced control plot for measuring browsing impact on forest regeneration in Upper Austria.

To produce an overall evaluation per hunting ground, assessments of individual enclosure/control pairs and transects were combined. If the majority of the surveys within one hunting ground indicated a tolerable game impact, the overall evaluation was also considered tolerable. If the majority of the surveys displayed an intolerable game impact, the overall assessment was intolerable.

When selecting new enclosure/control pairs or transects, areas as representative as possible were chosen for the respective hunting grounds. Forest areas smaller than 3 ha were not suitable. Regarding our study, the overall classification (tolerable vs. intolerable) was consistent throughout the years 2010 to 2015 within each of the 20 regions. Data regarding game impact were provided by the Upper Austrian government.

### 2.3. Data Processing

For each study region, land use was classified into four categories: forest, forest-edge habitat, agricultural land (arable land, meadows, pastures, set-asides), and areas not suitable for hunting. This classification was performed via remote sensing and based on digital orthophotos and airborne laser-scanning data provided by the geographical information system of Upper Austria. The area of each category was measured in  $m^2$  using QGIS 3.10.12-A Coruña [36]. Forest edges, defined as areas with a buffer width of 50 m around forests, were included in the land use category to consider habitats favoured by roe deer [30]. Cities, roads, and water bodies were summarised into areas not suitable for hunting. As no hunting takes place in this specific land use category, it was excluded from further statistical analyses.

To answer our second hypothesis, we generated a high-resolution proxy variable for hunting pressure. In this study, we defined hunting pressure as the actual effect of hunting activities on game, triggering physiological (e.g., increase in heart rate) and behavioural (e.g., spatio-temporal) responses. This concept differs from hunting effort, which we defined as the sum of all human investment in hunting activities (mostly measured within a temporal context, e.g., time invested by hunters to harvest game). As not all hunting activities exert effects on game, while also taking habituation of game to hunting activities into account, variables measuring hunting pressure must be carefully chosen. We chose hunting locations as measurable and verifiable variables, as gunshots trigger stronger responses in roe deer compared to other stimuli [37], and surviving individuals are assumed

to adapt their behaviour the most if they witnessed the death of a conspecific individual. To specify hunting pressure in each classified land use category, individual hunting location during the hunting season 2014/15 were added virtually as point data to each study region. These data were based on georeferenced hunting protocols and provided by local hunting communities. If several roe deer were harvested at a single hunting locations on different dates, this specific location was counted multiple times, based on the number of harvested deer. The number of hunting locations ranged between 39 and 421 per region. On average, 186 roe deer individuals were harvested per region per year. Based on hunter estimations, the distribution of hunting locations within each region in 2014/15 corresponded to previous years. Finally, we assigned the respective land use category to each hunting location and used 'number of locations = number of gunshots' as a variable for hunting pressure within each category.

#### 2.4. Statistical Analyses

For testing both hypotheses, we analysed the distribution of hunting locations separated by groups of forest cover (group A, group B) and game impact (tolerable, intolerable). For all statistical analyses, we used R version 3.6.1 [38] and the packages *adehabitatHS* version 0.3.14 [39] and *car* version 3.0-12 [40]. To test for hunting location preferences by hunters regarding different land use categories, we calculated Manly selection values [41] and analysed selection (positive or negative) of forests, forest-edge habitats, and agricultural land, respectively. Based on Manly et al. [41], we linked available and used areas for hunting within each study region (selection ratio = used/available areas). Available areas were expressed as the size of each land use category in m<sup>2</sup>. The number of hunting locations within each category represented the intensity of use (used areas). Thus, the selection of forests, forest-edge habitats, and agricultural land by hunters was based on the number of hunting locations within those land use categories in relation to their availability.

By measuring available and used land use categories for each study region separately, we considered that the proportions of each category and the use of it by hunters varied between each region. Hence, we treated hunting locations between regions as independent events, and calculated selection ratios for each region using a type III log-likelihood test statistic (Khi2L) approach. Next, we combined regions based on forest cover and game impact and again computed selection values. Chi-square tests were used to examine the selection of hunting locations by hunters. To test for statistical significance, *p*-values were calculated and compared with a Bonferroni-corrected alpha-level of 0.01667. Subsequently, selection values were plotted to compare regions of tolerable and intolerable game impact within each group of forest cover.

