

ARE TREE LOGS SCARY?

The behavioural responses of deer to tree logs in a human-dominated area



Esther Swankhuisen S2749149
Primary supervisor: prof. dr. ir. Chris Smit
Daily supervisor: Bjorn Mols
University of Groningen, March 2020

ABSTRACT

Large carnivores have direct and indirect effects on ungulates, with the latter modifying ungulate behaviour in a created “landscape of fear” with varying levels of predation risk in the landscape. Ungulates change their behaviour on a large spatial scale due to the presence of large carnivores in high-risk areas, like cores of territories. On a small spatial scale escape impediments, like tree logs, change the perceived predation risk and also shape ungulate behaviour. In the current anthropogenic landscapes, humans are also known to modify ungulate behaviour on a large spatial scale, with human recreation functioning as a key disturbance factor. However, it is not yet completely clear what the behavioural response of ungulates is to escape impediments on a small spatial scale in a human-dominated area. For the first time, we studied how human recreation can interact with habitat characteristics impeding escape. Therefore, we performed a camera trap study to compare deer spatial distribution and vigilance levels at locations with and without fallen tree logs, in zones with and without recreation and at varying distances to trails. We found a higher number of deer visits in the refuge zone than in the recreation zone and deer showed higher vigilance levels in the recreation zone. In the recreation zone vigilance levels increased with a decrease of distance to trails, with the opposite effect in the refuge zone. No effect of tree logs on the number of visits or on the vigilance levels was found, neither with an interaction with human recreation. To conclude, human recreation functions as a key disturbance factor changing both deer spatial distribution and vigilance levels of deer. However, escape impediments like tree logs do not modify deer behaviour in a human-dominated area. This study shows that humans only induce the same risk effects as large carnivores on a large spatial scale, with possible cascading effects on the lower trophic levels in the landscape.

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INTRODUCTION

Direct and indirect interactions between trophic levels importantly structure ecosystems. Large carnivores have a direct impact on their ungulate prey because of predation (e.g. Kuijper *et al.*, 2013). Several studies have also shown indirect effects of carnivore presence on the behaviour of prey, resulting in a changed spatial distribution (Creel *et al.*, 2005; Thaker *et al.*, 2011); ungulates change their habitat use while making a trade-off between the need for resources and the risk of predation (Lima & Dill, 1990; Creel *et al.*, 2005; Kuijper *et al.*, 2013). In line with this trade-off, ungulates showed increased vigilance levels at the cost of foraging when a carnivore was present (Lung & Childress, 2006; Kuijper *et al.*, 2015; Van Ginkel *et al.*, 2018). These direct and indirect effects of carnivores are intensively studied in Yellowstone National Park (YNP) in the United States, where the wolf (*Canis lupus*) was reintroduced after they were eradicated by humans years ago. Many studies showed how the recruitment of trees recovered and increased in the YNP because of this reintroduction, after years of intensive browsing by deer (Laundré, Hernández & Altendorf, 2001; Ripple & Beschta, 2004, 2006; Painter *et al.*, 2015; Beschta, Painter & Ripple, 2018). So, these effects of carnivores can have cascading effects on lower trophic levels. Carnivores can therefore structure ecosystems via density mediated trophic cascades, which is caused by suppression of the ungulate population, but also via behaviourally mediated trophic cascades; ungulates show behavioural responses because of the fear to become predated (Macarthur & Pianka, 1966; Ripple & Beschta, 2006; Kuijper *et al.*, 2013). This is the basis of the “ecology of fear” concept (Brown, Laundré & Gurung, 1999), which was later on expanded to the “landscape of fear” (Laundré *et al.*, 2001; Laundré, Hernández & Ripple, 2010).

A “landscape of fear” is created by varying levels of predation risk in the landscape (Laundré *et al.*, 2001). The core of a wolf territory could be defined as a high-risk area, because the probability of becoming predated is higher and therefore the perceived predation risk is also higher for deer. In response to these risky areas in the landscape, deer change their behaviour (Ripple *et al.*, 2001; Van Ginkel *et al.*, 2018). With the reintroduction of the wolves in YNP, Ripple & Beschta (2003, 2004) found that deer behaviour is also associated with landscape conditions at a small spatial scale. They found less browsing pressure in areas with steep hills or deep gullies, because certain habitat characteristics decrease predator detection and impede escape, therefore also called escape impediments. So, the perceived predation risk on this small spatial scale depends on the capability of deer to detect predators and the possibilities to escape from them (Underwood, 1982; Halofsky & Ripple, 2008; Kuijper *et al.*, 2015). Furthermore, very small spatial scale escape impediments have recently been found to be important: fallen tree logs. Halofsky & Ripple (2008) found increased vigilance levels in the vicinity of tree logs, in addition both Ripple & Beschta (2007) and Painter *et al.*

(2015) found increased heights of young trees close to tree logs. Not only in the YNP, but also in the Białowieża forest in Poland, studies showed reduced browsing intensity in the vicinity of tree logs, which supports growth of saplings (Kuijper *et al.*, 2014; Van Ginkel *et al.*, 2018). Additionally, the different spatial scales are likely to interact, as the perceived risk induced by escape impediments increases when there are carnivores close by. The study of Kuijper *et al.* (2015) found that red deer (*Cervus elaphus*) were more vigilant near tree logs or even avoid these escape impediments, especially when these tree logs were located inside the core of a wolf territory (high-risk area). Likewise, the study of Van Ginkel *et al.* (2018) showed that in low-risk areas foraging behaviour in red deer was reduced at a distance of 4.0-6.0m from the tree logs, whereas in high-risk areas (inside the wolf core) the foraging behaviour was reduced up till a distance of 16m from the tree logs. The different spatial scales interacting create a dynamic “landscape of fear”, that modifies deer behaviour.

Large carnivores show enormous declines in the current anthropogenic landscapes (Ripple *et al.*, 2014), therefore humans are now the main factor shaping deer behaviour. They do this with hunting, which has not only direct effects suppressing deer densities (e.g. Proffitt *et al.*, 2009), but also indirect effects. Hunting for fear induces a behavioural response in ungulates, to move them from areas where they are undesired (Cromsigt *et al.*, 2013). Moreover, the risk-disturbance hypothesis states that other human activities like recreation also affect the behavioural responses of ungulates, because ungulate prey have a generalized-response to threatening stimuli in a similar way to predation risk (Frid & Dill, 2002; Benhaiem *et al.*, 2008; Rogala *et al.*, 2011; Ciuti *et al.*, 2012). Other studies showed that deer avoided high-risk areas like recreation zones, or showed increased vigilance levels as a response to human recreation (Taylor & Knight, 2003; Jayakody *et al.*, 2008; Lambers, 2019). Not only the zones where recreation takes place are perceived as high-risk areas modifying the behaviour of ungulates, also the trails that are used by the recreationists were avoided (Coppes *et al.*, 2017; Mathisen, Wójcicki & Borowski, 2018; Lambers, 2019). However, no study is done yet to investigate the behavioural response of deer to escape impediments on a small spatial scale located in a human-dominated area and its possible interaction with human recreation in the high-risk areas.

In this study, we investigated how tree logs functioning as escape impediments affect the spatial distribution and vigilance levels of deer in relation to human recreation as the key disturbance factor. We performed a camera trap study in two areas of the Veluwe, located in the Netherlands. With the videos conducted from these camera traps we were able to observe the number of deer in the vicinity of a tree log, as well as their behaviour and then especially their vigilance levels. These observations were compared with observations from videos made in a similar location without a tree

log functioning as a control. Additionally, the distance to human disturbance (distance to trails and forest edges) and the different zones (recreation or refuge) were taken into account. Therefore, we were able to look at a possible interaction between the tree logs and its location in the large spatial scale. On the large spatial scale we expected that deer would avoid these high-risk areas (namely the recreation zones and the trails) or would show increased vigilance levels when they were present in a high-risk area. We expected on the small spatial scale to find fewer deer close tree logs compared with locations without tree logs and increased vigilance levels close to tree logs. In addition, we hypothesised an interaction between the small and the large spatial scale: tree logs located in a high-risk area would evoke the strongest behavioural response in deer.

