



Nothing else matters? Food as a driving factor of habitat use by red and roe deer in winter?

Authors: Bobrowski, Maria, Gillich, Benjamin, and Stolter, Caroline

Source: Wildlife Biology, 2020(4)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00723>



Nothing else matters? Food as a driving factor of habitat use by red and roe deer in winter?

Maria Bobrowski, Benjamin Gillich and Caroline Stolter

M. Bobrowski (<https://orcid.org/0000-0002-9660-1614>) ✉ (maria.bobrowski@uni-hamburg.de), B. Gillich (<https://orcid.org/0000-0001-5241-4449>) and C. Stolter (<https://orcid.org/0000-0003-4059-9786>), Dept of Animal Ecology and Conservation, Univ. of Hamburg, Martin-Luther-King Platz 3, DE-20146 Hamburg, Germany. MB also at: Center for Earth System Research and Sustainability, Inst. of Geography, Univ. of Hamburg, Bundesstraße 55, DE-20146 Hamburg, Germany. BG also at: Dept of Wildlife Biology, Wildlife Management and Hunting Practice, Eberswalde Univ. for Sustainable Development, Eberswalde, Germany.

Habitat use by cervids can have large effects on vegetation. Therefore, factors influencing habitat use are pertinent to ecology, nature conservation as well as management of forests and hunting. The aim of this study was to identify factors influencing habitat use by red and roe deer, *Cervus elaphus* and *Capreolus capreolus*, in the Lüneburger Heide, Germany. We used faecal pellet counts as an indicator of habitat use and applied generalized linear models to conclude that habitat use by both cervids was largely explained by the availability of food plants. In particular, the occurrence of bilberry *Vaccinium myrtillus* and deciduous trees such as beeches *Fagus sylvatica* were of major importance. Nonetheless, red and roe deer showed preferences for different plant species, but for both deer, the presence of large trees and conifers, with exception of young Norway spruce *Picea abies* providing shelter for roe deer, was less attractive. Furthermore, the proximity of mineral licks was important for both cervids. Relative to roe deer, red deer showed a stronger avoidance of well-used paths. Surprisingly, landscape features such as distance to settlements and elevated hunting standshad no significant effect. Our study demonstrates similarities and differences in habitat use of two important herbivores of the Northern temperate forests. We propose that managers establish 'decoy' sites for deer: areas with a high proportion of ground vegetation and young trees of lower forestry value. This will serve to divert deer from valuable trees and thereby enhance biodiversity. These open stands could be interspersed with dense islands of young coniferous trees to offer shelter and should be distant to frequently used pathways. Mineral licks may help enhance use of these sites. Providing an attractive resource for both species of cervids is the best way to manage large herbivores in economically valuable forests.

Keywords: anthropogenic influences, browsing, *Capreolus capreolus*, *Cervus elaphus*, decoy feed, food availability, landscape features, ungulates, vegetation composition

Habitat use is an important issue in the ecology of every species (Rosenzweig 1981) and is always a tradeoff between many factors like forage availability, disturbance, shelter, competition and predation risk. However, no habitat offers all these factors in equal balance. For example, human disturbance and predation risk influence deer behaviour and can cause increased vigilance (Jayakody et al. 2008, Sönnichsen et al. 2013, Eccard et al. 2017), temporary departure from disturbed areas, or a change in diet composition (Sibbald et al. 2011). As remote areas become more and more accessible to a greater number of people, disturbance to wildlife from human recreation is increasing (Staines and Scott

1994, Sibbald et al. 2011). For example, free-roaming dogs accompanying walkers may result in red deer *Cervus elaphus* becoming more vigilant and concentrated than those in undisturbed areas (Jayakody et al. 2008). Moreover, cervids may adjust their foraging behaviour by browsing far from roads (Bonnot et al. 2013) as road traffic and hikers disturb them. Nonetheless, red and roe deer *Capreolus capreolus* may differ in their response to human disturbance (Latham et al. 1997, Jiang et al. 2008). This has implications for how browsing by both species is managed in Europe where they are seen as detrimental to high value forestry.

Browsing by cervids on trees, saplings and seedlings can affect subsequent tree growth and wood quality (Lavsund 1987, Vila et al. 2003, Bobrowski et al. 2015). Since both red and roe deer feed on twigs of trees in wintertime, at high density they may change forest structure and species composition (Partl et al. 2002, Hester et al. 2006, Bobrowski et al. 2015). Especially young deciduous trees may suffer from

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

severe browsing by both species (Bobrowski et al. 2015), which might lead to reduced tree recruitment, a severe problem for silviculture in times of dying coniferous forests due to heat stress in Germany.

Notwithstanding, red and roe deer share resources (i.e. habitat quality and food availability), which may trigger competition among species (de Boer and Prins 1990). However, due to differences in gut morphology and physiology (Hofmann 1988), they differ in their nutritional needs and consequently in their diet preferences (Gebert and Verheyden-Tixier 2001, Felton et al. 2018, König et al. 2020) and thus may use available habitat differently. Furthermore, seasonality and interspecific interactions constitute environmental constraints which likely influence food availability, and hence the use of food resources by individuals of sympatric populations (Storms et al. 2008). It has been shown that competition between red and roe deer negatively affected life history traits, whereas high red deer density negatively influenced roe deer body mass (Richard et al. 2010). Latham et al. (1997) pointed out that red deer prefer a high proportion of older, more open thickets, whereas roe deer prefer sites with a higher proportion of young plants and thickets.

