

2018

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Suzanne T.S. van Beeck Calkoen

Dries P.J. Kuijper

Hakan Sand

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Recommended Citation

van Beeck Calkoen, S. T. S., D. P. Kuijper, H. Sand, N. J. Singh, S. E. van Wieren, and J. P. Cromsigt. 2018. Does wolf presence reduce moose browsing intensity in young forest plantations? *Ecography* 41:1-12.

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Research

Does wolf presence reduce moose browsing intensity in young forest plantations?

Suzanne T. S. van Beeck Calkoen, Dries P. J. Kuijper, Håkan Sand, Navinder J. Singh, Sip E. van Wieren and Joris P. G. M. Cromsigt

S. T. S. van Beeck Calkoen (<http://orcid.org/0000-0002-2574-9056>) (suzanne.vanbeeckcalkoen@ziggo.nl), N. J. Singh and J. P. G. M. Cromsigt, Dept of Wildlife, Fish, and Environmental Studies, Swedish Univ. of Agricultural Sciences, Umeå, Sweden. STSvBC also at: Dept of Conservation and Research, Bavarian Forest National Park, Grafenau, Germany. JPGMC also at: Centre for African Conservation Ecology, Dept of Zoology, Nelson Mandela Univ., Port Elizabeth, South Africa. – D. P. J. Kuijper, Mammal Research Inst., Polish Academy of Sciences, Białowieża, Poland. – H. Sand, Grimsö Wildlife Research Station, Dept of Ecology, Swedish Univ. of Agricultural Sciences, Riddarhyttan, Sweden. – S. E. van Wieren, Dept of Environmental Sciences, Resource Ecology group, Wageningen Univ., Wageningen, the Netherlands.

Ecography

41: 1776–1787, 2018

doi: 10.1111/ecog.03329

Subject Editor: Eric Post

Editor-in-Chief: Miguel Araújo

Accepted 24 January 2018

Large carnivores can be a key factor in shaping their ungulate prey's behavior, which may affect lower trophic levels. While most studies on trade-offs between food acquisition and risk avoidance by ungulate prey species have been conducted in areas with limited human impact, carnivores are now increasingly returning to highly anthropogenic landscapes. Many of these landscapes are dominated by forestry, and ungulate-forestry conflicts are an increasing issue. The aim of this study was to test if the indirect effects of a re-colonizing large predator, the wolf *Canis lupus*, results in a change in browsing intensity by moose *Alces alces* in young forest plantations in a boreal forest in Sweden. We selected 24 different forest plantations, with 12 located in low-wolf and 12 in high-wolf utilization areas. In each plantation, we measured browsing intensity, tree height, tree density, distance to the closest forest edge and we counted the number of moose pellet groups. In contrast to our predictions, wolf utilization was not the main driver of moose browsing patterns. Instead, moose browsing intensity declined with tree density and height. Separate analyses on the main tree species showed that wolf utilization had an influence, but browsing intensity was in fact higher in the high-wolf utilization areas for three out of five tree species. This pattern seemed to be driven by a strong confounding relationship between wolf utilization, tree density and height, which were both lower in the high-wolf utilization areas. We argue that this confounding effect is due to wolves being pushed towards the less productive parts of the landscape away from human activity centers. Therefore, we concluded that in order to better understand carnivore driven risk-mediated effects on herbivore behavior in anthropogenic landscapes we need to better understand the complexity of human-carnivore-prey-ecosystem interactions.

Keywords: behaviorally-mediated trophic cascades, anthropogenic landscapes, wolf-ungulate interactions



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Introduction

Large carnivores are now rapidly recolonizing large parts of Europe and North America (Chapron et al. 2014, Ripple et al. 2014). These carnivores can strongly influence the foraging behavior of their herbivore prey by shifting their distribution towards less risky habitat types (Lima and Dill 1990, Laundré et al. 2001, Creel et al. 2005) or by changing the intensity at which they exploit food patches (Fortin et al. 2005, Kuijper et al. 2015). Such risk-mediated changes in foraging behavior may affect browsing patterns with resulting consequences for plant communities, such as increased growth and recruitment of certain tree species in risky places (Hebblewhite et al. 2005, Beyer et al. 2007, Kuijper et al. 2013). A key feature of the current large carnivore comeback is that they are often returning to highly anthropogenic landscapes (Chapron et al. 2014, Ripple et al. 2014). Recent studies have started to show how human activity may strongly modify the ecological effects of large carnivores (see Kuijper et al. 2016 for a review); e.g. by changing the distribution of carnivores and their prey (Theuerkauf and Rouys 2008, Muhly et al. 2011) or by influencing bottom-up effects through shaping the herbivore's food landscape (Muhly et al. 2013). While most current studies focus on how humans affect predator-prey-ecosystem dynamics, the return of large carnivores to human-modified landscapes also results in a different kind of question: (how) do large carnivores affect interactions between humans and herbivores in anthropogenic landscapes? We look at this question by considering the ungulate-forestry conflict.

Forestry is a dominant land-use across the anthropogenic landscapes in the northern hemisphere where carnivores are now returning. In many areas, the dominant practice is a clear-cutting approach followed by replanting of production trees, which leads to a heterogeneous patchwork of younger plantations and more mature forest stands (Esseen et al. 1997, Edenius et al. 2015). Ungulates benefit from these alterations in forest structure as the young forest plantations provide a high availability of forage (Esseen et al. 1997, Kuijper et al. 2009, Massé and Côté 2009, Edenius et al. 2015). However, the impact of ungulates on these young forest plantations has resulted in strong conflicts with the forestry industry (Danell et al. 2003, Ezebilo et al. 2012). Several studies have, therefore, focused on revealing the potential factors that determine the level of ungulate impact on economically valuable tree species (Andrén and Angelstam 1993, Bergqvist et al. 2001, Edenius et al. 2015). Predation risk has so far hardly been considered as a driver of ungulate impact on forestry. Recent work, however, suggests that the openings in forest habitat created by forestry may change the reaction of ungulates in response to predation risk (Sahlén et al. 2015). In this study, ungulates reduced their use of forest habitat after the introduction of brown bear scent, but not if this habitat was relatively open due to human influence (e.g. forest clearings). So this begs the question: how do returning large carnivores affect the ungulate-forestry conflict?

