Recreation influences deer behavior and browsing more than returning wolves

A field study at the Veluwe, the Netherlands

[redacted]

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Content

Pictures titlepage:

Wolf: https://en.wikipedia.org/wiki/File:Wolf_-_populations_in_Europe.png

Humans: https://www.fietshurenharderwijk.nl/verhuur/fietsroutes-harderwijk/

Red deer: https://depoortvancyriel.be/wp-content/uploads/2016/10/Hert-op-de-Hoge-Veluwe.jpg

Background & vegetation: Self-made pictures

Abstract

After a long time of disappearance the wolf has returned to most human dominated areas in western Europe. The wolf is known to have large effects on ecosystems, it is however questionable if wolves have the same effect in human dominated ecosystems. Therefore, we here studied the effect of wolves and human recreation on deer behavior and vegetation browsing damage at the Veluwe, in the Netherlands. First, we tested how wolves and recreation affected deer distribution (visitation rate) and vigilant and foraging behavior. Therefore, data on wolves (distance from the wolf core), human recreation (path effect and the amount of human recreation, performing repetitive countings), the behavior of deer (using camera-traps) was collected. Additionally, the effect of forest path on deer behavior was included, by setting up cameras and performing the measurements at 20 and 100 meter distance from a forest path. Secondly, we tested how wolves and humans affected the browsing damage on vegetation (blueberries and deciduous tree saplings). Therefore, additional data on the browsing damage of vegetation was collected, at 20 and 100m distance from forest paths. Our results show that wolves indeed have an influence by decreasing the visitation rate and increasing the vigilance behavior of red deer. However, we did not find any evidence of an effect of wolves on the browsing behavior of red deer and the browsing damage on vegetation. Human recreation on the other hand did show effects on both deer behavior and vegetation browsing damage. Red deer showed more vigilance and less browsing behavior if there was more human recreation. Also we found less browsing damage in areas with more recreation. From this can be concluded that at the moment human recreation influences deer behavior and vegetation more than wolves at the Veluwe. Additionally, we show the importance of including the effect of human activity in studies that look at the effect of predators in human dominated systems.

Introduction

Nowadays, after a long time of absence, some large predators are again colonizing parts of Europe (Chapron et al., 2014). One example is the grey wolf (*Canis lupus*), the most important predator of ungulates in Europe, which disappeared in Western Europe due to human hunting activities. Since wolves are protected by law they started to return to several west European countries (Chapron et al., 2014; Heurich, 2015; Ripple et al., 2014) . Their return is expected to have a large impact on the structure of the ecosystem, because the wolves will form an additional trophic level that has been absent for a long time (Heurich, 2015). However, now the most important predator of ungulates in Europe has returned after been absent for a long time, it is still a question what their exact impact on ecosystems will be.

A very well-known example on the possible impact of wolves on an ecosystem is the reintroduction of wolves in Yellowstone National Park. The study of Ripple & Beschta (2012) in Yellowstone park suggests, that returning wolves do not only have influence on the habitat use, movements, group size and vigilance of elk (their prey), but also indirectly affect many other trophic levels, causing a trophic cascade (Ripple & Beschta, 2012; Ripple et al., 2016). In this case, wolves may indirectly alter the browsing behavior of elk, which decreases the browsing damage on woody vegetation. This gives the woody vegetation the change to recover, which in addition has an positive effect on many vertebrates and invertebrates that are depending on this vegetation (Ripple & Beschta, 2012). Even if these results are often discussed by scientist who claim that human harvest, climate and a sapling bias could also have caused this trophic cascade (Brice et al., 2020; Kauffman et al., 2010; Vucetich et al., 2005), we still find multiple other studies that show otherwise. These studies suggest wolves cause a trophic cascade and therefore give a good example of the impact wolves may have on an ecosystem (Ausilio et al., 2021; Halofsky & Ripple, 2008; Ripple & Betscha, 2004; Ripple & Larsen, 2000; Smith et al., 2003). All these studies, however, have been performed in national parks, which are protected wild areas without much human activity. The situation in national parks like for example Yellowstone national park differs from the situation in Europe. National parks are less influenced by anthropogenic influences as Europe (Ausilio et al., 2021; Beyer et al., 2007; Kuiper, 2016). Humans have similar effects on deer as wolves, they can induce antipredator behavior like more vigilance (Jayakody et al., 2008; Proudman et al., 2020). Moreover, humans can create corridors of fear along forest paths and roads, by disturbing ungulates. This means ungulates avoid habitats or alter their vigilance and browsing behavior near forest roads to avoid humans (Marie et al., 2018). Moreover, anthropogenic activities are expected to influence and possibly overshadow the effects of wolves on ecosystems, thus wolves are expected to have an different effect on the ecosystems in Europe (Ausilio et al., 2021; Ciuti et al, 2012; Coppes, 2017; Heurich, 2015; Kuiper et al., 2016). This lets us wonder what influence wolves will have in a strongly anthropogenic affected ecosystem.

In some European countries wolves are already recolonizing anthropogenic influenced areas for some years and multiple researchers studied their influence on the ecosystem. On the one hand there are studies indicating that the return of wolves first will lead to more vigilant behavior, by creating a landscape of fear. Resulting in a decrease in the foraging behavior of deer and the increasing abundance of vegetation. Furthermore deer will start to avoid areas with danger of wolves and result in changes in the composition of the vegetation (Hebblewhite et al., 2005; Kupferschmid et al. 2016. After some time also the abundance of deer will decrease due to wolves (hunting and creating fear), resulting in more changes in the composition of vegetation in forests (Kupferschmid et al. 2016). On the other hand there are multiple studies that suggest that wolves have no or less influence on the ecosystem, because these influences are overshadowed by anthropogenic influences. However, the effect of humans on deer behavior (e.g. avoidance of humans, higher vigilance levels, decrease browsing activity) is often depending on the context, the amount of people, the season and if hunting is allowed or not can all play an important role (Ausilio et al., 2021; Ciuti et al, 2012; Coppes, 2017; Hebblewhite, 2005; Heurich, 2015; Kuiper et al., 2016).

Even in the most human dominated areas in Western Europe, like the Netherlands, Belgium and Luxembourg the wolf is returning (Chapron et al., 2014; Natuurmonumenten, 2021). In the Netherlands the Veluwe in Gelderland is a good area to study the effect of this returning wolf in area full of anthropogenic activities. The Veluwe is the largest natura 2000 nature area of the Netherlands, including forest and heath landscapes (natura 2000, 2021). It is an area with much human activity like human recreation and hunting to keep the deer abundance controlled. In addition, wolves have returned here in 2018 and reproduced here three times resulting in a pack of more than 10 individuals (Dekker & Bruinderink, 2010; Klees et al., 2019; Natuurmonumenten, 2021; Wolfen in Nederland, 2021). This makes the Veluwe an interesting area to study the influence of both wolves and humans on other trophic levels (eg. ungulates and vegetation) in this forest ecosystem, as a model for areas in the northern-hemisphere that are colonized by both humans and wolves.

The aim of this research is to study the effects of wolves on deer and vegetation in an highly anthropogenic influenced ecosystem. Therefore we need to take a look at the influence of both wolves and humans on deer and vegetation (see fig. 1). We chose to focus on human activity from human recreation during this study and excluded hunting activities. Leading to the following research question: How do wolves and human recreation influence deer behavior and vegetation at the Veluwe in the Netherlands?

We expected to find that the presence of each wolves and humans alone decrease the visitation rate of deer and increases vigilant behavior of red deer (Hebblewhite, 2005; Marie et al, 2018). Furthermore we expected that the decreased visitation rate and the increased vigilant behavior would result in decreased time for foraging behavior of red deer. Which was expected to lead to less browsing damage on the vegetation (Heurich, 2015; Marie et al, 2018). However, combined with the presence of humans, wolves were expected to have less effect on deer behavior and vegetation (Hebblewhite, 2005). This has three reasons. First, humans have an higher direct (abundance) and indirect (behavior) impact on deer, which would overshadow the effect of wolves (Ausilo et al., 2021; Ciuti et al., 2012; Kuiper et al., 2016). Second wolves avoid places near human settlements, which gives deer the chance to go to predation save places (Berger, 2007; Heurich, 2015; Kupfersmid and Bollman, 2016). Last, humans can change the landscape were prey and predator depend on and therefore also alter the effects of predators on their prey (Kuiper et al., 2016). Furthermore, we expect to find an effect of forest paths on deer behavior and browsing damage, since path can create an corridor of fear (Marie et al., 2018). We expect to more vigilant behavior and less browsing behavior near the path (20m) as further away from the path (100m), resulting in more browsing damage further away from the path (100m).

We tested the hypothesis in two steps. First, we tested how wolves and recreation affected deer distribution (visitation rate) and vigilant and foraging behavior. Therefore, data on wolves (distance from the wolf core), human recreation (the amount of human recreation, by performing repetitive couns), the behavior of deer (using camera-traps) was collected. In addition we included the effect of the path by placing cameras and measuring variables at 20 and 100m distance from the path. Secondly, we tested how wolves and humans affected the browsing damage on vegetation (blueberries and deciduous tree saplings). For which we additionally collected data on vegetation browsing damage at 20 and distance from the path (performing counts on browsing damage on saplings and blueberries).