METHODS

Study area

The fieldwork was conducted in the National Park of Veluwezoom (5000ha) and Nature Reserve Deelerwoud (2380ha), which are part of a larger area called the Veluwe, located in the Netherlands (52°4'N, 5°56'E). These two areas are divided into hunting zones and hunting-free zones and both zones contain recreation and refuge zones. During the hunting season (August-February) several ungulates are regulated by shooting. Since we conducted our fieldwork in March, April, May and June (2019), which is in the non-hunting season, only two zones were classified: recreation and refuge zones. Hiking, biking and horse-riding are the types of recreation that are allowed in the recreation zones between dawn and dusk. Motorised traffic is restricted in all zones, only managers use 4WD to do work in all the zones.

Veluwezoom and Deelerwoud predominantly consist of temperate lowland mixed forest and heathland. However, birch-oak (*Betulo-Quercetum*) and beech-oak (*Fago-Quercetum*) forests only cover small areas, whereas 60% of the area is covered by pine-plantations (Kuiters & Slim, 2002). Therefore, only the coniferous part of the forests in the two areas were used for our study, as this is the most representative forest of the areas and in this way the effect of confounding factors related to forest type were minimized. The underground of this forest type is dominated by billberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea*), but also wavy hair-grass (*Deschampsia flexuosa*) and purple moor-grass (*Molinia caerulea*) can be found. The climate is temperate maritime, with a mean annual precipitation of 790 mm year⁻¹ and the average annual temperature is 9.4 °C, with a minimum of 2.5 °C in January and a maximum of 16.4 °C in July (Kuiters & Slim, 2002).

Both areas support populations of ungulates: red deer (*Cervus elaphus*, 7 ind. km⁻¹ in Deelerwoud and 2 ind km⁻¹ in Veluwezoom), fallow deer (*Dama dama*, 28 ind. km⁻¹ in Deelerwoud and 4 ind. km⁻¹)

in Veluwezoom) and wild boar (*Suis scrofa*, 2 ind. km⁻¹ in Deelerwoud and 3 ind. km⁻¹ in Veluwezoom) (pers. Comm. A. ten Hoedt, area manager, April 2018). Roe deer (*Capreolus capreolus*) have become absent in the Deelerwoud, but are still present in the Veluwezoom in very low densities. Both areas have restricted parts that are grazed by Scottish Highland Cattle (170 ind. km⁻¹). The red deer and the fallow deer were the study species of our study, since they are the most abundant species. Furthermore, these two deer species are the main browsers of tree saplings and therefore preventing tree regeneration. All the ungulates mentioned above can roam freely between the two areas (Veluwezoom and Deelerwoud) using a wildlife passage and deer are also able to reach other parts of the Veluwe by jumping over fences.

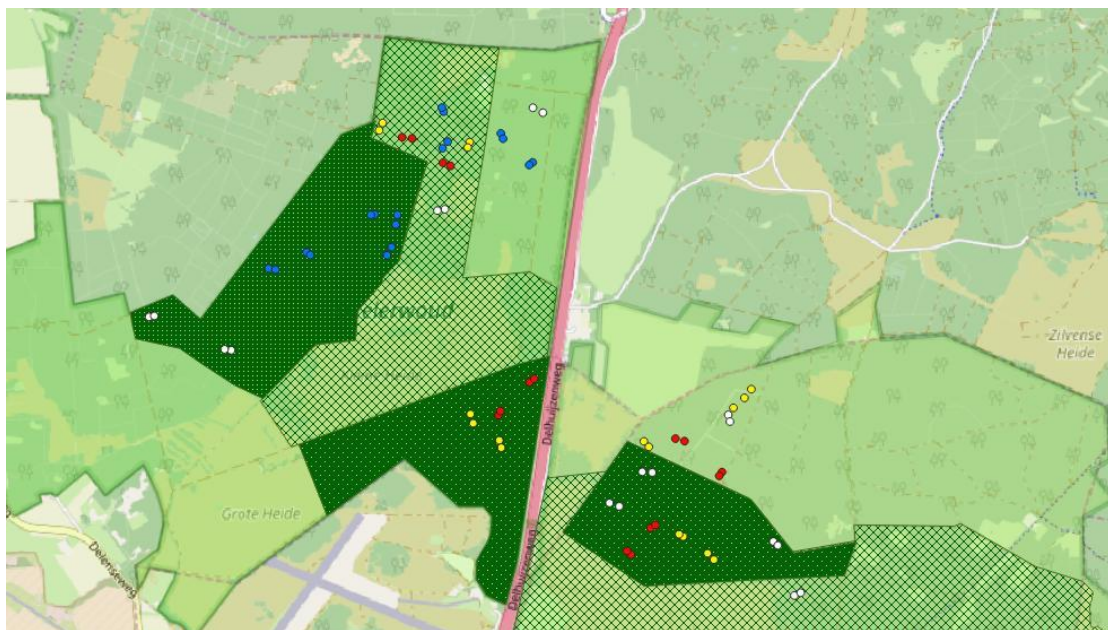


Figure 1: Map showing the two study areas (left: Deelerwoud, right: Veluwezoom) with their two zones (darkgreen: refuge, lightgreen: recreation/hunting and hatched: recreation/hunting-free) and the dots are the pairs from four different sessions (shown by four different colours).

Plot selection

To examine the behavioural responses of deer towards fallen tree logs, we performed a camera trap study in a pairwise design in which we compared observations of deer at fallen tree logs with observations in controls without fallen tree logs. We selected 34 tree logs in the coniferous forests of Veluwezoom (n = 13) and Deelerwoud (n = 21), distributed over the recreation (n = 16) and the refuge (n = 18) zones (Fig. 1). Tree logs were located at least 20m from the trail or the forest edge, to minimize direct human disturbance. The distance to the trails ranged up from 20m to 270m and there was a minimum distance of 100m between the different tree logs to make them independent from each other. Our tree logs were on average 24.64 + 1.04m long and because Kuijper *et al.* (2015) showed that tree logs longer than 12m resulted in increased vigilance levels, we could define our

tree logs as significant escape impediments. The tree logs in the study of Kuijper *et al.* (2015) had a diameter of minimal 1m, however tree logs with a diameter of at least 1m were not present in our study area. Therefore, we selected tree logs that were at least 1m from the ground in the middle of the tree log (Fig. 2). The tree logs were accessible to ungulates from all directions, except for one (where the tree log was positioned).



Figure 2: An example of a tree log plot (left) with a camera trap (right).

Secondly, locations (hereafter: plots) with tree logs were paired with control plots without a tree log, which were located on approximately the same distance from the trail. The controls were at least 30m away from the tree log, as deer were found no longer to respond with vigilant behaviour when further away than 30m from impediments (Halofsky & Ripple, 2008). Furthermore, we ensured the absence of other tree logs of similar size within 30m radius of the tree log and its corresponding control. Therefore, we were able to measure the behavioural responses of deer to a single tree log (Halofsky & Ripple, 2008; Van Ginkel *et al.*, 2018). In addition, the controls were positioned in a comparable site as the paired tree log. That means that they both occurred in patches of the plant species best representing the forest (billberry (*Vaccinium myrtillus*) and cowberry (*Vaccinium vitis-idaea*)). If the selected tree log was located parallel or perpendicular to frequently used 'high-way' deer trails, the corresponding control was chosen to have a different deer trail at the same angle to control for potentially higher visitation rates near those 'high-ways'. Additionally, we avoided large forest gaps avoided during plot selection, because large forest gaps could have been created by multiple, already removed, tree logs. Furthermore, Kuijper *et al.* (2009) found that deer visitation rates and time spent on foraging were higher in forest gaps, because the increased light availability changes the quality and quantity of plant species.

Camera trapping design

Deer behavioural responses were observed with camera traps on all tree log plots and their corresponding control plots (68 in total). We used 19 Bushnell (Trophy Cam Aggressor 2017, Wildlife Monitoring Solutions) camera traps that use no-glow invisible infrared flash light. These camera traps are triggered by a motion sensor reacting on movement and body heat, with a detection range of 30m. The camera traps were attached at one tree next to the tree log and was oriented in such a way that the camera traps could cover the entire plot in the photos and videos. The camera trap was placed at approximately a height of 1m at an angle that the camera trap direction was oriented sideways past the tree log (Fig. 2), without detecting the tree log. The corresponding control also got a camera trap attached to a tree and this camera was oriented towards the same direction as the camera of the paired tree log. After detection of movement or body heat by the motion sensor within the detection range (30m), a photo was taken with a time lag of 0.15s. Thereafter a video of 15s was made with a delay of 0.69s (recover time of photo) + 0.72s (time lag after detection for videos). When the animal stayed, this process was repeated without any delay. During low-light conditions or during night the flash light of the camera traps automatically turned on, also called the night modus. When we switched on the camera traps, we always started with a test video to ensure the camera trap functioned properly. If the test video failed, this camera trap was excluded from the analysis. Camera traps were left at plots for 19-22 days (except for two cameras that only worked for 2 or 7 days), after which they were moved to unused pairs. Every session of 19-22 days contained eight or nine pairs (this changed due to a broken camera trap) and were divided equally, except for the first session, among the two areas and the two zones.

