

# University of Natural Resources and Applied Life Sciences, Vienna



### **DECLARATION IN LIEU OF OATH**

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

01.04.2019

Date

Signature

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# ABSTRACT

Europe is a heavily human altered continent, where large natural areas have become scarce and are often protected by national parks. These, however, are often too small to ensure a protection of large-scale ecological processes, such as the distribution of ungulates, from external anthropogenic influences. The Bieszczady and especially its national park, is amongst the last more natural areas within Europe and provides the opportunity to investigate ungulate distributions in an area with contrasting management of wild life. The present study attempts to evaluate how much the winter and spring distribution of red deer (Cervus elaphus), roe deer (Capreolus capreolus) and wild boar (Sus scrofa) is influenced by anthropogenic and environmental factors in the Bieszczady National Park and its surroundings. Ungulate densities were estimated with faecal pellet group counts on 466 cleared strip transects (500m x 2m) in a study area of 466km<sup>2</sup>. Generalized additive models (GAM) and relative importances were used to analyse the influence of environmental and anthropogenic predictors. To include potential predatory effects, a regional wolf (Canis lupus) habitat model was calculated. The results revealed that the distribution of red deer, roe deer and wild boar in the Bieszczady is driven to 77%, 79% and 85%, respectively, by environmental and to 23%, 21% and 15%, respectively, by anthropogenic factors. The ungulate distribution in the Bieszczady is dominated by environmental, but also influenced by anthropogenic factors. The area is an example for management influences which do not stop at legislative boundaries, potentially causing conflicts between contrasting wildlife management.

Keywords: ungulates, winter\_habitat, pellet\_group\_count, generalized\_additive\_model, national\_park, Bieszczady, Poland

### ZUSAMMENFASSUNG

Europa ist ein stark vom Menschen geprägter Kontinent, wo große natürliche Gebiete selten geworden und oft durch Nationalparke geschützt sind. Jedoch sind diese meistens zu klein um großräumige ökologische Prozesse wie die Schalenwildverteilung vor externen menschlichen Einflüssen zu schützen. Der Bieszczady und besonders sein Nationalpark, ist eines der wenigen naturbelasseneren Gebiete und bietet die Möglichkeit die Schalenwildverteilung in einem Gebiet mit gegensätzlichem Management zu erforschen. Diese Arbeit untersucht, zu welchen Teilen die Winter- und Frühjahrsverteilung von Rothirsch (Cervus elaphus), Reh (Capreolus capreolus) und Wildschwein (*Sus scrofa*) durch menschliche oder natürliche Faktoren im Bieszczady National Park und seiner Umgebung beeinflusst wird. Mit Hilfe von Losungszählungen auf Linientransekten (500m x 2m, 1Transekte/km<sup>2</sup>) wurden die Wilddichten auf 466km<sup>2</sup> bestimmt. Anschließend wurde mit generalisierten additiven Modellen (GAM) und der Bedeutung einzelner Modellvariablen, die Verteilung der Paarhufer analysiert. Um Prädatoreinflüsse zu berücksichtigen, wurde ein regionaler Index zur Habitateignung für Wölfe (Canis lupus) berechnet. Die Ergebnisse zeigen, dass die Verteilungen von Rothirsch, Reh und Wildschwein im Bieszczady jeweils zu 77%, 79% und 85% von natürlichen und jeweils zu 23%, 21% und 15% von menschlichen Faktoren beeinflusst ist. Natürliche Faktoren dominieren zwar die Verteilung von Paarhufern im Bieszczady, jedoch ist auch der menschliche Einfluss signifikant. Dieses Gebiet ist ein Beispiel dafür, dass sich der Managementeinfluss nicht an legislative Grenzen hält und zu Konflikten zwischen gegensätzlichem Management von angrenzenden Gebieten führen könnte.

Schlagwörter: Schalenwild, Winterhabitat, Losungszählung, Bieszczady, Nationalpark, generalisierte\_additive\_Modelle, Polen

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## **1. INTRODUCTION**

The habitat of wild ungulates has become fragmented, concentrated and diminished, due to anthropogenic influences (Weisberg and Bugmann 2003). Especially on the fragmented European continent (Crooks et al. 2011), natural areas with wilderness qualities comprise only around 2.3% of the landmass (EEA 2019). These scarce areas are often protected by national parks. The protection through national parks focuses on the protection of ecological processes, species protection, education and recreation (IUCN 1994). Nevertheless, national parks are often too small to protect ecological processes, such as the natural spatial-temporal distribution of large herbivores (Keiter and Boyce 1991). They can thus be seen as a habitat island lacking sharp borders with its environment (Janzen et al. 2007). This leads to external circumstances affecting the inside of the actual management free national park and internal circumstances affecting the surroundings of the national park (Janzen et al. 2007). These effects vary with the size of the national park in their intensity, with smaller national parks being more affected by external factors (Janzen et al. 2007). Outside of national parks, the wildlife management usually aims for high ungulate densities in economically less important forests, to increase recreation opportunities for hunters without reducing economic benefits for foresters or farmers (Porter and Underwood 1999). Consequently, different management aims can cause conflicts between bordering areas with a different protection status (Porter and Underwood 1999). This conflict can even lead to a landscape that is rather driven by management, even within national parks (Möst et al. 2015). Management measures like hunting (Cromsigt et al. 2013), supplemental feeding (Putman and Staines 2004) and different levels of protection (Heurich et al. 2015) directly affect wild ungulate distributions. Hunting is known to have a similar effect on ungulates like natural predation and is actively used to manage the game distribution by creating areas which are avoided by game (Cromsigt et al. 2013). In the opposite way, supplemental feeding is applied to attract game to certain areas (Putman and Staines 2004). The management of protected areas typically tries to reduce the human influence with increasing protection status which can create an attractive refuge area for wild ungulates (Tolon et al. 2009) or contrary be avoided when external management improves habitat quality in national park surroundings, by providing supplemental feed (Heurich et al. 2015). Other anthropogenic factors like settlements, roads, and recreational activities usually cause an unintended avoidance by wild ungulates (Andrea et al. 1995; Debeljak et al. 2001; Jayakody et al. 2008; Kuemmerle et al. 2010; Sibbald et al. 2011; Jerina 2012; Perzanowski et al. 2015). However, human infrastructure can also be attractive to wild ungulates by providing food resources (Thurfjell et al. 2009) or a shield against predators (Berger 2007; Atickem 2014).

When anthropogenic influences are reduced, the distribution of wild ungulates is driven by environmental factors. These typically comprise topography (Andrea et al. 1995; Mysterud 1999; Košnář and Rajnyšová 2012; Heurich et al. 2015; Morelle et al. 2015), food(Fonseca 2008; Morelle et al. 2015), shelter (Prokešová et al. 2006; Borkowski and Ukalska 2008; Perzanowski et al. 2008; Millington et al. 2010; Perzanowski and Januszczak 2010) and predator presence (Laundré et al. 2001; Hernández et al. 2005). In mountainous habitats, an increasing elevation is usually associated with higher precipitation, lower temperatures, as well as higher and longer lasting snow covers, which limits the access to food and increases the energy expenditure of movement (Mysterud et al. 1997; Náhlik et al. 2005; Borkowski and Ukalska 2008). Therefore, a dense vegetation, plays a major role in providing shelter against harsh winter conditions and poses preferred winter habitats for ungulates (Prokešová et al. 2006; Fonseca 2008; Perzanowski et al. 2008; Perzanowski and Januszczak 2008; Millington et al. 2010). On the other hand, this habitat offers unfavourable foraging conditions (González-Hernández and Silva-Pando 1999), leading to a trade-off between food and shelter (Borkowski and Ukalska 2008). Also, more favourable living conditions are found in lower elevations during winter, which leads to a seasonal migration along an elevational gradient, especially in regions with a high seasonality, where conditions vary considerably throughout the year (Mysterud 1999). Predators also play an important role for the distribution of their prey by a direct reduction through consumption (Kanzaki and Perzanowski 1997; Śmietana 2005b) and second, by indirect effects of their presence(Creel et al. 2005). The avoidance of areas that are perceived as more dangerous can ultimately create a landscape of fear (Laundré et al. 2001; Hernández et al. 2005)

Consequently, the distribution of wild ungulates always results from the trade-off between anthropogenic and environmental factors.