To test whether regions with tolerable impact and regions with intolerable impact differ in hunting location selection by hunters, we performed two-way analyses of variance (ANOVAs). We defined Manly's selection values as dependent variables. As values larger than 1 represent positive selection and values smaller than 1 represent negative selection [41], we converted the measurement into a continuously increasing index of selection through calculating the differences (absolute value) between Manly's selection values and 1. This method resulted in an index of absolute selection strength regarding hunting locations. In this context, low indices indicated no or weak selection and high values indicated strong selection (positive or negative). Absolute selection strength values, therefore, did not equal Manly's selection values. Within all of our 20 regions, we computed three selection strength indices corresponding with the land use categories (forest, forest-edge habitat, and agricultural land). Two-way ANOVAs were then performed separately for each land use category using the respective selection strength index as a dependent variable and the classification of the regions based on game impact and forest cover as independent variables. In doing so, we were able to test whether the selection of hunting locations was significantly different in respect to forest cover (group A, group B) and game impact (tolerable, intolerable). Additionally, we included an interaction term in every ANOVA. Hereby, we accounted for the possibility that effects of hunting location

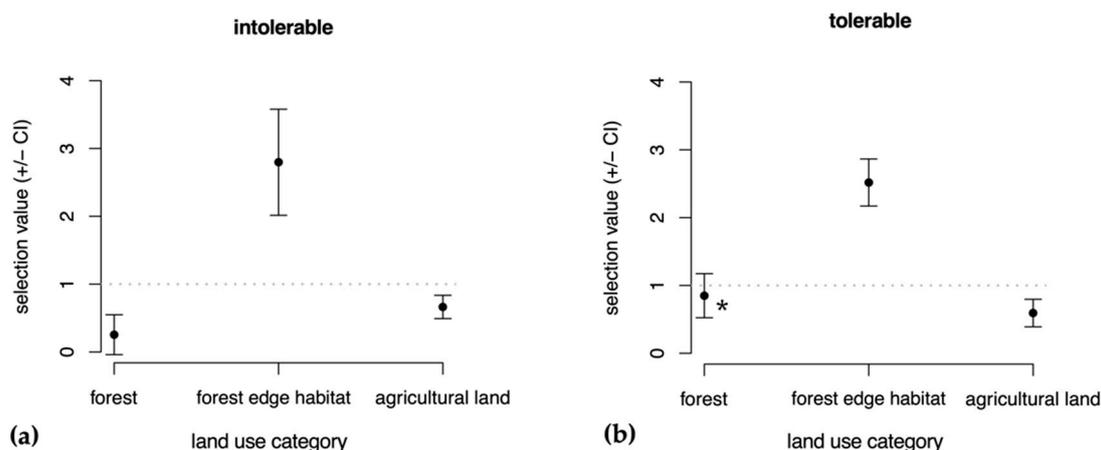
distribution on game impact might also be influenced by forest cover. Tukey's honestly significant difference (HSD) tests were used for post hoc analyses. The selection strength index for the land use category "forest-edge habitat" was reciprocally transformed to meet the assumptions of normality and homogeneity.