Landscape features clearly influence the risk of predation for prey (Laundré et al. 2001, Gervasi et al. 2013). Although wolves can profit from habitat edges or obstacles in the forest to more easily catch their prey (Kuijper et al. 2013, Bojarska et al. 2017), there are several studies that suggest that predation risk by wolves is higher in open habitats than in closed forest habitat (Creel et al. 2005, Gervasi et al. 2013). For example, for North American elk the risk of encountering and being killed by wolf was higher in open grasslands than in forests (Hamilton et al. 1980, Kauffman et al. 2007, Gervasi et al. 2013) and, in the presence of wolves, elk increase their use of forested areas (Creel et al. 2005). Similarly, Swedish moose experienced increased predation risk from wolves in open areas such as clear-cuts and young forest stands (Gervasi et al. 2013). Following this, one would predict that in a forestry mosaic of open, recently planted, areas in a matrix of mature forest the recolonization of wolves should reduce the use of, and impact on, these young plantations by their main ungulate prey. Returning large carnivores may, in this way, mitigate the ungulate-forestry conflict. However, prey constantly face trade-offs and have to balance avoiding risk with other needs, particularly the acquisition of food (Lima and Bednekoff 1999). In situations where food availability in mature forest stands is relatively low young plantations form an important food source for ungulates (Kuijper et al. 2009). Ungulates may thus not be able to afford avoiding these young plantations, despite a potentially increased predation risk (Schmidt and Kuijper 2015). In such a situation, ungulate prey may choose to adapt their foraging behavior at the within-plantation scale to reduce risk. In fact, previous studies have hypothesized that under predation risk ungulates should browse closer to the forest edge to facilitate an early escape if necessary (Molvar and Bowyer 1994, Weixelman et al. 1998).

We tested effects of predation risk on the patterns of ungulate browsing, at the plantation and within-plantation scale, in young plantations using a wolf-moose model system in central Sweden. We used detailed data on the ranging behavior of wolf packs to contrast moose browsing patterns in high- versus low-wolf utilization areas. We hypothesized that, if predation risk effects are substantial and override resource needs, overall moose browsing intensity should be lower in plantations found in high-wolf utilization than those in low-wolf utilization areas. Secondly, we predicted that within a recently planted area, moose browsing intensity should decline more strongly with distance away from the forest edge in high compared to low-wolf utilization areas.

Methods

Study area

In October 2015, we measured browsing patterns in young forest plantations in the counties of Örebro, Värmland and Västmanland, Sweden, which are situated in the boreal forest

zone. This area is intensively managed by forestry, resulting in a network of forest roads and a landscape mosaic characterized by clear-cut areas of different sizes (varying between 0.1–156.9 ha in the studied counties) and forest plantations of different ages and heights. Although forest roads were present in the study area as result of intensive forestry practices, we did not expect these to influence our design as forest roads were present in all areas. Forests within the study area are dominated by, predominately planted, Norway spruce *Picea abies* and Scots pine *Pinus sylvestris* (Andrén and Angelstam 1993). Naturally regenerating deciduous tree species, such as silver birch *Betula pendula*, downy birch *Betula pubescens* and rowan *Sorbus aucuparia*, are abundant in young forest plantations in the area (Andrén and Angelstam 1993). In the 1960s the grey wolf *Canis lupus* was functionally extinct in all of Scandinavia. However, after the settlement of a few wolves from the Finnish-Russian population in the early 1980s, the wolf population in Scandinavia rapidly increased (Zimmermann 2014). Nowadays, the Scandinavian wolf population is mainly confined to the south-central parts of Sweden, including our study area, and was estimated at 460 individuals in the winter of 2014–2015 (Svensson et al. 2015). Moose *Alces alces* constitute the main prey species of Scandinavian wolves, particularly in winter (Sand et al. 2008, Wikenros et al. 2009). Moose was the dominant ungulate browser in our study system with estimated winter densities of 12.5 ± 1.54 1000 ha⁻¹ around the Grimsö Wildlife Research Area located at the center of our study area (Lindqvist 2012). Other browsers are present in the study area but occur in lower densities; roe deer *Capreolus capreolus* with an estimated population density of 9.87 ± 1.48 1000 ha⁻¹ in 2011 (Lindqvist 2012, Edenius et al. 2015). Red deer *Cervus elaphus* also sporadically occurs in some parts of the study system but overall their densities were extremely low at the time of study (Lindqvist 2012, Edenius et al. 2015). Since these estimated densities are regional densities, they reflect the average ungulate densities in our entire study area and do not take into account fine-scale variation in densities that might exist between our studied plantations. Therefore, we performed pellet counts, particularly to estimate possible differences in moose densities between plantations in high versus low wolf areas. During winter, moose are the main browser of Scots pine twigs and several deciduous tree species (Andrén and Angelstam 1993). Although roe deer forages on the same species, it selects the needles and buds rather than the larger twigs that we measured (Bergquist and Örlander 1996). As a result, we are confident that most of the browsing we recorded in this study reflected moose browsing. Further support for this assumption came from the pellet group counts.

Moose hunting season started in the middle of October 2015. Several studies found that human hunting pressure directly influenced large ungulate behavior in terms of movement activity and home ranges size (Root et al. 1988, Kilgo et al. 1998), in contrast to, Neumann et al. (2009) who found no effect on moose movement patterns during hunting

season. Within our study area, we do not expect that hunting activity directly influenced our measurements of the browsing intensity and pellet group counts as they result from moose activity in the months before the hunting season.