The present study evaluates to what degree the distribution of red deer (*Cervus elaphus*) roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*) and European bison (*Bison bonasus*) is shaped by anthropogenic and environmental factors within the Bieszczady in south-eastern Poland, where a national park is surrounded by less protected and more managed areas. Within anthropogenic factors it was tested if settlements (A1) and,due to absent supplemental feeding practices, the national park (A2) have a negative effect on ungulate densities and if supplemental feeding sites have a positive effect on ungulate densities (A3). Within environmental factors it was tested if an increase in elevation and slope has a negative effect on ungulate densities (E4), if the presence of wolves has a negative effect on ungulate densities (E5) and if coniferous forests, high canopy closure and coverage of *Rubus* spp. have a positive effect on ungulate densities (E6).

### 2.1. Study area

The study was conducted in the Bieszczady National Park (293km<sup>2</sup>, hereafter BNP) and its vicinity on 466 km<sup>2</sup>. Situated in the polish part of the eastern Carpathians, this area is also referred to as the Bieszczady with a size of 1115 km<sup>2</sup> (EEA 2015). The BNP forms the core zone of the transboundary Biosphere Reserve East Carpathians (2081 km<sup>2</sup>) that additionally comprises two landscape parks (277 km<sup>2</sup> and 510 km<sup>2</sup>) in Poland, the Poloniny National Park (298 km<sup>2</sup>) in Slovakia and the Nadsanski Landscape Park (194 km<sup>2</sup>) and Uzanski National Park (392 km<sup>2</sup>) in the Ukraine (Winnicki and Zemanek 2001).

In the Bieszczady National Park (hereafter BNP) elevations range from 600 m a.s.l to 1346 m a.s.l. The continental climate causes an annual precipitation of 800-1200 mm, a mean annual temperature of 4.9°C and a snow cover lasting 4-5 months with depths of up to 150 cm. The mixed mountain forest covers around 80% of the BNP area and is dominated by European beech (Fagus silvatica), silver fir (Abies alba) and Norway spruce (Picea abies). Additional common species are grey alder (Alnus incana) and sycamore (Acer pseudoplatanus) (Zarzycki 1963). Open landscapes are found in the valleys (Winnicki and Zemanek 2001) and above 1150 m a.s.l. as "połoninas", a subalpine meadow with blueberries and а variety of grasses (Zarzycki and Glowaciński 1986). With only 6 inhabitants/km<sup>2</sup>, the human population density is very low all over the Bieszczady (Śmietana 2005a).

The Bieszczady sustains a natural ungulate composition, with red deer, roe deer, wild boar, and European bison, which was reintroduced in the 1960's and hunted outside the BNP soon afterwards. The population of European bison grew constantly until the suspicion arouse, that one of the two herds was infected with bovine tuberculosis, leading to the culling of one herd (30 individuals) in 2016. To enforce recolonisation, the state forestry tried to relocate individuals from another herd together with five individuals from an enclosure during spring 2017 (while this study was conducted).

The carnivore populations of brown bears (*Ursus arctos*, 83 individuals, 2.6 individuals/100km<sup>2</sup>) (Śmietana et al. 2014), Eurasian lynx (*Lynx lynx*, 60 individuals, 3 individuals/100km<sup>2</sup>) and the gray wolf (*Canis lupus*, 65-100 individuals) are in a stable situation (Śmietana 2000). Śmietana and Wajda (1997) estimated a wolf density within the BNP and its surroundings of 5.1 ind./100km<sup>2</sup> in early winter and 3.3 ind./100km<sup>2</sup> in late winter/km<sup>2</sup>, whereas data from 2006 to 2012 resulted in a density of 2.6 ind./100km<sup>2</sup> within the BNP (BNP, internal Reports).

Only minimal active management measures are carried out in the BNP. One is the protection of livestock and beehives with livestock guardian dogs and electric fences. Another is to mow meadows in the valleys once a year in late summer to preserve open landscapes (pers. comm. BNP). Hunting, winter enclosures and supplemental feeding were prohibited since 1999 (Winnicki and Zemanek 2001). However, these measures are organised outside of the national park area by the State Forest National Forest Holding and local hunting associations, without any buffer zone to the national park. Supplemental feeding with corn (Śmietana and Wajda 1997), silage and hay (personal observation) is very common. In the voivodship of Subcarpathia (17.844 km<sup>2</sup>) a total of 4984 (0.28 ind./km<sup>2</sup>) red deer, 10633 (0.6 ind./km<sup>2</sup>) roe deer and 12850 (0.73 ind./km<sup>2</sup>) wild boar were harvested in the hunting season of 2016/2017 (Domaszewicz et al. 2017).

Economy within the BNP is mainly based on summer tourism from April to October with around half a million visitors every year (Holly et al. 2017). Outside the national park borders, forestry is the dominant source of income (Domaszewicz et al. 2017).



Fig.1 Location of the Study area in the Bieszczady and Europe (inset), sample squares, area of the BNP and national borders. Created in Arc GIS 10.5

#### 2.2. Pellet group counts

Pellet group counts were permitted by the authorities of Bieszczady National Park and the State Forests. The census was designed as a clearance strip census (Buckland et al. 1993), meaning that the strip transects were considered as completely covered by the leave fall in autumn. The exact date used for this event was the 15<sup>th</sup> of November 2017, as suggested in Holly et al. (2017), since most leaves are assumed to have fallen by this date and to cover old faecal pellet groups. Resulting differences in accumulation periods, between leave fall and different dates of data collection, were accounted for in the transition to ungulate densities (see 2.5). Similar to former studies in the BNP (Holly et al. 2017) the study area of 466km<sup>2</sup> was partitioned into 1km<sup>2</sup> squares(Fig.1). Within each square one transect was walked, resulting in a total of 466 transects. Each transect had a length of 500m and was two meters wide, covering an area of 0,1ha. The transects were placed by the fieldworkers as straight lines into a square, so that it did not exceed the boundaries of a square. To walk transects as straight lines, one followed the beforehand determined bearing of a planned transect with a field compass. To take the terrain ruggedness into account, the walked transect length was controlled with the trip odometer function of a handheld GPS (GARMIN GPSMAP 64s), that records the distance travelled since it was reset. The handheld GPS was also used to record the endpoints and the path of the transect for the subsequent spatial analysis. The transects were placed on an elevational range of 553-1339 m a.s.l.. The number of pellet groups with a minimum of five pellets of red deer, roe deer and wild boar that were lying more than half on the transect were counted, whereas bison pats were counted as one pellet group. Pellet groups of different species were differentiated by their size and shape. The survey was conducted after snow melt, between March 29 th and June 8 th 2017, starting with transects that were snow free first (usually in low elevations and with a southern aspect).