### 3. Results

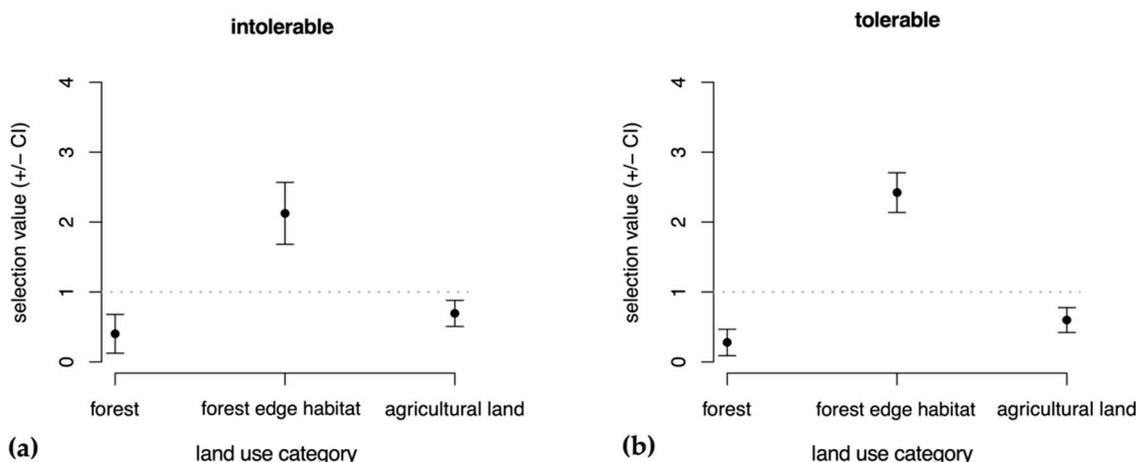
The comparison of available and used land types revealed distinct patterns of hunting location preferences by hunters. Manly's selection values displayed highly significant overall selection of hunting locations regarding both groups of forest cover and game impact ( $p < 0.001$ , Table 1). The tested selection of hunting locations for each region was always highly significant ( $p < 0.001$ ). Regardless of forest cover or game impact, forest-edge habitats were always positively selected and agricultural lands always negatively selected (Figures 3 and 4). Concerning regions covered with <20% forest, differences in selection of forests between regions with tolerable and intolerable game impact were found. Within regions showing an intolerable game impact, hunters negatively selected forests (Figure 3a). In contrast, hunters used forests corresponding to their availability within regions having a tolerable game impact (Figure 3b). In regions covered with 30–50% by forest, hunters always negatively selected forests for hunting. In latter regions, no differences between regions of tolerable and intolerable game impact could be found regarding the selection of hunting locations (Figure 4a,b).

**Table 1.** Log-likelihood test statistic (Khi2L), degrees of freedom (df) and  $p$ -values based on Manly's selection values. Selection of land use categories by hunters for harvesting roe deer in 20 regions of the Austrian province Upper Austria was analysed based on forest cover (<20%, 30–50%) and game impact on forest vegetation through browsing (tolerable, intolerable). Land use categories: forest, forest-edge habitat, and agricultural land (including all types of open land).

	Group A: <20%			Group B: 30–50%		
	Khi2L	df	$p$ -Value	Khi2L	df	$p$ -Value
Tolerable	284.64	12	<0.001	336.64	8	<0.001
Intolerable	488.11	10	<0.001	178.2	8	<0.001



**Figure 3.** Selection of land use categories by hunters for harvesting roe deer in regions of the Austrian province of Upper Austria. Regions were covered with <20% forest and classified based on game impact (intolerable, tolerable). Points represent mean Manly's selection values. Values larger than 1 represent positive selection, whereas values smaller than 1 represent negative selection. Confidence intervals (99% CI) including 1 (\*) indicate non-significant effects, i.e., utilisation of areas conforms with their availability. Number of regions: (a)  $n = 6$ , (b)  $n = 6$ .