Study design – comparing areas with different levels of predation risk

The intensity of land use by wolves differed strongly across our study area (Fig. 1). We used polygons of the annual home ranges of wolf packs and pairs for the period 1999–2015 as provided by the Scandinavian Wolf Research Project (Skandulv) (<www.slu.se/skandulv>). These locations are based on data from annual monitoring using a mixture of three methods including snow tracking, scat DNA-analysis, and radio telemetry when available (Liberg et al. 2011). These estimates of annual wolf territories most likely underestimate the true range sizes somewhat (except for territories where wolves were GPS-collared) and we, therefore, increased each annual range with an additional buffer of 3 km from the edge of the estimated home range. We used these extended annual home ranges (i.e. including the buffer area) to delineate contrasting levels of wolf predation risk; high-wolf utilization areas were located inside annual home ranges of wolf packs or pairs at the time of study (2014–2015) and, additionally, had been part of an annual home range of a wolf pack or pair for at least 9 of the 17 yr prior to our study. In contrast, low-wolf utilization areas were not occupied by a wolf pack or pair at the time of study and had not been during the 17 yr prior to the study (Fig. 1). The low-wolf utilization areas would only have received occasional visits from single dispersing wolves. We assumed that these single wolves pose a limited threat to moose and should result in minimal predation risk in contrast to wolf packs and pairs (Carbyn and Trotter 1987).

For the purpose of our study we selected the high-wolf utilization areas within the annual home ranges of three different wolf packs at the time of study and paired each of these with the closest low-wolf utilization area (Fig. 1). In each of these six different areas we selected four different young forest plantations (24 in total), where we measured the spatial pattern and intensity of browsing. From a database provided by the Swedish Forest Agency (Skogsstyrelsen), we selected forest plantations that were clear-cut between 2008 and 2010 and planted between 2009 and 2011. These recent forest plantations, hereafter plantations, of similar age were selected as to achieve a similar tree height among the plantations. Plantations showed an average tree height of 80 cm (± 4 cm) at the time of study. The reason to select plantations within this height class is that we assumed that saplings up to this height would still be potentially perceived as risky open areas by moose; i.e. tree height < 1 m does not allow moose to hide from wolf. Further, all plantations were at least three kilometers apart, reflecting the average radius of a moose home range (Allen et al. 2016), to maximize the likelihood that plantations were visited by different moose individuals.

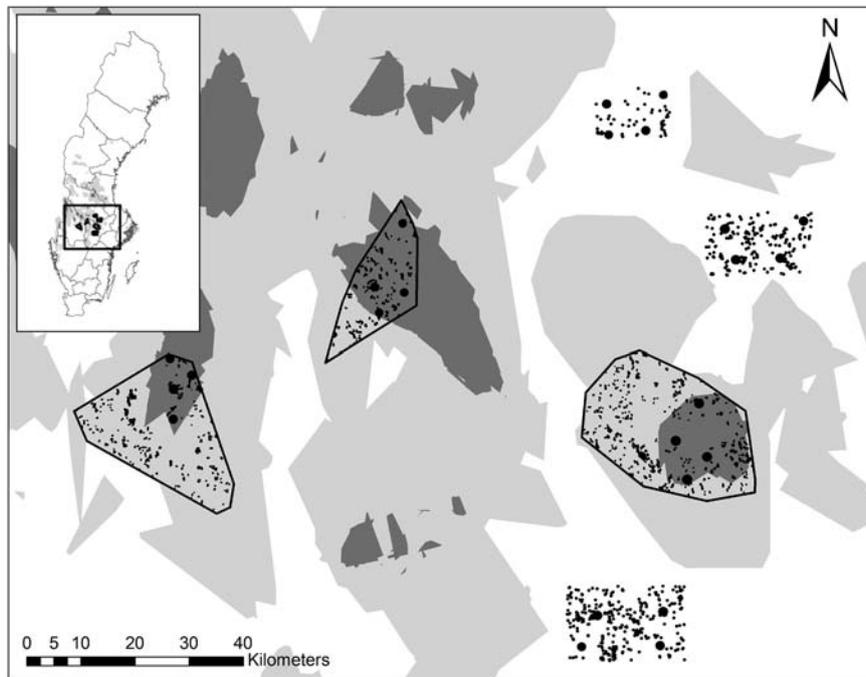


Figure 1. Study area, dark grey areas represent high-wolf utilization areas where wolf home ranges overlap for at least 9 of the 17 yr prior to the study. The white areas are low-wolf utilization areas, which have not been part of any annual wolf pack range for at least 17 yr prior to the study. Line polygons represent the 2014–2015 home ranges of the three different wolf packs used for this study design and the light grey areas represent the areas where wolf packs have been present for at least one year between 1999 and 2015. The small black dots represent the young forest plantations which fit with our criteria, inside the high- and low-wolf utilization areas. Big black dots indicate the measured young forest plantations inside the high- and low-wolf utilization areas.

Apart from these criteria, plantations were selected randomly inside high- and low-wolf utilization areas, respectively.

Quantifying browsing patterns

Matlack (1993) found that forest edges affect the micro-environment in plantations up to 50 m from the edge. Particularly due to shading, tree regeneration was lower on the south side of plantations, while there was no difference between eastern and western orientated edges (Matlack 1993). To account for these differences, we recorded browsing along two perpendicular line transects relative to the forest edge, one set in the northern and one in the eastern direction starting at the center of a plantation. The measured plantations had an average size of 4.9 ± 0.64 ha and transect lengths in northern and eastern direction varied between 39 and 138 m, depending on the shape and size of the plantation. In virtually all cases distance to the closest forest edge was not greater than 138 m and transects were therefore not measured further. Starting from the forest edge, we measured each tree within the moose browsing range of 0.4–3.5 m (Bergqvist et al. 2001, 2013, Kalén and Bergqvist 2004) that fell within 0.5 m on each side of the transect line. For each tree individual we recorded its species and two types of browsing following Kuijper et al. (2013); 1) we noted whether the current year's apical shoot was browsed or not (apical browsing) and 2) we counted the number of the top

10 lateral shoots that were browsed (lateral browsing). For Scots pine we used a slightly different approach than for the deciduous species because Scots pine is mainly eaten in winter whereas deciduous trees are also eaten during summer (Andrén and Angelstam 1993, Courtois et al. 2002). Since our study was conducted in October, fresh browsing on Scots pine was not yet extensive in contrast to that on deciduous species. To account for this difference in timing of browsing, we included (besides the current year's apical shoot browsing) browsing on the apical shoot of the previous year for pine in our measurements. If the previous year's apical shoot had been browsed, it was counted as one of the top 10 lateral shoots browsed. In addition, for each individual we measured tree height using a measurement pole and distance to the closest forest edge using a Nikon Forestry Pro laser. Afterwards, we calculated overall tree density for each young forest plantation by dividing the total sum of trees for each transect by the transect length (m).