### 2.3. Model predictors

#### 2.3.1. Predictors in the field

The dominant habitat (13 categories: Norway spruce (*Picea abies*), grey alder (*Alnus incana*), silver fir(*Abies alba*), European beech (*Fagus sylvatica*), European larch (*Larix decidua*), sycamore (*Acer pseudoplatanus*), common hazel (*Corylus avelana*), Scots pine (*Pinus sylvestris*), birch (*Betula spec.*), European rowan (*Sorbus aucuparia*), aspen (*Populus tremula*), polonina and meadow/wetland), the estimated canopy closure and estimated rubus cover (*Rubus spp.*) (4 categories each; breaks at 10%, 40% and 70%, predictor names "canopy" and "rubus") were recorded in the field. For the analysis, the recorded habitats were summarized into six categories

of broadleaf, conifer, mixed, meadows and peatlands, polonina and for transects that contained more than one habitat type the category other habitat within the predictor "habitat". The estimated canopy cover and rubus cover were integrated as numeric variables, by using the means of estimated categories (5%, 25%, 55% and 85%).

Predictor name	Definition	Resolution	Range	Categories	Models	Predictor Set
dist.to.Urban	distance to closest settlement	10mx10m	0.0- 6483.0m	-	**	
dist.to.Roads	distance to sealed roads	10mx10m	47.9- 12668.6m	-	-	
dist.to.Forestroads	distance to forest roads	10mx10m	16.2- 8697.0m	-	-	Ant
NP	More than 50% of transect in or out of the BNP	-	-	inNP/outNP	**	hropoge factors
dist.to.Feed	distance to closest artificial supplemental feeding site	10mx10m	274.1- 10112.5m	-		enic
dist.to.Trail	distance to closest hiking trail	10mx10m	0.1-3139.1 m	-	-	
rubus	percentage of rubus spec. covering the ground	-	5%-85%	-		
canopy	percentage of canopy closure	-	5%-85%	-		
habitat	habitat type	-	-	broadleaf, conifer, mixed forest (mixed), polonina (pol), meadows and peatlands (mead/peat), other		Enviro fac
Wolf_HSI	Habitat Suitability Index for wolves	100mx100 m	0.0-1.0	-		nmen tors
Elevation	meter above sea level	10mx10m	574.1- 1314.5m	-		Ital
Slope	slope	10mx10m	3.3-58.2°	-	<b>*</b>	
TRI	terrain ruggedness	10mx10m	-	1,2,3,4,5,6,7,8,9	-	
SolRad	total solar radiation	10mx10m	770.0- 2373.0 kWh/m²	-	-	

**Table 1** Predictors, their usage in the final models for red deer, roe deer and wild boar and the according predictor set,used for the game distribution analysis.

#### 2.3.2 Predictors in GIS

A digital elevation model with a raster size of 10mx10m was generated from contour lines (provided by BNP) and used to extract elevational data (predictor name "Elevation"). It also served for the calculation of slope (predictor name "Slope") and the total solar radiation (predictor name "SOL") for the time between leaf fall and the day of fieldwork, based on elevation, surface orientation, atmospheric conditions and topography (Fu & Rich, 2002). The terrain ruggedness was measured with an index (ranging from 1 to 9) based on differences in elevation of one raster cell to its eight neighbouring cells (predictor name"TRI") (Riley et al. 1999). The administration of the BNP provided maps of supplemental feeding sites, human settlements, sealed roads, forest roads, hiking trails and the Bieszczady National Park border in Poland. National borders, settlements, sealed roads and forest roads in Slovakia and Ukraine were obtained from Openstreetmap (http://download.geofabrik.de) ("dist.to.Feed", "dist.to.Urban", "dist.to.Roads", "dist.to.Forestroads", "dist.to.Trail", "NP"; Table 1). To have one measurement of each predictor for each transect, the mean of 100 points set every five meters along the transect was calculated. Distances to features were calculated as Euclidean distances. Transects were categorised as inside or outside the national park, based on the mean distance to the BNP boundaries. All mapping and spatial analysis was done using ArcGIS 10.5(ESRI, Redlands, CA, USA).

To evaluate the influence of environmental and anthropogenic factors in this study, sets of corresponding predictors were created (Table 1).

#### 2.4 Habitat suitability for wolves

To account for the presence of wolves as main predators in this area (Śmietana et al. 2000), a habitat suitability model (HSM) was calculated with long-term observation data and validated by telemetry data of one individual.

#### 2.4.1 Wolf telemetry data

Telemetry data were obtained from a female wolf (two to three years old at capture) that was live trapped with a Belisle foot snare (Belisle, Labelle, Canada) with combined GSM alarm system and collared with a Vectronic GPS plus (Vectronic Aerospace, Berlin, Germany) in April 2015. Field observations suggest that it stayed with the parental pack and in its territory in the BNP and adjacent areas until she migrated to Slovakia in November 2015. Theuerkauf et al. (2007) additionally concluded, that activity patterns in north-eastern Poland did not differ even between packs of the same area, so that single wolves are able to represent the movements of the whole pack, also in the Bieszczady. Thus, it was assumed, that the space use of the collared wolf is

representative for the full pack. However, the GPS locations for the analysis were restricted until the start of the migration to Slovakia. In these eight months positions were recorded in 2h intervals, resulting in 2122 locations.

### 2.4.2 Wolf observations

1415 observations from 12 years of wolf monitoring (2006-2018) in the BNP and its vicinity were used to for the analysis. Data from this dataset can be divided into three types.

The first type comprises data from standardized snow tracking counts that were organized in large areas of the BNP. Therefore, the Staff of the BNP simultaneously walked predetermined transects through the BNP and recorded wolf tracks in the snow.

The second type consists of data from the regular snow tracking in the BNP and adjacent area. The search effort for snow tracks shifted periodically in patches through the complete area. The tracking always followed the same method. First, searching for wolf tracks crossing a road and then follow the track from the road as long as possible. The number of wolves and all signs and markings (e.g. urine marking) were recorded with a handheld GPS.

The third type includes all random observations, such as reported sightings by staff during their field work (direct sightings, scats, footprints, wolf kills) as well as random camera trap records (only BNP). Nevertheless, all of these observations and records needed approval by the wildlife management of the BNP. For some observations a definite number of individuals was missing (e.g. uncertainty in snow tracking). Thus, the count data were transformed into a binomial framework, with equal weights of observations. In addition, the binominal data is more conservative and reliable, especially when it comes to predictive modelling (Guisan et. al. 2017) as in this study.

#### 2.4.3 Wolf habitat suitability model (HSM)

For the HSM of the collared wolf (Wolf\_GPS), the locations were reduced to one nighttime (02:00 am) and one daytime (02:00 pm) location per calendar day first to avoid spatial autocorrelation, resulting in 332 locations (Moran's / of total locations: 0,87; p<0,01 and after reduction: -0,26; p=0,65). Thus, the studied locations were assumed as independent. To study the habitat selection, these locations were compared to the available habitat. Following the suggestions of Barbet-Massin et al. (2012), 10.000 pseudo-absence points were therefore selected within the territory (95 % minimum convex polygon (hereafter MCP95) of GPS locations). The factors affecting the GPS locations were analyzed by applying a binominal generalized additive model (GAM) with the 'gam' function of mgcv package (Wood 2019), which seemed to fit best,

due to the adaptive character (Guisan et al. 2002). Predictors included dist.to.Roads, dist.to.Urban, Slope, Elevation and SOL and were checked for correlations using the Spearman's correlation coefficient. The correlation threshold for two predictors was a Spearman's correlation coefficient of 0.7 or higher. As a consequence of occurring correlations, only the more meaningful predictor was kept within the model (Dormann et al. 2013). Thus, the predictor dist.to.Urban was preferred over dist.to.Roads since model performance was better in this constellation.

