

# 1 **Effects of forest roads on oak trees via cervid habitat use and browsing**

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## 21 **Abstract**

22 Roads can affect animals in several ways, by affecting movement, space use, foraging behaviour and  
23 mortality. As roads often have a negative effect on populations of birds and mammals, their effects  
24 are important for wildlife management. However, the effect of roads differ between different types  
25 of roads, and most studies of road ecology have focused on major roads with high traffic intensity,  
26 whilst effects of smaller unpaved forest roads in northern ecosystems are less known. We  
27 investigated the effects of forest roads in a mixed conifer forest in central Europe on cervid habitat  
28 use and browsing impact on forest regeneration during the winter season. We found that hunted  
29 cervid species avoided forest roads, and that browsing pressure was higher within the core of forest  
30 areas rather than close to roads. This led to an increased density of undamaged trees (by browsing)  
31 close to forest roads, whilst browsing damages were relatively high in the interior. Hunters often use  
32 these forest roads in the hunting season. We suggest that human disturbance creates corridors of  
33 fear along forest roads, and that cervids alter their habitat and browse use to avoid humans. This in  
34 turn has implications for forest and cervid management. This is the first study to document that  
35 gravel roads can affect oak trees through modifying cervid behaviour. Future studies should use  
36 experiments to explore this question further and separate different effects of forest roads to  
37 understand the mechanisms; edge effects on vegetation, traffic, effects on natural predators and  
38 human disturbance.

39

40 **Keywords:** deer; oak; damage; fear; hunters; edge

41

## 42 **1. Introduction**

43 Roads can affect animals in numerous ways. Roads lead to fragmentation of habitat, and major roads  
44 can create movement barriers (Bartzke *et al.*, 2015). Major roads can also cause direct mortality by

45 traffic accidents, as well as indirect effects through creating disturbance and affecting animal  
46 behavior (Leblond *et al.*, 2013). On the other hand, roads can also increase movement by facilitating  
47 more energy-efficient travel and access to new areas (Bruggeman *et al.*, 2007). The effect of roads is  
48 important for wildlife conservation, as both birds and mammals often show either avoidance or  
49 reduced population density close to human infrastructure and roads (Fahrig and Rytwinski, 2009;  
50 Benitez-Lopez *et al.*, 2010). Especially densities of hunted wildlife species are often negatively related  
51 to the density of roads, or positively with the distance to roads (Coffin, 2007). The effect of roads  
52 varies with road type and traffic intensity, and avoidance of roads by large mammals generally  
53 increases with increasing disturbance intensity (road width, traffic density, human disturbance)  
54 (Eldegard *et al.*, 2012; Leblond *et al.*, 2013; D'Amico *et al.*, 2016). However, roads with low traffic  
55 intensity may also influence animal behavior (Ciuti *et al.*, 2012; D'Amico *et al.*, 2016). The majority of  
56 studies on the effects of roads on wildlife have focused on roads with high traffic intensity, traffic  
57 accidents and barrier effects. The effect of forest gravel roads with low traffic intensity on ungulates  
58 is less known.

59 The road edge environment may differ from the surroundings, as roads create gaps in forested  
60 environments, increasing light and nutrient availability and creating soil disturbance, which can lead  
61 to changes in the vegetation (Coffin, 2007). These edge effects on vegetation can also affect  
62 herbivores in different ways which may have cascading effects on vegetation, potentially important  
63 for forest management (Cadenasso and Picett, 2000). The effect on the road-edge environment is  
64 different among road types and road surfaces, as high traffic levels on paved roads may cause local  
65 pollution, but on gravel or dirt roads, dust may spread from the road onto the vegetation nearby.  
66 Several studies have investigated effects of logging roads in tropical forest, particularly in the  
67 Amazon, which increase human access to forest areas (including effects of disturbance but also  
68 poaching) see review in Coffin (2007). Few studies have been carried out on forest roads in northern  
69 and temperate forests.

70

71 Changes in ungulate habitat selection and movement, or changes in roadside vegetation, may in turn  
72 have both positive and negative effects on ungulate browsing, and affect browsing damage on  
73 commercial forests. Aggregations of moose (*Alces alces*) due to barrier effects of major roads on  
74 migration, led to increased moose browsing on pine within 3 km from major highways (Ball and  
75 Dahlgren, 2002). Moose have also been observed to avoid major roads with high traffic intensity, and  
76 select for browse far from the road (Eldegard *et al.*, 2012). However, according to our knowledge,  
77 how forest roads with low traffic intensity affect ungulate browsing, is unknown.

78 Roads affect predation risk from hunters and natural predators, which often use roads for transport  
79 and access to new areas (Coffin, 2007; Lone *et al.*, 2014; Zimmermann *et al.*, 2014). However, if  
80 natural predators also tend to avoid roads, prey may benefit from predator free areas close to  
81 human disturbance (Berger, 2007; Muhly *et al.*, 2011). The effects of roads on predation risk may  
82 also differ with disturbance intensity. Large predators may avoid roads with high traffic intensity  
83 (Muhly *et al.*, 2011), but are known to use forest roads with low human disturbance for travel and  
84 scent marking (Barja *et al.*, 2004; Zimmermann *et al.*, 2014). As forest roads can be used by both  
85 hunters and natural predators, the risk of encountering a predator is higher close to forest roads, and  
86 roads may affect ungulates indirectly by creating a “landscape of fear” (Brown *et al.*, 1999) in the  
87 near vicinity of roads. The presence of predators may affect ungulate browsing on plants either  
88 through density-mediated effects (McLaren and Peterson, 1994; Beyer *et al.*, 2007), or by indirect  
89 non-lethal effects. Predators can affect ungulate spatio-temporal distribution, by avoiding risky  
90 habitats or risky periods (Edwards, 1983; Fortin *et al.*, 2005; Lone *et al.*, 2017). Predators may change  
91 ungulate behavior, such as increased vigilance or increased group size (Laundre *et al.*, 2001). Earlier  
92 studies have shown that group vigilance in elk increased close to roads, with reduced foraging time  
93 (shorter feeding bouts, less total time feeding) (Ciuti *et al.*, 2012). Both avoidance of high risk areas  
94 and behavioral changes can mediate browsing pressure on plants growing in these areas (Ripple *et*

95 *al.*, 2001). The effects of predators on prey behavior may also change with vegetation type, as  
96 predation risk from humans may be higher in open landscapes, whilst predation risk from lynx is  
97 higher in dense understory (Ciuti *et al.*, 2012; Lone *et al.*, 2014).

98 On the other hand, roads may be attractive habitats for wildlife. In road-edge habitats, increased  
99 light availability, disturbance and nutrients, may favor growth of early successional, fast-growing  
100 plants, usually preferred by herbivores (Price, 1991; Månsson *et al.*, 2009). Management of road-  
101 edge vegetation may also affect browse availability and palatability (Rea *et al.*, 2010). However,  
102 spreading of dust from gravel roads may render plants less palatable (Forman and Alexander, 1998;  
103 Ndibalema *et al.*, 2008). In addition, herbivores may also use roads for the ease of transport, similar  
104 to predators. In areas with snow where roads are plowed during wintertime, animals may prefer to  
105 travel on roads (Bruggeman *et al.*, 2007). Use of forest roads may therefore represent a trade –off for  
106 ungulates, between the risk of encountering predators or vehicles, and the benefits of foraging on  
107 edge vegetation and efficient travelling (Eldegard *et al.*, 2012). If predation is temporally predictable,  
108 e.g., human hunters are usually active in the daytime, this trade-off can be solved by temporal  
109 allocation of use of roads. A study of roe deer in France showed that roe deer use of open habitats  
110 increased with distance to roads and during the night, whilst use of forest increased during daytime,  
111 most likely to avoid humans (Bonnot *et al.*, 2013).