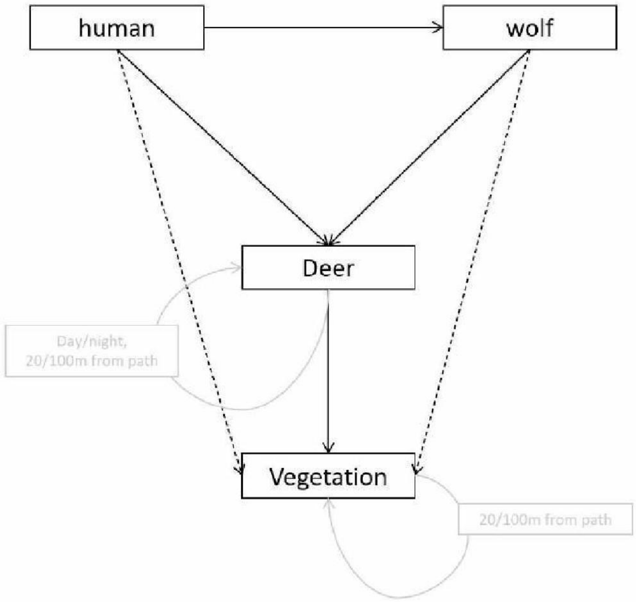

FIGURE 1: OVERVIEW OVER THE VARIABLES INFLUENCING EACH OTHER

Methods

Study area and population

The study area is located at the north-Veluwe in Gelderland, the Netherlands, with 88436 hectares the largest natura 2000 nature reserve in the Netherlands (natura 2000, 2021). Located between Zwolle (52°30'50.0"N 6°06'30.0"E), Apeldoorn (52°12'46.9"N 5°58'26.5"E) and Harderwijk (52°20'45.0"N 5°37'41.5"E). The nature reserve consists of different landscapes including forest (both coniferous and deciduous) and heath. Red deer (*Cervus elaphus)*, fallow deer (*Dama dama*)), Roe deer (Capreolus capreolus), and wild boar (Sus scrofa) are common species on the Veluwe. In addition, the wolf has resettled in the area since 2018 (Klees et al., 2019; Natuurmonumenten, 2021). The area is open for recreational visitors between sunrise and sunset. Hunting is allowed during the hunting seasons, this season differs per species, red deer are for example hunted between august and February (nederlandse jagers vereniging, 2021). At the Veluwe only two types of hunting are allowed, hunting of an high chair & pressure hunt (one hunter at a fixed point and one person pushes deer slowly to the hunter). Battue with hounds is not allowed on the Veluwe. The data of this research was collected outside of the hunting season.

Our study area consists of multiple parts, managed/owned by different organizations: Kroondomein (10400 ha managed by the Royal family), Boswachterij nunspeet (2388 ha managed by Staatsbosbeheer), Leuvenumse bos (837 ha managed by Natuurmonumenten) and Elspeterstruiken (1100 ha managed by Staatsbosbeheer) (see fig. 2). Together the area consists of 14725 ha. All parts are connected to each other, allowing animals to migrate between all parts of the area.

At 25 paired (sapling) locations within the study area data on wolf presence, human recreation pressure, spatiotemporal distribution and behavior of deer and vegetation browsing damage were collected (see fig. 2). The locations were grouped in pairs (due to the camera set-up, see below), with one location at 20m from a path and the other location at 100m from the path (see fig. 4).

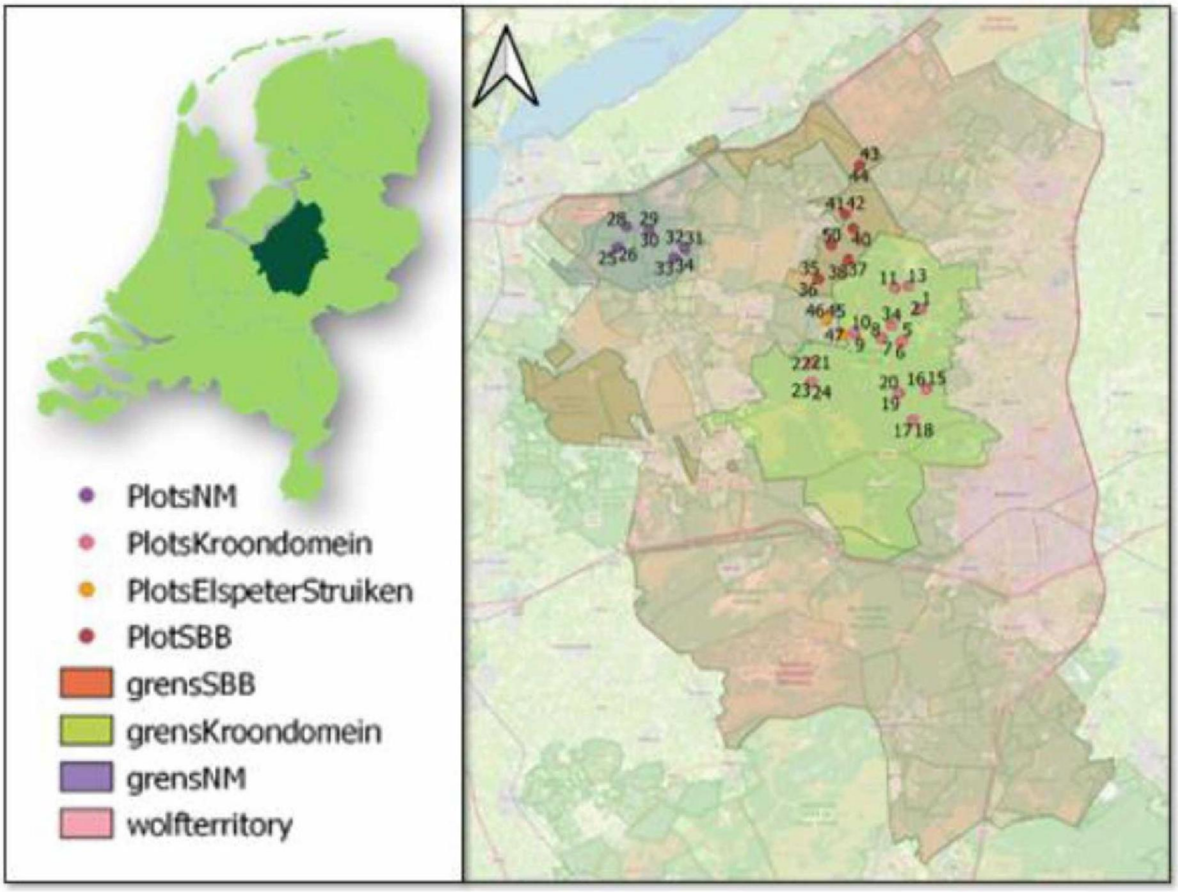

FIGURE 2: MAP OF THE STUDY AREA WITH THE 50 CAMERA LOCATIONS LOCATED AT EITHER >20 OR >100M FROM TRAILS, AT VARIABLE DISTANCES FROM THE WOLF CORE TERRITORY (NOT SHOWN HERE). DARK GREEN AREA IN THE LEFT MAP INDICATES THE LOCATION OF THE VELUWE IN THE NETHERLANDS (HTTPS://LEKKERPLAKKERIG.NL/NATIONAAL-PARK-DE-HOGE-VELUWE-ONTDEKKEN/)

Wolf monitoring

The distance of each location of the wolf core, based on location of the wolf den, was used as a measure for the presence of wolf at each location. It is assumed that a higher abundance of wolves are present near than further away from the wolf core, forming a gradient of wolf abundance. The location of the wolf core was based on information provided by managers of this area, which was confirmed by the data on wolf presence of the zoogdierenvereniging (Klees et al., 2019).

To test if the distance from the wolf core was an appropriate variable to represent the presence of wolf, the distance from the wolf core was correlated to data on the presence of wolves on the north Veluwe retrieved from the Zoogdierenvereniging (Klees et al., 2019). The dataset contained different keys on wolf presence: direct wolf observations by humans and wolf observations by camera traps (C1) and indirect wolf observation through wolf traces or faeces (C2). First the data of the Zoogdierenvereniging was used to define the amount of present wolves in a radius of 1 km around the locations from 2018 to June 2021 using the package geosphere (Robert J. Hijmans, 2019) in R. Finally, the amount of present wolves in a radius of 1 km was correlated to the distance from the wolf core. The results showed that the distance from the wolf core was significantly correlated to the presence of wolfs 1 km around the locations (for both C1 and C1 keys), making distance from the wolf core an appropriate variable to represent the presence of wolf (See Appendix A, for graphs, tests & figures).

Human recreation pressure

The pressure of recreation was measured on the path next to 12 paired locations during May and June, which were a subset of the 50 camera trap locations, see figure 3). Students and volunteers were standing 3 hours (between 14:00-17:00) on Wednesdays and Saturdays between 12 may and 29 june 2021 along the path and counted the amount and type of humans that passed by (e.g. hikers, mountain bikers, horse riders etc.) . Every location was monitored 1-5 times, depending on the amount of volunteers that were available (see appendix B for additional information and the field formular used during the counting).

To compensate for locations that had been monitored for less than 3 hours (appeared during 6 of 43 counts) the data was extrapolated. And to compensate for the different amount of repetitions the average of all repetitions per location was used for further statistics (see appendix B for additional information).