The local HSM (Wolf\_OBSERVE\_local) based on the observation data was created similarly. Only observations within the MCP95 of GPS locations and within the months of the study period (November to June) were used for the analysis, resulting in 379 observations. For the comparison to possibly available locations, the same pseudoabsence locations as used in the Wolf\_GPS model were used here. The used GAM only included predictors, that were not used in ungulate models. The best fitting model was evaluated by comparing basic diagnostic plots for the best deviance residual fit and applying a stepwise selection function (*'step.Gam'* function) from *gam* package (Hastie 2018) to the initial set of predictors, that selects the best fitting predictor combination based on the BIC. The restrictiveness of the BIC compared to the AIC is resulting in more conservative predictions (Hastie et al. 2009).

The third step was to fit a regional HSM, based on the total amount of observations (Wolf\_OBSERVE\_regional). Following an equal procedure as in the local HSM, the binominal GAM consisted of equally weighted 985 presence points and 10.000 randomly created pseudoabsence points within the MCP95 of the total observations. To crosscheck the validity of the local and regional HSM, predictions were compared to the ones from the HSM of GPS locations with the correlation. Therefore, the predicted HSI by all three HSM was calculated for a new set of 10.000 random points within the Bieszczady. Finally, the Spearman's correlation coefficient between the predicted values of the models was calculated to compare the three HSM. The predictions of the regional HSM (Wolf\_OBSERVE\_regional) were then normalized to 1 and integrated into the ungulate models as the predictor "Wolf\_HSI".

### 2.5 Transformation of pellet group counts to game densities

To estimate the abundance of the researched species, the pellet data were transformed to game densities for each transect with the following formula after Neff (1968), considering number of pellets found per transect, a species-specific defecation rate and the number of days between local leaf fall (15.11.) and date of count:



**Formula 1** Formula for estimating game densities *N* [individuals/km<sup>2</sup>]), based on the absolute number of found pellet groups (*P*), the species-specific defecation rate(*D*[defecations/day]) and the number of days (*t*) from local leaf fall (15.11.) until the date of count, after Neff (1968).

The defecation rate depends on several factors like species, food quality, food quantity and food variability. Thus, defecation rates found in literature for red deer range from 19,0 to 25,0 (Mitchell & McCowan 1984, Mitchell et al.1985, Dobiáš et al.1996), for roe deer from 14,0 to 23,0 (Neff 1968, Dobiáš 1996, Fuller 2003, Mitchell 2009), for wild boar from 4,5-5,0 (Cristescu 2007; Massei Smith, Zentral UK Science Laboratory, unpublished) and is 20,0 for bison (Herrig 1969). Since exact defecation rates are missing for the study area and for comparability with former studies in the BNP (BNP, internal Reports), the used defecation rates to calculate the ungulate densities for further modelling, were 22 for red deer, 19 for roe deer, 4.75 for wild boar and 20 defecations per day for bison.

#### 2.6 Ungulate distribution models

The calculated densities of ungulate species per transect was modeled separately, but with identical fitting strategies and model types. First, spearman correlations for all predictors were calculated. The pairs of dist.to.Urban and dist.to.Roads, dist.to.Feed and dForestroad as well as Wolf\_HSI and Slope were 0.7 or higher, thus, the predictors dist.to.Urban, dist.to.Feed and Wolf\_HSI were kept in the three initial models of all species (Table 2). The *'step.Gam'* function from the *gam* package (Hastie 2018) was used to select the best fitting predictor combination based on the AIC. Since this function excluded the predictor Wolf\_HSI from the models of red deer and roe deer, the process was repeated, this time with slope and the distance to the closest settlement as predictors instead of Wolf\_HSI in the initial model. This did not influence the selection of the other predictors.

The final predictors for red deer densities were rubus cover, canopy closure, habitat, slope, the distance to urban areas, elevation and the distance to supplemental feeding sites. The final predictors for roe deer densities were rubus cover, habitat, slope, the distance to urban areas, elevation and the location of the transect inside or outside the national park. The final predictors for wild boar densities were canopy closure, habitat, elevation, distance to supplemental feeding sites and the habitat suitability for wolves. Furthermore, all models showed a better fit, after the dependent variable was squared with 0,3.

The relative predictor importance expresses the share of one predictor in a model to explain the response variance of the depended variable. It was calculated for predictors of each model with the 'variables\_importance' function from the biomod2 package (Thuiller et al. 2009). Therefore, the predictions of ungulate densities of the original models were compared by predictions of a model including randomized values of the predictor under investigation with a Pearson correlation. The raw relative predictor importance was calculated as one minus the mean of 100 of such correlations. To express the relative predictor importance as a percentage, these raw importances were normalized to a sum of 100.

All statistical analysis was performed with the software R Studio version 3.4.4 (R Core Team 2018).

Predictor 1	Predictor 2	Spearman correlation index	р
dist.to.Urban	dist.to.Roads	0.82	<0.001
dist.to.Feed	dForestroad	0.70	<0.001
Wolf_HSI	slope	-0.81	< 0.001

**Table 2** Spearman correlation indices and p-value (p) of predictor pairs with a value of  $\geq |0.7|$ .

## **3.1** Pellet group counts and ungulate densities

The pellet group counts of red deer, roe deer, wild boar and European bison on 466 transects showed a great variance. Of 466 transects, 330 were inside the BNP and 136 outside. A total of 2826 red deer pellet groups on 365 transects, a total of 765 roe deer pellet groups on 213 transects, a total of 353 wild boar pellet groups on 135 transects and a total of 21 European bison pellet groups on only 13 transects were found. Mean densities per square kilometre were 1.70 (SD± 2.4) for red deer, 0.54 (SD± 1.1) for roe deer, 0.98 (SD± 2.1) for wild boar and 0.01 (SD± 0.08) for European bison. Because of the limited dataset the European bison was excluded from further statistical analyses. The total population size for each species within the study area was estimated to be 792 red deer (SD± 1118), 252 roe deer (SD± 513), 457 wild boar (SD± 978) and 5 European bison (SD± 37) individuals (Table 3).

**Table 3** Number of transects with pellet groups of the respective species (PG), number of pellet groups found, the estimated population and densities for the total study area, within and outside of the BNP for red deer, roe deer, wild boar and European bison, including standard deviation (SD).