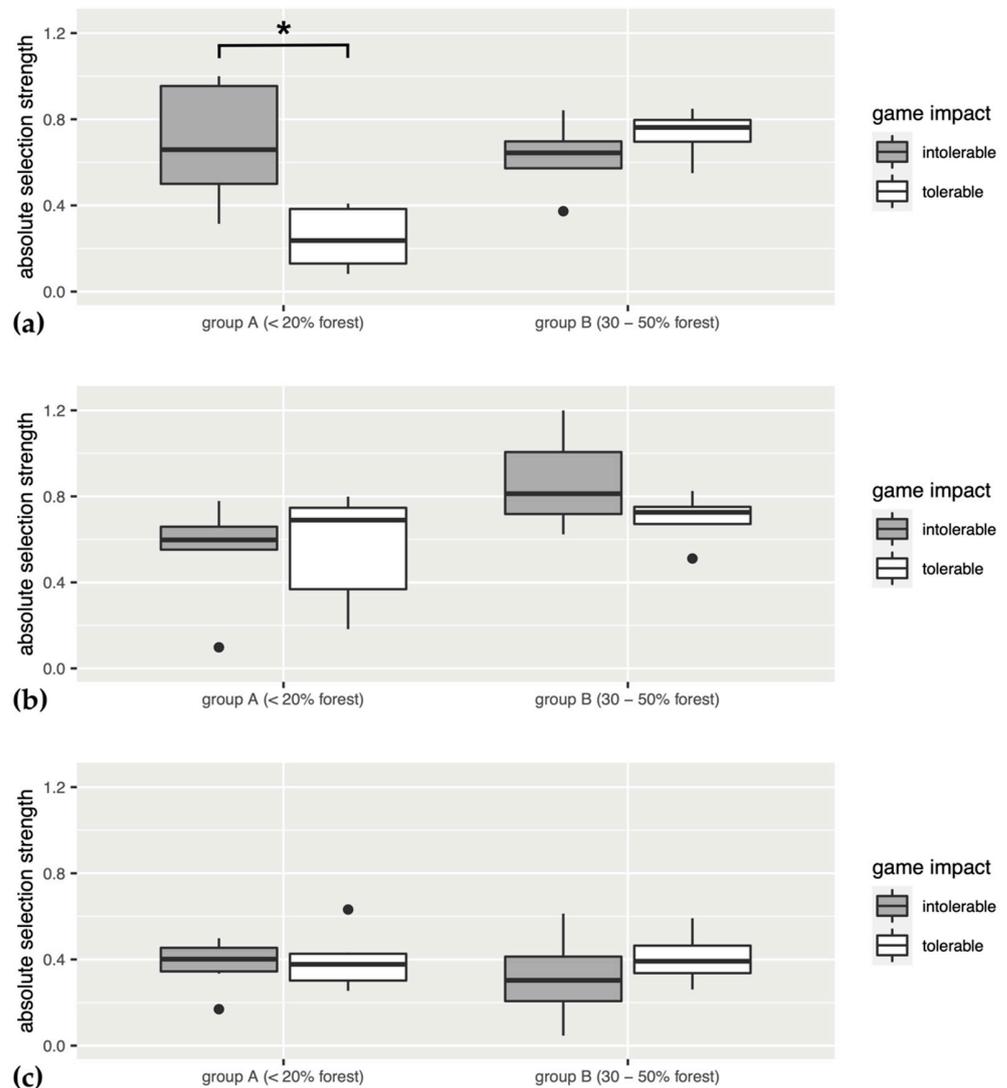


**Figure 4.** Selection of land use categories by hunters for harvesting roe deer in regions of the Austrian province of Upper Austria. Regions were covered with 30–50% forest and classified based on game impact (intolerable, tolerable). Points represent mean Manly’s selection values. Values larger than 1 represent positive selection, whereas values smaller than 1 represent negative selection. Confidence intervals (99% CI) including 1 indicate non-significant effects, i.e., utilisation of areas conforms with their availability. Number of regions: (a)  $n = 4$ , (b)  $n = 4$ .

Concerning absolute selection strength, two-way ANOVAs revealed significant differences between groups of forest cover and game impact for the land use category “forest” (Table 2). The interaction term within this land use category was also significant. Concerning the land use category “forest-edge habitat”, significant differences were found between groups of forest cover. Apart from this, no further significant differences were found. Post hoc testing (Figure 5) confirmed that the selection of forests by hunters was significantly different between regions of tolerable and intolerable game impact, but only in regions with <20% forest cover (group A,  $p < 0.05$ ,  $\text{diff} = -0.44$ ). There was no difference in selection strength between tolerable and intolerable game impact in regions with 30–50% forest cover (group B,  $p = 0.89$ ).

**Table 2.** Two-way ANOVAs describing differences in selection strength regarding hunting location preferences by hunters for harvesting roe deer. Differences were analysed between groups of forest cover (group A: < 20%, group B: 30–50%), game impact (tolerable, intolerable), and interaction of both. ANOVAs were calculated for each land use category (forest, forest-edge habitat, and agricultural land) separately. Sum Sq: Sum of squares, df: degrees of freedom.