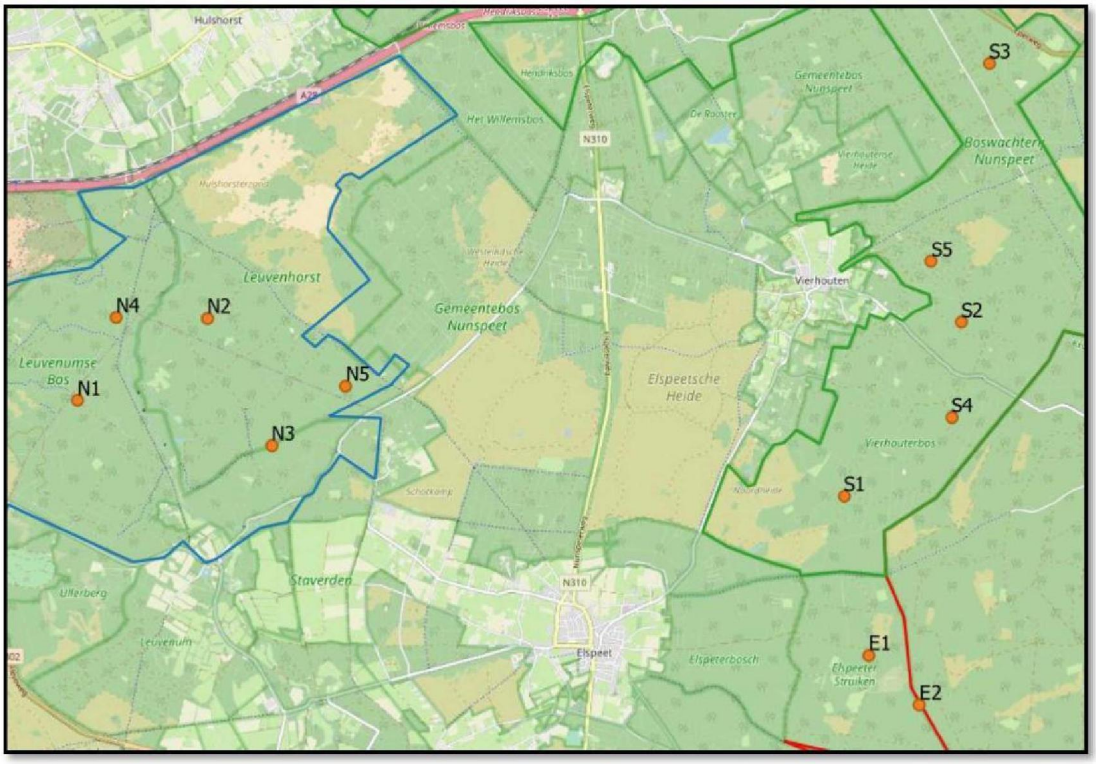

FIGURE 3: MAP WITH LOCATIONS WHERE RECREATION DATA WAS COLLECTED, EACH LOCATION IS CONNECTED TO A PAIRED PLOT WITH CAMERAS AT 20 AND 100 METER FROM THE PATH.

Spatiotemporal distribution and behavior of red deer

Data on spatiotemporal distribution (visitation rate) and behavior (vigilance and browsing behavior) of red deer was retrieved by analyzing the camera data from the 25 paired camera traps that were installed at the 25 paired sample locations, during 4 months from March until June. The cameras traps were installed in pairs, with one camera on 20 m distance of the path and the other 100m distance of the path, to include the influence of the distance of a path as a variable (see figure 4). A camera trap was placed at a height of 100-120cm on a tree which was standing in a plot covered in blueberries, if there were less blueberries (e.g. locations in the Leuvenumse bossen) the camera was directed to a patch of blueberries. If possible, it was avoided to place the camera traps near to tree logs and wildlife tracks. Three types of camera traps were used Bushnell Trophy Cam HD Agressor 2017, Bushnell Trophy Cam HD 2013; LTL ACORN 5210; LTL ACORN 5310. For the set-up of each camera type see table (see appendix C) .

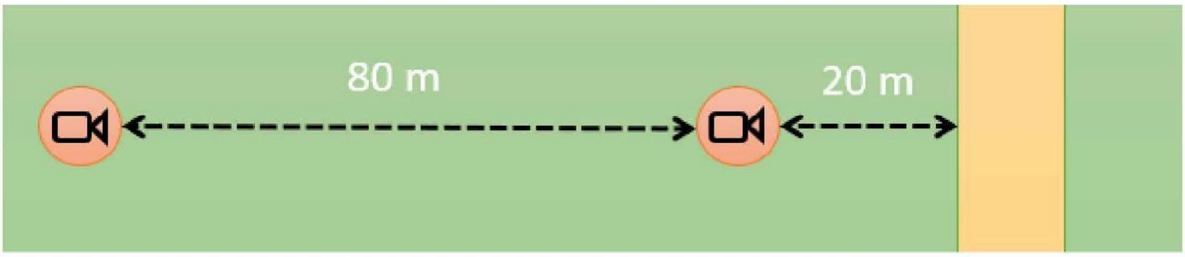

FIGURE 4: SET-UP OF A PAIR OF CAMERA TRAPS

The video material received from the camera traps has been analyzed on different behaviors with the program Boris (v 7.10.5). To analyze different kinds of vigilant and non-vigilant behavior an ethogram was made which includes the subjects and behaviors we wanted to analyze (see appendix C for the ethogram with the different behavior types). We analyzed the behavior of one individual per observation, in case that their was a group of deer we chose to analyze the animal in the center of the video or the animal that appears first in sight of the camera. In addition we wrote down for each observation if it was day or night, so we could include this as an variable in our statistical analyses. Furthermore we kept track of the date, time, temperature and weather, but did not use these variables in our statistical analyses.

Visitation rate was calculated by dividing the amount of observations through the amounts of days the camera was present in the field. One observation includes one or more videos that are recorded not more than 5 minutes after each other and contained the same species (assuming that all videos in one observation are about the same individual). The visitation rate had to be transformed with log to get a normal distribution. The vigilance and browsing time of the deer were used to calculate the proportion of vigilance and foraging of deer at one location. For the proportion of vigilant behavior all time performing vigilant behavior was added together, excluding vigilant behavior induced by the camera trap. For the proportion of browsing behavior the time performing all kinds of browsing behavior were added together. In the end both the time performed on vigilant behavior and on browsing behavior were divided by the time that deer were present, to calculate the proportions of vigilant and browsing behavior.

For the analysis data on spatiotemporal distribution and deer behavior has been summarized per location and day & night, excluding variables as observation, camera type, date, time and weather. In addition we chose to only include red deer to represent the deer population, since this was the most present deer species during the research and occurred on most locations (see Appendix C for the amount of observations per species).

Vegetation browsing damaging

Vegetation is measured at the same 24 paired locations were data on human recreation was collected. The following variables were measured:

1. Browsing of blueberries was measured by taking 5 samples of 10 random shoots in a quadrants of 1x1cm (see fig. 5). The quadratic was laid within 5 meters from the camera location, opposite from the camera direction (to avoid that the camera plot will be visited by humans and scare away deer). If there was no suitable blueberry patch within 5 meters, we would go

to the closest patch to the camera trap (opposite from the camera). The proportion of browsed shoots was calculated and the average of the 5 samples was taken.

2. Tree height , stem diameter and browsing damage of all deciduous tree saplings, between 35 and 150 cm (as these where in reach of red deer), were measured at the same distance of the path (+- 3m) as the camera traps and not further than 50 m to left and right of the camera (see fig. 6). Browsing is measured on the ten highest shoots, following the method of Kuiper et al. (2013). The proportion of browsed shoots of each was calculated and the average of all trees per location was taken. The proportion of browsed shoots was log transformed to obtain normal distribution.

Data on vegetation has been summarized per location, excluding length, stem thickness and tree species. Trees were treated as one group of deciduous trees (see appendix D for the amount of different species that were encountered) .

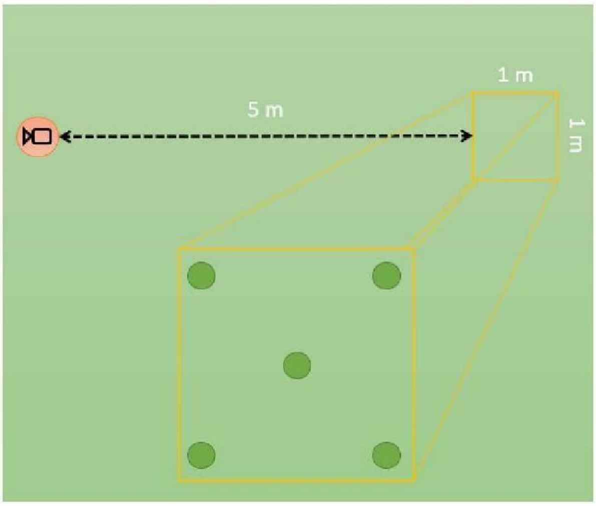

FIGURE 5: SET-UP OF MEASUREMENT ON BROWSING OF BLUEBERRIES. GREEN DOTS ARE THE 5 DIFFERENT SAMPLES OF EACH 10 SHOOTS

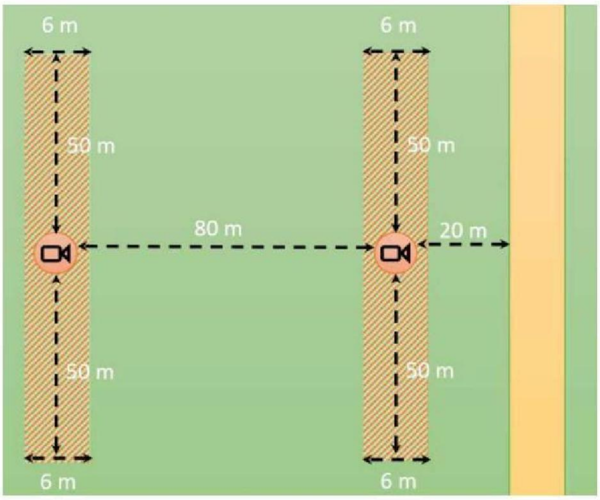

FIGURE 6: SET-UP OF MEASUREMENT ON BROWSING OF TREES, IN ORANGE THE AREA WITHIN TREE SAPLING LENGTH, THICKNESS AND BROWSING DAMAGE WERE MEASURED

Statistical analysis

Data analyzes was conducted with R studio (v. 1.4.1717). To test the influence of wolves and human recreation on deer behavior (visitation rate, proportion vigilance and proportion foraging) and vegetation (proportion browsing of blueberries and trees) 5 linear mixed models have been made. These models included amount of human recreation, distance to wolf core, distance to trail as fixed variables and paired locations as a random variables to account for the paired design. The models with deer behavior as the response also included day and night as a fixed variable. For the models with vegetation as response two-way interactions between distance wolf core & distance trail and a two way-interaction between amount of recreation & distance trail were included. The models with deer behavior included a tree-way interaction between distance wolf core, distance trail & day/night and a tree-way interaction between amount of recreation, distance trail & day/night (see table 1) .