	Red Deer	Roe Deer	Wild Boar	European Bison
Number of Transects with PG				
total area	365 (78%)	213(45%)	135(29%)	13(3%)
inside NP	251 (76%)	119(36%)	96(29%)	13(4%)
outside NP	108 (79%)	94(69%)	39(29%)	0(0%)
Number of PG (total area)	2826	765	353	21
Mean Population (total area, ± SD)	792 (±1118)	252 (±513)	457 (±978)	5 (± 37)
Densities [ind./km <sup>2</sup> ]				
total area Mean (± SD)	1.70 (± 2.4)	0.54 (±1.1)	0.98 (±2.1)	0.01 (±0.08)
inside NP Mean (± SD)	1.21 (± 1.6)	0.27 (± 0.5)	0.84 (± 1.7)	0.02 (± 0.1)
outside NP Mean (± SD)	2.91 (± 3.3)	1.21 (± 1.7)	1.32 (± 2.7)	0 (± 0)

# 3.2 Wolf habitat suitability model (HSM)

The most important factor influencing a high wolf presence was slope (Fig.2). All three models showed the highest significance level and chi-square values for this factor. A decreasing distance to urban areas had a significant positive effect within the Wolf\_GPS model but was more ambiguous within the models based on observational data. In the models Wolf\_OBSERVE\_local and Wolf\_OBSERVE\_regional, a preference for a distance to the next human settlements of about 900 meters is displayed and declines rapidly towards both lower and higher distances. In the Wolf\_GPS model elevation had a significant effect on wolf presence and displayed the highest presence in an elevation about 700m and declined towards both lower and higher elevations. The models Wolf\_GPS (n = 10.332, adjusted R<sup>2</sup> = 0,056), Wolf\_OBSERVE\_local (n = 10.379, adjusted R<sup>2</sup> = 0,087) and Wolf\_OBSERVE\_regional (n = 10.985, adjusted R<sup>2</sup> = 0,082) explained 14,2%, 19,2% and 12,4% of the deviance, respectively (Table 4).

**Table 4** Summary of generalized additive mixed models predicting habitat selection by wolves in the Bieszczady, based on GPS locations of the individual (Wolf\_GPS), the observations within the MCP95 of GPS locations (Wolf\_OBSERVE\_local) from November to June and observations within the regional MCP95 (Wolf\_OBSERVE\_regional) from November to June. The estimated degrees of freedom (edf), residual degrees of freedom (Ref.df), chi-square test statistics ( $\chi$ 2), and p-values (p) refer to the spline functions summary statistics for the continuous predictors.

Predictors	Wol	f_GPS			Wol	Wolf_OBSERVE_local			Wolf_OBSERVE_regional			
Fredictors	edf	Ref.df	χ2	р	edf	Ref.df	χ2	р	edf	Ref.df	χ2	р
parametric co	efficients											
(intercept)	-4.003	0.089	-45.1	<0.001	-4.318	0.104	-41.5	<0.001	-2.751	0.049	-56.1	<0.001
approximate	significanc	e of smoo	th terms									
s(Slope)	2.345	2.966	112.4	<0.001	1.005	1.011	286.1	<0.001	5.325	6.454	466.2	<0.001
s(dist.to. Urban)	1.135	1.257	33.4	<0.001	6.179	7.276	53.5	<0.001	8.531	8.935	114.2	<0.001
s(Elevation)	7.875	8.670	36.0	<0.001	-	-	-	-	-	-	-	-
s(SOL)	3.616	4.596	11.9	0.025	~	1000	177	-	a.	-	9599	155
model fit												
dev. exp		14,	2%			19,	2%			12,	4%	
r²(adj)		0,0	56		0,087			0,082				
n		103	332			103	379			109	985	



**Fig.2** Plots of significant smooth terms from the generalized additive models Wolf\_GPS, Wolf\_OBSERVE\_local and Wolf\_OBSERVE\_regional, predicting habitat selection of wolves in the Bieszczady.

The predictions of the three HSM showed high correlations on local and regional scale. Especially the predictions of the models Wolf\_GPS and Wolf\_OBSERVE\_local, which correlate with 0,87 on the local scale and the predictions of the models Wolf\_GPS and Wolf\_OBSERVE\_regional, which correlate with 0,71 (Table 5) show the reliability of the observation data to resemble the habitat usage of wolves in the Bieszczady.

**Table 5** Spearman correlation coefficients between the predictions of Wolf\_GPS, Wolf\_OBSERVE\_local and Wolf\_OBSERVE\_regional on the two prediction scales of 10.000 random points within the 95%MCP of GPS location (local, white background) and 10.000 random points within the 95%MCP of regional field observations (regional, grey background).

	Wolf_GPS	Wolf_OBSERVE_local	Wolf_OBSERVE_regiona	
Wolf_GPS	local regional	0.87	0.87	
Wolf_OBSERVE_local	0.89		0.98	
Wolf_OBSERVE_regional	0.71	0.80		

**Fig. 3** Predicted wolf habitat suitability index (1=high and 0=low suitability) by the Wolf\_OBSERVE\_regional model, based on data from the 95% MCP of 12 years of field observation and for the study period (November to June). The equivalent predictions from the Wolf\_GPS model are included (inlet).



# 3.3 Ungulate distribution models

The red deer model explained 47.6 percent of the deviance and had an adjusted R<sup>2</sup> of 0.449

(Table 6).

**Table 6** Red deer model: Summary of final generalized additive mixed model predicting red deer densities between

 November and June in the Bieszczady, the importance of each predictor (pi) and its corresponding predictor set.

Red deer							
predictors	Estimate	Std. error	t-value	Pr(> t )	sig. codes	pi (%)	predictor set
parametric coefficients							
(Intercept)	0.586	0,109	5,354	<0,001	***	-	-
rubus	0.007	0.001	6.458	<0,001	***	28	Environment
canopy	0.004	0.001	2.805	0,005	**	10	Environment
veg_broadleaf	-0.240	0.054	-4.426	<0,001	***		
veg_other	-0.009	0.069	-0.138	0.890			
veg_mead/peat	-0.297	-0.136	-2.180	0.03	*	20	Environment
veg_conifer	0.162	0.110	1.474	0.141			
veg_polonina	-0.025	0.193	-0.129	0.897			
	edf	Ref.df	χ2	р			
approximate signifi	icance of smo	ooth terms					
s(Slope)	3.901	4.882	3.972	0.002	**	9	Environment
s(dist.to.Urban)	2.250	2.850	3.718	0.021	*	6	Anthropogenic
s(Elevation)	3.115	3.960	2.977	0.018	*	10	Environment
s(dist.to.Feed)	6.337	7.490	4.015	<0.001	***	17	Anthropogenic
Sum predictor impo	ortance:					100	
Model fit							
dev. exp(%)			47.	5			
r²(adj.)			0.44	.9			
n	466						

Model formula:

reddeer^0.3 ~ rubus + canopy+ veg + s(Slope) + s(dist.to.Urban) + s(Elevation) + s(dist.to.Feed) The estimate, standard error (Std.error) t-value and p-value (Pr(>|t|)) refer to the summary of parametric coefficients. The intercept includes: rubus\_0-10%, canopy\_0-10% and veg\_mixed. The estimated degrees of freedom (edf), residual degrees of freedom (Ref.df), chi- square test statistics ( $\chi$ 2), and p-values (p) refer to the spline functions summary statistics for the continuous predictors (smooth terms). The relative predictor importance sums up to 100%.

Significance codes(sig. codes):  $0'^{**'} 0.001'^{*'} 0.01'^{*'} 0.05'.0.1'' 1$ , with bold letters for significances of p<0.05.

The roe deer model explained 37.6 percent of the deviance and had an adjusted  $R^2$  of 0.36 (Table 7).

**Table 7** Roe deer model: Summary of final generalized additive mixed model predicting roe deer densities between

 November and June in the Bieszczady, the importance of each predictor (pi) and its corresponding predictor set.