Finally, to confirm that moose was the main browser in the study area we counted the number of fresh (< 1 yr) pellet groups per ungulate species within a maximum distance of 1 m on each side of the transect lines within the young forest plantations on which we recorded browsing. To test if moose would shift its use from plantations to closed mature forest inside wolf territories, we continued the transect line into the mature forest for the same length as we walked in the young forest plantations. Due to differences in decomposition rates

between clear-cuts and forested areas (Fairbanks 1979), we compared the pellet group counts between high- and low-wolf utilization areas separately for the plantation and mature forest areas respectively. All pellet group counts were conducted by the same single observer.

Statistical analyses

Pellet group counts

For each transect we calculated the number of pellet groups found 100 m⁻², to account for differences in transect length. To test if the total number of pellet groups 100 m⁻² transect differed between high- and low-wolf utilization areas, we used a non-parametric Mann–Whitney U-test. We performed this test separately for the plantations and the mature forest areas, where the number of pellet groups found per transect was the dependent variable and wolf utilization, a factor with two levels (high/low wolf presence), was the independent (predictor) variable. Because of small sample size and non-normality of errors we decided to use the non-parametric Mann–Whitney U-test instead of an ANOVA.

Browsing variables

Since predation risk effects may depend on the quality of the food item, we tested the different types of browsing; apical shoot versus lateral shoot browsing in separate models. As five tree species represented > 95% of the measured trees (rowan, downy birch, silver birch, Scots pine and spruce), only these 5 tree species were included in the statistical analyses. Similarly, these tree species differ in palatability which potentially could influence our results. Predation risk effects may depend on the quality of the food item, which we took into account in two different ways. Firstly, we calculated Jacobs' selection index (Jacobs 1974) as an index of selectivity and tested whether the selection for each tree species differed between high and low wolf areas. For this a Jacobs' index was calculated separately for apical- and lateral shoot browsing per plantation in both high- and low-wolf utilization areas according to the formula: $D = (r - p) / (r + p - 2rp)$, where r is the proportion of species y browsed relative to all browsed trees (apical or lateral), and p is the proportion of species y relative to all trees

(Jacobs 1974, Kauhala and Auttila 2010). Differences in the Jacobs' index for each of the five species (for apical- and lateral shoot browsing separately) between the wolf utilization areas was tested using a Mann–Whitney U-test. Secondly, at both the plantation scale and within-plantation scale we tested for effects of wolf presence on browsing of all tree species and for each tree species separately.

Plantation scale

At the plantation scale we tested if the average proportion of browsed trees was lower in the high- than the low-wolf utilization areas. Hence, as response variables we used the proportion of trees of which the apical shoot was browsed ('apical browsing') within each plantation. We also converted the lateral shoot variable (proportion of top 10 lateral shoots browsed) to a binomial variable and scored for each individual tree if any of its lateral shoots were browsed or not. As response variable we then used the proportion of trees of which at least one lateral shoot was browsed for each forest plantation. Both response variables (apical and lateral browsing) were arcsine transformed to normalize the proportion data. We first combined all data of the five most common tree species to look at overall browsing patterns. We used a linear mixed effect model with either the proportion of apical shoot browsing or lateral shoot browsing as the response variable and wolf pack ID as the random effect. Furthermore, a spatial autocorrelation structure was added to account for the fact that some young forest plantations were closer to each other than others. We used the following three variables as fixed effects; wolf utilization (high vs low), average tree density (total number of trees m⁻² within each forest plantation) and average tree height per plantation (cm). Despite our random placement of plantations within high and low wolf utilization areas, we found that tree density (two-sample t test, $t = -3.5$, $df = 18.5$, $p = 0.002$) and height (two-sample t test, $t = -3.5$, $df = 17$, $p = 0.002$) were both higher in the low-wolf utilization areas (Fig. 2), and thus strongly collinear with our wolf utilization treatment. We, therefore, never included these three variables in the same model. We then used corrected Akaike information criterion (AICc) to compare model fits. We used all models with $\Delta AICc < 2$ in our interpretation

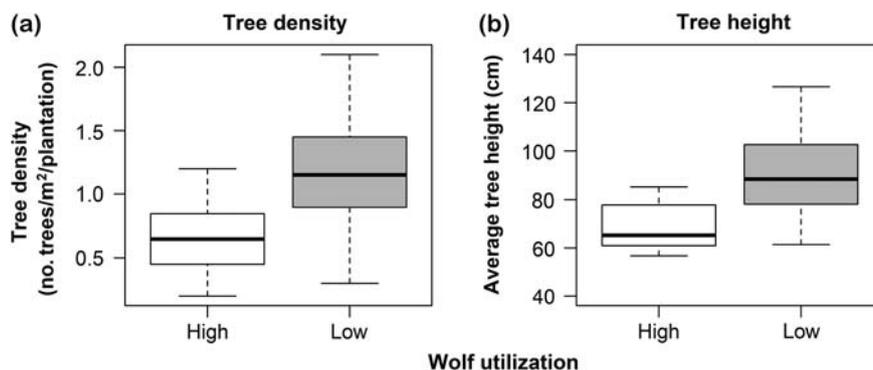


Figure 2. Boxplots of tree density and average tree height in areas with different levels of wolf utilization levels (high/low). The thick line shows the median and the box shows 25% of the data. The whiskers show the minimum and maximum value in the dataset.