In many parts of Europe coniferous forests (mainly *Picea abies*) have been decimated by insect outbreaks, and so natural regrowth or plantations of native broadleaf species (e.g. beech and oak) is essential to adjust forests to future climate changes. However, an abundance of young trees is attractive to deer (Gill et al. 1996, Latham et al. 1996, 1997, Bobrowski et al. 2015), resulting in conflicts with forest managers. Therefore, understanding the factors influencing the habitat use is critical in developing management approaches that balance the needs of foresters, hunters and those who use the forests for recreation as well as wild ranging large herbivores, which often have an iconic status for humans (Linnell et al. 2020). In this study, we investigated the effects of human disturbance, food availability, vegetation composition (including different tree heights), browsing and different anthropogenic landscape features on habitat use of sympatric red deer and roe deer, at sites in the Lüneburger Heide, Lower Saxony in northern Germany. We assume a stronger negative influence of roads, paths and settlements as well as elevated hunting stands for hunting on the habitat use of red deer compared to roe deer. On the other hand, cover and food availability should be the most important factors driving the habitat use of roe deer at small scales. Specifically, we addressed the following research questions: 1) are red deer more affected by human disturbance than roe deer? 2) Do red and roe deer use the same habitat, preferring the same vegetation composition? 3) Is food availability the most important factor influencing habitat use for both species?

Material and methods

Study area

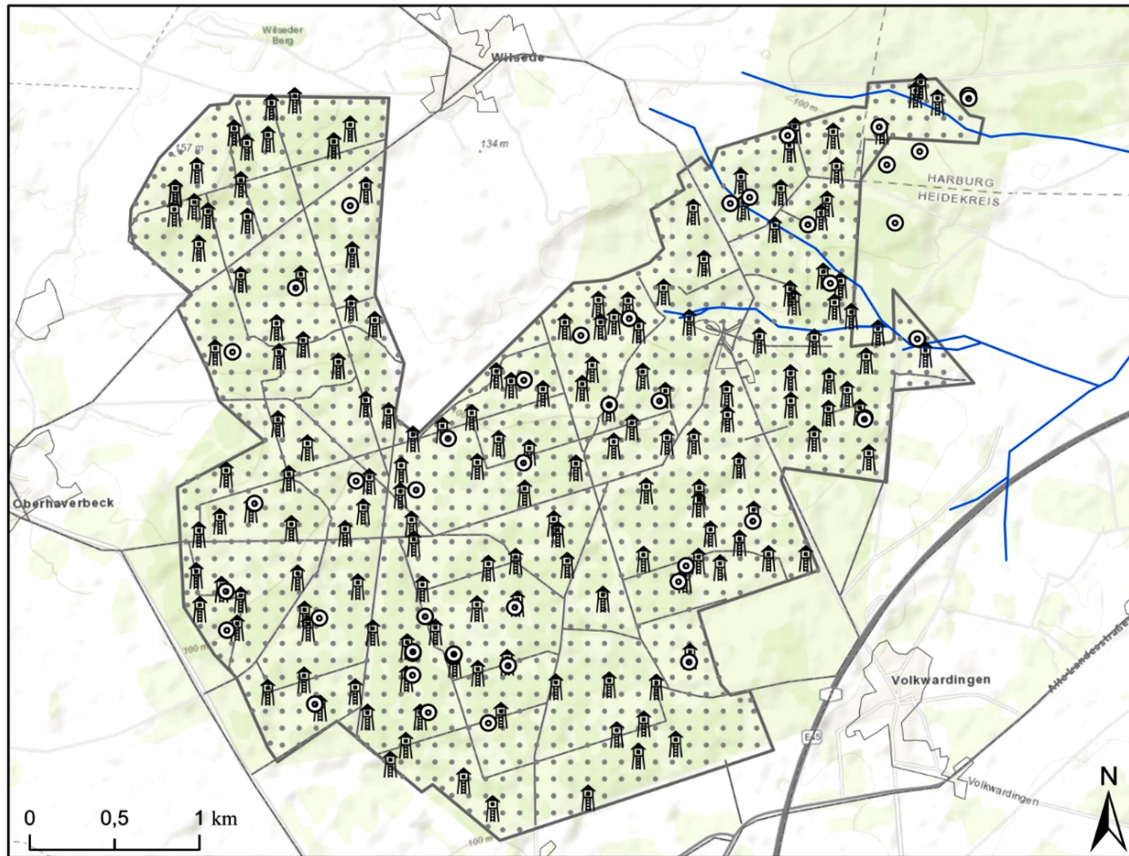
The study was conducted at Wilsede, Forestry Department Sellhorn (53°9'N, 9°59'E, 100 m a.s.l.), located southeast in the conservation area 'Lüneburger Heide', Lower Sax-

ony, Germany. The study area is characterized by a yearly precipitation of around 800 mm and a mean annual temperature of 8°C. Most of the 1240 ha study site is forested; the vegetation is dominated by coniferous trees, planted as monocultures over 200 years ago. Dominant overstorey trees are Scots pine *Pinus sylvestris*, Norway spruce *Picea abies*, Douglas fir *Pseudotsuga menziesii* and European larch *Larix decidua*. The existing deciduous forest stands, such as beech *Fagus sylvatica*, birch *Betula* spp. and oak *Quercus* spp., are relatively small and often mixed with other deciduous trees (alder buckthorn *Frangula alnus*, hackberry *Prunus padus*, holly *Ilex aquifolium*, rowan *Sorbus aucuparia* and willow *Salix* spp.). Dominant ground cover plant species include bilberry *Vaccinium myrtillus*, blackberry *Rubus fruticosus*, raspberry *Rubus idaeus* and common bracken *Pteridium aquilinum*. The dominant large herbivore species at the site are roe deer at an estimated density of about 20 individuals per 100 ha. The density of red deer is estimated at about two individuals per 100 ha and the sex ratio is 1:1 (K. Sierk, Forestry commission office, unpubl.). Hunting of both species takes place in autumn and winter (until end of February). At the time of the study large predators were not known to be present but wolves have been observed in other parts of the Lüneburger Heide since 2007. The Lüneburger Heide is a well known destination in Germany and frequently used for outdoor recreation. Consequently, there is a well-developed network of pathways throughout the forest.

Data collection

Fieldwork was conducted between February and March 2012. A systematic design was used for data collection. The position of the sampling grid was randomly selected and the sampling plots were regularly distributed 100 m apart (Fig. 1). Each sampling point represented a 2 × 2 m sampling plot, whereas 1309 plots were investigated covering a total area of 5236 m². Within each sampling plot we recorded 1) groups of faecal pellets from both red and roe deer, 2) tree species, 3) tree height (in three categories), 4) browsing damage according to three tree height categories 5) ground vegetation cover (Table 1).