Video analysis

Five cameras failed (wrong settings/broken) and were therefore excluded from the video analysis. Eight cameras did not succeed to film deer, hence they were settled as NA in the vigilance analysis part, but as zero included in the number of visits analysis part. In the end, a total of 29 pairs and 5 loose cameras were used for the video analysis (14 pairs, 3 loose at control plot and 1 loose at a tree log plot in the refuge zone and 15 pairs and 1 loose at a control plot in the recreation zone, 1270 camera trapping days).

The video analysis was done with Behavioural Observation Research Interactive Software (Friard & Gamba, 2016). Only videos showing any deer were used for the video analysis in BORIS. Because it was not possible to identify individuals, visits of deer more than 5 min apart were considered as two separate visits and therefore became separate observations (according to Kuijper *et al.*, 2015). The species and sex were defined, after which the behaviour scoring was performed. The behaviour types

that we scored were focused on the first individual present or the most centred individual at the beginning of the video in case of groups. Either non-vigilant behaviour (foraging, walking, scratching, lying, social interaction) or vigilant behaviour (visual vigilant, auditory vigilant, running, looking into the camera) was scored (Winnie & Creel, 2007; Kuijper *et al.*, 2014). Both visual and auditory vigilant were defined as the individual holding the head above shoulder level while standing still and possibly also looking around, either with chewing (visual or 'routine') or without (auditory or 'induced'), with the latter being more costly as it leads to less time left for foraging opportunities (Lima & Bednekoff, 1999; Blanchard & Fritz, 2007). Observations shorter than 5 seconds were excluded, as these observations were only deer running or walking by without knowing the cause of this behavioural response and could therefore not be defined as a real visit. During the video analysis also some background information was saved for every video: day/night, temperature, number of individuals. From the number of individuals that we saved per video, together with the number of days the camera trap stayed in the field, the number of visits was calculated, which is the number of individuals per day per plot. The vigilance levels were determined with the time deer were scored as vigilant calculated as a percentage of the total time spent on both non-vigilant and vigilant-behaviour. For our vigilance levels, we chose to take only auditory vigilance, which is being vigilant without chewing, because it was difficult to see visual vigilance; deer could just be chewing while foraging instead of being vigilant. Choosing only auditory vigilance also fits with our interest till which extent deer increase their vigilance levels at the cost of foraging, especially when this vigilance was induced by risk. In the end, visual vigilance was therefore grouped with non-vigilant behaviour.

Habitat visibility and canopy openness

To control for existing variation in light availability between pairs, we estimated the canopy openness. During the camera trap retrieval an upward photo was taken with a regular digital camera (Nikon Coolpix B700) 1m above ground level and 8m away from the camera trap in the centre of the plot. The photos were analysed with ImageJ which resulted in an estimate of the percentage canopy openness (a measure of canopy light) (Rueden *et al.*, 2016). We found that canopy openness did not significantly differ between pairs ($p = 0.10$; t-test).

Additionally, the visibility at the plots during the camera trap retrieval was measured to correct for differences between pairs as well. Visibility is reduced by dense vegetation which limits view and therefore changes the amount of perceived predation risk (Halofsky & Ripple, 2008; Kuijper *et al.*, 2015). The visibility was defined as the distance at which the laser of a handheld rangefinder hits any object. While measuring, the rangefinder was held at a height of 1m and 1.5m (as this is approximately the range the adult deer scan its surroundings while foraging (1m) and while being

vigilant (1.5m)). The rangefinder was pointed to all the cardinal directions, because there was no significant difference between the average visibility between both sub-cardinal and cardinal directions, or cardinal directions only (Supplementary Table Appendix A Table A1). We found that visibility at 0.5m did not significantly differ between pairs ($p = 0.10$; t-test), however visibility at 1.5m was found to differ significantly between pairs ($p < 0.001$; t-test). Therefore, we included visibility at 1.5m in the statistical analysis.

Statistical analysis

First, we separated the dataset into a day and a night dataset, because the number of visits was significantly different for day and night ($p < 0.001$; Supplementary Table Appendix B Table B1). This significant difference could be explained by the errors that the video analysis of night videos contain, because it was harder to define which species and which sex were showing behaviour and with how many they were. The vigilance levels did not significant differ for day and night ($p = 0.58$; Supplementary Tables Appendix B Table B2), however, we think that also this night data set contained many errors, because the behaviour types shown by deer were difficult to observe during the night. We were interested in the effect of tree logs in relation to human disturbance, and human recreation is only allowed during the day in our study area. Therefore, in this report we only focus on the number of visits and the vigilance levels of deer during the day, the night analysis is shown in Supplementary Tables Appendix C Table C1, C2, C3 and C4.

Due to an unequal number of observations in the two different sexes, we ignored sex and focused only on species in our statistical analysis. Females with calf and calves on their own were already excluded, because mothers are constantly vigilant to be able to protect herself and the calf (Halofsky & Ripple, 2008, Costelloe 2018), and calves tend to search for their mothers, so show overall higher vigilance levels. Observations scored for unknown deer where excluded as well, as these had an extremely low number of observations. The two species (fallow deer and red deer) never significantly differed from each other and species as a predictor variable was never included in the final model (see below). Therefore, species was ignored as well and results only show the behavioural responses of deer in general.

To examine the number of visits and the vigilance levels, generalized linear mixed effect models were built. For the number of visits a negative binomial GLMER was used, as the number of individuals was count data and included many zeros which caused overdispersion. In the model, number of individuals was used as the response variable and days was included as an offset with a log transformation, to be able to adjust for sessions of different lengths of days. To clarify the effect on

the number of individuals per day, the graphs are shown with the number of visits as response variable. For the vigilance levels a GLMER with family binomial was used, as the vigilance levels were proportional data. We started with the full model and tested for an effect of treatment (tree log present/control without tree log), zone (refuge/recreation) and distance to the trail or forest edge and their 3-way interaction, plus visibility at 1.5m and species as predictor variables, on the number of visits and the vigilance levels. The 3-way interaction was included as others (Kuijper *et al.*, 2015; Van Ginkel *et al.*, 2018) found effects of tree logs that interacted with the location of the escape impediment (high or low risk area). Since our study was a pairwise design, pair ID was added as a random factor to link the tree logs with the corresponding controls.

To find the best model, we used backward model selection based on p-value and Akaike information criterion (AIC) (Burnham & Anderson, 2004). Starting with the full model we checked if the 3-way interaction was significant, if not we simplified the model with 2-way interactions to see if this improved the model. Otherwise the interactions were stepwise deleted, based on the p-value and AIC scores. After that, the model was simplified by deleting the non-significant predictor variables and with AIC the best model could be found. If multiple models were less than 2 points away from the lowest AIC score, the most complex model with the most predictor variables and interactions was accepted as the best model (Burnham & Anderson, 2004). In the end we also performed a post hoc test on the interactions of variables left in the model to clarify any significant differences between groups. All our data was analysed with R, version 3.6.1 using the lme-4 package (glmer) (<https://cran.r-project.org/>).

RESULTS

We collected a total of 406 observations in 63 plots in 12 weeks (Supplementary Table Appendix D Table D2). In detail, 102 of these observations were collected in the recreation zone and 304 in the refuge zone. Looking and the tree log plots with their controls, 198 of these observations were collected at the tree logs and 208 observations at the controls. This amounts to 16.098 seconds of behaviour, with 4.068 seconds of behaviour in the recreation zone and 12.092 seconds in the refuge zone. At the tree logs 8.181 seconds of behaviour were observed and 7.917 seconds at the controls. A total of 1.009 deer individuals were observed, with in the recreation zone 242 individuals and 767 individuals in the refuge zone. At the tree logs 481 of these number of individuals were present and 528 individuals at the controls. More details about observations during the night and specified for the two species (fallow deer and red deer) and unknown deer can be found in the Supplementary Tables Appendix D Table D1 and D2.