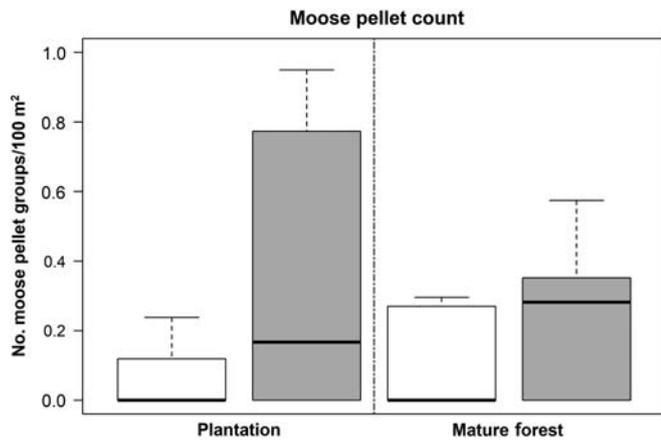


Figure 3. Boxplots of the number of moose pellet groups 100 m⁻² inside young forest plantations and mature forest for high-wolf utilization areas (white) and low-wolf utilization areas (grey). The thick line shows the median and the box shows 25% of the number of moose pellet groups. The whiskers show the minimum and maximum number of moose pellet groups found on a transect.

(following Burnham and Anderson 2002). Subsequently, we followed the same procedures on the data of the five most abundant tree species separately.

Within-plantation scale

At the within-plantation scale, we were interested in testing if browsing intensity declined more strongly with distance to forest edge in the high-wolf utilization areas. For apical shoot browsing we tested how the probability of an individual tree being browsed differed inside and outside wolf territories using a generalized linear mixed model with a binomial family. For the top10 proportion of lateral shoots browsed we used a linear mixed effect model, after arcsine transforming the proportions. In all models, the nested structure, wolf territory/plantation ID, was used as the random effect. Tree height (for each individual in cm), tree density (total number of trees m⁻² within each forest plantation), wolf utilization level (high or low) and distance to the closest forest edge (m) were used as fixed effects. Model selection was based on the AIC and Δ AIC. First, univariate models for each fixed effect

were tested. As we were interested in the indirect effect of wolf predation and distance to the forest edge on moose browsing patterns in this study, distance and wolf utilization were included in two-way interaction models. As a result, multiple univariate or multivariate models were tested and their AIC's compared (Table 4). For each browsing response (apical or lateral) the model with the lowest AIC was selected for interpretation. The same method was applied in the model selection for the five most abundant tree species separately.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.5vm5g2f> > (van Beek Calkoen et al. 2018).

Results

From the 47 pellet groups that were found, 36 belonged to moose and 4 to roe deer while 7 could not be identified to species. The number of moose pellet groups did not differ between high- and low-wolf utilization areas for plantations ($Z = -1.33$, $n = 24$, $p = 0.200$) or for mature forest stands ($Z = -1.20$, $n = 24$, $p = 0.250$, Fig. 3).

Downy and silver birch were the most dominant tree species recorded, followed by Norway spruce, rowan and Scots pine (Table 1). These five species represented 98.7% of all trees measured. Moose strongly selected for rowan, while Norway spruce was selected the least ($H = 111$, $df = 4$, $p \leq 0.001$, Table 2). No differences were found in Jacobs' indices for apical- and lateral browsing between high- and low wolf utilization areas for any of the tree species (Table 2).

Moose browsing at plantation-scale: inside versus outside wolf territories

Variation in browsing intensity at the plantation scale was best explained by variation in tree density since models which included tree density performed better than models including tree height or level of wolf utilization (Table 3). For apical shoot browsing, the model with wolf utilization performed

Table 1. Study area characteristics in high-wolf utilization areas and low-wolf utilization areas in south-central Sweden. The five tree species below represented 98.7% of all trees measured. Further, one other tree species was measured in the high-wolf utilization areas and 39 individual trees from other tree species were measured in the low-wolf utilization areas.

Description	High-wolf utilization areas	Low-wolf utilization areas
Total number of young forest plantations	12	12
Total number of trees	1148	2025
Apical shoot browsing (%)	13.3	10.4
Lateral shoot browsing (%)	32.2	23.9
Mean tree density young forest plantations (m ⁻²)	0.78	1.36
Mean tree height young forest plantations (cm)	72	88
No. of downy birch	516 (45%)	737 (36%)
No. of silver birch	253 (22%)	647 (32%)
No. of Norway spruce	239 (21%)	344 (17%)
No. of rowan	32 (3%)	133 (6%)
No. of Scots pine	107 (9%)	125 (6%)

Table 2. Differences in the average Jacobs' index scores for the five most common tree species. For each of the common tree species an average Jacob's index score was calculated for apical- and lateral shoot browsing within both high- and low-wolf utilization areas separately (n=12). Consequently, differences in the Jacobs' index scores were tested between the wolf utilization areas for apical- and lateral shoot browsing. Tree species are ranked from most to least preferred.

Species	High-wolf utilization	Low-wolf utilization	Z-value	n	p-value
Apical browsing					
Rowan	0.10 ± 0.16	0.33 ± 0.05	-0.812	24	0.431
Downy birch	-0.49 ± 0.09	-0.64 ± 0.08	1.328	24	0.193
Silver birch	-0.49 ± 0.14	-0.73 ± 0.07	0.994	24	0.341
Scots pine	-0.87 ± 0.08	-0.53 ± 0.13	-1.875	24	0.061
Norway spruce	-0.82 ± 0.16	-0.96 ± 0.02	-0.244	24	1.000
Lateral browsing					
Rowan	0.41 ± 0.08	0.50 ± 0.07	-0.870	24	-0.407
Downy birch	-0.07 ± 0.09	-0.03 ± 0.09	-0.115	24	0.932
Silver birch	-0.03 ± 0.12	-0.09 ± 0.09	0.924	24	0.378
Scots pine	-0.11 ± 0.15	-0.01 ± 0.12	-0.319	24	0.765
Norway spruce	-0.61 ± 0.12	-0.79 ± 0.07	0.890	24	0.396

similarly well as the model with tree density ($\Delta AICc \leq 2$), but the effect of wolf utilization was not significant. Browsing intensity decreased with tree density for lateral shoot browsing (-0.13 ± 0.06 , $t = -2.3$, $df = 20$, $p = 0.029$), and there was a similar tendency for apical shoot browsing (-0.05 ± 0.03 , $t = -1.8$, $df = 20$, $p = 0.083$, Fig. 4).