TABLE 1: OVERVIEW OF THE MODELS AND THE CONTAINING FIXED AND RANDOM VARIABLES

Response	Fixed variable(s)	Random variable	Model	Type data	Distribution
Visitation rate		Paired location	lmer	count	Gaussian

red deer	# Human recreation				(Log-transformed)
Vigilance behavior red deer	Distance wolf core Distance path	Paired location	lmer	proportion	Gaussian
Foraging behavior red deer	Day/night	Paired location	lmer	proportion	Gaussian
browsed shoots blueberries	# Human recreation	Paired location	lmer	proportion	Gaussian
browsed shoots trees	Distance wolf core Distance path	Paired location	lmer	proportion	Gaussian (Log-transformed)

To conduct the statistical analysis the package lme4 (Bates et al., 2015) was used. Model selection was performed by stepwise exclusion of variables with the highest P-value. All models were tested for normality and variances simulations using the "DHARMA" package (Florian Hartig, 2021) (see appendix E for more information on the residual diagnostics). For graphs the packages ggplot2 (Wickham 2016) and ggpurb (Kassambara, 2020) were used. In addition, the packages The data was organized using the packages dplyr (Wickham et al., 2019) and reshape2 (Wickham, 2007) have been used for the organization of the data.

Results

Effects of wolves and human recreation on red deer behavior

During the study 258 observations of deer were made using camera traps. The observation included 85% red deer, 6% fallow deer, 7% roe deer and 2% of the deer we not recognizable by species (see appendix C). All species other than red deer were excluded from the analysis, because of their small sample size.

Spatiotemporal distribution of red deer: visitation rate

Wolf presence decreases red deer visitation rate

The best model for testing the effect of wolves on the visitation rate of red deer, included a two way interaction between distance form the core and day/night. Furthermore, it included the distance from the trail. The model shows a significant effect of the wolf core, the effect is however depending on whether it is day or night . During the day the visitation rate is significantly lower near the wolf core, while during the night the visitation rate is lower further away from the wolf core (see table 2 and figure 7A). In addition the model contains a significant path effect, with a lower visitation rate near the path (see table 2 and figure 7B). Also these paths can be used by wolves, why they may have an additional effect on deer visitation rate via paths.

Human recreation has no direct effect on red deer visitation rate, but paths do

The best model did exclude human recreation as a variable, thought it still includes the significant path effect. We find a lower visitation rate nearer to the path (20m) than further away from the path (100m), indicating that humans still may have an effect on deer via forest paths (see table 2 and figure 7B). A summary of all used variables and an overview on the residual diagnostics can be found in appendix E.

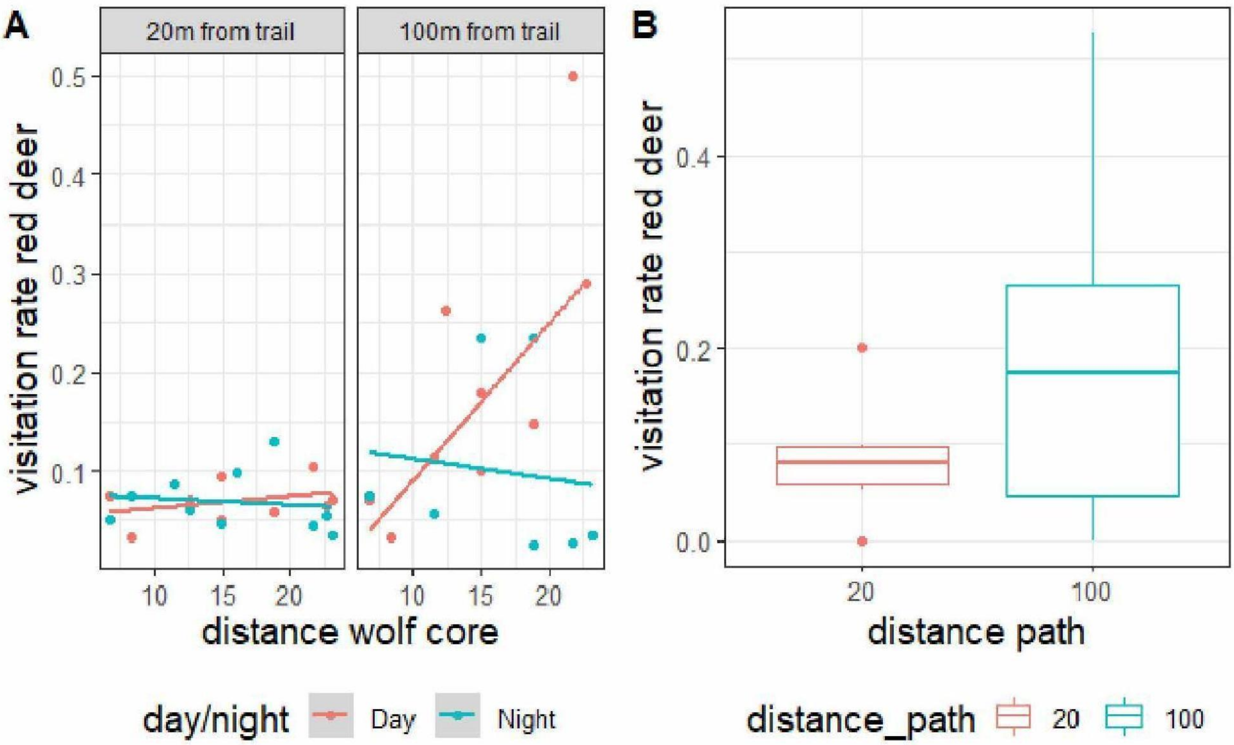

FIGURE 7: THE INFLUENCE OF (A) THE DISTANCE OF THE WOLF CORE, INCLUDING DAY NIGHT AND DISTANCE PATH (B) DISTANCE PATH FROM THE TRAIL ON THE VISITATION RATE OF RED DEER.

TABLE 2: OUTPUT OF THE LMER VISITATION RATE (BEST MODEL)

	Chisq	Df	Pr(>Chisq)	
distance_core	0.0652	1	0.79842	
day_night	1.8096	1	0.17855	
distance_path	4.2957	1	0.03821	*
distance_core:day_night	4.1347	1	0.04201	*

Behavior of red deer: vigilance and foraging

Wolf presence increases red deer vigilance behavior near the path

The best model to test the effect on vigilant behavior included an significant three-way interaction between distance from the core, distance from the path and day/night. This means we see a higher amount of vigilant behavior near the path during the night, further away from the wolf core. However, the amount of vigilant behavior was higher during the day, nearer to the wolf core, possibly because wolves move between day and night (see table 3 and figure 8A). Distance of the wolf core was excluded from the best model to test the effect of wolves on foraging behavior. So wolves have no significant effect on red deer foraging behavior.

Human recreation increases vigilance and decreases foraging behavior

The best model to test the effect on vigilant behavior also included a significant two-way interaction between human recreation and day/night. Human recreation increased vigilance, but only during the night. (see table 3 and figure 8B). Also we found an trend indicating an effect of human recreation on the foraging behavior of red deer. More recreation may decrease the foraging behavior of red deer (see table 4 and figure 8C). A summary of all used variables and an overview on the residual diagnostics can be found in the appendix E.

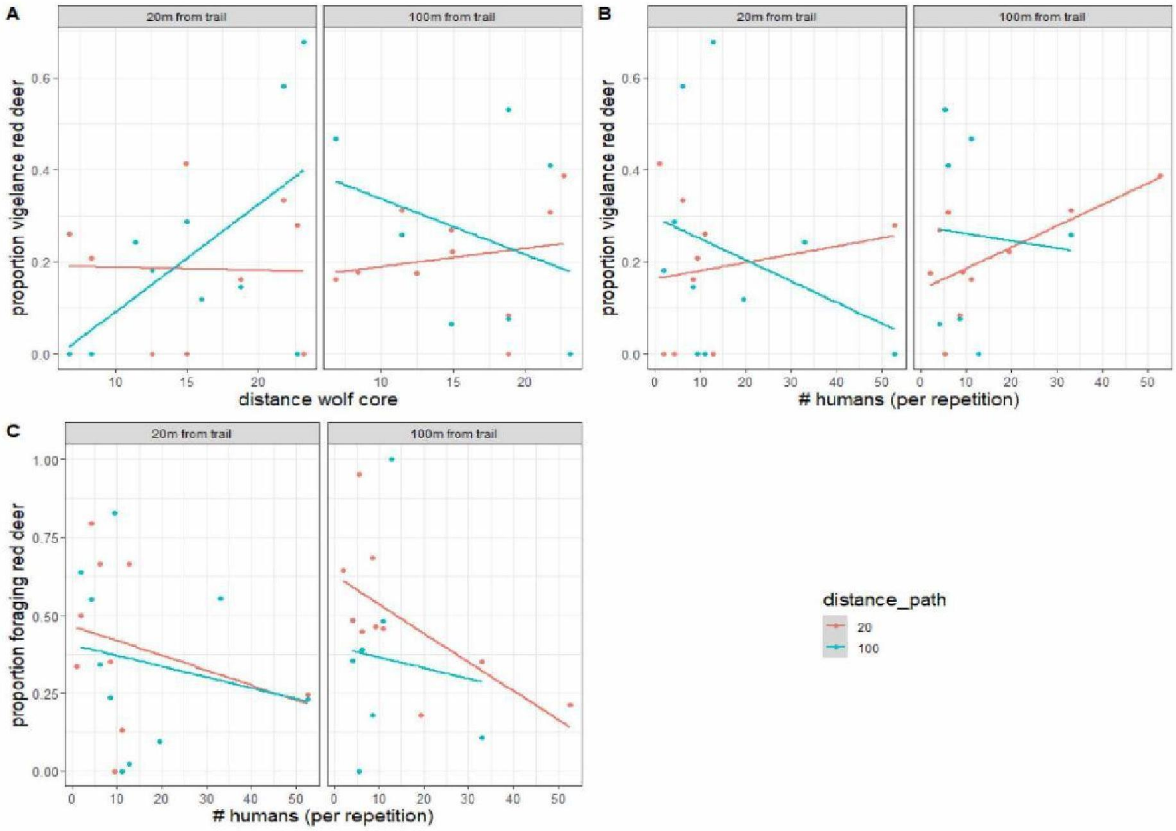

FIGURE 8: THE INFLUENCE OF (A) DISTANCE OF WOLFCORE (B) AMOUNT OF HUMAN RECREATION ON THE PROPORTION OF VIGILANCE OF RED DEER AND THE INFLUENCE OF (C) THE AMOUNT OF HUMANS ON THE PROPORTION OF FORAGING BEAHVIOR OF RED DEER. ALL GRAPHS INCLUDE DAY/NIGHT AND THE DISTANCE FROM THE TRAIL (20/100M).