Number of visits

Based on the AIC scores, we found two models with good support for the number of visits ($\Delta AIC < 2$; Table 1). The best predictive model (with the lowest AIC) for the number of visits only contained zone as predictor variable.

However, we also accepted the most complete model within 2 points away from the lowest AIC score as the best model.

This model contained not only zone, but also visibility at 1.5m as predictor for the number of visits. Table 2 shows the estimates and their standard errors of this model. The number of visits of deer was significantly higher in the refuge zone ($p < 0.01$) compared with the recreation zone (Table 2, Fig. 3). Visibility at 1.5m was also included as a predictor variable in the best model, however this was not significant and the standard error was larger than the estimate suggesting that the direction of the effect is unknown ($p = 0.53$; Table 2, Supplementary Fig. Appendix E Fig. E1).

Table 1: All the general linear mixed effects models predicting the number of visits. The AIC scores and the ΔAIC with the lowest AIC score are shown. The models with a ΔAIC lower than 2 are depicted in bold. SP = species, X1.5 = visibility at 1.5m, ZO = zone, TR = treatment, DIS = distance to walking trails/forest edge.

| Model | AIC | ΔAIC |
|---------------------------------|---------------|--------------|
| ZO | 646.42 | 0.00 |
| X1.5, ZO | 648.02 | 1.60 |
| X1.5, TR, ZO | 649.30 | 2.88 |
| SP, X1.5, TR, ZO | 651.00 | 4.58 |
| SP, X1.5, TR, ZO, DIS | 652.84 | 6.42 |
| SP, X1.5, ZO, TR*DIS | 653.51 | 7.09 |
| SP, X1.5, TR*DIS, ZO*DIS | 653.84 | 7.42 |
| SP, X1.5, TR*ZO, TR*DIS, ZO*DIS | 655.22 | 8.80 |
| SP, X1.5, TR*ZO*DIS | 656.91 | 10.49 |

To be able to compare the effect of tree logs on number of visits and vigilance levels, the third model from Table 1 was used ($\Delta AIC = 2.88$). We found no significant effect of tree logs on the number of visits and again the standard error was larger than the estimate ($\beta = 0.19 \pm 0.23$, $p = 0.40$; Fig. 4).

Table 2: Estimates of the best model predicting the number of visits. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold. X1.5 = visibility at 1.5m, ZO = zone.

| Random | | | | |
|------------------|----------------|---------------|--------------|----------------------|
| Variable | Variance | St.Dev | | |
| plotID | 0.6342 | 0.7964 | | |
| Fixed | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -1.8206 | 0.4598 | -3.96 | <0.001 *** |
| X1.5 | 0.0052 | 0.0082 | 0.64 | 0.53 |
| ZO-refuge | 0.9702 | 0.3759 | 2.58 | <0.01 ** |

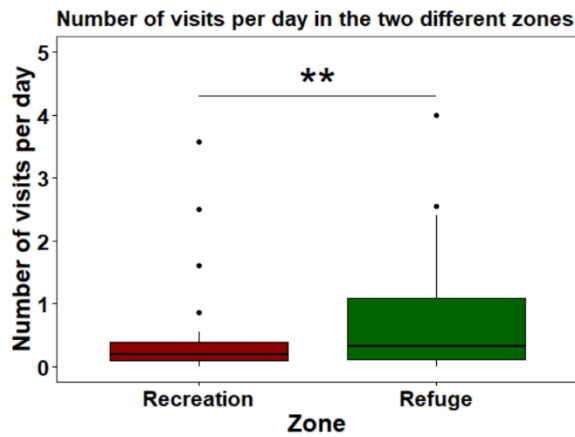


Figure 3: The number of visits (number of individuals per day) of deer in the recreation zone compared with the refuge zone.

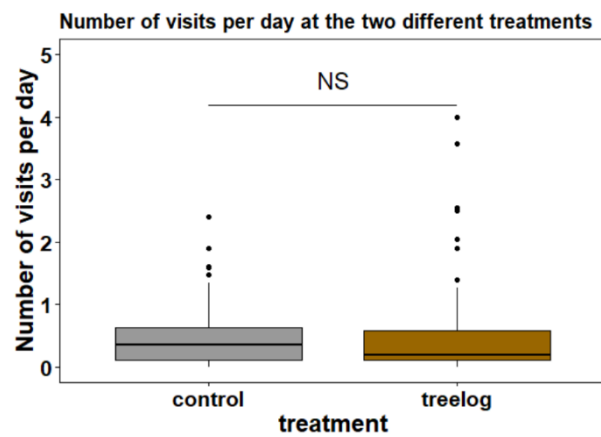


Figure 4: The number of visits (the number of individuals per day) of deer at the control plot without a tree log compared with the plot with a tree log.

Vigilance levels

From all models predicting the vigilance levels of deer, there are three candidate models based on the AIC scores (Table 3). The most complete model included species, visibility at 1.5m and the 3-way interaction. The 3-way interaction was not significant ($p = 0.10$; Table 4), while this model is one of the candidate models and, following our criteria, the best model. Only the interaction between treatment and zone was significant ($p < 0.05$; Table 4), although no significant differences between the different groups could be revealed with a post-hoc Tukey test ($p = 0.82$; Table 5). This is also confirmed by Figure 5, where no clear differences can be seen.

Table 3: All the general linear mixed effects models predicting the vigilance levels. The AIC scores and the Δ AIC with the lowest AIC score are shown. The models with a Δ AIC lower than 2 are depicted in bold. SP = species, X1.5 = visibility at 1.5m, ZO = zone, TR = treatment, DIS = distance to walking trails/forest edge.

| Model | AIC | Δ AIC |
|---------------------------------|---------------|--------------|
| ZO*DI | 60.523 | 0.00 |
| TR, ZO*DI | 61.212 | 0.689 |
| SP, X1.5, TR*ZO*DIS | 61.484 | 0.961 |
| X1.5, TR, ZO*DIS | 62.678 | 2.155 |
| SP, X1.5, TR*DIS, ZO*DIS | 63.333 | 2.810 |
| SP, X1.5, TR*ZO, TR*DIS, ZO*DIS | 63.633 | 3.110 |
| SP, X1.5, TR, ZO*DIS | 64.568 | 4.045 |

The second best model contained treatment and an interaction of zone with distance as predictor variables (Table 3). First, zone had a significant effect on the vigilance levels, with lower vigilance levels in the refuge zone than in the recreation zone ($p < 0.05$; Table 7, Fig. 6). Secondly, the interaction of zone with distance was also significant ($p < 0.05$; Table 7), with increasing vigilance levels in the recreation zone and decreasing vigilance levels in the refuge zone when getting closer to trails (Table 6, Fig. 8). However, both the estimates of the change in vigilance levels with their standard error were close to zero. Figure 7 shows the effect of treatment on the vigilance levels. Even though treatment was included in the best model, there was no significant effect of the presence of a tree log on the vigilance levels ($p = 0.27$; Table 7).