We found some varying effects when the five tree species were analyzed separately (Supplementary material Appendix 1 Table A5). Moose lateral shoot browsing decreased with tree density for silver and downy birch and moose browsing intensity was higher in high-wolf utilization areas for apical shoot browsing on silver and downy birch and for lateral shoot browsing on Norway spruce. Tree density, or wolf utilization, did not affect browsing intensity on Scots pine and rowan.

Within-plantation variation in moose browsing

Within plantations, browsing intensity was best explained by variation in individual tree height (Table 4). Distance to forest edge, wolf utilization and tree density strongly reduced the fit of models and thus were poor predictors of browsing intensity (Table 4). The probability of apical shoot browsing declined with tree height (-0.01 ± 0.00 , $z = -5.3$, $p \leq 0.001$) and the proportion of the top10 lateral shoots

browsed also declined with tree height (-0.001 ± 0.00 , $z = -6.3$, $p \leq 0.001$) (Fig. 5).

Variation in browsing intensity for the five tree species separately was best predicted by wolf utilization and tree height. Distance to the closest forest edge was only maintained as a significant factor in the model for apical shoot browsing for rowan (Supplementary material Appendix 1 Table A6). Moose browsing on individual trees only decreased with tree height for apical shoot browsing for downy birch. Further, moose browsing was higher in high wolf utilization areas for silver birch, downy birch and Norway spruce. Distance to the forest edge had no effect on browsing of any of the tree species (Supplementary material Appendix 1 Table A6).

Discussion

We hypothesized that at the plantation scale increased wolf utilization should reduce moose browsing, whereas at the within-plantation scale moose should browse closer to the forest edge. In contrast to our predictions, we did not find evidence for an effect of wolf utilization on moose browsing at either scale. The most important factors that explained variation in moose browsing intensity were tree density and tree height. At the plantation scale, browsing intensity declined with increasing tree density while at the within-plantation scale browsing intensity declined with increasing tree height and did not depend on distance to forest edge. We also found an unexpected strongly confounding effect between wolf utilization and tree density/ height. Tree density in high-wolf utilization areas was only half that of low-wolf utilization areas, and tree height was also clearly lower (Fig. 2). This led to an apparent effect of wolf utilization on moose browsing, where moose browsing intensity was higher in the high-wolf utilization areas (Fig. 6). However, our data analyses clearly indicate that this apparent positive effect of wolf utilization reflected a confounding effect of tree density and height. Below we speculate how this confounding effect may be caused by differences in productivity in relation to distance

Table 3. Model selection for the factors influencing browsing intensity between young forest plantations (plantation scale) for all species combined. The bold text show the models which are selected based on their corrected Akaike information criterion (AICc and $\Delta AICc$).

Browsing variable	Fixed factor	AICc	$\Delta AICc$
Apical shoot	Tree density	-41.1	
	Wolf utilization	-39.6	1.5
	Average tree height	-34.7	6.4
Lateral shoot	Tree density	-8.7	
	Wolf utilization	-5.8	2.9
	Average tree height	2.1	6.6

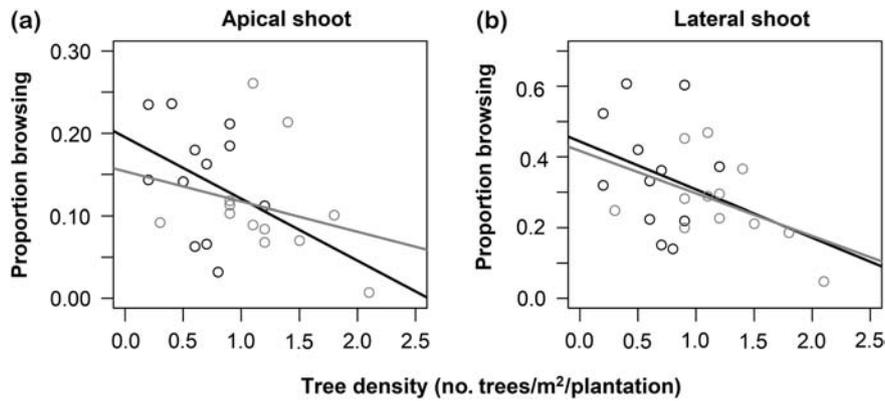


Figure 4. Browsing intensity for all tree species combined in relation to tree density for (a) apical- and (b) lateral shoot browsing at the plantation scale. The black line represent the high-wolf utilization areas and the grey line represent the low-wolf utilization areas. Browsing intensity was measured as the proportion of individuals with top shoot browsed (for apical) and proportion of top10 shoots browsed (for lateral).

from human settlements. This suggests that in order to better understand possible ecological effects of large carnivores in anthropogenic landscapes we need to better understand the complexity and context dependence of human–carnivore–prey–ecosystem interactions.

Differences in tree height and density, not wolf predation risk, explain moose browsing

At the plantation scale we found that browsing intensity generally declined with increasing tree density. This suggests that on plots with higher tree density, where the number of food items is higher, the plot was browsed less intensively. This result supports earlier findings that, as sapling density increases, the proportion of plants browsed by moose decreases (Vivas and Saether 1987, Andrén and Angelstam 1993, Wallgren et al. 2013).