TABLE 3: OUTPUT OF LMER VIGILANCE BEHAVIOR RED DEER (BEST MODEL)

	Chisq	Df	Pr(>Chisq)	
distance_core	0.4227	1	0.515603	
distance_path	0.0005	1	0.981298	
day_night	0.8864	1	0.346467	
all_human_per_repetition	0.1321	1	0.716276	
distance_core:distance_path	3.4383	1	0.063701	.
distance_core:day_night	1.6266	1	0.202178	
distance_path:day_night	0.013	1	0.909394	
day_night:all_human_per_repetition	9.1343	1	0.002509	**
distance_core:distance_path:day_night	7.5312	1	0.006064	**

TABLE 4: OUTPUT OF LMER FORAGING BEHAVIOR RED DEER (BEST MODEL)

	Chisq	Df	Pr(>Chisq)	
all_human_per_repetition	3.2824	1	0.07003	.

Effects of wolves and human recreation on vegetation

During the study the browsing the proportion of damage on 257 deciduous tree saplings and 120 blueberry shrubs was determined. The deciduous tree sapling species which were studied existed of 30% Silver birch (*Betula pendula*), 16% European beech (*Fagus sylvatica*), 14% Pedunculate oak (*Querus robur*), 12% Rowan (*Sorbus aucuparia*), 11% Alder buckthorn (*Frangula alnus*) and 17% of other not very common species (see appendix D).

Wolves have no effect on browsing damage of vegetation

The distance to the wolf core was excluded from the best model, thus we found no significant effect wolves on the browsing damage of both blueberries and deciduous tree saplings (table 5&6).

Human recreation has different effects on browsing damage of different plant types

We found a significant effect of human recreation on the browsing damage of deciduous tree saplings, however the effect different between the distance from the path. We found more browsing damage on the tree saplings with more recreation nearer to the path (20m) as further away from the path (100m) (see table 5 and figure 9A). We also found a trend of an effect of human recreation on the browsing damage of blueberries, here the effect also differs between the distance from the path. This effect is the opposite from the effect human recreation had on the saplings. Now we find a trend of more browsing damage on blueberries with more further away from the path (100m) as nearer to the path (20m) (see table 6 and figure 9B). A summary of all used variables and an overview on the residual diagnostics can be found in the appendix E.

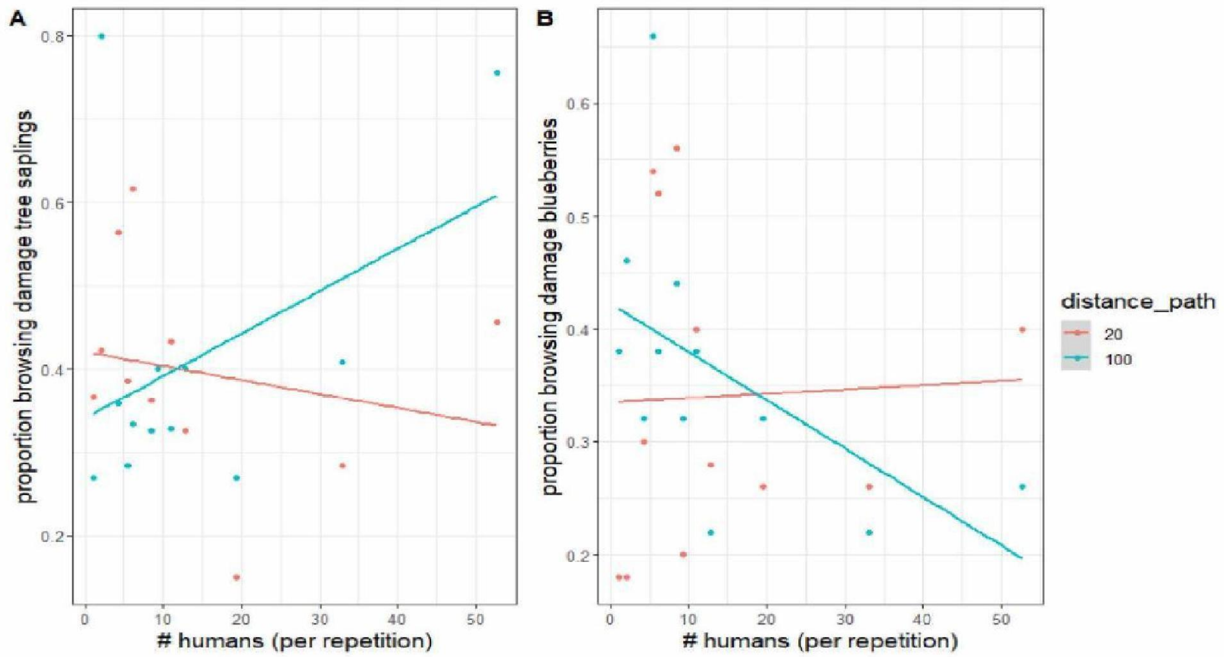

FIGURE 9: THE INFLUENCE OF THE AMOUNT OF HUMAN RECREATION ON (A9 THE PROPORTION OF BROWSED SHOOTS OF DECIDUOUS TREES (B) THE PROPORTION OF BROWSED BLUEBERRIES. BOTH GRAPHS INCLUDE THE DISTANCE FROM THE PATH.

TABLE 5: OUTPUT OF LMER BROWSING DAMAGE DECIDUOUS TREE SAPLINGS (BEST MODEL)

	Chisq	Df	Pr(>Chisq)	
all_human_per_repetition	0.2341	1	0.6285	
distance_path	0.0299	1	0.8626	
all_human_per_repetition:distance_path	4.305	1	0.038	*

TABLE 6: OUTPUT OF LMER BROWSING DAMAGE BLUEBERRIES (BEST MODEL)

	Chisq	Df	Pr(>Chisq)	
all_human_per_repetition	0.7367	1	0.39072	
distance_path	0.4368	1	0.50867	
all_human_per_repetition:distance_path	3.6299	1	0.05675	.

Discussion

The goal of the research was to study the effect of wolves and human recreation on red deer and vegetation at the Veluwe. Therefore, we first looked at the effect of wolves and human recreation on the spatiotemporal distribution (visitation rate) and the behavior (vigilance and foraging) of red deer. After this, we additionally studied the effect of wolves and human recreation on browsing damage on blueberries and deciduous tree saplings.

We found that wolves were indeed correlated to the visitation rate of deer and also on the vigilance behavior, but we did not find any evidence for an effect on the browsing behavior of red deer. Wolves caused a lower visitation rate and an higher proportion of vigilance, depending on whether it is day or night and whether deer are near or further away from the path. Human recreation did also show an effect on both the vigilant and browsing behavior of red deer, but we did not find an effect on the visitation rate. Red deer were more vigilant during the day and spent less time on foraging if there was more recreation. Vegetation was only effected by human recreation and not by wolves. Both blueberries and tree saplings had decreased browsing damage if there weas more human recreation, the effect however depended on the distance from the trail. Blueberries were browsed less further away from the trail (100m) and tree saplings were browsed less nearer to the trail (20m). These results show that human recreation do create a trophic cascade and wolves do not, concluding that human recreation has an bigger effect on red deer and vegetation than wolves have.

Effect of wolves and human recreation on the spatiotemporal distribution and behavior of red deer

Wolves decrease visitation rate and increase vigilance in red deer, but do not effect browsing

In line with our hypothesis we find a lower visitation rate of red deer nearer to the wolf core during the day. This result is not unexpected, because we expect an higher probability of wolf presence near the wolf, why red deer avoid this area out of fear to be predated. This is in accordance with previous findings of a Hebblewhite et al. (2010), who found that elk density and presence where lower in an area with high wolf presence than in an area with low wolf presence in an human dominated landscape. Additionally, this study showed that the high wolf presence area was linked to an higher predation rate. Suggesting that there is a similar link between wolf presence and predation rate on the Veluwe, it is not surprising that we find lower visitation rates in areas with a higher probability of wolf presence. On the other hand we also find a lower visitation rate of red deer further away from the wolf core during the night. This is unexpected, because we do expect a lower probability of wolf presence further away from the wolf core. To find an explanation for this unexpected result, we need to look at the spatio-temporal activity and moving patterns of wolves. Research from Poland shows that the temporal distribution of wolf predation and activity are bimodal, with peaks at dawn and dusk (Theuerkauf et al., 2003). This means that wolves are mostly hunting deer during the dawn and dusk, which can be explained be two factors. First, wolves adjust their activity patterns to periods when red deer are most active (Kamler et al., 2007; Ję drzejewskiet al., 2002; Theuerkauf et al. 2009) And second, the vision of wolves is better with crepuscular light, why they can easier locate their prey during sunrise and sunset. So wolves hunt in crepuscular periods providing them an better hunting success. Hunting by wolves at night (including dawn and dusk) may explain the unexpected result of lower visitation rate further away from the wolf core during the night. Because wolves are leaving the nest site and move further away from the core to go hunting during the night, red deer get disturbed by the wolf further away from the core and therefore we find a lower visitation rate in this area.