Roe Deer									
predictors	Estimate	Std. error	t-value	Pr(> t )	sig. codes	pi (%)	predictor set		
parametric coefficie	parametric coefficients								
(Intercept)	0.598	0.053	11.198	<0.001	***	-			
rubus	0.003	0.001	3.292	0.001	**	10	Environment		
veg_broadleaf	-0.115	0.051	-2.267	0.024	*				
veg_other	-0.026	0.058	-0.453	0.651					
veg_mead/peat	-0.529	0.100	-5.274	<0.001	***	26	Environment		
veg_conifer	-0.035	0.106	-0.335	0.738					
veg_polonina	-0.073	0.164	-0.445	0.657					
inNP	-0.218	0.048	-4.557	<0.001	***	20	Anthropogenic		
	edf	Ref.df	χ2	р					
approximate signific	cance of smo	ooth terms							
s(Slope)	1	1	13.229	<0.001	***	16	Environment		
s(dist.to.Urban)	1	1	4.319	0.04	*	5	Anthropogenic		
s(Elevation)	2.567	3.282	4.600	0.002	**	23	Environment		
sum predictor impo	ortance:					100			
Model fit									
dev. exp(%)			37.0	5					
r²(adj.)			0.30	5					
n			466	5					

Model formula: roedeer^0.3 ~ rubus + veg + inNP +s(Slope) + s(dist.to.Urban) + s(Elevation)

The estimate, standard error (Std.error) t-value and p-value (Pr(>|t|)) refer to the summary of parametric coefficients. The intercept includes: rubus\_0-10%, canopy\_0-10% and veg\_mixed. The estimated degrees of freedom (edf), residual degrees of freedom (Ref.df), chi- square test statistics ( $\chi$ 2), and p-values (p) refer to the spline functions summary statistics for the continuous predictors (smooth terms). The relative predictor importance sums up to 100%.

Significance codes(sig. codes):  $0'^{**'} 0.001'^{*'} 0.01'^{*'} 0.05'.01'' 1$ , with bold letters for significances of p≤0.05.

The wild boar model explained 27.6 percent of the deviance and had an adjusted  $R^2$  of 0.249 (Table 8).

**Table 8** Wild boar model: Summary of final generalized additive mixed model predicting wild boar densities between

 November and June in the Bieszczady, the importance of each predictor (pi) and its corresponding predictor set.

Wild boar							
predictors	Estimate	Std. error	t-value	Pr(> t )	sig. codes	pi (%)	predictor set
parametric coeffic							
(Intercept)	0.053	0.139	0.384	0.701	•	-	
canopy	0.005	0.002	3.243	0.001	**	14	Environment
veg_broadleaf	-0.226	0.069	-3.289	0.001	**		
veg_other	0.082	0.088	0.938	0.349			
veg_mead/peat	0.287	0.168	1.714	0.087		18	Environment
veg_conifer	0.061	0.143	0.429	0.668			
veg_polonina	0.382	0.251	1.524	0.128			
	edf	Ref.df	χ2	р			
		approxima	te significa	nce of smoo	oth terms		
s(Elevation)	3.348	4.230	7.198	<0.001	***	17	Environment
s(dist.to.Feed)	4.153	5.140	5.610	<0.001	***	16	Anthropogenic
s(Wolf_HSI)	2.830	3.566	10.058	<0.001	***	35	Environment
sum predictor importance:						100	
model fit							
dev. exp(%)	dev. exp(%) 27.6						
r²(adj.)	(adj.) 0.249						
n			466	5			

Model formula: wild boar^0.3 ~ canopy+ veg + +s(Elevation) + s(dist.to.Feed) + s(Wolf)

The estimate, standard error (Std.error) t-value and p-value (Pr(>|t|)) refer to the summary of parametric coefficients. The intercept includes canopy\_0-10% and veg\_mixed. The estimated degrees of freedom (edf), residual degrees of freedom (Ref.df), chi- square test statistics ( $\chi$ 2), and p-values (p) refer to the spline functions summary statistics for the continuous predictors (smooth terms). The relative predictor importance sums up to 100%.

Significance codes(sig. codes):  $0'^{**} 0.001'^{**} 0.01'^{*} 0.05'.0.1'' 1$ , with bold letters for significances of p≤0.05.

With summed importances of 77%, 75% and 84%, respectively, environmental factors are more important than anthropogenic factors with summed importances of 23%, 25% and 16%, respectively (Table 9).

**Table 9** Summary of predictor importances of anthropogenic (distance to Settlements, national park and distance to supplemental feeding sites) and environmental predictors (rubus cover, canopy cover, vegetation, wolves, elevation, slope) for the generalized additive models of red deer, roe deer and wild boar.

Species	Environmental influence	Anthropogenic influence	SUM
Red deer	77%	23%	100%
Roe deer	75%	25%	100%
Wild boar	84%	16%	100%

Contrary to the first prediction (A1) the distance to the next urban area had a positive influence on roe deer densities (Fig.4) and an importance of 5%. Red deer responded more ambiguously, with highest densities at around 2000 meters and a similar predictor importance of 6%. This factor was not included in the wild boar model.

The second prediction was a negative influence of the national park area due to the absence of additional feeding practices (A2). Red deer and wild boar reacted indifferent to the national park, so that this predictor was not included in their final models (Table 6 and Table 8.), but roe deer significantly preferred areas outside of the national park (Table 7). This predictor was as important as 20% in explaining the distribution of roe deer.

Coherent with the third prediction (A3), decreasing distance to supplemental feeding sites had a significant positive influence on red deer and wild boar densities, but was excluded from the final roe deer model. In contrast to the predictions, red deer densities were highest in about 1600m distance to feeding sites and declined towards both lower and higher distances. The importance was 17% and 16% for red deer and wild boars, respectively.

In conformity with the fourth prediction (E4), increasing elevation had a significant negative influence on roe deer densities and an importance of 23%. The significant response of wild boar and red deer densities to elevation, displayed the highest densities in an elevation about 900m and 730m, respectively and declined towards both lower and higher elevations. The predictor importance was 17% for wild boar and 10% for red deer. Roe deer also reacted in line with the predictions towards slope, which had a negative influence and an importance of 9%. However, red deer displayed the highest densities at slopes of around 22% and which was also more important with 16%. Since the wild boar model contained the presence of wolves, slope was not included.



**Fig.4** Plots of significant smooth terms from generalized additive models explaining habitat selection by red deer, roe deer and wild boar in the Bieszczady.

In contrast to the fifth prediction (E5), the increasing presence of wolves had no effect on the densities of red deer and roe deer but a significant positive effect for values up to 0.15 on the wild boar densities. With 35% it is the most important predictor within the wild boar model.

Coherent with the sixth prediction (E6), habitat aspects have a strong influence on ungulate distributions with importances of 20%, 26% and 18% for red deer, roe deer and wild boar, respectively. Compared to mixed forests, pure broadleaf forest has a significant negative effect on all three species. The rubus cover shows a significant positive influence on red deer and roe deer densities and has importances of 28% and 10%, respectively, but did not influence wild boar densities. Canopy cover shows a positive influence on red deer and wild boar densities with importances of 10% and 14%, respectively, but was not included in the roe deer model.

### 4. DISCUSSION

This study indicates that the influence of environmental factors on the winter and spring distribution of red deer, roe deer and wild boar in the Bieszczady is around three to five times higher than the influence of anthropogenic factors.