At the within-plantation scale we hypothesized that moose in high-wolf utilization areas should browse more in closer proximity to the forest edge as this would facilitate escape

following a wolf attack (Molvar and Bowyer 1994, Weixelman et al. 1998). However, moose browsing intensity did not differ with distance to the closest forest-edge in either high- or low-wolf utilization areas. These results are in contrast with studies on moose conducted in North America where wolves were present (Hamilton et al. 1980, Molvar and Bowyer 1994, Hernández and Laundré 2005). Molvar and Bowyer (1994) found that moose spent less time feeding when at 200–500 m away from cover than at 0–50 m from cover. Similarly, Hamilton et al. (1980) concluded that most browsing by moose took place within 80 m from forest cover and browsing intensity dropped significantly beyond 80 m. Both these studies suggest that effects of predation risk on moose only occur in larger clear-cuts, with at least 100 m distance to edge. The clear-cuts that we measured in the present study were generally smaller, with a shorter distance to the closest forest edge, which may explain why we did not find an effect. Since we took a random selection of clear-cuts in our study area, this indicates that clear cuts in our study region are generally smaller (i.e. no longer distance to the closest forest edge) than in the before-mentioned North American studies. Finally, the lack of a consistent effect of forest edge could also be related to anti-predator behavior being context dependent with wolf density. For example Eisenberg et al. (2014) found that elk in areas with high wolf population density tended to increase vigilance levels with increasing distance from the forest edge. As a result elk moved into the protective cover of wooded areas when wolves were often present. In contrast, in areas with low to moderate wolf presence, elk did not increase vigilance levels with increasing distance to forest edge (Eisenberg et al. 2014) and increased their use of preferred grassland foraging habitats (Creel et al. 2005). Hence, the wolf density and the frequency at which wolves are present in an area can determine the perceived risk of their prey species for potential risk factors, such as a forest edge.

The main driver of browsing intensity at the within-plantation spatial scale in our study was tree height, with the probability of browsing decreasing with tree height. This

Table 4. Model selection for the factors influencing browsing intensity within young forest plantations (within-plantation scale) for all species combined. The bold models are the models which are selected based on their Akaike information criterion (AIC and Δ AIC).

Browsing	Fixed factor	AIC	Δ AIC
Apical shoot	Tree height	2164.3	
	Wolf utilization	2193.3	29
	Distance	2193.7	29.4
	Wolf utilization + Distance	2194.1	29.8
	Tree density	2194.9	30.6
	Wolf utilization \times Distance	2196.1	31.8
Lateral shoot	Tree height	107.8	
	Wolf utilization	135.2	27.4
	Tree density	137.1	29.3
	Distance	144.3	36.5
	Wolf utilization + Distance	150.9	43.1
	Wolf utilization \times Distance	166.6	58.8

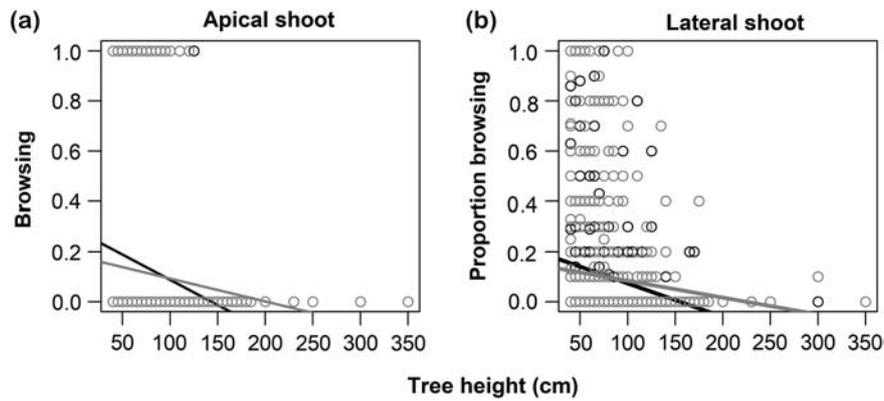


Figure 5. The probability of browsing for all tree species combined in relation to tree height for (a) apical- and (b) lateral shoot browsing at the within-plantation scale. The black line represent the high-wolf utilization areas and the grey line represent the low-wolf utilization areas.

finding confirms the results from previous studies that large ungulates select smaller trees (30–60 cm) (Staines and Welch 1984, Welch et al. 1991). This declining probability of browsing with tree height may be the result of trade-offs between food quality, food quantity and chemical defense (Staines and Welch 1984, Welch et al. 1991). Nordengren et al. (2003), e.g. showed that, although food quality (nitrogen to fiber ratio) and quantity (bite size) increased with tree height, the concentration of defensive compounds also increased.

Confounding relation between wolf utilization and tree density and height

As mentioned above, in contrast to our hypothesis, we found browsing pressure to be higher in high wolf utilization areas but also concluded that this likely reflected a strong confounding relationship between wolf utilization levels, tree density and tree height (Fig. 2). As described in the methods, we made sure to standardize for plantation age (4–6 yr old) and randomly selected young plantations from a database before going out in the field. There were also no obvious differences in forestry management practices between the high- and low-wolf utilization areas (unpubl.). It is important

to emphasize that the difference in tree density was mainly caused by differences in natural recruitment of the deciduous trees and not due to planting differences. So why were tree densities on average lower in high-wolf utilization areas? In hindsight, we speculate that the relationship between tree density and wolf utilization may have resulted from an interaction between human activity, wolf behavior, and site productivity. Several studies have shown that wolves avoid centers of human activity such as towns and agricultural areas (Theuerkauf et al. 2003, Rogala et al. 2011, Wam et al. 2012). To test a posteriori if wolves in our study area avoided areas of higher human activity, we compared average ‘human influence index’ values between the high- and low-wolf utilization areas. This human influence index (from Wildlife Conservation Society – WCS 2005) is based on human population density, human land use and infrastructure, and has been mapped globally in 1-km grid cells. For the high-wolf utilization areas we used all available wolf territories (n = 68) at the time of study (2014–2015) and selected only those that had been part of an annual home range for at least 9 of the 17 yr prior to our study (following our study design). This resulted in 29 high-wolf utilization areas. For each of the high-wolf utilization areas, a low wolf-utilization area of similar size was