We found similar effects of wolves on the vigilant behavior of deer, as we see more vigilance further away from the wolf core during the night and less vigilant behavior nearer to the wolf core during the day. The increased vigilance further away from the wolf core during the night, again indicates that wolves move away from the core during the night to go hunting, as already explained above (Theuerkauf et al., 2003). However, this result is only found near to the forest path (20m), as further away from the path (100m) we find more vigilance near the wolf core during the night and less vigilant behavior further away from the wolf core during the day. This indicates that the distance from the forest path has an additional effect on the vigilant behavior of red deer. As already declared by multiple studies do wolves use forest path for hunting (Ausilio et al., 2021; Houle et al., 2010; James & Stuart, 2000; Whittington et al., 2005; Zimmermann et al., 2014). Forest path give wolves the advantage to travel two to three times faster compared to the natural forest (Dickie et al., 2016) and provide wolves of open areas to hunt and locate their prey (Heurich, 2015). The use of forest path by wolves, can explain why red deer have more vigilance nearer to the path if there is a higher probability of wolf presence, because further away from the path means also further away from the wolves that use this path.

Contrary to our expectations we do not find any evidence of an effect of wolves on the browsing behavior of red deer. According to previous research do wolves induce more vigilant behavior in red deer, why they have less time for foraging, resulting in less browsing damage on vegetation (Kupferschmid & Bollmann, 2016). We indeed found an increase in red deer vigilance through wolves, but this does not result in less foraging behavior in red deer. A possible explanation could be Prey naivety towards the returned wolf (Kuiper et al., 2018). Red deer could forgotten their antipredator behavior and therefore wolves still not have have enough influence on red deer behavior to cause a trophic cascade. Since the wolf only returned to the Veluwe a few years ago and has been away for centuries, this would be a logical explanation (Berger et al., 2001; Sand et al., 2006). Another explanation could be that the effects of wolves are suppressed by the much larger influence of humans. Kupfersmid & Bolmann (2016), state that if prey has two different predators (including humans) they only can adjust to one of these predators if they have different hunting techniques. At the Veluwe red deer are hunted by wolves and humans, who have two different hunting techniques. Here red deer may adjust primarily to humans, suppressing the effect of wolves on the browsing behavior of deer.

Human recreation increase vigilance and decrease browsing behavior of red deer

Against our expectations we do not find evidence for an effect of the amount of human recreation on red deer vigilance. We found, however, that the visiting rate of deer is positive influenced by the distance of the path. Nearer to the path we see less red deer than further away from the path. This can be due to the presence of human at the path. According to previous research are deer avoiding forest paths and decrease there forage behavior in areas near path, because these paths used by humans and predators create a corridor of fear (Coppes, 2017; Marie et al., 2016).

Although there is no effect on the visitation rate, we do find a higher level of vigilant behavior due to humans during the day then during the night. This can be explained by the rules that only allow human recreation at the Veluwe during the day (between dusk and dawn), which means only during the day humans are present and can influence red deer behavior. Coppes et al. (2017) found a similar difference in the effect of roads during day and night and also suggested that deer avoid roads during the day because of more human activity, whereas they return at night if there is less human pressure. According to other literature on the effect of human activity on deer, is one car per 2 hours already enough to induce vigilant behavior in deer (Ciuti et al., 2012). This result supports our finding that human recreation have indeed an impact on deer vigilant behavior and also the foraging. Nonetheless, it should be taken into account that most vigilance is induced during the hunting season (Ciuti et al., 2012) and because red deer are not able to distinguish between a hunter and a recreationist, they show vigilant behavior towards human recreation (Coppes et al., 2017).

Effect of wolves and humans on the browsing damage of blueberries and deciduous tree saplings

Wolves have no effect on vegetation browsing damage at the Veluwe

Contrary to our expectations we do not find any influence of wolves on the browsing damage of blueberries and deciduous tree saplings. If we, however take into account that we also found no evidence of an effect of wolves on the browsing behavior of red deer, the missing effect on vegetation damage is not unexpected. As Hebblewhite et al. (2010) already declared, there is 60 % less predation by wolves in ecosystems with increased human activity. If human activity suppresses wolf predation this much, it is not surprising that they do not show any effects on the vegetation. Furthermore Hebblewhite et al. (2010) stated, that the direct effects on ungulates are stronger than the indirect effect of wolves on the vegetation, which is in line with our results. We indeed found some direct effects on the spatiotemporal distribution and the vigilant behavior of red deer, but the effect did not reach to an indirect effect on the vegetation.

Human recreation increase vegetation browsing damage of deciduous tree saplings

In line with our hypothesis we found an effect of the amount of human recreation on the foraging damage on blueberries and deciduous tree saplings. Since, we already found that the proportion of foraging behavior of red deer was influenced by the amount of human recreation, it is not surprising that we also found an effect on the browsing damage on the vegetation. Moreover, this findings agree with the previous research that human recreation indirectly influences the proportion of browsing trees, by influencing the foraging behavior of red deer (Marie et al, 2018; Mathisen et al., 2018). In addition, Coppes et al. (2017) declare that the avoidance of red deer increases with higher amounts of humans. This may explain that we find lower vegetation damage if there is more human pressure (only at 20m), because more avoidance by deer leads to less browsing. The effect of the amount of human recreation however differs with the distance from the path. We find more browsing damage on deciduous trees further away from the path (100), than nearer to the path (20m). Similar results were obtained in previous research from Boriwski et al. (2021), who found an lower proportion of browsed oak seedlings near roads, than at an further distance. Humans create corridors of fear along forest path and therefore red deer change their behavior to avoid humans (Mathisen et al., 2018). Looking at our results these corridors of fear, could be an explanation for our finding. Deer avoid habitats near the path (20m) or are more vigilant in these areas, resulting in less browsing behavior and decreased browsing damage near the path.

On the other hand we see for blueberries the opposite effect, more blueberries seem to be browsed at 20 meter from the path if there are more humans , but less at 100 meter from the path if there are more humans. Even if this result is a not significant trend this is striking, because we would expect that red deer choose to eat more blueberries further away from the path if there are more humans on the path. So how the vegetation damage is effected by recreation and path seems to be depending on the vegetation species (more browsing on blueberries in areas with more humans and more browsing of tree saplings in areas with less human recreation). Similar result were obtained by Boriwski et al. (2021) who suggest that the choice for vegetation is a result of a trade-off between predation risk and resource attractiveness. They found that places with a higher abundance of the blueberries, which is a preferred plant of red deer, were more visited by deer even if there was an high (predation) risk. In our study area there is indeed a high abundance of blueberries, making our result comparable to the study of Browski et al. (2021). Concluding that red deer seem to prefer to eat the more abundant blueberry in areas with more risk (20m form the path) and the tree saplings in areas with less risk (100m from the path). Moreover, it may be the case that the data on tree saplings is more reliable than the data on blueberries, since the browsing damage on trees was measured more precise than the browsing damage on blueberries. During the measurements on the deciduous tree samplings all trees in a area of ~ $600m^2$ were checked on browsing damage, whereas for the blueberries we only took a sample of 5 time 10 shoots within a square of $1m^2$ per location. Since most of the locations were completely covered in blueberries one square meter is a very small sample, resulting in a small probability of finding browsing. For future research it would be interesting to increase the sample size of the blueberry browsing damage measurement to check if the same results are found as we did now.

Expectations for the future

In the end we can conclude that humans influence vigilant behavior and foraging behavior and therewith indirectly also influence the proportion of browsing on vegetation. Wolves influence the visitation rate and also vigilance behavior, but do not influence the foraging behavior and the browsing of vegetation. This indicates that red deer might favor to stay away from the wolves instead of being more vigilant. On the other hand red deer may favor to be more vigilant near humans, but not to stay away more.

For the situation at the Veluwe this means that wolves do already scare red deer more away, but not yet influence their direct behavior. Humans on the other hand cause red deer to change their behavior to more vigilant behavior, and less foraging behavior, but do not scare them away. An explanation for this different response to wolves and human could be that red deer are more accustomed to humans than to wolf and do expect less danger from humans than from wolves. Multiple studies report on the naivity of prey for returning predators (Berger et al., 2001; Kuiper et al., 2018; Sand et al., 2006). The behavior in red deer caused by wolves may however change in the coming years, if wolf naivety disappear. Nonetheless, the small effect of wolves on deer and vegetation also can also be caused by the suppressing function of humans as an far more riskier predator (Hebblewhite, 2005; Kupfersmid & Bolmann, 2016). This would suggest that the behavior of red deer caused by wolves keeps the same, as it is suppressed by the much larger influence of humans. Dit moet future research uitwijzen.

All in all the results of this research show that wolves may have a very different impact on deer and vegetation in human dominated landscapes, than in a natural environment without humans. Furthermore, this study shows the importance of taking the effect of human activity into account when studying the effect of wolves on ecosystems in human dominated areas. We see that humans can have an large effect on ecosystems, as the effects of humans reach much further than we often think (e.g. humans influence not only deer but also vegetation and possibly also many other species depending on vegetation). Maybe human effects can be managed, but more research is needed to find out how. For further research it would also be interesting to take a closer look at the effect of spatiotemporal movements of wolves and the effect of different kinds of human activity on deer and vegetation.

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Appendix

A. Additional information on collection of wolf data

Graphs correlation between distance to wolf core and amount of wolf observations (C1, C2).