In each sampling plot the total number of tree species were recorded and allocated to three height categories (HC) (HC1: 40–100 cm, HC2: 101–150 cm and HC3: > 150 cm). Trees under 40 cm were excluded from the data set, since they are commonly browsed by rodents and lagomorphs. The impact of browsing was estimated as the total number browsed trees per species in each height category. Thereby, 'old' browsing damage was not counted (older than a few months, which is recognizable by the dark colour). The classification in number of browsed and unbrowsed trees was less subjective than assessing browsing scores for tree species and was conducted to minimise observer bias. Furthermore, this method was less time-consuming than quantifying the exact browsing damage by counting twigs (Stolter 2008). To avoid identification errors of winter-dormant trees, *Betula pubescens* and *Betula pendula* were not separated and were treated as *Betula* spp. A detailed description concerning the tree composition and browsing damage can be found in Bobrowski et al. (2015).



- ⊙ Mineral lick
- 🏠 Elevated hunting stand
- Sampling plots

Service Layer Credits: Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Figure 1. Study area (grey polygon) in the Forestry Department Sellhorn (53°9'N, 9°59'E, 100 m a.s.l.), Lüneburger Heide, Niedersachsen, Germany (N = 1309). Paths and forest roads are in grey.

Euclidean distances to human settlements, roads and paths) as well as to elevated hunting stands (n = 176) and mineral licks (n = 46) were included (Table 1) in the data set.

The habitat use was studied using faecal pellet counts. This method is widely accepted for assessing habitat use and even for estimations of population numbers (Archibald et al. 2005, Månsson et al. 2011, Hema et al. 2013, Schwarz et al. 2017). However, our intention was neither the estimation of population numbers nor the investigation of activity patterns. We counted faecal pellet groups to determine sites that were favoured by deer compared to other sites. The method is feasible for both deer species as neither uses latrines. Counting faecal pellets has been proven to represent a valuable approach if the number of occurring ungulate species is low (Spitzer et al. 2019). Since only red and roe deer are

known to inhabit the studied area, faecal pellets can easily be distinguished by size, which minimizes the risk of misidentification with other deer species (Spitzer et al. 2019). Counts of faecal pellet groups were conducted at the same time as the vegetation assessment, and in the same plots and only at a single time in late winter (February–March). Only pellet groups consisting of more than seven individual pellets (Schwarz et al. 2017) were counted to avoid overestimations, as lower numbers of individual pellets in one pellet group might indicate moving animals.

Statistical analyses

All statistical analyses were performed by using the programming language R (<www.r-project.org>, ver. 3.6.0).

Table 1. List of all measured variables, tree species were measured in three different height categories (HC1–3) and separated into number of trees and number of browsed trees (b).

Anthropogenic landscape features	distance to paths and roads, settlements, mineral licks, elevated hunting stands
Ground cover vegetation	bilberry, blackberry, raspberry
Tree species	all trees total and total b
All species were measured as total, total b and in different height classes (HC1, HC1b, HC2, HC2b, HC3, HC3b)	birch, beech, Douglas fir, European larch, hackberry, holly, Norway spruce, oak, rowan, Scots pine

Table 2. Measured variables included in the model development. Spearman's rank correlations between faeces distribution from red and roe deer and explanatory variables are given, with *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Variables which were included in the principal component analyses are indicated by 'X'. Tree species were measured in three different height categories (HC1–3) and separated into number of trees and number of browsed trees (b).

Variables used for modelling	Red deer		Roe deer	
		Spearman's coefficient		Spearman's coefficient
Anthropogenic landscape features				
Distance to paths (m)	X	0.1***		
Distance to mineral licks (m)	X	-0.063*	X	-0.101**
Ground cover vegetation				
Blackberry			X	0.055*
Bilberry	X	0.098***	X	0.262***
Tree species				
Birch	total		X	0.077***
	total (b)	X	X	0.092**
	HC1	X	X	0.065**
	HC1 (b)	X	X	0.069**
Beech	total			
	total (b)	X	X	0.075**
	HC1	X		
Norway spruce	total		X	0.072**
	total (b)		X	0.059*
	HC1		X	0.075**
Rowan	total	X		0.061*
	total (b)	X		0.083**
	HC1	X		0.062*
	HC1 (b)	X		0.055*

Generalized linear models (GLM) incorporated in the *stat* package (<www.r-project.org>, ver. 3.6.0) were used to analyze the impact of different factors on habitat selection of red and roe deer. Because of the distribution of the data (high number of zero values) we used Tweedie-distribution for modelling (*tweedie* package, Dunn 2017). We analyzed each species individually using their count of faecal pellets groups as dependent variables. We included vegetation parameters, browsing damage on different tree species and the distance to geographical features as potential covariates. We restricted our analyses to the ten most common tree species in the area (Stolter unpubl.) to avoid multiple co-variables. Furthermore, to reduce the number of variables and to avoid multiple correlations we pre-examined our covariates for relationships with our dependent variables using Spearman's rank correlations (Table 2) using the *psych* package (Revelle, 2019) and scatter plots (Zuur et al. 2010, see also Stolter et al. 2013 for details).

High correlation coefficients ($r_s \geq 0.7$ according to Dormann et al. 2013), were found between most of the predictor variables indicating multi-collinearity. Therefore, we applied factor analyses (principal component analyses, PCA, for extraction) implemented in the *psych* package (Revelle 2019) to group variables into principal components (PCs; factor loadings can be found as Supplementary material Appendix 1 Table A1, A2) to eliminate multi-collinearity. To ensure independence of the extracted PCs in the modelling process, we used the Anderson–Rubin-method (Anderson and Rubin 1956). By using PCA, we reduced the number of explanatory variables and grouped them into new variables without losing information. Difficulties may arise in interpretation of the PCs, but since most variables were multiply correlated and the calculated PCs were often reasonably combined, we decided to use PCs, which gave us the ability to include all relevant measured variables. The model with the lowest

Akaike information criterion value (AIC) is considered to be the most revealing model (Anderson 2008). In addition, we calculated Δ AIC and Akaike weights (AICc) to evaluate relative model performance in order to identify the most parsimonious model (Akaike 1974, Wagenmakers and Farrell 2004). All maps were created using ArcGIS (ESRI 2017).