112 This study focuses on the effects of unpaved forest roads with low traffic intensity on cervid habitat  
113 use and browsing in Central Europe, to our knowledge, an area previously little investigated. We  
114 studied the effect of distance to forest roads at a small spatial scale (20-400 m) on cervid habitat use  
115 and browsing impact during winter in a commercial mixed conifer forest dominated by Scots pine  
116 (*Pinus sylvestris*) and oak (*Quercus robur*) in North-East Poland, where roe deer, red deer and moose  
117 are present. In this area, humans are the most important predator; hence, we expect that cervids  
118 would avoid forest roads during the hunting season. We also expected that avoidance of forest roads  
119 would lead to reduced browsing pressure on the vegetation near forest roads, with impacts for

120 commercial forestry. In Poland, roe deer and red deer are hunted, whilst moose is a protected  
121 species, hence roe and red deer would be expected to avoid roads more than moose. In addition,  
122 cervids have to handle the trade-off between being vigilant and foraging. In habitats with high forage  
123 availability, we expect less avoidance of roads than in habitats with low forage availability, where the  
124 cost of avoiding roads is less in terms of missed foraging opportunities.

125 We therefore predict that:

- 126 1. Habitat use by cervids will increase with increasing distance from forest roads
- 127 2. Hunted species (roe deer and red deer) show stronger avoidance of roads than non-hunted  
128 species (moose)
- 129 3. Avoidance of roads will be strongest in habitats with low forage availability
- 130 4. Browsing pressure will increase far from road
- 131 5. Density of commercial trees undamaged by browsing will decrease with increasing distance  
132 to forest roads

133

## 134 2. Materials and Methods

### 135 2.1 Study area

136 The study was carried out in the state forest district of Czarna Białostocka with an estimated area of  
137 26 066 ha in northeastern Poland (from 53°13' to 53°43' N and from 22°56' to 23°44' E). This forest  
138 district is part of a larger forest complex called the Knyszyńska Forest (62 319 ha) which is located near  
139 the Polish-Belarussian border. The forest stand is dominated by Scots pine (up to 50% cover) and oak  
140 (up to 20%), the average age of the forest is 64 years. Other major species include birch (*Betula spp.*),  
141 Norway spruce (*Picea abies*), alder (*Alnus spp.*), hornbeam (*Carpinus betulus*), larch (*Larix spp.*), ash  
142 (*Fraxinus excelsior*) and maple (*Acer spp.*). Most tree stands of the forest district were regenerated by  
143 planting. The region is characterized with a continental climate. The coldest month is January with

144 average temperature -3.4 °C and the warmest month is July with average temperature 17.2 °C. The  
145 average number of days with snow cover between December and March between years 2014 – 2017  
146 is approximately 51, but average snow depth rarely exceeds 16 cm. The growing season lasts 122 days,  
147 starting in May and ending in September. The area is flat, and its elevation ranges between 125 and  
148 157 m.a.s.l. Seasons were defined based on phenological patterns as follows: spring 16 March-15 June,  
149 summer 16 June-15 September, autumn 16 September-15 December, winter 16 December-15 March.

150 There were three deer species present in the study area: red deer (3 ind./ km<sup>2</sup>), roe deer (5.8 ind./  
151 km<sup>2</sup>) and moose (1 ind./ km<sup>2</sup>). Density of deer populations were estimated based on drive counts  
152 (Borkowski *et al.*, 2011) by hunting associations and foresters in the study area. Previous tracking  
153 studies in the area showed that wolves were present at low densities (1-5 individuals) in the area, but  
154 lynx were not (Borowik and Schmidt, 2013). Human hunting pressure therefore represented the largest  
155 predation risk for ungulates in this area. The hunting season for red deer stags starts 21. August, whilst  
156 for hinds and calves it starts at 1.October. For stags and calves, the hunting season ends the last day in  
157 February, but for hinds the end of the hunting season is 15.January. For roe deer, the hunting season  
158 is similar to red deer for females and calves, but the hunting season for bucks is 11 May – 30 August.  
159 For red deer, the hunting quota in the area during the winter 2015-2016 was for 231 animals, and 62  
160 % were shot. For roe deer, the hunting quota was for 449 animals, and 85% were shot. During the  
161 hunting season 2015-2016, 144 red deer and 380 roe deer were registered shot in the study area. Red  
162 and roe deer are hunted individually, usually from high seats or hunting towers, for a few hours at  
163 dawn and dusk. Hunters use forest roads and paths for transport, and usually only enter the forest if  
164 they detect and stalk a deer. Drive hunts with dogs and groups of hunters are sometimes used, during  
165 the season 1.October – 15.January. In addition, wild boar hunters are present most of the same period.  
166 Moose are totally protected from hunting since 2001. We surveyed winter habitat use by pellet group  
167 counts and winter browsing impact in spring 2016. The winter season overlaps mostly with the hunting  
168 season for cervids, and the results will therefore reflect mainly habitat and browse use during the  
169 hunting season.

## 170 2.2 Selection of forest stands, and plots within stands

171 Although both oak and pine are important commercial species in the area, most pine plantations  
172 were protected from deer browsing by fences. We therefore focused on cervid browsing in oak  
173 stands in this study. We chose two forest types: old (>80 years) oak forest (minimum 30% oak) and  
174 young oak thickets (7-20 years old). All stands in the area with this classification were selected using  
175 forest maps in ArcGIS, and visited according to a list of random numbers. We surveyed all stands in  
176 early spring (April/May 2016) to estimate habitat use and browsing from last winter. We alternated  
177 between old and young stands to avoid any bias in time of registration related to age of stand. Some  
178 young oak stands had plastic tube protection against deer browsing around the tree trunk. These  
179 stands were excluded from our survey, in case protection would affect deer browsing. Because of  
180 this, the number of thickets was somewhat lower than old forest surveyed; we surveyed totally 32  
181 old forest stands and 26 thickets.

182 In this study, we focused on unpaved forest roads with low traffic intensity. Forest roads were  
183 maximum 6 meters wide, and were either gravel or dirt roads. The forest is divided into forest  
184 management blocks, with a road or forest block edge occurring approximately every 500 m, hence  
185 the maximum distance from a forest road to the block interior was approximately 250m. In each oak  
186 stand we selected one plot center close to the nearest forest road (placing the edge of the plot  
187 minimum 20 m from the road to avoid edge zone effects on vegetation), and one plot far from a  
188 forest road (> 200 m from road). For each plot center, we established two circular plots using a  
189 measuring rope. The plot area was 100 m<sup>2</sup> for cervid pellet counts, and 12.5 m<sup>2</sup> for browsing  
190 surveys. In some stands, both 20 m and 200 m from road were not possible to obtain; here we  
191 selected the closest and furthest plot possible from the road. In 9 stands we had two close or two far  
192 plots. Two of 58 stands visited were too small to fit two plots and had only one plot. In total, we  
193 sampled 112 plots, 57 plots close to roads, and 55 plots far from roads. "Close" plots were from 20-  
194 100 m from forest roads (mean distance = 34 m, median distance = 20 m), and "far" plots were from  
195 120-380 m from forest roads (mean distance = 187 m, median = 163 m). These plots were distributed



196 between the 2 forest types, with 62 plots in old oak forest and 50 plots in oak thicket. For all plots,  
197 we measured the distance to the closest forest road. If two roads were present, we measured the  
198 distance to both roads, and we used the shortest distance in the analysis.