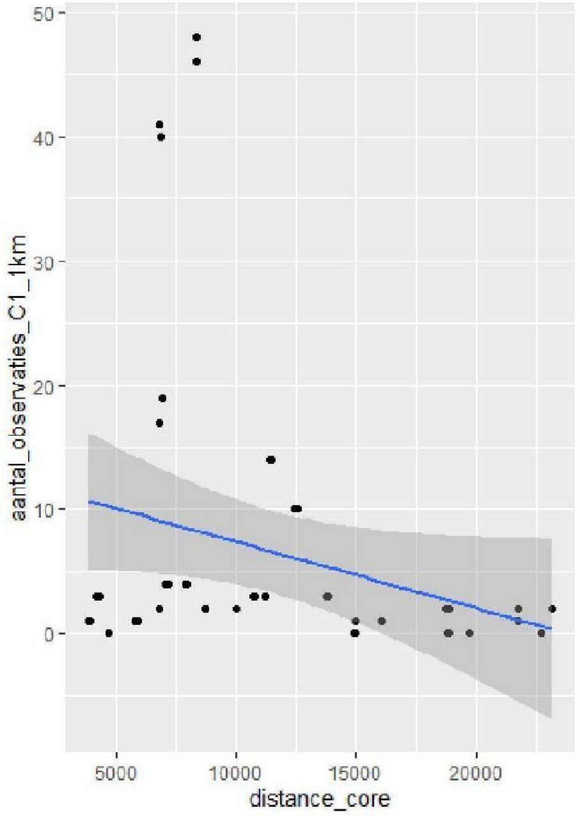

FIGURE 1: CORRELATION BETWEEN DISTANCE WOLF CORE AND AMOUNT OF C1 OBSERVATION IN 1 KM AROUND EACH LOCATION

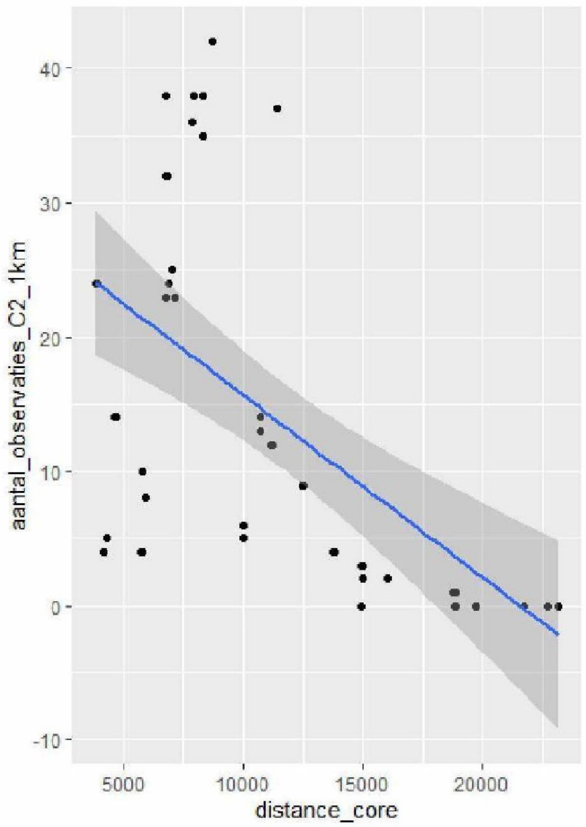

FIGURE 2: CORRELATION BETWEEN DISTANCE WOLF CORE AND AMOUNT OF C2 OBSERVATION IN 1 KM AROUND EACH LOCATION

Output tests correlation between distance to wolf core and amount of wolf observations (C1, C2)

TABLE 1: OUTPUT OF LM WITH CORRELATION BETWEEN WOLF CORE AND AMOUNT OF WOLF OBSERVATIONS (C1)

	estimate	Std. error	T value	Pr(>|t|)	
Intercept	12.7351724	3.6433618	3.495	0.00103	**
distance_core	-0.0005328	0.0002786	-1.912	0.06183	.

TABLE 2: OUTPUT OF LM WITH CORRELATION BETWEEN WOLF CORE AND AMOUNT OF WOLF OBSERVATIONS (C2)

	estimate	Std. error	T value	Pr(>|t|)	
Intercept	29.273658	3.543344	8.262	8.89e-11	***
distance_core	-0.001359	0.000271	-5.015	7.65e-06	***

Maps with amount of wolf observations per location (C1, C2)

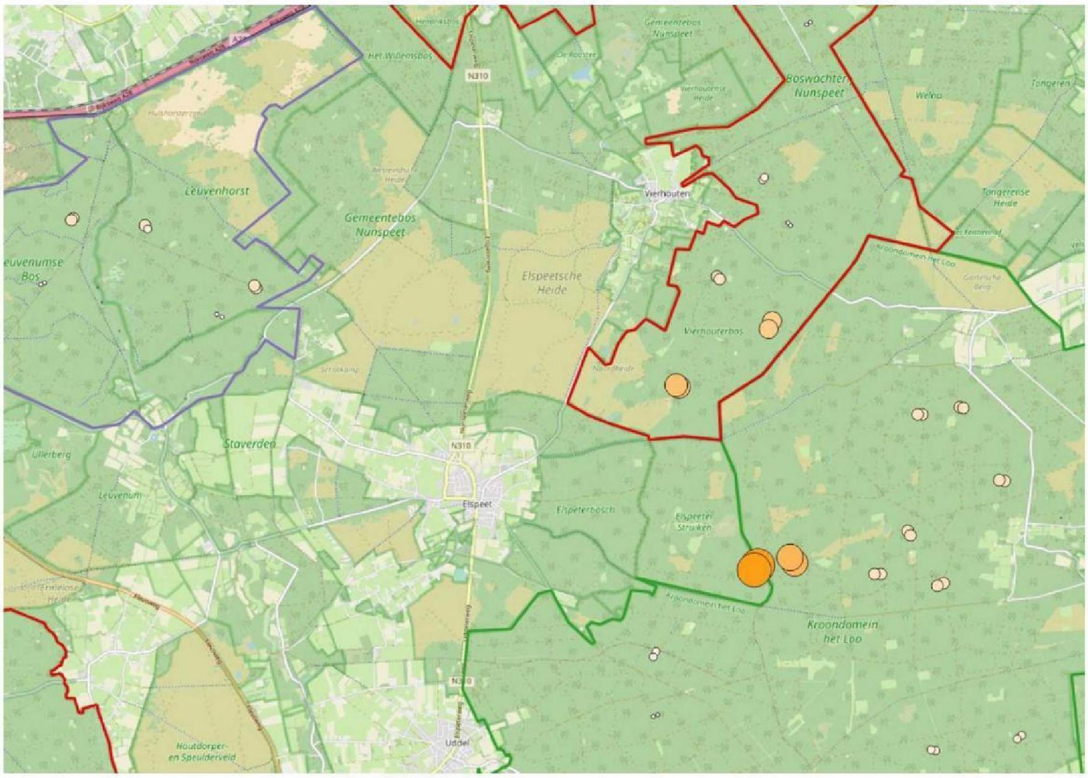

FIGURE 3: MAP OF THE AMOUNT OF WOLF OBSERVATIONS PER LOCATION (C1)

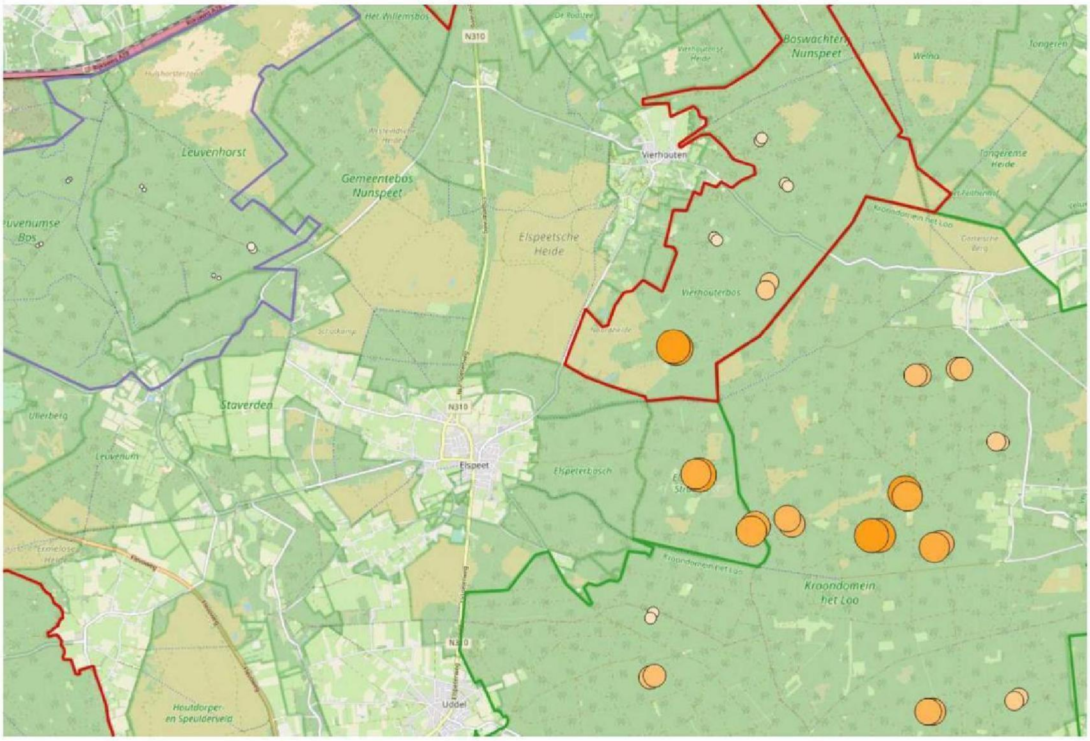

FIGURE 4: MAP OF THE AMOUNT OF WOLVE OBSERVATIONS PER LOCATION (C2)

B. Additional information on collection human recreation data

The data on human recreation has been summarized per location for further analyzing, excluding variables as time, date and weather which did not have an significant effect on the amount of human recreation. Furthermore, we choose to only include humans recreation (by bike & on foot) and exclude pets and vehicles as type of recreation, because of their small sample size. We also did not take into account that different types of human recreation (e.g. mountain-bikers, joggers, bikers...) could have a different impact on deer and vegetation (for the different types of human recreation see table 1) .

TABLE 3: THE AMOUNT OF OBSERVATIONS PER RECREATION TYPE

Recreation type	Amount of observations
By bike	**448**
Biker	46
Race biker	4
Mountain biker	396
E-mountain biker	2
On foot	**190**
Walker	176
Jogger	14
Horserider	**4**

TABLE 4: AMOUNT OF MONITORING REPETITIONS PER LOCATION ON WENSDAY & SATURDAY (ONE REPITITIONS IS 3 HOURS OF MONITORING BETWEEN 14:00-17:00).