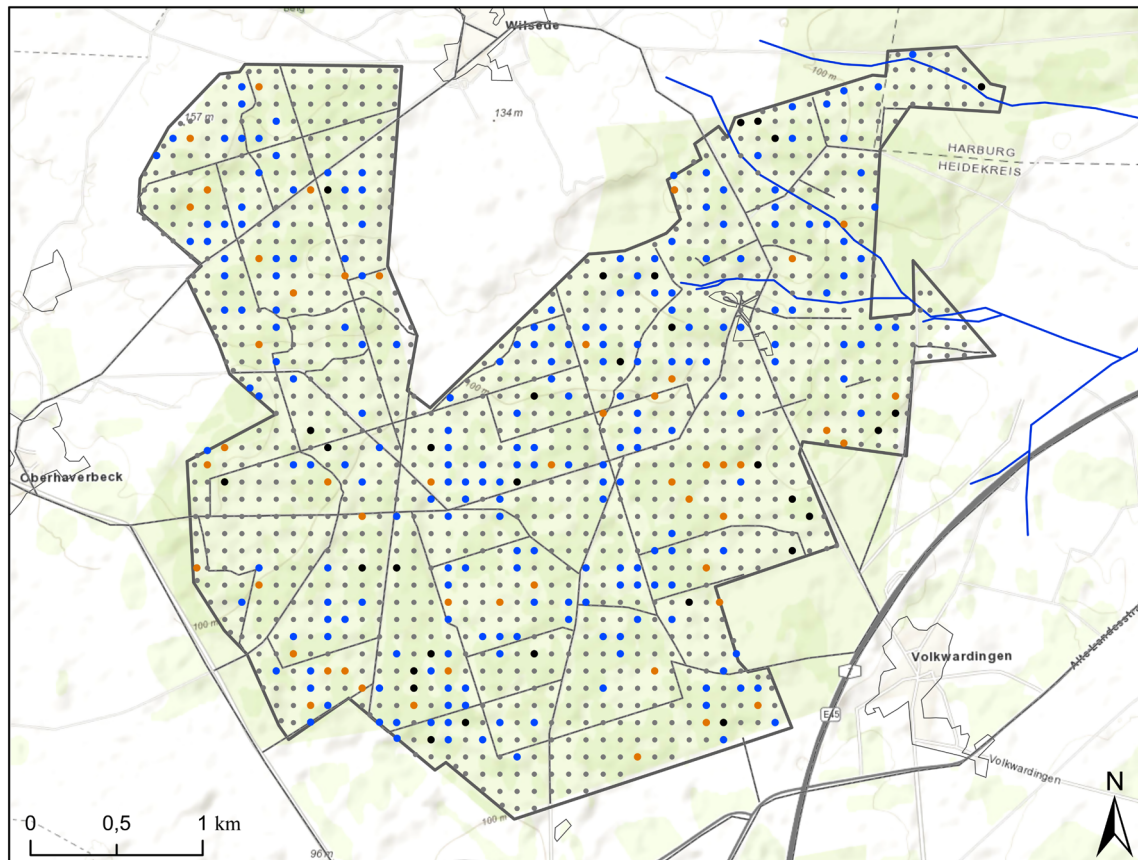
Results

Based on 1309 sample plots, faeces of both red and roe deer were found on 301 plots (24%). Faeces from red deer were found on 81 plots and from roe deer on 251 plots. On 31 plots, faeces from both species were found (Fig. 2, 10% of all plots with faecal pellets). Although highly significant, the correlation coefficient for faeces from red and roe deer was quite low $r_s = 0.122$, $p \leq 0.001$, $n = 1309$ including all plots investigated). Further correlation analyses revealed difference between faeces distribution from red and roe deer and other measured variables (Table 2). In order to highlight differences between factors in influencing habitat use, we calculated models for red and roe deer, respectively.

Models for habitat use of red deer

The pre-examination resulted in 13 variables which were significantly correlated with the counts of red deer pellet groups (Table 2). These variables were summarized in a PCA and subsequently used as co-variables in GLMs in order to identify the major influences on habitat use. All other measured variables were excluded from the final model as they were not related to faecal pellet counts. Surprisingly, this was the case for some of the anthropogenic landscape features thought to be important, e.g. distance to settlements.

The GLM (Table 3) results revealed a negative influence of paths on the occurrence of red deer (PC5), followed by the



- Faecal pellet count both
- Faecal pellet count red deer
- Faecal pellet count roe deer
- Sampling plots

Service Layer Credits: Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Figure 2. Distribution of faecal pellet groups from red deer (n=81) and roe deer (n=251). Faeces from both species were found on 31 plots.

positive effects of the distance to mineral licks and bilberry (PC4), followed by the occurrence of rowan (PC2) and beech (PC3), both mainly resembled by HC1, whereas birch was less important (PC1). Because PC4 summarizes the occur-

Table 3. Upper section: results of the GLM of red deer including all relevant PCs (AIC=651.8); lower section: explanation of the variables summarized in the different PCs.

	Estimate	SE	z-value	p-value
Intercept	-2.85	0.13	-22.49	≤ 0.001
PC1	0.06	0.07	0.84	0.402
PC2	0.13	0.06	2.52	0.012
PC3	0.15	0.06	2.39	0.017
PC4	0.34	0.11	3.08	0.002
PC5	0.38	0.09	4.24	≤ 0.001
PC1	PC2	PC3	PC4	PC5
Birch HC1	Rowan total	Beech HC1	Bilberry	Dist. path
Birch spp. HC1b	Rowan total b	Beech HC1 b	Dist. mineral licks	
Birch spp. total b	Rowan HC1	Beech total b		
	Rowan HC1b			

rence of bilberry and mineral licks, we conducted further models to elucidate which of these two variables had a greater influence on the occurrence of red deer. Therefore, these two variables were considered separately with the other significant PCs (Table 4). The results showed that bilberry was marginally more important than the distance to mineral licks.