Table 4: Estimates of the best model predicting the vigilance levels. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold. SP = species, X1.5 = visibility at 1.5m, TR = treatment, ZO = zone, DIS = distance.

| <i>Random</i> | | | | |
|-----------------------------|----------------|---------------|--------------|-------------------|
| Variable | Variance | St.Dev | | |
| plotID | 0.0009 | 0.0298 | | |
| <i>Fixed</i> | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -0.7372 | 2.6600 | -0.28 | 0.78 |
| SP-RedDeer | -0.4374 | 0.8936 | -0.49 | 0.62 |
| X1.5 | -0.0203 | 0.0280 | -0.72 | 0.47 |
| TR-treelog | 4.1252 | 3.5971 | 1.15 | 0.25 |
| ZO-refuge | 0.0546 | 2.8294 | 0.02 | 0.98 |
| DIS | -0.0090 | 0.0273 | -0.33 | 0.74 |
| TR-treelog:ZO-refuge | -9.9661 | 5.0547 | -1.97 | <0.05 * |
| TR-treelog:DIS | -0.0526 | 0.0560 | -0.94 | 0.35 |
| ZO-refuge:DIS | -0.0043 | 0.0329 | -0.13 | 0.90 |
| TR-treelog:ZO-refuge:DIS | 0.1057 | 0.0636 | 1.66 | 0.10 |

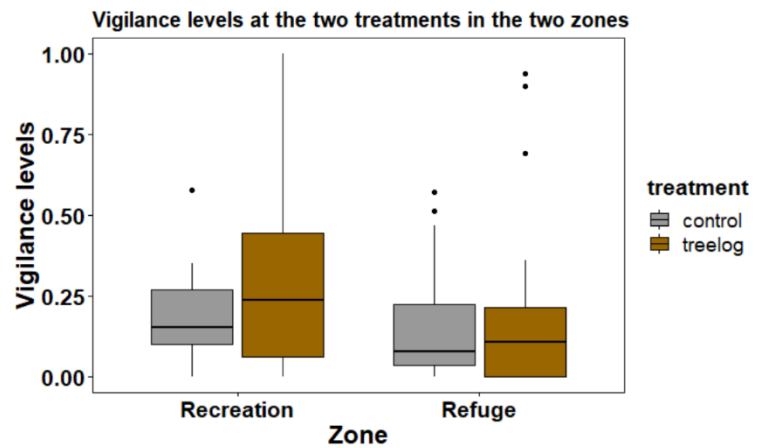


Figure 5: The vigilance levels of deer in the recreation zone compared with the refuge zone, in combination with the presence or absence of tree logs.

Table 5: Post hoc comparisons of zone-treatment interaction in the best model predicting the vigilance levels. The estimates, standard error, z-value and p-value are shown for all the possible groups. Significantly different groups are in bold ($\alpha=0.05$). TR = treatment, ZO = zone.

| Variable | Estimate | SE | z-value | p-value |
|--------------------------|----------|------|---------|---------|
| TR-control:ZO-recreation | 0.601 | 1.21 | 0.50 | 0.82 |
| TR-treelog:ZO-recreation | -0.418 | 1.78 | -0.24 | 0.82 |
| TR-control:ZO-refuge | 0.231 | 1.02 | 0.23 | 0.82 |
| TR-treelog:ZO-refuge | -0.414 | 1.24 | -0.34 | 0.82 |

Table 6: Post hoc comparisons of zone-distance interaction in the second best model predicting the vigilance levels. The estimates, standard error and p-value are shown for both zones and their distance trend. Significantly different groups are in bold ($\alpha=0.05$). ZO = zone.

| Variable zone | Variable distance trend | SE | p-value |
|---------------|-------------------------|--------|-------------------|
| ZO-recreation | -0.0302 | 0.0198 | <0.05 * |
| ZO-refuge | 0.0121 | 0.0064 | <0.05 * |

Table 7: Estimates of the second best model predicting the vigilance levels. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold. TR = treatment, ZO = zone, DIS = distance.

| Random | | | | |
|----------------------|----------------|---------------|--------------|-------------------|
| Variable | Variance | St.Dev | | |
| plotID | 6.035e-05 | 0.0078 | | |
| Fixed | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -0.3219 | 1.4045 | 0.22 | 0.82 |
| TR-treelog | 0.8766 | 0.7869 | 1.11 | 0.27 |
| ZO-refuge | -3.8602 | 1.6764 | -2.30 | <0.05 * |
| DIS | -0.0302 | 0.0198 | -1.52 | 0.13 |
| ZO-refuge:DIS | 0.0423 | 0.0208 | 2.03 | <0.05 * |

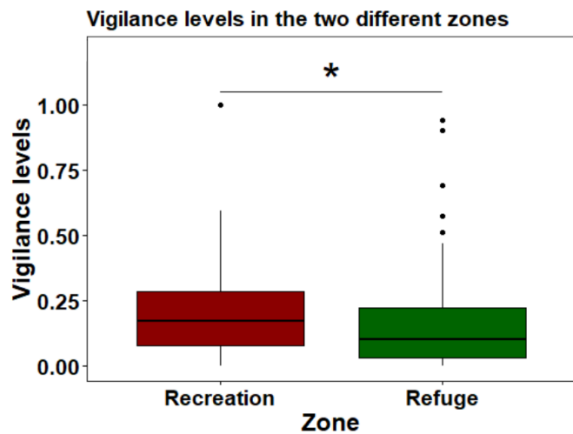


Figure 6: The vigilance levels of deer in the recreation zone compared with the refuge zone.

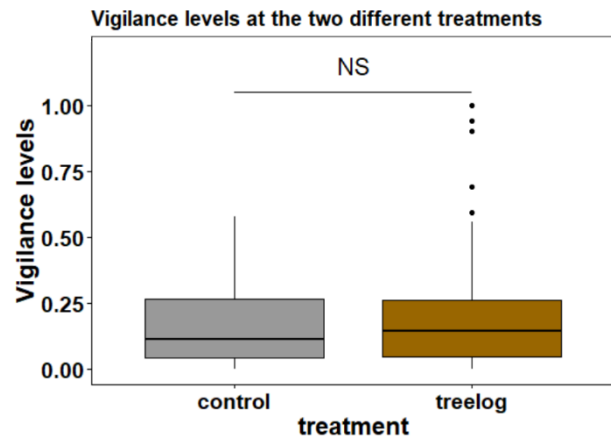


Figure 7: The vigilance levels of deer at the control plot without a tree log compared with the plot with a tree log.

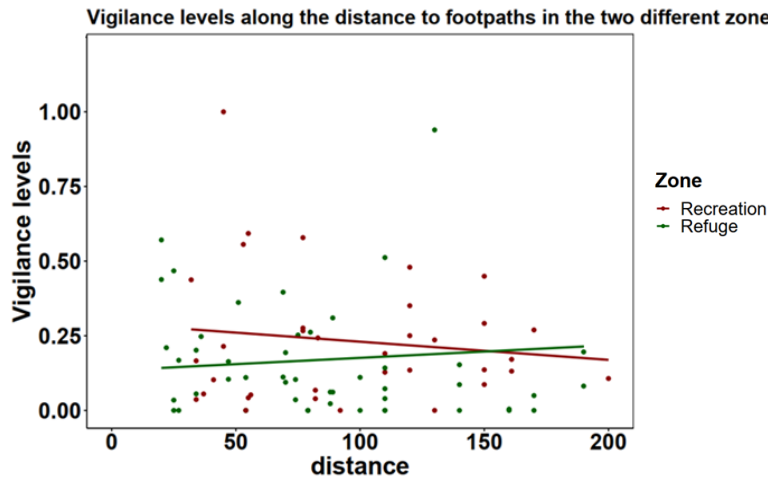


Figure 8: The vigilance levels of deer in the recreation zone compared with the refuge zone, along the distance to the walking trails/forest edge in meters.

DISCUSSION

In this study we investigated whether human recreation affected the number of visits and the vigilance levels in two species of deer at two different spatial scales. On the large spatial scale the behavioural responses of deer were studied in recreation zones (humans are allowed) and refuge zones (humans are not allowed) and at different distances to trails. On the small spatial scale we investigated the effect of tree logs (as escape impediments), compared with plots without tree logs (controls). Because we were interested in the effect of tree logs on the behaviour of deer in relation to human recreation, we also looked at the interaction between the two spatial scales, i.e. meaning that the effect of tree logs could be dependent on their location at the large spatial scale.

On the large spatial scale we found a higher number of visits in the refuge zone than in the recreation zone. Furthermore, deer showed lower vigilance levels in the refuge zone than in the recreation zone. The distance to trails only had an effect on the vigilance levels, but this effect was different for the two zones: vigilance levels were increasing in the recreation zone with decreasing distance to trails and for the refuge zone the effect was the opposite. At the small spatial scale, the presence of tree logs did not affect the number of visits or the vigilance levels of deer. Moreover, it also did not matter in which zone or at which distance the tree logs were located, as there was no interaction found between the two different spatial scales.