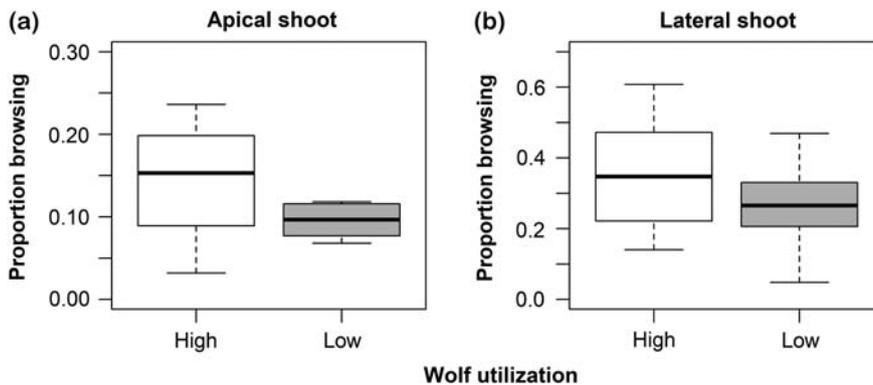


Figure 6. Boxplots of browsing intensity between the different wolf utilization levels (high/low). The thick line shows the median and the box shows 25% of the proportion browsed. The whiskers show the minimum and maximum proportions browsed within the different wolf utilization levels.

randomly selected within 50 km distance to ensure they were in comparable areas. Within each of these high- and low-wolf utilization areas 'human influence index values' were extracted and averaged. We found that the human influence index was indeed more than 1.5 times lower in the high-wolf utilization areas than in the low-wolf utilization areas (Mann–Whitney U-test, $Z = -4.73$, $n = 29$, $p < 0.001$). This confirms that in our study, similar to elsewhere, human activity determines the areas that wolves use intensively. Moreover, areas of human activity are generally associated with the more productive parts of the landscape (Huston 1993). Thus, if wolves avoid areas of higher human activity, high-wolf utilization areas would likely be associated with the less productive parts of the landscape (Worrell 1987). Indeed, despite the careful random selection of the studied plantations, we found a posteriori that the high-wolf utilization areas were, on average, situated at higher altitude (mean \pm SE: 214 ± 24.5 m) than the low-wolf utilization areas (mean \pm SE: 141 ± 20.4 m; two-sample t test, $t = 2.3$, $df = 21$, $p = 0.032$). In boreal landscapes, site productivity is generally negatively related to altitude (Lindgren et al. 1994) and lower productivity will result in lower density of naturally recruiting tree saplings (Kuijper et al. 2010). In summary, our a posteriori tests provide evidence for our hypothesis that the pattern of increased browsing in high-wolf utilization areas reflects the fact that wolves are pushed into less productive parts of the landscape where lower overall tree densities lead to higher moose browsing.

Can wolves mitigate ungulate–forestry conflicts in anthropogenic landscapes?

Moose is the dominant browser in most parts of Sweden as well as in large parts of the boreal zone. Forestry is often the main economic activity in these regions and moose browsing damage is a serious concern for this activity (Angelstam et al. 2000, Bergqvist et al. 2001). This wildlife–forestry conflict is not unique to the boreal zone; across Europe (Apollonio et al. 2010) and North America (McShea and Brian 1997, Côté et al. 2004) growing ungulate populations have led to growing concerns about both the ecological and economic consequences and pleas for stronger population control (Côté et al. 2004, Gordon et al. 2004). Following the recent thinking on large carnivore-mediated trophic cascades (Estes et al. 2011, Ripple et al. 2014), it is easy to speculate that the comeback of large carnivores in Europe and parts of North America (Chapron et al. 2014) should influence the ungulate–forestry conflict by steering the distribution of ungulates across the landscape. However, our results suggest one should be careful with simple views on possible ecological effects of large carnivores in anthropogenic landscapes without full recognition of possible indirect effects of human activities on carnivore and prey behavior (Kuijper et al. 2016). Human activities can influence the ecological roles of large carnivores and their influence on their prey through top-down mediated effects (hunting/poaching on both carnivores and ungulates) or by changing the resource landscapes as a result of forest management and nutrient deposition (Kuijper et al. 2016). Our

results already state the importance of these intricate interactions as areas of human activity are generally associated with the more productive parts of the landscape (Huston 1993, Kuijper et al. 2016) and the avoidance of areas with higher human activities by wolves. Further, our results could also be influenced by other complex-human–predator–prey interactions that occur in anthropogenic landscapes. In most parts of Scandinavia, human harvest replaced natural predation on moose by wolves (Sand et al. 2006). During the last decades, moose harvest constituted approximately 95% of the total moose mortality in Scandinavia (Cederlund and Sand 1991, Sæther et al. 1996, Stubbsjøen et al. 2000). The methods and extent of human harvest as a mortality factor compared to natural predators is likely to have resulted in more naïve moose with reduced behavioral response to recolonizing wolves in the Scandinavian moose population (Sand et al. 2006). Besides, Wikenros et al. (2015) showed how hunters reduced their harvest of moose within wolf territories to compensate for wolf predation. Interestingly, hunters seemed to overcompensate for wolf mortality and harvest size was reduced more than the estimated reduction needed to account for wolf predation (Wikenros et al. 2015). As a result of this overcompensation in harvest by humans moose densities may be higher in wolf areas than in non-wolf areas, which may lead to higher browsing intensity in stands within the high-wolf utilization areas. It is important to note that in our study the results of our pellet counts do not support this and our analyses at the plantation and within-plantation scale show that tree density and tree height are more important in explaining the variation in browsing intensity.

In conclusion, our results show that in anthropogenic landscapes carnivore effects on prey and lower trophic levels may follow complex, context-dependent, indirect relations. In order to give more insight in the controversies that exist about the impact of large carnivores on lower trophic levels and subsequently design appropriate conservation policies we need a better understanding of the full implications of human activity on carnivore–ungulate–ecosystem interactions.

Acknowledgements – We would like to thank the Scandinavian Wolf Research Project (Skandulv) for providing access to the wolf data and the Swedish Forest agency (Skogsstyrelsen) for access to the database on clear-cut areas in Sweden. Further, we would like to thank E. Le Roux for her support with the statistics.

Funding – JPGMC and NJS were supported by a grant from the Swedish EPA ('Beyond Moose' grant number NV-01337-15). In addition, the work of DPJK was supported by funding of the National Science Centre, Poland (grant number 2015/17/B/NZ8/02403)

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Supplementary material (Appendix ECOG-03329 at <www.ecography.org/appendix/ecog-03329>). Appendix 1.