	Sum Sq	df	F-Value	p-Value
<b>Forest</b>				
Group of forest cover	0.21078	1	4.8756	<0.05
Game impact	0.24675	1	5.7075	<0.05
Group of forest cover: game impact	0.35661	1	8.2489	<0.05
<b>Forest-edge habitat</b>				
Group of forest cover	0.37299	1	6.1585	<0.05
Game impact	0.05059	1	0.8353	0.37431
Group of forest cover: game impact	0.10311	1	1.7024	0.21043
<b>Agricultural land</b>				
Group of forest cover	0.00253	1	0.1056	0.7494
Game impact	0.01072	1	0.4466	0.5135
Group of forest cover: game impact	0.00712	1	0.2968	0.5934



**Figure 5.** Differences in absolute selection strength regarding hunting location preferences by hunters for harvesting roe deer in three different land use categories—((a) forest, (b) forest-edge habitat, and (c) agricultural land)—separated by groups of forest cover (group A, group B). Low absolute selection strength values indicate no or weak selection, and high values indicate strong selection (positive or negative). Grey coloured boxplots illustrate regions with intolerable game impact ( $n = 10$ ). White coloured boxplots represent regions with tolerable game impact ( $n = 10$ ). Asterisk (\*) indicates a significant difference between regions of tolerable and intolerable game impact based on Tukey’s honestly significant difference (HSD) tests.

#### 4. Discussion

The overall objective of this study was to investigate whether the selection of hunting locations by hunters can be a valuable component in roe deer management to reduce browsing impact on forest vegetation. Our findings support hypothesis (i), which stated that hunting locations concerning roe deer were not randomly distributed across the landscape but driven by specific selection preferences of hunters. By associating hunting location distribution with game impact, we found significantly reduced impact on forest vegetation when hunters used forests in proportion to their availability rather than avoiding them. This effect is consistent with hypothesis (ii). This correlation, however, was only found for regions with <20% forest cover. Regarding study regions with 30–50% forest cover, no difference in selection of hunting locations was detected between regions of tolerable and intolerable game impact. Our results highlight that targeted selection of

hunting locations might be an important component in preventing intolerable browsing impact, at least in regions with low forest cover.

The significant results we found in regions covered with <20% forest might be explained according to the “landscape of fear” (LOF) concept [20]. Based on this concept, landscapes are built up of valleys and peaks illustrating the level of fear a prey animal experiences. Thus, this model of a three-dimensional landscape helps to understand how animals will alter and adjust their behavioural patterns and habitat use to reduce the probability of being killed [5,20]. Hunting can induce a LOF [42] and, therefore, influences the spatial distribution of game species [1] such as roe deer. Based on our results, hunters might have increased anthropogenic predation risk within forests using forests up to their availability. Based on the LOF concept, roe deer probably responded to that risk using avoidance behaviour. In this context, the use of forests by roe deer decreased, and game impact on forest vegetation consequently declined.

The emergence and extent of forest damage by ungulates, however, depends on numerous factors and their ecological context. Thus, there are further explanations that might contribute to the significant correlations we found. Hunting, for instance, not only has the potential to alter the spatial distribution of roe deer [13], but also influences populations directly through reducing their numbers through harvesting [19]. If hunting quotas exceed yearly population growth, this management instrument can reduce roe deer densities, relieving some of its impact on forest vegetation [9]. Consequently, tolerable game impact in certain areas might also be explained based on reduced population sizes of roe deer due to increased harvest. Further important factors influencing the browsing impact on forest vegetation are habitat suitability (e.g., shelter, forage supply) and predisposition of forests to game impact. Both factors interact with each other and influence the probability of damage occurring to forest vegetation [43]. In this context, many studies [8,44–51] have mentioned that good forage supply (i.e., quality, quantity, and distribution of natural forage resources, such as grasses or non-timber tree species) lessens the predisposition of forested areas to deer impact. This phenomenon is explained via the balance between food-independent settling stimuli (e.g., hiding cover for deer) and food supply [9]. More productive forests with unsuitable settling stimuli tend to be less vulnerable to browsing impact as they supply more feeding resources in relation to the abundant number of deer [52]. In short, browsing impact of wild ungulates on forest vegetation is a very complex issue, with many factors interacting with each other. A literature analysis by Gerhardt et al. [9] revealed, in total, 80 distinct factors determining game impact of deer on European forests, and mentioned the spatial distribution of hunting as one of them.