### 199 **2.3 Variables measured**

200 For each plot, we counted cervid pellet groups from winter. Pellet group counts are a good indicator  
201 of species present and habitat use (Alves *et al.*, 2013), in this case representing habitat use of two  
202 different forest types and distance to road. We identified pellet groups to species in early spring  
203 (April) before pellets from last winter had started to decompose. We assume no decay of pellets  
204 during winter, due to low temperatures. We counted only pellets on top of leaf litter, representing  
205 habitat selection by cervids during winter, and excluding pellets from the summer period before  
206 deciduous trees lost their leaves. Pellet groups were identified to species (moose, red deer, roe deer)  
207 based on size, color and shape (Bang *et al.*, 2001).

208 We measured browsing on trees in a smaller circular plot of 12.5 m<sup>2</sup> because of the high density of  
209 small trees. We included all trees and tall shrubs > 0.5 m height. Browsing marks cannot be identified  
210 to deer species with certainty, so browsing from all deer species was grouped. In each plot, we  
211 identified all trees taller than 0.5 m to species with height and browsing impact measured. We  
212 measured diameter at breast height (1.37 m) for trees  $\geq$  1.37 m height. Occurrence of browsing last  
213 winter (0/1) was defined per tree as if there was  $\geq$  1 fresh bitten twig within browsing height (0.5-3.0  
214 m). The effect of previous browsing, i.e. browsing occurring over several years, was registered using  
215 an accumulated browsing index (Skarpe *et al.*, 2000; Mathisen *et al.*, 2017) as follows: 0=no old  
216 browsing, 1=old browsing present but the architecture of the tree had not changed, 2= old browsing  
217 had changed the architecture of the tree (i.e. crooked stem or increased branching), 3= old browsing  
218 had strongly modified the architecture of the tree (i.e. multiple stems, brooming). Lastly, we  
219 registered if bark stripping was present or absent (0/1), including both fresh and old bark stripping.

## 220 2.4 Statistical analysis

### 221 2.4.1 Cervid pellet groups

222 We carried out all statistical analysis using the program R 3.3.1. (R Development Core Team, 2016),  
223 the model for each response variable is described in Appendix A. The effect of distance to road,  
224 forest type and the interaction between distance and forest type on cervid pellet group counts per  
225 plot was analyzed using a generalized linear mixed model using the package lme4 (Bates *et al.*, 2017)  
226 and the function glmer. Distance to road was a categorical variable classified as “close” = 20-100 m  
227 from road, and “far” = 120-380 m from road. Forest type was classified as either “thicket” (7-20 years  
228 old) or “old forest” (> 80 years old). Forest block number was included in the model as a random  
229 intercept, to account for pairwise plots (close and far) in most stands. For moose pellet counts,  
230 limited sample size precluded running a complex model, so we used a glm rather than a mixed  
231 model, with a Poisson distribution and a log-link function. Red and roe deer pellet group counts were  
232 overdispersed (variance > mean), so they were analyzed with a negative binomial model, and a log-  
233 link function. The significance of explanatory variables was investigated using the drop1 function  
234 with Chi square tests according to (Zuur *et al.*, 2009), which drops each variable, and compares the  
235 full model with the nested model, excluding this variable. We carried out model validation of each  
236 model by plotting the deviance residuals versus fitted values and all explanatory variables, and  
237 looking for patterns. We checked for overdispersion by evaluating if the dispersion parameter  
238 (residual deviance/df ) was larger than 1 (Zuur *et al.*, 2009). We also checked for outliers by plotting  
239 each response variable versus all explanatory variables using dotcharts. We reported the Chi-square  
240 and p-value per variable in the model selection step where this variable or interaction was dropped  
241 (comparing the full model with the nested model), considering p values < 0.05 statistically significant.  
242 The estimates for least square means for the combinations of the factors distance to road and forest  
243 type were estimated from each model using the lsmeans function in the package lsmeans (Russell,  
244 2016), and back transformed from log scale to counts, together with 95% confidence intervals, and  
245 were presented in figures.

246

247 In order to investigate if the vegetation composition was similar close to and far from forest roads,  
 248 we compared plot characteristics using a multivariate analysis of variance (using the function  
 249 manova), with distance to road (close/far) and forest type as explanatory variables. Variables  
 250 describing vegetation characteristics analyzed included total tree density, oak density, species  
 251 richness, mean tree diameter at breast height, mean tree height and a feeding site attractiveness  
 252 value. The feeding site attractiveness value (FSAV, adopted after Manly *et al.* (1992) and Stokke  
 253 (1999)), was defined per plot as

254

$$FSAV = \sum_{i=1}^n P_i * B_i$$

255 Where  $P_i$  is the preference index per  $i$  tree species (proportion browsed/proportion of species in all  
 256 trees measured) and  $B_i$  is the proportion of the species available in the plot, and  $n$ = the number of  
 257 species per plot.

#### 258 **2.4.2 Cervid browsing**

259 We analyzed the proportion of all trees per plot that had fresh browsing from last winter using a  
 260 generalized linear model, with a binomial distribution and a logit link function. We added distance,  
 261 forest type and the interaction between them as fixed effects, and number of trees per plot as model  
 262 weights. We used a quasibinomial correction for slight overdispersion of the response variable.

263 To examine the effect of distance to road on distribution of accumulated browsing among trees, we  
 264 analyzed the number of trees per plot in the different accumulated browsing categories as a  
 265 response variable. We used distance to road, accumulated browsing category and the interaction  
 266 between these as fixed effects, and forest block number as a random intercept in a generalized linear  
 267 mixed model with a Poisson distribution and a log-link function. In old oak forest, there were only  
 268 three trees in the class accumulated browsing 3 (trees highly modified by browsing in previous

269 years), and all of these were close to the road. Hence, accumulated browsing class 3 and 2 were  
270 pooled for old forest, to analyze the effect of the interaction between accumulated browsing and  
271 distance to road. We analyzed old forest and thicket separately.

272 For bark browsing and density of undamaged trees for forestry, we examined only oak trees in  
273 thickets, as this is where most of the browsing damage to commercial species occurs. We analyzed  
274 the effect of distance to road on proportion of bark stripped oak trees per plot using a generalized  
275 linear model with a binomial distribution and a logit link function, with total number of oak trees per  
276 plot as weights. Undamaged oak trees were defined as trees with no bark stripping, and an  
277 accumulated browsing index of zero or 1. We analyzed the effect of distance to road on number of  
278 undamaged trees per plot with a generalized linear model, a Poisson distribution and a log-link  
279 function. We used a quasipoisson correction to correct p-values for slight overdispersion.