Zonation

We found a higher number of visits in the refuge zone compared to the recreation zone, so deer were preferably in zones where no humans were present. Likewise, in other studies they found that

ungulates preferred refuge zones over zones with human recreation (Coppes *et al.*, 2017; Lambers, 2019) or altered their spatial distribution in other ways to avoid areas with humans as much as possible (Nellemann *et al.*, 2001; Vistnes & Nellemann, 2001; Manor & Saltz, 2005; Mathisen *et al.*, 2018). In our study, deer in the recreation zones showed higher vigilance levels than deer in the refuge zones, suggesting a clear trade-off between food and safety. Previous studies showed similar results (e.g. Duchesne, Coã Teã & Barrette, 2000; Jayakody *et al.*, 2008; Ciuti *et al.*, 2012) namely that deer increased their vigilance levels at the cost of foraging as a response to disturbance from human recreation. So, deer perceive a certain risk of human recreation, which is also in accordance with the risk-disturbance hypothesis (Frid & Dill, 2002); deer should have a generalized-response to threatening stimuli like human disturbance in a similar way to predation risk. This generalized-response is also shown in other animals; for example (Suraci *et al.*, 2019) found that mountain lions altered their movements by only hearing the sound of humans talking.

Distance to trails

The distance to trails or forest edges did not have an effect on the number of deer visits, which is in contrast with our expectation that deer would avoid trails in the recreation zone. Our expectation was based on multiple studies that found that ungulates tend to avoid trails used by humans (Nellemann *et al.*, 2001; Vistnes & Nellemann, 2001; Manor & Saltz, 2005; Coppes *et al.*, 2017; Mathisen *et al.*, 2018; Lambers, 2019). Especially, when deer were within 100m distance of a trail, they flee away (Taylor & Knight, 2003). As our plots were located on distances from 20m up to 270m to the trails, it would have been possible to find the 100m effect. However, animals are able to adapt to the presence of human disturbance, therefore we think deer did not avoid trails because they are habituated to human recreation (Schultz & Bailey, 1978). This habituation of ungulates is in accordance with several studies (e.g. Colman, Jacobsen & Reimers, 2001; Stankowich, 2008) that concluded that ungulates get used to the presence of humans and reduce their flight responses. Especially, when deer experience the human disturbance frequently and both spatially and temporally predictable (e.g. Colman, Jacobsen & Reimers, 2001; Stankowich, 2008). The lacking distance effect could therefore be caused by relative high numbers of deer staying close to trails, because of their reduced flight responses. Taylor & Knight (2003) showed this as well; flight responses of deer decreased when the distance to a recreationist decreased. Because escaping from a potential threat is energetically costly, ungulates only flee away when a certain threshold termed avoidance distance is reached (Lima & Dill, 1990; Jayakody *et al.*, 2008). Hence, deer are habituated to human recreation (Colman, Jacobsen & Reimers, 2001; Stankowich, 2008), however, increased vigilant behaviour is still needed to estimate the potential threat. This is in accordance with our findings that vigilance levels increased closer to trails located in the recreation zone. Further away

from trails deer showed decreased vigilance levels as the perceived risk was different; the trails can be seen as a source of information. Other studies showed as well that ungulates close to trails switch to vigilant behaviour, especially when they perceive a high frequency of recreation (Ciuti *et al.*, 2012).

Animals are able to adapt to the presence of human disturbance; they react most to temporally unpredictable activities (Schultz & Bailey, 1978; Taylor & Knight, 2003). For example, Rogala *et al.* (2011) showed that only when human recreation increased above two people/hour the avoidance distance became larger than 50m. In our study, we did not collect information about trail use by humans. Possibly, values were lower than the average two people/hour. Moreover, human recreation reaches its peak of activity on certain moments during the day, even during the week. We did not take the hours of the day into account, neither the days of the week. We could have missed a distance effect on the number of visits in deer, because they are habituated to human recreation and only avoid the trails at certain moments. It is also argued that the type of recreation shapes ungulate distribution, possibly even more than the frequency (e.g. Stankowich, 2008; Ciuti *et al.*, 2012). Bikers and equestrians rarely leave trails and that makes them more predictable than hikers. Humans on foot are more likely to go off trail and therefore they evoke a stronger behavioural response of ungulates. However, hikers are not correlated with hunting because hunting does not impose enough negative stimuli towards humans on foot after the hunting season, as hunters shoot without being noticed by ungulates (Colman *et al.*, 2001). Distance to trails could trigger an avoidance effect, but only to certain types of human recreation that are spatially unpredictable like recreation off trail, at which deer are not habituated to. To get a better insight in the behavioural response of deer to human recreation, we suggest that detailed information on the frequency of certain types of recreation per specific trail and time of the day would be favourable for quantifying how recreation triggers an avoidance response and therefore change the number of visits in deer close to trails.

We also found that the distance to trails had an effect on the vigilance levels of deer in the refuge zone. In the refuge zone we found increasing vigilance levels with distance from trails, even though it was a minimal increase. The result we found could be caused by individual differences between deer. Deer moved to the refuge zones in large numbers, which we also showed with higher number of visits in the refuge zones. Then, less risk taking deer avoided the trails and stayed deep in the forest, while maintaining increased vigilance levels. High risk taking deer did not avoid trails in the refuge zones and also did not increase their vigilance levels. Further research of these possible deer personalities is needed to better understand individual differences within populations.

Tree logs as escape impediments

Since deer avoid fallen tree logs in response to wolf predation risk (e.g. Eisenberg *et al.*, 2014; Kuijper *et al.*, 2015), we expected tree logs to function as escape impediments as well in response to human induced risk. However, we did not find an effect of tree logs on the number of visits of deer, neither did the vigilance levels differ between plots with and without tree logs. This is in contrast with our expectation based on other studies (Halofsky & Ripple, 2008; Eisenberg *et al.*, 2014; Kuijper *et al.*, 2015), that vigilance levels would increase at the small spatial scale by the presence of escape impediments, like tree logs. More time spent on vigilant behaviour leads to reduced foraging opportunities, this release of browsing pressure is shown in multiple studies (Kuijper *et al.*, 2013; Beschta *et al.*, 2018; Van Ginkel *et al.*, 2018). However, most of these studies have in common that the strength of the behavioural response is dependent on where the tree log is located. Van Ginkel *et al.* (2018) found that browsing pressure was reduced at tree logs, but only in small patches when these tree logs were located in a low-risk area, whereas in high-risk areas (the wolf core) the browsing pressure was reduced up to large patches. In addition, Kuijper *et al.* (2013) only showed a decrease in browsing pressure in the high-risk area, no behavioural response was observed in the low-risk area.

We also expected such an interaction between tree logs and their location in the large spatial scale (which zone or distance to trails). Even though the best model included a 3-way interaction between zones, distance to trails and treatment, none of the combinations showed a significant behavioural response. Risk perceived from escape impediments in the presence of natural predators is therefore not comparable with the perceived risk in the presence of human disturbance. Which could be due to habituation to human recreation, which is mostly spatially and temporally predictable and not associated with tree logs. Another human disturbance factor shaping the behaviour of deer is hunting. However, in our study area hunting takes mainly place on the heathlands and therefore the forest and its escape impediments are likely not to be associated with risk, which is in accordance with our results. Furthermore, hunters use a different hunting method than wolves, as wolves are coursing hunters chasing their prey through the landscape. Human hunting often aims at minimizing ungulate fear response by shooting from a long distance using silencers to minimize the possibility that ungulates link risk effects with specific habitat characteristics or humans on foot (Cromsigt *et al.*, 2013).

Multiple other studies focussed on the cascading effects of wolves on woody species living close to tree logs, rather than on the behavioural response of ungulates. These studies found that saplings species increased in height in the vicinity of tree logs or other escape impediments like coarse woody

debris (Ripple & Beschta, 2006; Pellerin *et al.*, 2010; Painter *et al.*, 2015). These studies confirmed that their results are caused by ungulates showing anti-predator behaviour at these small spatial scales. Besides the fear-effect that tree logs induce in areas with large carnivores, growth of saplings could also be supported by coarse woody debris giving physical protection against ungulate browsing (Smit *et al.*, 2012) or by the higher light availability, as fallen tree logs create forest gaps with increased canopy openness. However, it is also discussed that due to the factors mentioned above deer preferentially forage close to tree logs because of this enhanced growth of saplings in forest gaps (Kuijper *et al.*, 2015) or because saplings emerging from the coarse woody debris and growing beyond the physical protection are more visible to deer (e.g. Pellerin *et al.*, 2010; Beschta *et al.*, 2018). We found neither an avoidance nor an attraction response of deer towards tree logs. We corrected for vegetation differences caused by forest gaps by estimating the canopy openness, therefore it was not likely to expect that deer would be attracted to our tree logs. Moreover, tree logs were accessible from all sites and no other escape impediments were present within 30m, physical protection supporting saplings growth could therefore not have played a role. Deer also did not show an avoidance response to our tree logs, confirming that human recreation does not induce risk effects on the small spatial scale. This provides support for the explanation of studies performed in areas with large carnivores present; they found increased saplings growth close to escape impediments because of fear and not because of changing environmental factors.