Environmental conditions that positively influenced ungulate densities were cover providing habitats, high coverage of rubus, high canopy closure, low to medium elevations and low slopes or wolf presence. Anthropogenic conditions that negatively influenced ungulate densities were larger distances to the next supplemental feeding site, the national park area and larger distances to the next settlement.

Unfortunately, only few studies have investigated the factors which influence the distribution of ungulates in a quantitative approach. One was carried out in the Bohemian Forest Ecosystem, where environmental and management related factors where of equal importance (Heurich et al. 2015).

Environmental factors with a similar influence on red deer and roe deer were rubus cover, broadleaf forests, meadows and peatlands. In line with former studies (Mysterud et al. 1997), open spaces were avoided and a high canopy cover or areas with dense understory was selected (Ewald et al. 2014; Müller et al. 2017). This pattern is explained by site selection for sheltered resting sites and high quality foraging sites deer, since brambles are a year round preferred food source (Moser et al. 2006), also in the Carpathians (Perzanowski et al. 1986). Of these two factors, shelter can be more important than browse availability (Borkowski and Ukalska 2008), which is also known for north American white-tailed deer in deep snow conditions (Odocoileus virginianus) (Morrison et al. 2003) and in line with the high predictor importance of habitat type for all species in the present study. Broadleaf forests are the only type of habitat with a significant negative influence on all ungulate species in this study. This is contrary to the findings of Fonseca (2008) where wild boars selected European beech-hornbeam forests in the foothills of the Bieszczady. Food availability was mentioned as the main reason for this behavior. However, the snow cover in the foothills was only 10-40 cm and reached only half of the threshold of 80cm, proposed by Andrea et al. (1995), when snow heights start to significantly influence the habitat use of wild boars, and thus might not have effected wild boars as much as in the present study. Similarly, red deer and roe deer avoid the high snow and missing cover within pure broad leaf forests, even if broadleaf forests might be a better source of forage (Ewald et al. 2014; Müller et al. 2017). In line with the third prediction (A3) and former studies (Cagnacci et al. 2011) steeper slopes and higher elevation have a negative effect on roe deer densities in winter. As the smallest of the studied species, roe deer seems to have more problems with high snow covers (Guillet et al. 1996; Jiang et

al. 2008), harsher climate and less abundant food associated with higher elevations (Mysterud et al. 2011, Perzanowski 2000). This effect is also known to be amplified by steeper slopes (Richard et al. 2014) and consequently lead to a seasonal migration into lower areas and thus higher roe deer densities in the valleys (Perzanowski 2000). This pattern has also been observed in other areas with high seasonality (Mysterud et al. 1997, Mysterud 1999; Košnář and Rajnyšová 2012; Heurich et al. 2015). The bigger influence of snow height on roe deer densities is thus resembled by higher predictor importances of the topographical factors elevation and slope. In contrast to the clear reaction of roe deer, red deer and especially wild boar displayed a more ambiguous use of the elevational gradient. The pattern of a preference for an elevation of around 740 meters and 900 meters, respectively, could be explained with a trade-off between a suitable habitat, predator avoidance and influence of management. In general, wild boar and red deer are known to winter in lower elevations, too (Luccarini et al. 2006; Košnář and Rajnyšová 2012). However, the lowest and flattest parts of the study area are characterised by an open landscape with missing cover and forage in winter, high suitability for wolves and absent supplemental feeding sites, also outside the BNP. This combination consequently results in an avoidance of these areas. In addition, Carpathian red deer populations are known to be split into parts displaying a resident and migratory behaviour in winter (Kropil et al. 2015). This pattern might blur the general effect of elevation, too. The flexibility in behaviour towards the elevational gradient has also been reported in other areas for wild boar (Andrea et al. 1995; Morelle et al. 2015) and red deer (Heurich et al. 2015). The response of wild boar densities to the HSI of wolves fits this pattern, too. Very unsuitable areas for wolves are avoided, because of the steep terrain that also demands higher energetic costs of travelling for ungulates (Dailey and Hobbs 1989). On the other hand, very suitable areas for wolves are also avoided, maybe due to the actual presence of the predator that is known to prey on wild boar in the Bieszczady (Gula 2004) and even influence its population dynamics (Kanzaki and Perzanowski 1997). The influence of wolf presence on the distributions of roe and red deer is unclear, since slope and the distance to urban areas were included as predictors into the red deer and roe deer model (see 2.6). However, wolves and lynx do preferably prey on red deer and roe deer, respectively, in the Bieszczady, (Okarma 1984; Gula 2004) and are thus assumed to create a landscape of fear (Hernández et al. 2005) that influences the habitat selection of their prey. A possible reason why the used model was not able to represent such effects in this study, is the coarseness of used long term observation data, that does not cover small-scale effects.

Anthropogenic factors were less important for the distribution of ungulate densities in the Bieszczady, although the influence of supplemental feeding sites was significantly positive for red deer as well as wild boar densities and roe deer significantly avoided the area of the national park. The influence of supplemental feeding sites on ungulates in winter is well known to influence

home ranges (Jerina 2012; Morelle et al. 2015; Ossi et al. 2017), alter habitat selection (Van Beest et al. 2010; Plhal et al. 2014), concentrate individuals around supplemental feeding sites and even modify annual distribution patterns, especially with decreasing habitat conditions (Cross et al. 2007; Jerina 2006; Smith 2001). This can result in a local increase of forest damage and competition between ungulates, facilitate parasite and disease transmission and influence survival rates (Smith 2001; Putman and Staines 2004). Since some supplemental feeding sites are located directly at the national park border these influences are very likely to also have an effect within the actual management-free BNP. First, the higher survival rates lead to increased densities in the BNP during the vegetational period, because more ungulates live through the winter and migrate back to their summer ranges. However, the winter densities in the BNP are probably unaffected, since most individuals migrate out of the national park anyway (Perzanowski and Krzakiewicz 2000). Second, the possibly transmitted parasites and diseases (Smith 2001) are also carried with the migrating animals and in this way spread within the BNP. Third, the habitat around supplemental feeding sites is exposed to increased browsing pressure by higher deer densities (Smith 2001), sometimes up to a range of one kilometre as in the study of Van Beest et al. (2010). Roe deer densities are not influenced by supplemental feeding sites for two possible reasons. The first reason might be unsuitable feed that does not fit the narrow food spectrum of roe deer (Hofmann 1985). Second, an interspecific competition with red deer and wild boar. These ungulates are known as dominant food competitors (Latham 1999) that intimidate roe deer at shared feeding sites (Ferretti et al. 2008). Losing the interspecific competition against other ungulates can be a reason why roe deer is not able to benefit from supplemental feeding sites (Ossi et al. 2017). Instead, roe deer was the only species which avoided the national park area. These results are similar to (Heurich et al. 2015) who explained it with missing supplemental feeding, high snow-packs, high forest cover and lynx presence inside the Bavarian Forest National Park. The used models also included these factors, except of lynx occurrence, so that there must be another reason for this finding. The lynx presence is likely to also influence roe deer distribution in the Bieszczady, since it is the main predator of roe deers in the Bieszczady (Śmietana et al. 2000).Since lynx are known to avoid human settlements and to select for hunting areas in rugged terrain (Filla et al. 2017), the flat valleys with less hiding possibilities might be unfavourable hunting grounds close to human settlements, which thus could act as a human shield (Berger 2007; Atickem 2014) and pose a refuge area for roe deer resulting in higher densities close to human settlements. Red deer densities decreased only in distances to the next settlements larger than 2000 m. The influence within 2000 m is unclear due to a large variance. These findings are in line with former studies, which suggested, that the influence of settlements might play a minor role on wild life, due to the small size of the villages (Theuerkauf et al. 2007). Further more, roe deer generally do not avoid settlements as much as other ungulates (Jiang et al. 2008; Torres et al. 2011) . However Perzanowski et al. (2015) proposed a buffer of 500m around villages of up to 1000 inhabitants to protect migration routes of European bison in the Bieszczady, that seems similar with red deer ranging in distances to settlements between 600m and 3102m in Slovenia during winter (Debeljak et al. 2001). Still, this buffer accounts for an cultural landscape, which could increase the effect of settlement avoidance because of the missing cover (Sunde et al. 1998; Ciuti et al. 2012). The small settlements are also not able to provide a "human shield" protection (Berger 2007) against wolves, since they do not avoid human settlements in the Bieszczady (Theuerkauf et al. 2007). This is unlikely to be the same for lynx that do avoid human settlements between red and roe deer with different main predators. In addition, ungulates do not stay far away from the villages in the valley bottom, because of increasing elevations and associated conditions at the valley sides, which correlate with increasing distance to settlements.