280

## 281 **3 Results**

### 282 **3.1 Effect of distance to road on pellet density of cervids**

#### 283 **3.1.1 Red deer**

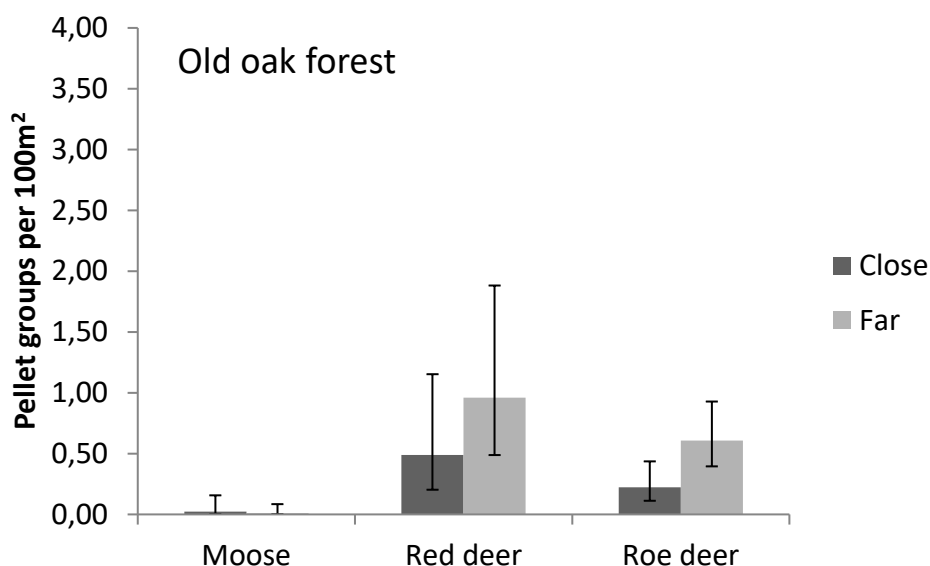
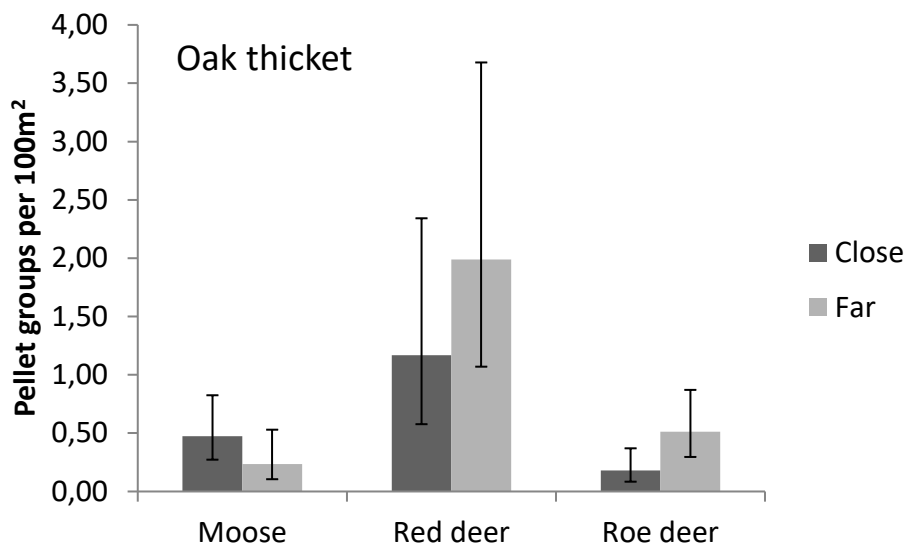
284 We found 122 pellet groups from red deer, in 41 of 112 plots surveyed (37% of plots). Red deer pellet  
285 group counts was higher than for moose and roe deer (Figure 1). Red deer pellet groups varied  
286 significantly with the interaction between distance to road and forest type ( $\chi^2 = 5.03$ ,  $df = 1$ ,  
287  $p=0.025$ ). The positive effect of far distance to road was larger in old forest compared to thicket,  
288 indicating less avoidance of roads in thicket than in old forest (Figure 1). Pellet groups also varied  
289 significantly with the effect of distance to road alone ( $\chi^2 = 7.19$ ,  $df = 1$ ,  $p= 0.007$ ) and near  
290 significantly with forest type alone ( $\chi^2 = 3.54$ ,  $df = 1$ ,  $p=0.059$ ). Red deer pellet group counts was  
291 higher far from road, compared to close, and higher in thicket compared to old forest (Figure 1).

### 292 **3.1.2** *Roe deer*

293 We found in total 48 pellet groups from roe deer, in 27 plots (24% of plots). Roe deer pellet group  
294 counts was intermediate between red deer and moose (Figure 1). Roe deer pellet groups did not vary  
295 significantly with the interaction between distance to road and forest type ( $\chi^2 = 0.86$ ,  $df = 1$ ,  $p =$   
296  $0.354$ ), nor with of forest type ( $\chi^2 = 0.19$ ,  $df = 1$ ,  $p = 0.659$ ). However, there was an effect of distance  
297 to road on roe deer pellet groups ( $\chi^2 = 5.27$ ,  $df = 1$ ,  $p = 0.022$ ). Roe deer pellet group counts was  
298 similar in oak thicket and old oak forest, with lower density close to road compared to far from road  
299 (Figure 1).

### 300 **3.1.3** *Moose*

301 For moose, we found 19 pellet groups, representing only 8% of plots. (9 of 112 plots). This indicates  
302 that moose was the least common of the cervid species (Figure 1). There was no significant  
303 relationship between the interaction of distance to road and forest type with moose pellet group  
304 counts ( $\chi^2 = 2.32$ ,  $df = 1$ ,  $p = 0.128$ ), nor any relationship with distance to road alone ( $\chi^2 = 2.14$ ,  $df = 1$ ,  
305  $p = 0.144$ ). However, there was an effect of forest type ( $\chi^2 = 22.12$ ,  $df = 1$ ,  $p < 0.001$ ), with more moose  
306 pellet groups in thicket compared to old forest. Moose pellets were present in eight plots in thicket,  
307 but only one in old forest (Figure 1).



310 **Figure 1** Distribution of cervid pellet groups from winter in relation to forest roads and forest type (mean and 95% CI).  
 311 Old oak forest = oak forest > 80 years, thicket = oak forest 7-20 years old. Close = 20-100m from forest road, Far=120-380  
 312 m from forest road.

313

### 314 3.2 Effect of distance to road on browsing by cervids

315 We found no differences in vegetation composition related to distance to forest road, but we found  
 316 differences between old forest and thicket, as expected (Table 1). Old forest and thicket differed in  
 317 species richness, total tree density, oak density, tree height and diameter, but were similar in feeding

318 site attractiveness value (Table 1). Thickets had higher densities of trees and more species per plot  
 319 than old forest (Table 1). Old forest had taller trees with bigger diameters (Table 1).

320 **Table 1** Species richness, tree density, mean height and diameter at breast height per 12.5 m<sup>2</sup> plot (mean and 2 SE) from  
 321 62 plots in old oak forest (> 80 years old) and 50 plots in oak thicket (7-20 years old). Feeding site attractiveness value  
 322 represents relative abundance of preferred browse species in the area (see methods for calculation). Results from a  
 323 MANOVA comparing plot characteristics such as tree density, species richness, diameter and height between forest types  
 324 (oak thicket versus old oak forest) and distance to road (close (20-100m) and far (120-380m) from road).