Plot.ID	N1	N2	N3	N4	N5	S1	S2	S3	S4	S5	E1	E2
Wednesday	3	3	3	4	4	0	1	1	1	1	4	1
Saturday	3	4	2	3	3	1	1	1	1	2	1	1

Form for data collection in the field

Veldformulier recreatie drukte Veluwe

Naam:		**Weer:*** **
Locatie:	**Datum:**	Regen ja/nee
Begintijd:	**Eindtijd:**	Zon ja/nee

Tijd	**Aantal voorbij komende mensen (per type)**										**zoogdieren**		**Notitie** (te weinig ruimte gebruik achterkant)
	Wandelaar (Op pad?)		Jogger	Fietser	Mountain biker*	Hond (aangelijnd?)		Auto	Ruiter	Anders **	Soort ****	aantal	
	ja	nee				ja	nee						

* op basis van fietstype (fiets heeft dikkere banden, recht stuur, hogere snelheid)

**in de notities precies beschrijven wat er langskomt en ook het aantal mensen/dieren goed aangeven (dus als er bijvoorbeeld een koets voorbij komt ook even aangeven hoeveel mensen erin zitten)

*** als het heeft geregend of de zon heeft geschenen tijdens de sessie (ook al is dat maar een minuut) "ja" aangeven.

**** de soort zo precies mogelijk beschrijven, bijvoorbeeld soort hert aangeven (damhert, edelhert, ree) als dit lukt (anders gewoon "hert"

C. Additional information on collection deer behavior data

TABLE 5: AMOUNT OF OBSERVATIONS OF ANIMALS ON THE VIDEO MATERIAL OF THE CAMERA TRAPS

Species	Amount of observations
Fallow deer (*dama dama*)	**15**
fallow deer female	12
fallow deer female + calf	1
fallow deer male	1
fallow deer female	1
Red deer (*cervus elaphus*)	**220**
red deer female	147
red deer female + calf	7
red deer male	62
red deer unknown sex	4
Roe deer (*capreolus capreolus*)	**17**
roe deer calf	2
roe deer female	6
roe deer male	9
unknown deer	**6**
Wild boar (*sus scrofa*)	**268**
wild boar	228
wild boar + young	40
wolf (*canis lupus*)	**2**
Other	**51**
Badger (*meles meles*)	3
fox (*vulpes vulpes*)	14
human (*homo sapiens*)	14
Other (Marten, birds etc.)	20

Camera trap set-up

TABLE 6: SET-UP OF THE THREE CAMERA TYPES

Camera type	Bushnell Trophy Cam Aggressor HD 2017	ecotone	Bushnell Trophy Cam HD 2013
Mode	Hybrid	Hybrid	Day
Image size	HD	HD	HD
Image format	Full screen	Full screen	Full screen
LED Control	High	High	High
Video size	1280x720	1280x720	1280x720
Interval	0.6s	0.6	1s
Sensor Level	High	High	High
NV Shutter	Auto	Auto	Auto
Camera Mode	24 Hrs	24 Hrs	24 Hrs
Video length	15s	15s	15s
Field scan	Off	Off	Off
Video sound	On	On	On

Video analysis

TABLE 7: ETHOGRAM USED IN ANALYSES PROGRAM BORIS

Behavior	Description
Non-vigilant behaviors	
unknown behavior	Behavior which does not fit in any category or is unclear
presence	If an animal is present which we do not study behavior on
social interaction	Interaction between animals
scratching	Animal is scratching
other non-vigilant	Everything not fitting in another non-vigilant category
rutting	Rutting animal
lying	Lying on the ground
walking	
foraging	Searching for food. Also if the animal is walking during foraging
Vigilant behaviors	
sudden rush due to camera	Sees camera trap and runs away
running	
visual vigilant	Head above shoulders, looking around and chewing
looking into camera	
unknown vigilant	Everything not fitting in another vigilant category
sudden rush	Running away, not seeing camera trap
auditory vigilant	Head above shoulders, looking around and chewing
other vigilant	Behavior which does not fit in any category or is unclear
vigilant while walking	If an animal is present which we do not study behavior on

D. Additional information on collection vegetation browsing damage data

TABLE 8: AMOUNT OF OBSERVATIONS OF EACH VEGETATION SPECIES

Species	Amount of observations
Blueberries	**120 ***
Deciduous trees	**257**
Birch (*Betula pendula*)	78
Beech (fagus sylvatica)	41
Blackberry (*rubus fruticosusi*)	1
Smooth shadbush (*Amelanchier laevis)*	18
Oak (*quercus)*	36
Holly (*Ilex*)	9
Rowan *(Sorbus aucuparia)*	32
Alder buckthorn (*Frangula alnus*)	29
Blach cherry (*Prunus serotina*)	13

**24 observations with each 5 samples*

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E. Additional information on performed tests

Summary of variables (n, mean, min, max) for each model

TABLE 9: SUMMARY OF VARIABLES RED DEER VISITATION RATE MODEL (24 LOCATIONS PER PLOT AND DAY/NIGHT)

	n	mean	min	max
Visiting rate red deer	36	0.10323	0.025	0.5
Distance wolf core	36	15.75	6.77	23.16
Human recreation	36	13.865	1	52.700

TABLE 10: SUMMARY OF VARIABLES RED DEER VIGILANCE BEHAVIOR MODEL: (24 LOCATIONS PER PLOT AND DAY/NIGHT)

	n	mean	min	max
Prop. Vigelance behaviour red deer	36	21.639	0	67.525
Distance wolf core	36	15.75	6.77	23.16
Human recreation	36	13.865	1	52.700

TABLE 11: SUMMARY OF VARIABLES RED DEER FORAGING BEHAVIOR MODEL: (24 LOCATIONS PER PLOT AND DAY/NIGHT)

	n	mean	min	max
Prop. foraging behaviour red deer	36	40.47	0	100
Distance wolf core	36	15.75	6.77	23.16
Human recreation	36	13.865	1	52.700

TABLE 12: SUMMARY OF VARIABLES BROWSING DAMAGE BLUEBERRIES MODEL: (24 LOCATIONS PER PLOT)

	n	mean	min	max
Prop. Browsed shoots blueberries	24	0.3517	0.18	0.66
Distance wolf core	24	16	6.77	23.16
Human recreation	24	13.783	1	52.700

TABLE 13: SUMMARY OF VARIABLES BROWSING DAMAGE DECIDUOUS TREE SAPLINGS MODEL : (24 LOCATIONS PER PLOT)

	n	mean	min	max
Prop. Browsed shoots deciduous trees	24	0.4041	0.15	0.80
Distance wolf core (km)	24	16	6.77	23.16
Human recreation	24	13.783	1	52.700

Residual diagnostics for each test

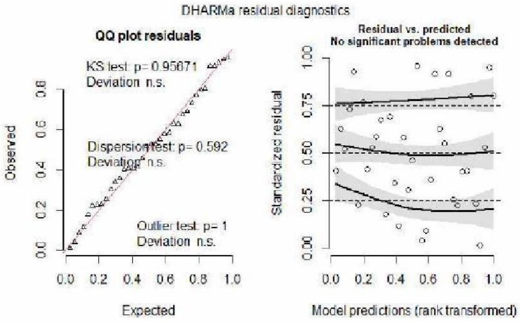

FIGURE 6: LMER VISITATION RATE

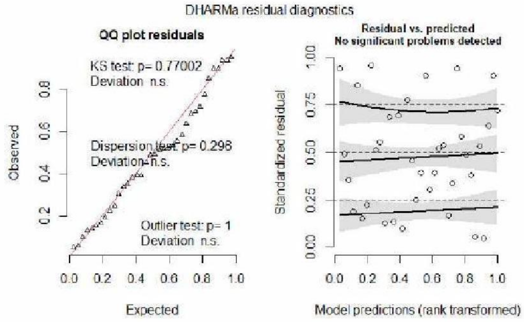

FIGURE 7: LMER VIGELANT BEHAVIOUR

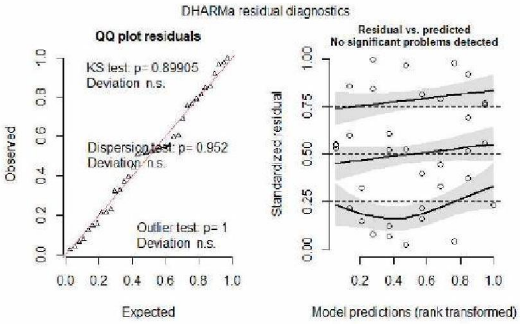

FIGURE 8: LMER FORAGING BEHAVIOUR

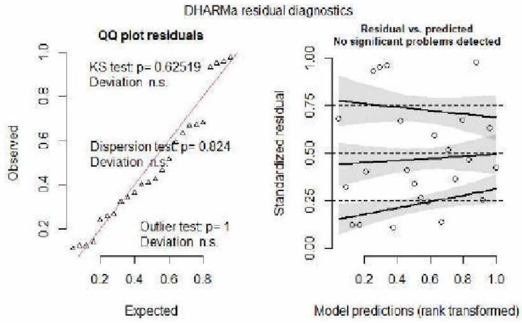

FIGURE 9: LMER BROWSING DAMAGE BLUEBERRIES

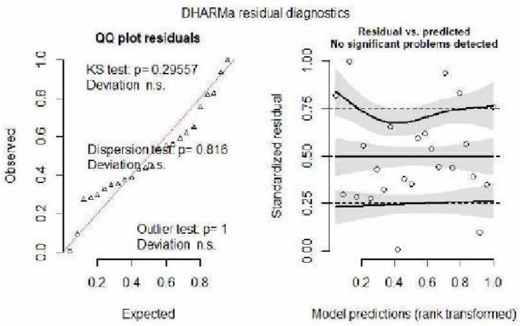

FIGURE 10: LMER BROWSING DAMAGE DECIDUOUS TREE SAPLINGS

F. Additional material (presentations)

During the research project I have supervised two students with their bachelor project and organized groups of students and volunteers for monitoring human recreation at the Veluwe. For this I have made some presentations and documents:

1. Guide on the use of BORIS
2. Introduction presentation for students & volunteers
3. Result presentation for students
4. Overview of the results for volunteers

This documents are included in an additional folder.