The used method to survey ungulate densities by counting faecal pellet groups is a noninvasive, practicable and cost effective census technique, that has proven its reliability in former studies (Daniels 2006; Prokešová et al. 2006; Borkowski and Ukalska 2008; Heurich et al. 2015). It is becoming a widely used tool in wildlife management (Marques et al. 2001) and is part of the regular monitoring programm in the BNP, also because it is well suited for areas of low aninmal densities and strong winters(Prokešová et al. 2006). The method was considered as a clearance design, although the transects were not actively cleared beforehand, because most of the study area is either covered with decidious trees or meadows (Winnicki and Zemanek 2001). Thus, the leave fall and the high grown gras squeezed to the ground by snow in winter, covered old pellet groups and naturally "cleared" the transects. Decay rates were not implied into the calculation, since pellet groups do not decay under the snow cover during winter, because of missing invertebrate activity (Mitchell et al. 1985; Welch et al. 1990; Heurich et al. 2015). Because of scarce vegetation directly after the snow melt, this time of the year allows the easiest detection of pellet groups (Latham et al. 1996). By starting the census at low elevations and south facing slopes, the early vegetational period was followed. However, some transects were sampled in May and even June, when vegetation started to grow and some decay might have taken place already. Considering the large elevational gradient sampled, the accumulation times and conditions varied accordingly to periods of snow cover, temperature and vegetation. This probably had the biggest influence on roe deer numbers, since the pellets are generally smaller, thus harder to spot and decay faster (Heurich et al. 2015). The polonina vegetation in higher elevations likely caused a bias due to a thick shrub cover decreasing the chances of finding pellet groups, even outside the vegetational period. The negative influence of boadleaf forests might have also been enhanced by

the fact, that old pellets were better covered by leave fall and that it was more probable to count old pellet groups in habitats with less decidious trees and little ground vegetation (eg. pure stands of norwegian spruce). Ideally, specific defecation rates should be considered, when ungulate densities are estimated, since they depend on various factors such as the population structure, food quality and habitat (Bobek et al. 1984; Mysterud et al. 2007) and have a large impact on the calculated absolute number of individuals (Andersen et al. 1992). This accounts especially for landscapes with a large variability in forage quality (Rönnegård et al. 2008). The two main food sources for ungulate species during winter come from forests and outside of the BNP additionally from supplemental feeding sites. These can provide high quality food (Śmietana and Wajda 1997), which would consequently lead to higher defecation rates. Therefore, when interpreting the results, it has to be considered, that ungulate densities in higher elevations, in areas close to supplemental feeding sites and of species with small faecal decay rates might have been overestimated. In habitats with much ground vegetation cover, such as poloninas, unglate densities might have been underestimated.

This method did not change since it was established, so that it is possible to compare the census results of different years. The densities in 2013 were much lower (BNP, internal Reports), suggesting that ungulate populations in the present study are on a population high and have similar densities as in the year 2011. Despite this population high, densities are still very low compared to other European populations, especially in the national park area (Ramirez et al. 2018).

During the present study, hunting took place in parts of the study area outside of the BNP. However, the only available data is a summary for the voivodeship of Subcarpathia, what made it impossible to estimate this influence.

The method for modelling wolf habitat suitability used to estimate the habiat usage of wolves in the Bieszczady has already proven to be reliable for a variety of presence only data (Torres et al. 2013; Almasieh et al. 2014; Raine et al. 2014; Filla et al. 2017). The preference of wolves for low elevations and slopes is in line with previous studies (Singleton 1995; Kunkel and Pletsher 2000; Ciucci et al. 2003; Lesmerises et al. 2012). However, contrary to the study of Theuerkauf et al. (2007), which also suffered from small sample size, no avoidance of main roads was discovered, which might be a particular behavior of the collared wolf, which is also supported by the fact, that it was roadkilled after leaving the Bieszczady. On the other hand, traffic casualities are the most common cause of death in wolves (Nowak and Mysłajek 2016). Also the response towards human settlements is contradictory between models. In the Wolf\_GPS model settlements are not avoided, which was also found by Theuerkauf et al. (2007). Additionally, Eggermann et al. (2013) concluded, that human activity is less important for the stress level of wolves, which would

also explain the non avoidance. Contrary, the observation models display an avoidance of settlements within a distance of around 750m and 1100m, respectively. This could be explained by a seasonal diference. The high grown meadows around settlements provide a good cover, so that wolves often use these areas for daybeds during summer in the Biesczcady (pers. comm. BNP). This cover is missing in winter, so that wolves probably stay within the forest. Also, higher snow covers and less favourable climatic conditions in the open landscapes close to settlements during winter could contribute to these findings. In conclusion, the settlements have only little influence on the distribution of wolves in the Bieszczady. This is also supported by Gula et al. (2009), who found no proof of an anthropogenic influence on the wolf dispersal in the Bieszczady. However, the reference model based on the GPS locations, would have gained credibility and accuracy with data of more individuals. It is in addition noteworthy, that the homerange of the collared wolf is fitting very well to the homerange of the same pack from 1995 (Smietana and Wajda 1997), suggesting that the territory border of this pack did not change much since then. This territory is located in the oldest part of the BNP, that was protected since the establishment of the park in 1973. This is the first reported indication for a longterm occupancy of the same territory by wolves in europe. Comparable periods of known occupancies are reported from North America (Phillips and Smith 1997) and with four years from the Bialowieza National Park in poland (Jedrzejewski et al. 2007).

# 5. CONCLUSION

This study shows, that the winter and spring distribution of ungulates in the Bieszczady is dominated by environmental factors, but management still has a significant effect. In contrast to national park management goals which aim to minimize the human impact inside the protected area (IUCN 1994), national management measures affect the Bieszczady National Park directly because of the proximity to the national park. Hence, the enlargement of the national park area towards the lower San Valley and Lake Solina (Winnicki and Zemanek 2001), to protect the ecosystem on the full elevational gradient is strongly supported. At least the creation of a management free buffer zone of 1km around the national park border to protect the protected area should be considered.

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