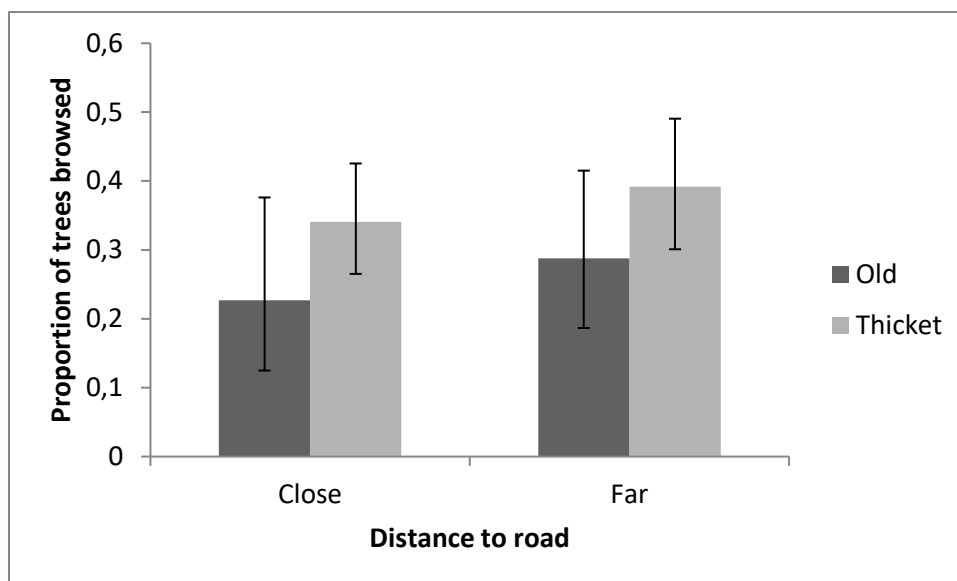
Plot characteristics	Old		Thicket		Results from Manova	
	Close	Far	Close	Far	Old/Thicket	Close/Far
Species richness	2.23 ± 0.44	2.23 ± 0.44	3.58 ± 0.56	4.42 ± 0.98	F <sub>1,101</sub> =28.63 p<0.001	F <sub>1,101</sub> =1.55 p=0.215
Feeding site attractiveness value	0.52 ± 0.15	0.49 ± 0.13	0.53 ± 0.17	0.48 ± 0.13	F <sub>1,101</sub> =0.05 p=0.828	F <sub>1,101</sub> =0.00 p=0.958
Tree density	5.55 ± 1.70	7.74 ± 3.18	20.77 ± 5.58	16.92 ± 5.18	F <sub>1,101</sub> =31.05 p<0.001	F <sub>1,101</sub> =0.01 p=0.924
Oak density	0.23 ± 0.15	0.23 ± 0.15	4.85 ± 1.14	4.96 ± 0.89	F <sub>1,101</sub> =192.56 p<0.001	F <sub>1,101</sub> = 0.17 p=0.682
Height (m)	4.95 ± 1.78	5.30 ± 1.98	3.48 ± 0.68	3.54 ± 1.12	F <sub>1,101</sub> =5.17 p=0.025	F <sub>1,101</sub> =0.00 p=0.978
Diameter at breast height (cm)	6.89 ± 2.52	8.21 ± 3.28	3.07 ± 0.60	3.34 ± 1.15	F <sub>1,101</sub> =13.54 p<0.001	F <sub>1,101</sub> =1.19 p=0.277

325

### 326 3.2.1 Proportion of trees browsed

327 Proportion of trees with fresh signs of browsing by deer from last winter showed no significant  
 328 relationship with the interaction between forest type and distance to road ( $\chi^2 = 0.03$ , df = 1, p =  
 329 0.854), nor with distance to road alone ( $\chi^2 = 1.09$ , df = 1, p = 0.297). However, there was a near

330 significant higher proportion of browsed trees in thicket compared to old forest ( $\chi^2 = 3.8$ ,  $df = 1$ ,  $p =$   
 331 0.051, Figure 2).



332

333 **Figure 2** Proportion of all trees per plot browsed by cervids last winter (mean  $\pm$  95% CI). Close = 20-100m from forest  
 334 road, Far=120-380 m from forest road. Old = oak forest >80 years old, Thicket = oak forest 7-20 years old.

335

### 336 **3.2.2 Accumulated browsing**

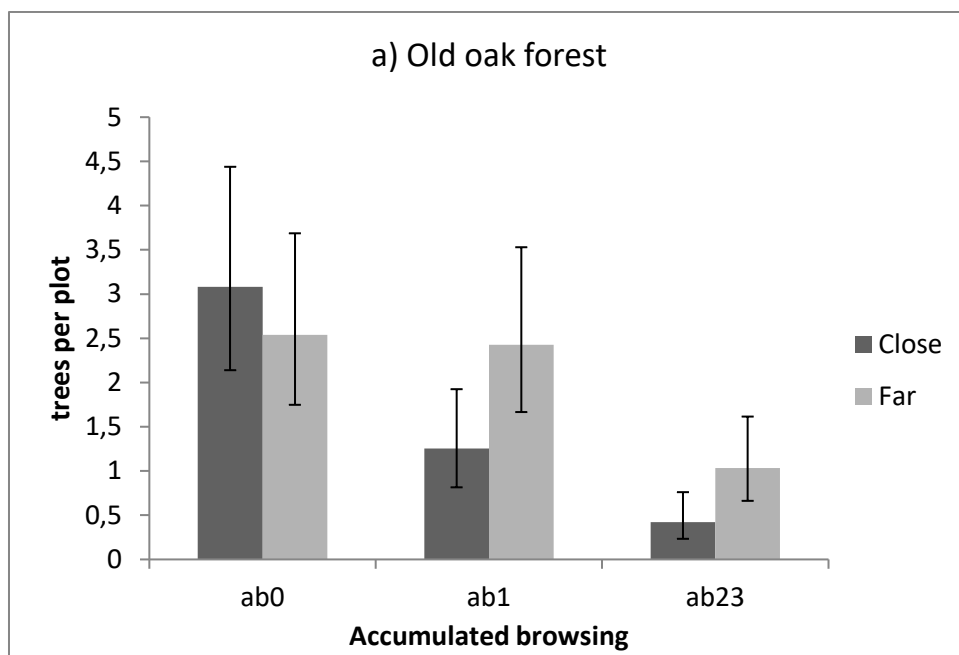
337 The density of trees in old oak forest among accumulated browsing classes differed with distance to  
 338 road (interaction distance to road and accumulate browsing:  $\chi^2 = 12.60$ ,  $df = 2$ ,  $p = 0.002$ , close vs far:  
 339  $\chi^2 = 4.61$ ,  $df = 1$ ,  $p = 0.032$ , accumulated browsing:  $\chi^2 = 64.18$ ,  $df = 2$ ,  $p < 0.001$ ). Density of trees with  
 340 signs of old browsing, both light and severe, was higher far from the road compare to close, but  
 341 density of unbrowsed trees showed little effect of distance to road (Figure 3a).

342 In oak thicket, the density of trees also varied with an interaction between distance to road and  
 343 accumulated browsing (interaction:  $\chi^2 = 10.95$ ,  $p = 0.012$ , close vs far:  $\chi^2 = 5.16$ ,  $p = 0.023$ ,  
 344 accumulated browsing:  $\chi^2 = 191.97$ ,  $p < 0.001$ ). Here the difference was largest close to road, where  
 345 density of unbrowsed trees was higher than far from road. The effect of road changed gradually to