Many studies have verified that hunting activities change habitat use by wild ungulates (e.g., [12–14]). Some studies (e.g., [25]) further analysed the spatial connection between hunting and browsing impact of deer on forest vegetation. Detailed knowledge regarding this connection is, however, still limited. Thus, we focused on correlations between spatial distribution of hunting and browsing impact of roe deer in a Central European context. Based on our findings, we were able to demonstrate that hunting locations concerning roe deer were not randomly distributed across the landscape but driven by selection preferences of hunters. In this context, the positive selection of forest-edge habitats by hunters in all study regions corresponded to the preferred use of forest edges by roe deer [30]. The overall negative selection of agricultural land by hunters is likely related to low hunting suitability during summer, when crops provide optimal shelter for roe deer [53] but block visibility for humans (see [23] for a general approach regarding hunting suitability of deer).

We further highlight potential connections between spatial distribution of hunting and browsing intensity in regions with <20% forest cover. In this context, hunters used forests up to their availability within regions of tolerable game impact compared to regions with intolerable impact, where hunters avoided forests. The selection of forests by hunters (selection strength) differed significantly between those low-forested regions of tolerable and intolerable browsing intensity. Although many of the factors mentioned in the literature analysis by Gerhardt et al. [9] are comparable between our study regions (e.g., the constitution

of roe deer habitats, topography, hunting regime, landscape characteristics, etc.), we cannot exclude the possibility that other factors besides the spatial distribution of hunting influenced browsing intensity. These other factors might also explain why game impact was tolerable in certain study regions covered with 30–50% forest, although hunters did not use forests up to their availability. While considering further factors (e.g., hunter effort as anthropogenic variable of investment, spatio-temporal behaviour of roe deer) would certainly improve knowledge, we excluded such variables as the underlying database was not available or based on oral communication without validation. Furthermore, we did not include hunting activities on other game species in our analyses. While this could be an important additional factor, our study regions are characterised by roe deer being the most abundant ungulate and most important game species, hence hunting activities on other species were neglectable.

Despite uncertainty about other factors shaping browsing intensity, our results highlight the potential connection of spatial distribution of hunting and game impact, at least in mosaic-like landscapes of Central Europe with low forest cover. Regarding management recommendations, such potential effects can be seen as an opportunity. By selectively altering the distribution of hunting locations and, therefore, anthropogenic predation risk, browsing impact on forest vegetation might be influenced. In particular, hunters can potentially reduce game impact on forest vegetation within low-forested regions by increasing hunting pressure within forests. This approach can be used to counteract conflicts (game impact) where they arise. Our results showed hunters' selection of forests up to their availability and we suggested that a positive selection of forests might further reduce browsing impact on forest vegetation. Since other ungulates such as red deer or mouflon also respond to anthropogenic predation risk [1,22,23], the transfer of this hunting strategy to the management of other species is conceivable. A careful selection of hunting locations might, therefore, serve as a cornerstone in the sustainable management of roe deer and other ungulates within human-dominated landscapes in Central Europe.

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## Appendix A. Guideline Values Regarding Game Impact on Longitudinal Transects in Upper Austria

Regarding Norway spruce (*Picea abies*), a browsing intensity up to 10% of branches/trees on a single transect is classified as tolerable. A higher intensity is categorised as intolerable. Regarding deciduous trees and silver fir (*Abies alba*), the assessment is carried out differently depending on stock density. On transects with a high stock density (more than 10,000 young trees/ha), a browsing intensity up to 50% of branches/trees is classified as tolerable. On transects with a low stock density (less than 10,000 young trees/ha), a browsing intensity

up to 20% is categorised as tolerable. To produce an overall evaluation per hunting ground, assessments of individual enclosure/control pairs and transects are combined. If the majority of the surveys within one hunting ground indicate a tolerable game impact, the overall evaluation is also tolerable as long as browsing intensity never reached certain values (percentages of browsed branches/trees) on any surveyed transect (Norway spruce: 20%; deciduous trees and silver fir (high stock density): 80%; deciduous trees and silver fir (low stock density): 50%).

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