Models for habitat use of roe deer

Eleven variables showed significant effects in preliminary analyses (Table 2). Again, the distance to settlements and paths were not related to the occurrence of faecal pellets.

The results of the GLM (Table 5) reveal the high influence of the occurrence of young beech trees (PC2), bilberry and the distance to mineral licks (PC4) on the occurrence of roe deer pellet groups. Additionally, the occurrence of blackberry (PC5) was important, whereas birch was less important (PC1), and spruce had only a minor influence (PC3). Similarly to the models of red deer, PC4 encapsulates the occurrence of bilberry and distance to mineral licks, and when these were considered individually we found that bilberry had a greater influence than the distance to mineral licks (Table 6).

Table 4. Results of two GLMs of red deer including PC 2, 3 and 5 and two different co-variates (either bilberry or distance to mineral licks).

Co-variate	Bilberry		Distance to mineral licks	
	Estimate	p-value	Estimate	p-value
Intercept	-2.93	≤ 0.001	-2.51	≤ 0.001
PC2	0.13	0.018	0.14	0.010
PC3	0.14	0.035	0.15	0.017
PC5	0.4	≤ 0.001	0.37	≤ 0.001
Covariate	0.015	0.012	-0.001	0.16
AIC	652.1		657.5	
ΔAIC	0		5.35	
AICw	0.936		0.065	

Discussion

Our results revealed that the habitat use by both cervids was largely determined by the availability of food plants, which were in our study broadleaf trees and ground vegetation, whereas, except from pathways, anthropogenic landscape features had no effects on the distribution of the animals.

We found faecal pellets of both cervids in our study area. Even though Spitzer et al. (2019) demonstrated the misidentification of faecal pellets, which might lead to misinterpretation of habitat use, we assume that in our study area, where only the two ungulate species are common, identification errors might be minor. Under these conditions faecal pellet group counts are a helpful tool of gathering the habitat use of animals in a study area more accurate than a few collar animals or visual observations (Hema et al. 2013).

Although we found a significant relationship between the occurrence of groups of faecal pellets from both red and roe deer, only 10% of the plots with faecal pellets had faecal pellets of both species, which suggests some differences in habitat use. In our study area the density of roe deer is quite high, while red deer occurs in smaller numbers. The territorial system of roe deer, with males occupying larger home ranges (Ellenberg 1978, Wang and Schreiber 2001) and the relative large home range size of red deer (Gillich et al. unpubl.) might explain our results of a small overlap of both cervids in our study area.

Indeed previous studies have documented shared habitat use as well as habitats with separate use (Latham et al. 1996, 1997, Prokešová et al. 2006, Borkowski and Ukalska

2008, Wu et al. 2016). We did not expect a total separation of both species but we expected differences in habitat use largely because of differences in the feeding behaviour based on the differences in the morphology of the digestive system of these two species (Hofmann 1988), but also because of differences in animals' flight behaviour (Jiang et al. 2008) due to differences in animal responses to anthropogenic disturbances.

However, recent studies demonstrate that roe deer is adapted to consume high amounts of fibre rich feeds (Dahl et al. 2020, König et al. 2020) which gives evidence that roe deer, which has been seen as a concentrate selector (sensu Hofmann 1988) might feed on similar food as the intermediate feeder, the red deer. This might lead to enhanced food competition between both species, when food availability declines (e.g. in winter).

We expected to find red deer in more open areas further away from human settlements and recreational paths, but also in older forest patches, which are typically used for shelter. In contrast, we expected to find roe deer in denser vegetation dominated by small deciduous trees.

Our analysis showed that a major factor determining habitat use was vegetation dominated by bilberry and young deciduous trees (HC1) which commonly showed signs of feeding by deer. Food availability might therefore be a common main driver of habitat use. The results are underpinned by the results by Bobrowski et al. (2015) who examined feeding damage of deer in the same area. Consistent with these findings, older forest stands (HC2, 3) and those with abundant coniferous trees are less important to the deer, as the number of faecal pellets groups in these sites were low, which is consistent with the study of Bobek et al. (1984).

However, there were some species-specific differences in the vegetation preferred by the two deer in the present study. Although red deer preferred areas with bilberry, followed by rowan and beech, roe deer preferred areas with beech, followed by bilberry and blackberry. For both cervids birch was important but to a lesser extent. Bilberry is a common food resource for both species and the deciduous trees are known to be a preferred source for feeding for deer (Saint-Andrieux et al. 2009, Mysterud et al. 2010, Bobrowski et al. 2015). The choice of specific food plants is mainly influenced by the nutritional quality (Hagemoen and Reimers 2002, Dussault et al. 2005, Stolter et al. 2005, Ferretti et al. 2008, Bjørneraas et al. 2012, Felton et al. 2018). The overall quality of a habitat differs between seasons (Stolter et al. 2013), whereas the food availability depends on the vegetation composition and therefore is often related to forest

Table 5. Upper section: results of the GLM of roe deer including all relevant PCs (AIC = 1535.9); lower section: explanation of the variables summarized in the different PCs.

	Estimate	SE	z-value	p-value
Intercept	-1.57	0.07	-23.28	≤ 0.001
PC1	0.08	0.04	1.95	0.052
PC2	0.14	0.03	3.91	≤ 0.001
PC3	0.05	0.05	1.12	0.26
PC4	0.37	0.06	6.55	≤ 0.001
PC5	0.08	0.03	2.54	0.011
PC1	PC2	PC3	PC4	PC5
Birch HC1	Beech HC1 b	Spruce HC1	Bilberry	Blackberry
Birch HC1 b	Beech total b	Spruce total	Dist. mineral licks	
Birch total				
Birch total b				

Table 6. Results of two GLMs of roe deer including PC2 and PC5 and two different co-variates (either bilberry or distance to mineral licks).