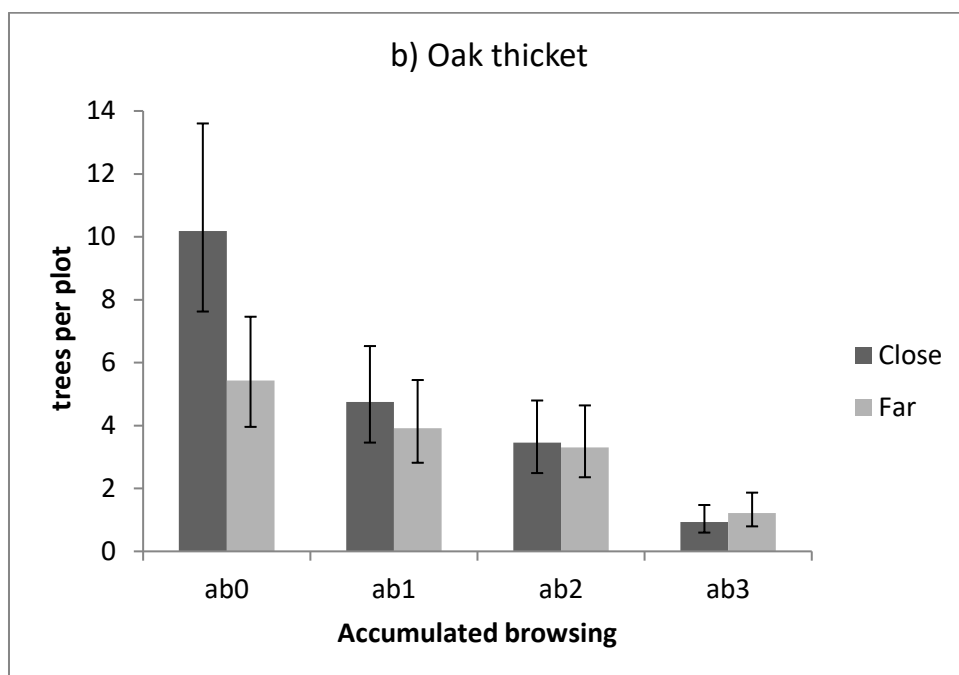


346 the opposite direction as we move from unbrowsed, lightly browsed, to trees highly modified by  
 347 browsing (ab3), in which density was slightly higher at far distance from road (Figure 3b).

348



349

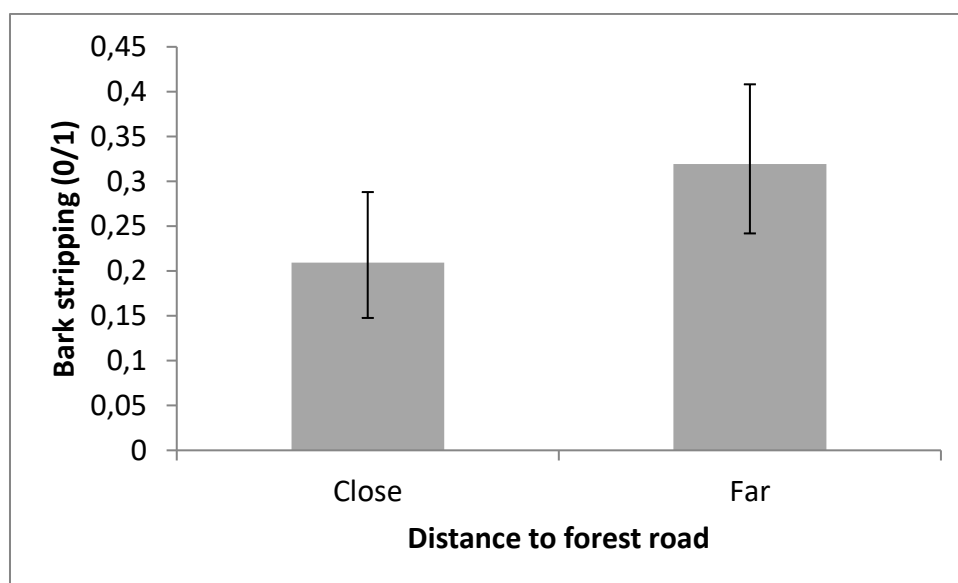


350 **Figure 3** Mean density of trees (with 95% CI) per 12 m<sup>2</sup> plot in different accumulated browsing classes, in relation to  
 351 distance to road (Close=20-100m, far=101-380m). Ab0 = no old browsing, ab1 = old browsing, but architecture of the tree  
 352 has not changed. Ab2&3 = old browsing had modified the architecture of the tree (i.e. crooked stem, increased  
 353 branching, multiple stems, brooming). a) Old oak forest (>80 years) b) Oak thicket (7-20 years).

354

355 **3.2.3 Bark stripping**

356 Of 1356 trees measured, only 98 had signs of bark stripping. Of these bark stripped trees, 65 were  
 357 oak and 14 were hornbeam. Other species where 1-4 bark stripped trees occurred were willow (*Salix*  
 358 sp.), aspen (*Populus tremula*), hazel (*Corylus avellana*), birch, ash, and Norway spruce. Only seven of  
 359 the bark stripped trees occurred in old forest, the remainder in thicket. For the analysis of how roads  
 360 affected browsing damages such as bark stripping, we focused on oak, as this was the most  
 361 important commercial species for forestry (N= 249 oak trees, Figure 4). Proportion of bark stripped  
 362 oak trees varied with distance from forest road ( $\chi^2 = 3.88$ ,  $p = 0.049$ ), and was 10 % higher far from  
 363 road compared to close (Figure 4).



364

365 **Figure 4 Probability of bark stripping by cervids on young oak trees in thickets (mean and 95% confidence interval). Close**  
 366 **= 20-100m from forest road, Far=120-380 m from forest road.**

367

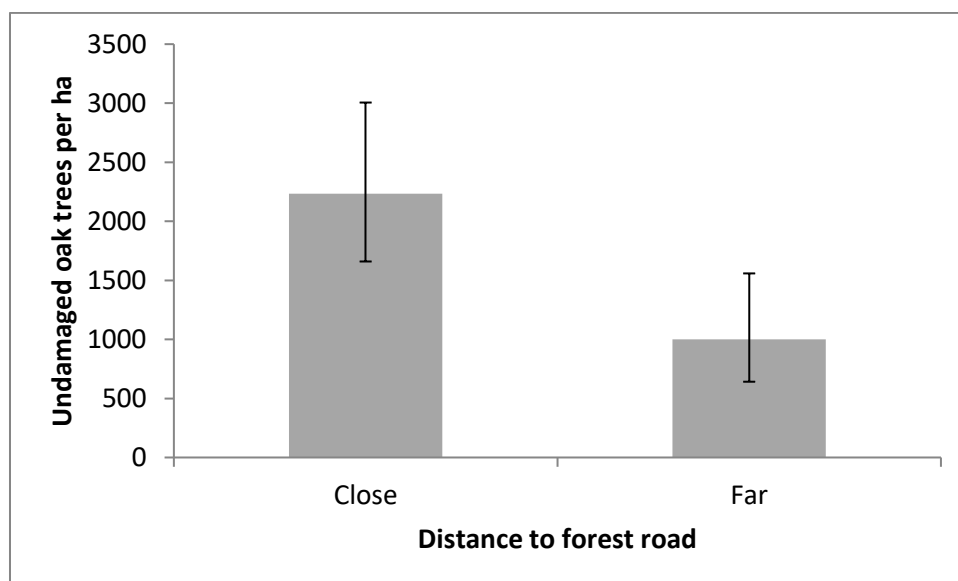
368 **3.2.4 Density of undamaged trees**

369 Of 249 oak trees in young thickets, only 42 % were undamaged by cervid browsing. The remaining  
 370 trees had browsing damage by bark stripping or severe repeated browsing over time (accumulated

371 browsing class 2 or 3). The total density of oak trees (both damaged and undamaged) was similar  
 372 close to road (mean 3969 trees/ha, 2SE= 876) and far from road (mean 3966 trees/ha, 2SE: 711, see  
 373 table 1 for density per plot). The density of undamaged trees was approximately double close to  
 374 road, compared to far from forest road ( $\chi^2 = 9.41$ ,  $p = 0.002$ , Figure 5).