Day/night differences

The day data contained 409 observations and a total of 1012 number of deer and the night data 84 observations and 144 number of deer (Supplementary Table Appendix D Table D1 and D2). It is known that deer leave the dense forest during the night to forage on the open heathlands. The open heathlands are their preferred foraging habitat, however during the day the perceived risk is higher in this habitat than in the dense forest (Creel & Winnie Jr, 2005; Stankowich, 2008; Lambers, 2019). We performed our study in the forest, not on the open heathlands, which could explain the lower amount of data during the night. Coppes *et al.* (2017), showed that zones and trails with human recreation were avoided during the day, but preferred during the night. However, because of the preferred open heathlands during the night the number of visits was expected not to differ between zones, which is in accordance with our results (Supplementary Table Appendix C). A distance effect is also not found, because trails are not used by recreationists during the night. For the same reason no differences in vigilance levels between zones or distances to trails were expected. Overall, it was expected the deer would show increased vigilance levels during the night than during the day. We only took auditory vigilance and it is shown that this type of vigilant behaviour is increased during the

night, because of the dark (Schuttler *et al.*, 2017), which makes visual vigilance less effective. It would be interesting to focus on both types of vigilance to clarify this difference between day and night. The differences that we found between species during the night are not trustworthy because of the difficulty in species recognition. There is no effect of tree logs found, which is in contract with our expectations that without recreation tree logs would not be perceived as risky. According to our result that tree logs do not trigger a behavioural response during the day, we suggest that for the same reason tree logs do not have an effect during the night.

It was hard to perform a video analysis during the night, because it was difficult to recognize the species, count the number of individuals or define the behaviour type deer were showing. Also, it was doubtful if the camera traps were always triggered at night, which could result in missing data. Therefore, we suggest for a following-up study that includes the open heathlands and possible different camera traps that works better during the night, to clarify the differences in deer behaviour during the day and the night.

CONCLUSION

We documented the behavioural response of deer towards recreation as the disturbance factor in a human-dominated area. On the larger spatial scale, deer changed their spatial distribution by avoiding recreation zones and preferred moving to the refuge zones. Furthermore, they showed higher vigilance levels when present in the recreation zone and when closer to used trails. The presence of humans affects the behaviour and spatial distribution of deer and could compromise the top-down regulation by predators (Kuijper *et al.*, 2016). Likewise, Suraci *et al.* (2019) concluded that humans can function as “super predators” and create the same “landscape of fear” as other predators (like wolves), which results in the recovery of trophic levels. We also observed the behavioural response of deer towards recreation on the small spatial scale, by looking at the effect of tree logs in relation to human disturbance. However, no differences were found in spatial distribution and vigilance levels close to tree logs compared to plots without these escape impediments.

In our study we did not test for possible cascading effects. However, with high densities of deer moving to refuge zones during the day, browsing pressure is released in the recreation zone, possibly leading to enhanced growth of saplings. In the recreation zone deer foraged less closer to trails, but in the refuge zone they foraged more closer to trails. This effect was only minimal, however it might be interesting to look at the vegetation differences close to the trails between the two zone. In our

study neither an attraction or an avoidance response to tree logs was found, suggesting that tree logs do not support the growth of saplings through release of browsing pressure.

The “landscape of fear” created by human recreation could play an important role in the management and conservation of human-dominated areas, as recreationists are able to change the behaviour of deer. Managers could influence the recreationists and therefore reduce the negative impacts on deer: prohibition for hikers to go off trail, planning of trails in the landscape. In addition, our study showed, just like many others, that refuge zones are very important for deer. Even though no effect of tree logs was found on the behaviour of deer, tree logs should be left in the forest, because dead wood is known to create micro-ecosystems for other taxa, e.g. insects.

The interesting question for now is, what if the wolves arrive in our study area? The wolf returned in the Netherlands after years of disappearance, therefore it is interesting to see if and how the behaviour of deer is going to change. Risk-effects from both humans and wolves could shape the spatial distribution between the zones completely different; the refuge zones are not any longer a zone to refuge to. Moreover, habitat choice and day-night rhythm could also become affected, because wolves are different hunters compared to human hunters; wolves use different habitats at different moments of the day. Due to this different hunting method of wolves, escape impediments possibly will create patches of fear according to multiple other studies (Kuijper *et al.*, 2015; Van Ginkel *et al.*, 2018).

To conclude, our results indicate that deer behaviour is shaped by recreation in a human-dominated area, however, only at the large spatial scale. On the small spatial scale escape impediments, like tree logs, do not induce risk effects with only recreationists present. So, human-induced cascading effects can only be found on the large spatial scale. This confirms that a “landscape of fear” created by humans is different than one created by large carnivores. The comeback of large carnivores like wolves probably will change these risk effects and therefore the cascading effects on both spatial scales, influencing the current ecosystem dynamics completely.

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APPENDIX

Appendix A

Table A1: The paired t-test (for session 1, height 0.5m and for session 2, height 1.5m) and the Wilcoxon signed rank test (for session 1, height 1.5m and for session 2, height 0.5m) predicting if the visibility measured towards either only cardinal

| Session | At what height | p-value |
|---------|----------------|---------|
| 1 | 0.5m | 0.23 |
| 1 | 1.5m | 0.76 |
| 2 | 0.5m | 0.06 |
| 2 | 1.5m | 0.64 |

Appendix B

Table B1: Estimates of the model predicting the number of visits, showing the differences between day and night. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold.

| <i>Random</i> | | | | |
|-----------------|----------|--------|---------|----------------------|
| Variable | Variance | St.Dev | | |
| plotID | 1.148 | 1.072 | | |
| <i>Fixed</i> | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -1.1960 | 0.1920 | -6.23 | <0.001 *** |
| Day.Night-Night | -1.5942 | 0.0889 | -17.94 | <0.001 *** |

Table B2: Estimates of the model predicting the vigilance levels, showing the differences between day and night. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold.

| <i>Random</i> | | | | |
|-----------------|-----------|-----------|---------|----------------------|
| Variable | Variance | St.Dev | | |
| plotID | 3.215e-10 | 1.793e-05 | | |
| <i>Fixed</i> | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -2.1595 | 0.3520 | -6.13 | <0.001 *** |
| Day.Night-Night | 0.3349 | 0.5968 | 0.56 | 0.58 |

Appendix C

Table C1: All the general linear mixed effects model predicting the number of visits during the night. The AIC scores and the Δ AIC with the lowest AIC score are shown. The models with a Δ AIC lower than 2 are depicted in bold. SP = species, X1.5 = visibility at 1.5m, ZO = zone, TR = treatment, DIS = distance to walking trails/forest edge.

| Model | AIC | Δ AIC |
|---------------------|---------------|--------------|
| SP | 233.07 | 0.00 |
| SP, TR | 233.73 | 0.66 |
| SP, TR*ZO | 234.28 | 1.21 |
| SP, TR*ZO*DIS | 240.78 | 7.71 |
| SP, X1.5, TR*ZO*DIS | 242.76 | 9.69 |

Table C2: Estimates of the best model predicting the number of visits during the night. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold. TR = treatment, ZO = zone, DIS = distance.

| <i>Random</i> | | | | |
|----------------------|----------------|---------------|--------------|----------------------|
| Variable | Variance | St.Dev | | |
| plotID | 1.189 | 1.091 | | |
| <i>Fixed</i> | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -4.0140 | 0.5170 | -7.76 | <0.001 *** |
| SP-RedDeer | 1.6379 | 0.4029 | 4.07 | <0.001 *** |
| TR-treelog | -0.3931 | 0.4970 | -0.79 | 0.43 |
| ZO-refuge | 0.1209 | 0.5797 | 0.21 | 0.83 |
| TR-treelog:ZO-refuge | 1.2071 | 0.6714 | 1.80 | 0.07 |