Co-variate	Bilberry		Distance to mineral licks	
	Estimate	p-value	Estimate	p-value
Intercept	-1.69	≤ 0.001	-1.15	≤ 0.001
PC2	0.13	≤ 0.001	0.14	≤ 0.001
PC5	0.08	0.004	0.07	0.02
Covariate	0.02	≤ 0.001	-0.001	0.002
AIC	1517.11		1549.0	
ΔAIC	0		31.89	
AICw	0.99		0	

management practices (Morrison et al. 2006). Therefore, the preference for specific food plants may not only depend on traits, such as chemistry and morphology (Stolter 2008, Stolter et al. 2013), but also on the surrounding vegetation (Bee et al. 2009).

Furthermore, the occurrence of mineral licks was positively related to the faecal pellet counts of both cervid species and thus seems to be important for habitat selection and use. Mineral licks offer sodium, magnesium and other trace elements, which are often limited to deer because of either a low concentration or lack of availability in the plants. In these situations, many species of animals rely on mineral licks or mineral rich soils (Laurian et al. 2008, Tobler et al. 2009).

Contrary to our expectations, we found no influence of the vicinity of settlements or elevated hunting stands on the distribution of faecal pellets of either deer species. However, our study site was surrounded only by small villages and we did not measure habitat use during the hunt and during summer, when human disturbance may be greater due to tourism and agricultural activity. Therefore, other study areas and times might lead to different results (Wu et al. 2016, 2019 but see Tinoco Torres et al. 2011).

However, there was striking difference between the two deer species in the impact of pathways, with this being a major effect on red deer but not for roe deer. The study area was well connected by a variety of forest roads and hiking paths. Our results showed that red deer avoided these paths, which are utilized mainly for hiking and cycling, but also by foresters and hunters. These activities can increase vigilance of red deer (Jayakody et al. 2008) or drive red deer from the source of disturbance (Reimoser and Gossow 1996, Sibald et al. 2011, Webb et al. 2011). However, other ungulates like the Rocky Mountain elk *Cervus canadensis nelsoni* also avoided roads (Cole et al. 1997) and although previous studies have demonstrated that roe deer and eastern roe deer *Capreolus pygargus bedfordi* also avoid roads (Hewison et al. 2001, Jiang et al. 2009), this was not the case in our study.

Nevertheless, unlike red deer, we found a minor influence of young Norway spruce (HC1) on habitat selection, which seem to be not connected to food availability as the trees were not browsed. Young Norway spruce is generally not a preferred food plant by cervids (Bobrowski et al. 2015) due to its poor digestibility and high concentrations in plant secondary metabolites (Stolter et al. 2009). Instead, these young spruce plants could provide cover for roe deer (Gill et al. 1996, Latham et al. 1997). San José et al. (1997) determined that roe deer favoured high cover and high botanical diversity of tree stratum. Additionally, roe deer preferred forest

with young trees (Welch et al. 1990), e.g. early successional stages (Henry 1981, Staines and Welch 1984), which might offer additional thermal cover in the case of young coniferous trees (Partl et al. 2002) and additional food resources in the case of deciduous trees in combination with under-ground vegetation such as bilberry (Latham et al. 1999).

Our results suggest similarities in habitat choice of the two cervids. For both cervids the availability of bilberry as a common food resource and the occurrence of deciduous trees as food seem to be the main driver of habitat use. However, the impact on the distribution is plant species-specific. Furthermore, the vicinity of mineral licks was important for both deer species. In contrast to roe deer, the results for red deer suggest a stronger anthropogenic influence on the choice of the habitat, but all other measured anthropogenic landscape features had no effects on both cervids (e.g. settlements, elevated hunting stands).

Conclusions

Our results could be used to design strategies for managing deer in commercial forests and for hunting. For example, our study site is characterized by two important factors: Firstly, typically for German forests, our study area contains many old trees, with a high proportion of coniferous trees. But we found that sites containing young trees were preferred as these offer more food resources. If the density of both species is maintained at a similar level a greater availability of young trees as a food resource will help to avoid deer stripping the bark from old trees but at a cost to recruiting forestry target species such as beech.

We therefore recommend the maintenance of open sites with ground vegetation such as bilberry and with young non-target deciduous tree species like rowan and birch as feeding sites. This could be useful 'decoy' to draw deer away from trees of high value to the forest industries and thereby enhance biodiversity. Our results show, that these young open forest stands should be interspersed with dense islands of young coniferous trees to offer shelter. Additionally, mineral licks could also be useful to attract deer and lure it to the created feeding sites. This attraction will be beneficial to hold the created feeding site in an early successional state. However, these young forest stands (feeding sites) should not be close to target tree species for forestry and pathways used by humans as disturbance may lead red deer retreating to old forest stands and possibly feeding on bark (Kiffner et al. 2008, Borkowski and Ukalski 2012). Subsequently

after implementing feeding sites, hunting strategies can be adapted to this kind of animal distribution management, e.g. hunting can be either banned or enhanced at these sites. These management options may improve existing forests and might be helpful to bring into accordance biodiversity, forestry, human recreation and wildlife.

Acknowledgements – We are grateful to Hans-Hermann Engelke, Knut Sierk from Niedersächsische Landesforsten for support, providing information and giving us permission to do fieldwork in the conservation area Lüneburger Heide. With many thanks for the language corrections to Sonja Schmidt and Bill Foley for his advice and language corrections.

Conflicts of interest – The authors declare no conflict of interest.