375

376



377

378 **Figure 5** Density of oak trees per ha (mean and 95% confidence interval) undamaged by browsing or bark stripping by  
 379 cervids in young oak thickets (7-20 years old). Close = 20-100m from forest road, Far=120-380 m from forest road.

380

## 381 4 Discussion

382 We found support for our predictions that 1) habitat use by cervids was higher far from forest roads  
 383 compared to close, 2) hunted species (red deer and roe deer) avoided roads, 3) avoidance of roads  
 384 was stronger in old forest with low food availability than in thickets with high forage availability, but  
 385 this was only the case for red deer, not for roe deer, 4) Browsing pressure (both proportion of  
 386 browsed trees last winter and accumulated browsing) was higher in the forest interior, and 5) density

387 of undamaged oak stems was higher close to forest roads. To our knowledge, this is the first study  
388 that documents effects of forest roads on ungulate browsing and impact on trees.

#### 389 **4.1 Habitat use in relation to forest roads**

390 Our results indicate that hunted cervids avoid forest roads, similar to a study in Spain, which found  
391 that presence of red deer and wild boar increased with increasing distance to unpaved roads with  
392 low traffic density (D'Amico *et al.*, 2016). Roads may represent a risk of mortality from traffic,  
393 hunters or natural predators. Predation risk from hunters on roe deer decreases with increasing  
394 distance from road (Lone *et al.*, 2014). As the traffic intensity is low on forest roads, and the density  
395 of natural predators in the area was low, we assume that fear of hunters is the most likely cause of  
396 this avoidance of forest roads. We studied habitat use through pellet group counts, which reflects  
397 habitat use during the winter period, largely overlapping with the hunting period for deer (August-  
398 February). Hunters are most active in the day, and wolves use roads more at night. Some studies  
399 show temporal avoidance of humans in the daytime, but not in the nighttime, i.e. Bonnot *et al.*  
400 (2013) found that roe deer in France used open areas further from road in the daytime than in the  
401 night. Red deer may exploit feeding habitats close to roads at times of low traffic burden (Meisingset  
402 *et al.*, 2013). However, the net effect in our study was an avoidance of roads. This may indicate that  
403 deer avoid roads both day and night, and might be affected both by human and wolf activity on roads.  
404 These assumptions are based on the ideal free habitat selection, that cervids will select the habitat  
405 with higher survival (Morris, 2003), if predation risk is higher close to forest roads. However,  
406 sometimes habitat selection may not be optimal, and prey may select a habitat despite a high  
407 predation risk, because of lack of information, or trade-offs with other needs (DeCesare *et al.*, 2014).  
408 As tree density, tree height and diameter, species diversity and feeding site attractiveness were  
409 similar at different distances from roads, we can assume that forage availability was approximately  
410 similar at different distances, which indicates that the avoidance of roads was caused by the road  
411 itself, not effects of the road on forage availability or occurrence of preferred species.

412 As the effect of roads was strongest for roe deer and red deer, and not for moose, this supports the  
413 idea that forest roads represent a predation risk from hunters. Moose have been protected from  
414 hunting in Poland since 2001 (Bobek *et al.*, 2005). Moose did not show any avoidance of road, which  
415 might indicate that they have adapted to reduce predation risk during 15 years of protection from  
416 hunting. Cervids may adapt temporally and spatially in relation to different hunting seasons, e.g. roe  
417 deer change their temporal and spatial habitat use in relation to hunting season, and different types  
418 of hunting (Bonnot *et al.*, 2013; Lone *et al.*, 2017). So, it is possible that moose have adapted to the  
419 hunting ban, and developed reduced fear of humans. However, this result should be interpreted very  
420 carefully, as moose density in the area was low; hence sample size for moose pellet groups in this  
421 study was very small. This hypothesis should therefore be further investigated in an area with higher  
422 moose density or a larger sample size.

423 Oak thickets represent a habitat with high forage availability compared to old forest, having a higher  
424 density of trees within browsing height; hence we would expect deer to select thickets over old  
425 forest. This was the case for red deer and moose, but not for roe deer. Possible reasons why roe deer  
426 do not show this pattern might be that they are more dependent on open habitat such as old forest  
427 for detection of predators, as oak thickets can be rather dense. Lynx, which is an efficient stalk-and-  
428 ambush predator (Nilsen *et al.* 2009), is specialized on roe deer (Odden *et al.* 2006), and the predation  
429 risk from lynx is higher in areas with dense understory vegetation (Lone *et al.*, 2014). Their best  
430 chance of escaping may be to discover the predator early. Oppositely, predation risk from humans  
431 would be expected to be higher in old forest, where visibility is higher. Visibility is often important for  
432 hunting success, and predation risk from hunters for roe deer is higher in more open habitats with  
433 less understory vegetation (Lone *et al.*, 2014). If there is no lynx present in the area, only predation  
434 risk from human hunters, we would expect roe deer to seek cover in thicket far from road. However,  
435 since roe deer seem to prefer older forest, maybe more lynx are present in the area than has been  
436 detected in tracking surveys (Borowik and Schmidt, 2013), and that roe deer prefer old forest far  
437 from road, with low risk of predation from both lynx and humans. An alternative explanation for the

438 higher use of old forest by roe deer, may be competition with red deer (Latham and Staines, 1997) in  
439 thickets.

440 In addition, we found an interaction between habitat type and distance to road for red deer, which  
441 was the most common species with most data. Our data showed that avoidance of road was higher  
442 in old forest than in thicket, representing the trade-off between foraging and predator avoidance  
443 (Myrsterud and Østbye, 1999). Avoiding habitats close to the road in thicket, represents lost foraging  
444 opportunities, as thicket has higher forage availability than old forest. However, this effect may be  
445 confounded with the effect of cover, as forest type affects both cover and forage availability. Cover  
446 may protect prey from detection by predators, but may also reduce the detection of predators by  
447 prey (Myrsterud and Østbye, 1999). In addition, dense vegetation may obstruct escape. Studies have  
448 shown that deer reduce foraging and increase vigilance levels in the vicinity of objects that reduce  
449 habitat visibility or can serve as objects obstructing escape (Halofsky and Ripple, 2008; Liley and  
450 Creel, 2008; Kuijper *et al.*, 2013). However, the response to human hunters may be opposite. During  
451 the hunting season, foraging may be safer in thicket than old forest as humans depend on visibility,  
452 and predation risk from hunters is higher in more open areas (Lone *et al.*, 2014). Deer may  
453 temporally adjust habitat selection to avoid risky habitats during the hunting season (Bonnot *et al.*,  
454 2013; Lone *et al.*, 2017). This could also explain the lower effect of road in thicket compared to old  
455 forest for red deer. It is therefore hard to separate effects of forage availability and visibility, as  
456 forage availability is higher and visibility lower in thicket compared to old forest, both may benefit  
457 red deer.