Table C3: All the general linear mixed effects model predicting the vigilance levels during the night. The AIC scores and the Δ AIC with the lowest AIC score are shown. The models with a Δ AIC lower than 2 are depicted in bold. SP = species, X1.5 = visibility at 1.5m, ZO = zone, TR = treatment, DIS = distance to walking trails/forest edge.

| Model | AIC | Δ AIC |
|---------------------------------|--------|--------------|
| - | 32.319 | 0.000 |
| SP | 33.012 | 0.693 |
| SP, TR | 34.131 | 1.812 |
| SP, X1.5, TR | 36.068 | 3.749 |
| SP, X1.5, TR, ZO | 38.035 | 5.716 |
| SP, X1.5, TR, ZO, DIS | 40.022 | 7.703 |
| SP, X1.5, ZO, TR*DIS | 40.539 | 8.220 |
| SP, X1.5, TR*ZO, TR*DIS | 41.956 | 9.637 |
| SP, X1.5, TR*ZO, TR*DIS, ZO*DIS | 43.838 | 11.519 |
| SP, X1.5, TR*ZO*DIS | 45.358 | 13.039 |

Table C4: Estimates of the best model predicting the vigilance levels during the night. For the random factors the variance and standard deviation are given. For the fixed factors the estimates, standard error, z-value and p-value are given. The significant ($\alpha=0.05$) fixed effects are in bold. TR = treatment, ZO = zone, DIS = distance.

| <i>Random</i> | | | | |
|---------------|-----------|-----------|---------|---------|
| Variable | Variance | St.Dev | | |
| plotID | 1.534e-09 | 3.916e-05 | | |
| <i>Fixed</i> | | | | |
| Variable | Estimate | SE | z-value | p-value |
| Intercept | -0.9929 | 0.7772 | -1.28 | 0.20 |
| SP-RedDeer | -1.6709 | 1.0177 | -1.64 | 0.10 |
| TR-treelog | 0.4572 | 1.0446 | 0.44 | 0.66 |

Table C5: Post hoc comparisons of treatment-zone interaction in the best model predicting the vigilance levels. The estimates, standard error and p-value are shown for both zones and their distance trend. Significantly different groups are in bold ($\alpha=0.05$).

| Variable | Estimate | SE | z-value | p-value |
|--------------------------|----------|-------|---------|---------|
| TR-control:ZO-recreation | -0.1657 | 0.330 | -0.51 | 0.82 |
| TR-treelog:ZO-recreation | -0.5588 | 0.395 | -1.41 | 0.32 |
| TR-control:ZO-refuge | -0.0448 | 0.339 | -0.13 | 0.90 |
| TR-treelog:ZO-refuge | 0.7692 | 0.357 | 2.16 | 0.12 |

Appendix D

Table D1: Overview of the number of observations, number of deer and number of seconds behaviour for all the species and unknown deer, for the two different zones and the two different treatment during the night.

| Night | | | | |
|-----------------|-----------------|---------------------------|-------------------|----------------------------|
| Zone | Tree log | Total observations | Total deer | Tot. sec. behaviour |
| Recreation (16) | Present | 8 | 18 | 439,247 |
| Recreation (16) | Absent | 30 | 50 | 669,837 |
| Refuge (18) | Present | 25 | 42 | 1.797,548 |
| Refuge (18) | Absent | 21 | 34 | 548,031 |
| | | 84 | 144 | 3.454,663 |

| Night | | | | |
|----------------|-------------|---------------------------|-------------------|----------------------------|
| Species | Zone | Total observations | Total deer | Tot. sec. behaviour |
| Fallow Deer | Recreation | 4 | 10 | 49,586 |
| Fallow Deer | Refuge | 10 | 33 | 112,274 |
| Red Deer | Recreation | 31 | 54 | 1.036,831 |
| Red Deer | Refuge | 31 | 38 | 2.180,687 |
| Unknown Deer | Recreation | 3 | 4 | 22,667 |
| Unknown Deer | Refuge | 5 | 5 | 52,618 |
| | | 84 | 144 | 3.454,663 |

| Night | | | | |
|----------------|-----------------|---------------------------|-------------------|----------------------------|
| Species | Tree log | Total observations | Total deer | Tot. sec. behaviour |
| Fallow Deer | Present | 6 | 18 | 74,620 |
| Fallow Deer | Absent | 8 | 25 | 87,240 |
| Red Deer | Present | 21 | 36 | 2.096,249 |
| Red Deer | Absent | 41 | 56 | 1.121,269 |
| Unknown Deer | Present | 6 | 6 | 65,926 |
| Unknown Deer | Absent | 2 | 3 | 9,359 |
| | | 84 | 144 | 3.454,663 |

Table D2: Overview of the number of observations, number of deer and number of seconds behaviour for all the species and unknown deer, for the two different zones and the two different treatment during the day.

| Day | | | | |
|-----------------|-----------------|---------------------------|-------------------|----------------------------|
| Zone | Tree log | Total observations | Total deer | Tot. sec. behaviour |
| Recreation (16) | Present | 49 | 108 | 1.798,541 |
| Recreation (16) | Absent | 56 | 137 | 2.269,927 |
| Refuge (18) | Present | 151 | 375 | 6.382,348 |
| Refuge (18) | Absent | 153 | 392 | 5.647,005 |
| | | 409 | 1012 | 16.097,821 |

| Day | | | | |
|--------------|------------|--------------------|------------|---------------------|
| Species | Zone | Total observations | Total deer | Tot. sec. behaviour |
| Fallow Deer | Recreation | 41 | 115 | 1.559,323 |
| Fallow Deer | Refuge | 141 | 467 | 6.095,998 |
| Red Deer | Recreation | 61 | 127 | 2.497,016 |
| Red Deer | Refuge | 163 | 300 | 5.933,355 |
| Unknown Deer | Recreation | 3 | 3 | 12,129 |
| Unknown Deer | Refuge | 0 | 0 | 0,000 |
| | | 409 | 1012 | 16.097,821 |

| Day | | | | |
|--------------|----------|--------------------|------------|---------------------|
| Species | Tree log | Total observations | Total deer | Tot. sec. behaviour |
| Fallow Deer | Present | 105 | 319 | 5.283,017 |
| Fallow Deer | Absent | 77 | 263 | 2.372,304 |
| Red Deer | Present | 93 | 162 | 2.888,744 |
| Red Deer | Absent | 131 | 265 | 5.541,627 |
| Unknown Deer | Present | 2 | 2 | 9,128 |
| Unknown Deer | Absent | 1 | 1 | 3,001 |
| | | 409 | 1012 | 16.097,821 |

Appendix E

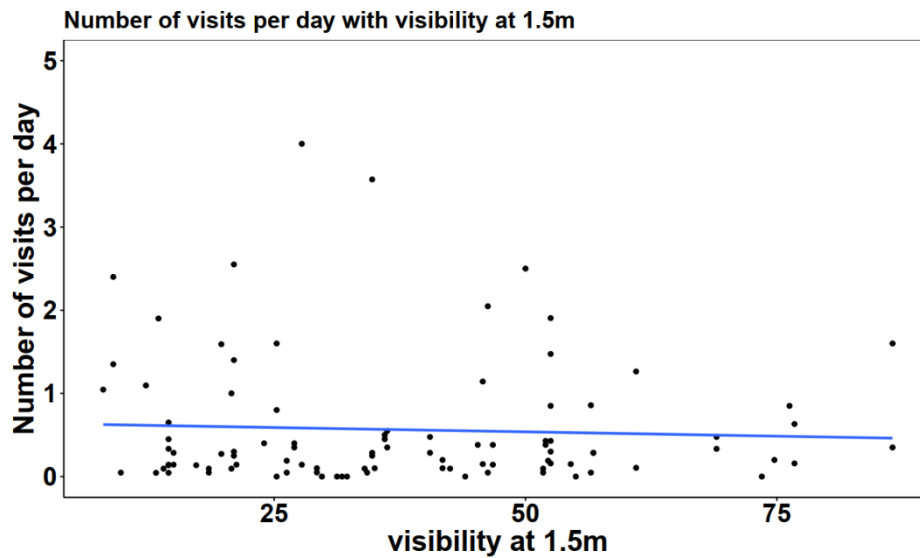


Figure E1: Number of visits per day with the visibility at 1.5m during the day.