References

- Akaike, H. 1974. A new look at the statistical model identification. – IEEE Trans. Autom. Control 19: 716–723.
- Anderson, D. R. 2008. Model based inference in the life sciences. – Springer Science and Business Media.
- Anderson, R. D. and Rubin, H. 1956. Statistical inference in factor analysis. – Proc 3rd Berkeley Symp. of Mathematical Statistics and Probability 5: 111–150.
- Archibald, S. et al. 2005. Shaping the landscape: fire–grazer interactions in an African savanna. – Ecol. Appl. 15: 96–109.
- Bee, J. N. et al. 2009. The benefits of being in a bad neighbourhood: plant community composition influences red deer foraging decisions. – Oikos 118: 18–24.
- Bjørneraas, K. et al. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. – Oecologia 168: 231–243.
- Bobek, B. et al. 1984. Factors affecting red deer (*Cervus elaphus*) population density in southeastern Poland. – J. Appl. Ecol. 21: 881–890.
- Bobrowski, M. et al. 2015. Modelling browsing of deer on beech and birch in northern Germany. – For. Ecol. Manage. 358: 212–221.
- Borkowski, J. and Ukalska, J. 2008. Winter habitat use by red and roe deer in pine-dominated forest. – For. Ecol. Manage. 255: 468–475.
- Borkowski, J. and Ukalski, K. 2012. Bark stripping by red deer in a post-disturbance area: the importance of security cover. – For. Ecol. Manage. 263: 17–23.
- Bonnot, N. et al. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. – Eur. J. Wildl. Res. 59: 185–193.
- Cole, E. K. et al. 1997. Effects of road management on movement and survival of roosevelt elk. – J. Wildl. Manage. 61: 1115–1126.
- de Boer, W. F. and Prins, H. H. T. 1990. Large herbivores that strive mightily but eat and drink as friends. – Oecologia 82: 264–274.
- Dahl, S. A. et al. 2020. High fibre selection by roe deer (*Capreolus capreolus*): evidence of ruminal microbiome adaption to seasonal and geographical differences in nutrient composition. – Anim. Prod. Sci. 60: 1303–1314.
- Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.
- Dunn, P. K. 2017. Evaluation of tweedie exponential family models. – <<https://cran.r-project.org/web/packages/tweedie/tweedie.pdf>>.
- Dussault, C. et al. 2005. Linking moose habitat selection to limiting factors. – Ecography 28: 619–628.
- Eccard, J. A. et al. 2017. European roe deer increase vigilance when faced with immediate predation risk by Eurasian lynx. – Ethology 123: 30–40.
- Ellenberg, H. 1978. Zur Populationsökologie des Rehes (*Capreolus capreolus* L., Cervidae) in Mitteleuropa. – Spixiana, Suppl 2: 212.
- Environmental Systems Research Institute (ESRI) 2017. ArcGIS Desktop: Release 10.5.1. – Environmental Systems Research Institute, Redlands, CA, USA.
- Felton, A. M. et al. 2018. The complexity of interacting nutritional drivers behind food selection, a review of northern cervids. – Ecosphere 9: e02230.
- Ferretti, F. et al. 2008. Intolerance amongst deer species at feeding: roe deer are uneasy banqueters. – Behav. Process. 78: 487–491.
- Gebert, C. and Verheyden-Tixier, H. 2001. Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. – Mamm. Rev. 31: 189–201.
- Gill, R. A. et al. 1996. Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. – For. Ecol. Manage. 88: 31–41.
- Hagemoen, R. I. M. and Reimers, E. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. – J. Anim. Ecol. 71: 883–892.
- Hema, E. M. et al. 2013. Elephants or excrement? Comparison of the power of two survey methods for elephants in West African Savanna. – Environ. Pollut. 2: 14–26.
- Henry, B. A. M. 1981. Distribution patterns of roe deer (*Capreolus capreolus*) related to the availability of food and cover. – J. Zool. 194: 271–275.
- Hester, A. J. et al. 2006. Impacts of large herbivores on plant community structure and dynamics. – In: Danell, R. et al. (eds), Large herbivore ecology, ecosystem dynamics and conservation. Cambridge Univ. Press, pp. 97–141.
- Hewison, A. J. M. et al. 2001. The effects of woodland fragmentation and human activity on roe deer distribution in agricultural landscapes. – Can. J. Zool. 79: 679–689.
- Hofmann, R. R. 1988. Morphophysiological evolutionary adaptations of the ruminant digestive system. – In: Dobson, A. and Dobson, M. (eds), Aspects of digestive physiology in ruminants. Proc. of a Satellite Symposium of the 30th Int. Congr. of the Int. Union of Physiol. Sci., Cornell Univ. Press, pp. 1–20.
- Jayakody, S. et al. 2008. Red deer *Cervus elaphus* vigilance behavior differs with habitat and type of human disturbance. – Wildl. Biol. 14: 81–91.
- Jiang, G. et al. 2008. Habitat use and separation between red deer *Cervus elaphus xanthopygus* and roe deer *Capreolus pygargus bedfordi* in relation to human disturbance in the Wandashan Mountains, northeastern China. – Wildl. Biol. 14: 92–100.
- Jiang, G. et al. 2009. Effects of human activities on the spatial distribution of eastern roe deer *Capreolus pygargus bedfordi* in the Lesser Khingan Mountains, northeastern China. – Acta Theriol. 54: 61–76.
- Kiffner, C. et al. 2008. Probability of recent bark stripping damage by red deer (*Cervus elaphus*) on Norway spruce (*Picea abies*) in a low mountain range in Germany – a preliminary analysis. – Silva Fenn. 42: 125.
- König, A. et al. 2020. Response of roe deer (*Capreolus capreolus*) to seasonal and local changes in dietary energy content and quality. – Anim. Prod. Sci. 60: 1315–1325.
- Latham, J. et al. 1996. The relative densities of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer and their relationship in Scottish plantation forests. – J. Zool. 240: 285–299.
- Latham, J. et al. 1997. Correlations of red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer densities in Scottish forests with environmental variables. – J. Zool. 242: 681–704.