#### 458 **4.2 Impact on browsing and densities of undamaged trees**

459 We have shown that browsing damage on commercial oak trees increased with increasing distance  
460 to road, and density of undamaged trees decreased. As both pellet counts and browsing impact  
461 indicated that red deer avoided roads in this study, we assume this is a cascading effect of presence  
462 of humans on roads affecting oak regeneration. Few studies have investigated the effect of predation

463 risk on browsing impact on the vegetation. Higher vigilance in areas with higher predation risk may  
464 reduce foraging effort and hence impact on vegetation (Laundre *et al.*, 2001). The most famous  
465 example of trophic cascades is probably from Yellowstone, where wolf reintroduction lead to a two-  
466 fold increased growth in willows (Beyer *et al.*, 2007). However, the effect of predation on browsing  
467 and vegetation recruitment are not always clear (Kauffman *et al.*, 2010). Examples of cascading  
468 effects of predators on plants in Europe are rare, but Kuijper *et al.* (2013) showed that increased  
469 predation risk from wolves lead to decreased browsing impact and increased tree regeneration with  
470 in areas with presence of coarse woody debris, that can reduce visibility and impede escape from  
471 predators. Hence effects of predation risk can occur at a rather fine spatial scale, in their study the  
472 area within 1 m around each seedling showed the strongest effects. This study also shows effects on  
473 browsing on a small-scale gradient, although larger than the previously mentioned study, with  
474 reduced browsing intensity within 100m from roads, and increased browsing intensity 120-380 m  
475 from roads. Other studies have found no effect of roads on vigilance in roe deer (Benhaiem *et al.*,  
476 2008).

477 Behaviorally, trophic cascades depend on the hunting mode of the predator. Sit-and-wait ambush  
478 predators are expected to create stronger behavioral responses in their prey than widely roaming  
479 active predators, because the predictability of areas of high predation risk is high for the first type,  
480 and low for the other (Schmitz, 2008). Roads are spatial structures that are permanent over longer  
481 times, hence if roads are linked to predation risk; it is spatially predictable and more cost-efficient for  
482 prey to respond to (Proffitt *et al.*, 2009; Crowsigt *et al.*, 2013). Roads may create corridors of fear by  
483 affecting the habitat use and way of travel of predators, for both hunters and natural predators. If  
484 increased predation changes the behavior of herbivores, so that they forage more locally and move  
485 less due to risk of predation, predation may increase browsing pressure locally and induce a change  
486 in landscape heterogeneity (Fortin *et al.*, 2005). The presence of predators can increase spatial  
487 variation in deer browsing pressure, as areas in the interior with less predation risk will be browsed  
488 more than areas close to road with high risk. If this differential risk pattern persists over several

489 years, this may lead to release from browsing pressure in high-risk road buffer zones. As roads are  
490 permanent linear features in the landscape, they present a spatially predictable risk of predation,  
491 which can in turn lead to changes in browsing pressure and vegetation dynamics in a gradient from  
492 roads.

493 As total browsing pressure was lower close to road, this indicates that the nightly compensation is  
494 not as great as the daytime avoidance, and might indicate a net cost of roads for ungulates in terms  
495 of missed forage opportunities. As oak density was equal in relation to distance to road, but density  
496 of undamaged oak (by cervids) was double close to road compared to far, this indicates a cascading  
497 effect of roads on oak production. We suggest this is due to disturbance by humans, but also other  
498 effects of road may be important. Disturbance from road traffic can also lead to reduced foraging  
499 effort (Ciuti *et al.*, 2012). Although the forest roads used in this study, have very little traffic, even  
500 low densities of traffic may affect ungulates (Ciuti *et al.*, 2012; D'Amico *et al.*, 2016). In addition,  
501 there may be other effects of roads than hunters and cars. I.e. dust from unpaved roads may affect  
502 the vegetation composition and growth (Farmer, 1993), and potentially reduce palatability of forage  
503 for ungulates. Effects of dust from roads has been found to negatively affect ungulate density in  
504 Serengeti National Park, however this was a more open habitat, with higher traffic density than our  
505 study, where the wind can affect dust deposition several 100 m from the road, especially when it is  
506 dry (Ndibalema *et al.*, 2008). In a forest, there is less wind and dust will also be trapped by taller  
507 vegetation, hence we consider this effect low in our study area. However, it is important to use  
508 experiments in future studies to try to separate different effects of roads on ungulate habitat  
509 selection and browsing pressure; effects of traffic disturbance, pollution and dust, hunters or other  
510 human disturbance, natural predators, light and nutrients.

### 511 **4.3 Management implications**

512 The implications of this study for forestry is that oak regeneration is improved in areas < 100 m from  
513 forest roads, and reduced in the core area of forest blocks. In order to increase densities of



514 undamaged trees for commercial forestry, the most preferred commercial tree species could be  
515 planted close to roads, and less preferred species could be planted in core areas. In addition, if we  
516 assume the reduction in browsing pressure close to roads is caused by fear of hunters, this may also  
517 be useful for management. By directing hunting activities to areas susceptible to browsing damage,  
518 such as young plantations, management of hunters habitat use could be used actively reduce  
519 browsing pressure by overabundant wildlife populations, as also suggested by Cromsigt *et al.* (2013).

520 However, planting unpalatable species in favorable habitat for deer at a landscape scale, would  
521 reduce forage availability for deer, and probably increase browsing damage on commercial species.  
522 In the area of this study, the forage resources were already under high pressure, as the majority of  
523 pine plantations were protected by fences, forcing deer to concentrate in non-fenced areas of the  
524 forest. In addition, plastic stem protection tubes protected many oak plantations, whilst the  
525 browsing pressure by deer was very high. Also, if hunting should be used to scare deer away from  
526 vulnerable plantations, there has to be sacrifice areas or refuges available where cervid browsing is  
527 tolerated, as alternative habitat for deer. These areas may be made more attractive to deer by  
528 facilitating growth of forage for wildlife, rather than commercial forestry. Hence landscape planning,  
529 that take into account deer habitat and forage availability in addition to forestry, together with a  
530 controlled harvest regime of deer is an important key to manage browsing damages.

#### 531 **4.4 Conclusion**

532 In this study, we have documented that unpaved forest roads with low traffic intensity affect  
533 ungulate habitat use and densities of undamaged oak trees. This is most likely caused by the indirect  
534 effects of the landscape of fear created by hunters using roads, cascading down to the vegetation  
535 and affecting commercial forestry. However, future studies should try to separate different  
536 mechanisms of road effects on cervid habitat use and browsing through experimental design. The  
537 results from this study can be useful for management of ungulate browsing damages, by using spatial

538 refuges for vulnerable tree species, and spatial manipulation of human disturbance to reduce  
539 browsing damage.

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544

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546

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Response variable	Models used
Pellet groups per plot	glm(moose pellet groups per plot~distance to road*forest type, family=poisson)
	glmer(red deer pellet groups per plot~distance to road*forest type+(1 forestblocknr), family=negative.binomial(theta=3.1))
	glmer(roe deer pellet groups per plot~distance to road*forest type+(1 Forestblocknr), family=negative.binomial(theta=1.68))
Multiple vegetation characteristics	> Y<-cbind(plotsummaries\$species per plot, plotsummaries\$trees per plot, plotsummaries\$mean tree height per plot, plotsummaries\$FSAV, plotsummaries\$oak trees per plot, plotsummaries\$mean DBH at breast height per plot)  fit<-manova(Y~plotsummaries\$forest type*plotsummaries\$distance to road)  summary.aov(fit)
Proportion of trees browsed last winter	glm(browsed trees/total trees per plot~distance to road*forest type, weights=total trees per plot, family=quasibinomial)
Distribution of trees in accumulated browsing classes	Separate analysis for old forest and thicket:  glmer(trees per plot~distance to road*accumulated browsing+(1 Forestblocknr), family=negative.binomial(theta=4.4 (old), 7.18 (thicket)))
Proportion of bark stripped oak trees in thicket	glm(bark stripped oak trees/oak trees per plot~CloseFar, weights=oak trees per plot, family=binomial)

Undamaged oak trees per plot in thicket	glm(undamaged trees per plot ~distance to road, family=quasipoisson)
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