- Latham, J. et al. 1999. Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. – *J. Zool.* 247: 409–418.
- Laurian, C. et al. 2008. Behavioral adaptations of moose to roadside salt pools. – *J. Wildl. Manage.* 72: 1094–1100.
- Lavsund, S. 1987. Moose relationship to forestry in Finland, Norway and Sweden. – *Swedish Wildl. Res. Suppl.* 1: 229–244.
- Linnell, J. D. C. et al. 2020. The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene – *Biol. Conserv.* 244: 108500.
- Morrison, M. L. et al. 2006. *Wildlife–habitat relationships: concepts and applications.* – Island Press, Washington, D.C.
- Mysterud, A. et al. 2010. Spatial patterns of accumulated browsing and its relevance for management of red deer *Cervus elaphus*. – *Wildl. Biol.* 16: 162–172.
- Månsson, J. et al. 2011. Can pellet counts be used to accurately describe winter habitat selection by moose *Alces alces*? – *Eur. J. Wildl. Res.* 57: 1017–1023.
- Partl, E. et al. 2002. Forest restoration and browsing impact by roe deer. – *For. Ecol. Manage.* 159: 87–100.
- Prokešová, J. et al. 2006. Density of red and roe deer and their distribution in relation to different habitat characteristics in a floodplain forest. – *Folia Zool.* 55: 1–14.
- Reimoser, F. and Gossow, H. 1996. Impact of ungulates on forest vegetation and its dependence on the sivilicultural system. – *For. Ecol. Manage.* 88: 107–119.
- Revelle, W. 2019. psych: procedures for psychological, psychometric and personality research. R package ver. 1.9.12. – Northwestern Univ., Evanston, Illinois, <<https://CRAN.R-project.org/package=psych>>.
- Richard, E. et al. 2010. High red deer density depresses body mass of roe deer fawns. – *Oecologia* 163: 91–97.
- Rosenzweig, M. L. 1981. A theory of habitat selection. – *Ecology* 62: 327–335.
- Saint-Andrieux, C. et al. 2009. Factors affecting beech *Fagus sylvatica* bark stripping by red deer *Cervus elaphus* in a mixed forest. – *Wildl. Biol.* 15: 187–196.
- San José, C. et al. 1997. Habitat use by roe and red deer in southern Spain. – *Miscellanea Zool.* 20: 27–38.
- Schwarz, K. et al. 2017. Influence of differently managed bush-enriched sites on the large herbivore distribution in the Namibian Savannah. – *Afric. J. Ecol.* 56: 290–300
- Sibbald, A. M. et al. 2011. Responses of red deer (*Cervus elaphus*) to regular disturbance by hill walkers. – *Eur. J. Wildl. Res.* 57: 817–825.
- Spitzer, R. et al. 2019. Doubting dung: eDNA reveals high rates of misidentification in diverse European ungulate communities – *Eur. J. Wildl. Res.* 65: 28.
- Sönnichsen, L. et al. 2013. Behavioural responses of European roe deer to temporal variation in predation risk. – *Ethology* 119: 233–243.
- Staines, B. and Welch, D. 1984. Habitat selection and impact of red (*Cervus elaphus* L.) and roe (*Capreolus capreolus* L.) deer in a Sitka spruce plantation. – *Proc. R. Soc. Edinb.* B 82: 303–319.
- Staines, B. W. and Scott, D. 1994. Recreation and red deer: a preliminary review of the issues. – *Scottish Natural Heritage* 31: 1–10.
- Stolter, C. 2008. Intra-individual plant response due to moose browsing: feed-back loops and impacts on multiple consumers. – *Ecol. Monogr.* 78: 167–183.
- Stolter, C. et al. 2005. Winter browsing of moose (*Alces alces*) on two different willow species: food selection in relation to plant chemistry and plant response. – *Can. J. Zool.* 83: 807–819.
- Stolter, C. et al. 2009. Comparison of secondary chemistry and digestibility of three different boreal coniferous trees. – *Basic Appl. Ecol.* 10: 19–26.
- Stolter, C. et al. 2013. Seasonal differences in the relative importance of specific phenolics and twig morphology result in contrasting patterns of foraging by a generalist herbivore. – *Can. J. Zool.* 91: 338–347.
- Storms, D. et al. 2008. Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. – *Wildl. Biol.* 14: 237–250.
- Tobler, M. W. et al. 2009. Habitat use, activity patterns and use of mineral licks by five species of ungulate in south-eastern Peru. – *J. Trop. Ecol.* 25: 261–270.
- Tinoco Torres, R. et al. 2011. Comparative use of forest habitats by roe deer and moose in a human-modified landscape in southeastern Norway during winter. – *Ecol. Res.* 26: 781–789.
- Vila, B. et al. 2003. Response of young *Tsuga heterophylla* to deer browsing: developing tools to assess deer impact on forest dynamics. – *Trees* 17: 547–553.
- Wagenmakers, E. J. and Farrell, S. 2004. AIC model selection using Akaike weights. – *Psychonomic Bull. Rev.* 11: 192–196.
- Webb, S. L. et al. 2011. Influence of land development on home range use dynamics of female elk. – *Wildl. Res.* 38: 163–167.
- Welch, D. et al. 1990. Habitat usage by red (*Cervus elaphus*) and roe (*Capreolus capreolus*) deer in a Scottish Sitka spruce plantation. – *J. Zool.* 221: 453–476.
- Wang, M. and Schreiber, A. 2001. The impact of habitat fragmentation and social structure on the population genetics of roe deer (*Capreolus capreolus* L.) in central Europe. – *Heredity* 86: 703–715.
- Wu, W. et al. 2016. Simulation of potential habitat overlap between red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in northeastern China. – *Peer J.* 4: e1756.
- Wu, W. et al. 2019. Anthropogenic effect on forest landscape pattern and Cervidae habitats in northeastern China. – *J. Geogr. Sci.* 29: 1098–1112.
- Zuur, A. F. et al. 2010. A protocol for data exploration to avoid common statistical problems. – *Methods Ecol. Evol.* 1: 3–14.

Supplementary material (available online as Appendix wlb-00723 at (<www.wildlifebiology.org/appendix/wlb-00723>). Appendix 1.