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The influence of variation in human disturbance on antipredator behaviour in ungulates

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Abstract

Prey have evolved several types of antipredator behaviour to respond to variation in perceived predation risk. Since predators are able to come and go, prey animals need to make a right perception of risk over time and space. Human recreation has been observed before to affect wildlife in a similar way as predators do. This study aims to describe correlations between ungulate behavioural responses and variation in human disturbance caused by recreation in an anthropogenic landscape. By means of camera trapping, ungulates in natural area the Veluwe, the Netherlands, were analysed in their behavioural response over different levels of human disturbance. The vigilance level, the duration of visits and the number of visits per plot were taken into account as behavioural responses. Both spatial (distance to the closest human path) and temporal (hour of the day, day or night, weather and day of the week) variation in human disturbance were used as predictors. We expected the stronger behavioural responses in areas and times where risk was high, which was during the day (when the park was open to visitors) and close to paths. We hypothesized stronger behavioural responses on days with pleasant weather and during weekends, when recreational pressure, and thereby human disturbance, is generally higher. We found that deer species (roe deer, red deer, and fallow deer) were influenced in their duration of their visit by the distance to the path, where they stayed longer in plots further from paths, but only during the day. During the night, the distance to the path had no effect on deer behaviour. We suggest that deer species in this area can adapt their behavioural response on both a spatial (day or night) and spatial (distance to path) scale. We found no such interactions in boar behaviour. We found no differences in behavioural responses of both deer and boar to weather indications or the day of the week and we therefore found no clear indication that deer or boar are able to adjust their behaviour to variation in human disturbance between days. From our results, we suggest that deer are more influenced by human disturbance than wild boar, and that human recreation creates a landscape of fear for deer species in anthropogenic landscapes. Gaining knowledge on how ungulates respond to human disturbance in an anthropogenic landscape is not only valuable for management of these areas, but also offers valuable insights for future studies on behavioural responses to perceived predation risks in prey species.

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Introduction

The unforgiving nature of predation and its effects on the fitness of prey species has caused animals to evolve many types of antipredator behaviours. One important antipredator behaviour is making the right trade-off between the costs of predation against the various benefits that might come with a certain location or time. Since predation pressure can change over time, as predators are able to move around and might migrate through different areas, prey animals have learned to respond quickly to temporal variation in predation risk (Kats & Dill, 1998). The risk allocation hypothesis claims that the level of antipredator behaviour is predicted by the frequency of the risk, the intensity of perceived risk and the prey's resource needs (Lima & Bednekoff, 1999). In a meta-analysis of fifteen studies on the risk allocation hypothesis, Ferrari et al. (2009) argues that the strength of the prey's response further depends on the predictability of the risk. If risk is predictable, prey may respond strongly by avoiding risky areas or times when predators are present. Creel et al. (2005) found that elk (*Cervus canadensis*) responded on a time scale of a day or less, and moved to coniferous forests, instead of open grassland foraging sites, when wolves were present. This knowledge of lurking predators creates what is called a 'landscape of fear' (Laundré et al., 2001), where prey perceive areas of relatively high and low predation risk and change their behaviour accordingly. This landscape of fear can therefore influence prey's behaviour, which in turn can cause a trophic cascade and shape an ecosystem (Beschta & Ripple, 2012; Ripple et al., 2015; Suraci et al., 2016).

Because predation risk is highly variable in time and space, as predators are able to come and go on a seasonal, lunar, diurnal or moment-to-moment basis (Ferrari et al., 2009), prey animals need to adapt to large-, as well as small-scale variation in perceived predation risk. Behavioural responses to this predation risk, amongst others, include increased vigilance (Elgar, 1989), reduced foraging time and movement (Hughes and Ward, 1993; Abramsky et al., 2002; Sih & McCarthy, 2002) and retreat to relatively safe habitats or locations (Bergerud et al., 1983; Formanowicz and Bobka, 1988; Blumstein and Daniel, 2002). An example of this adaptation to variation in predation risk was found in elk (*Cervus canadensis*), who were able to respond to a presence of wolves on a spatial scale of several kilometres, and a time scale of minutes to days (Winnie & Creel, 2007), showing adaptation to variation in both a spatial and temporal scale. Another example of this adaptation to variation in risk on both a diurnal and a seasonal scale was visible in vigilance levels of roe deer in Poland, which overlapped with the predation risk induced by the anthropogenic predator, human hunters (Sönnichsen et al., 2013), giving an example on how prey species can adapt to small-scale, circadian variating and human-induced predation risk.

The response in antipredator behaviour to variation in predation risk can therefore not only be induced by natural predators, but also by anthropogenic predators (Stankowich, 2008; Sönnichsen et al., 2013; Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019). Sönnichsen et al. (2013) tested the predictions of the risk allocation hypothesis in a natural environment, where both natural predators and human hunters were abundant. Natural predators were expected to show similar levels of predation activity throughout the season, but human hunters predated mainly during the daytime in a clearly defined hunting season. Sönnichsen and colleagues (2013) found that roe deer (*Capreolus capreolus*) in Białowieża Primeval Forest in Eastern Poland showed higher vigilance during the daytime and hunting season than outside of these periods, which, according to the authors, follows the risk allocation hypothesis and indicates that roe deer perceive the anthropogenic predator as a greater risk than their natural predator. It makes sense for prey species to take anthropogenic predators into account when making trade-offs in antipredator behaviours, as it was found that human hunters exploit prey populations in higher rates than the highest-exploiting terrestrial predator, in systems where humans compete with other predators over shared prey (Darimont et al., 2015). Human hunters in human-dominated North-America and Europe even exploited herbivores at median 7.2 and 12.5 times those of hunters in Africa (Darimont et al., 2015). The authors of this study therefore suggest that humans should be defined as a global "super predator". In fact, several studies have shown that humans have taken over

the role as apex predators in many ecosystems, creating strong landscapes of fear (Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019). Stankowich (2008) found evidence in a meta-analysis that ungulates respond with antipredator flight behaviours towards humans, and these flight responses are greater in populations that are subject to hunting by humans. But not only hunting, also recreation was found to negatively affect wildlife, especially on weekends (Nix et al., 2018). Mule deer (*Odocoileus hemionus*), who show crepuscular activity peaks, were found to reduce activity during weekends and avoided playgrounds. More nocturnal species showed less of an effect of weekends, indicating that as the temporal overlap increases between wildlife and humans, so does the influence that humans have on wildlife (Nix et al., 2018).

An adaptation in behaviour to predictable temporally variating perceived predation risks seems to be visible in the behaviour of ungulates in Natural Park the Veluwe, the Netherlands, as well. With no large carnivores present for a period of 150 years (van Ginkel et al., 2019), humans seem to have taken over the ecological role as apex predator and could be the main drivers in creating a landscape of fear. Human visitors are allowed to enter the park during daytime hours, creating a large temporal overlap with the natural activity rhythm of ungulates. The ungulates, as what seems to be a response to human presence, have shifted to a more crepuscular lifestyle, where the deer in the park mainly showed activity peaks at twilight (Ensing et al., 2014). It is hypothesized that this shift in activity rhythm is mainly due to the human disturbance induced by recreation in the area. However, to what extent ungulates are able to respond to variation in human disturbance remains unclear. It can be hypothesized that recreational pressure is affected on a day-to-day, as well as within a day basis, by several environmental predictors, such as the weather, the day of the week and the hour of the day (Brandenburg & Arnberger, 2001; Böcker et al., 2013). Recreational pressure is expected to be higher during the weekend (Nix et al., 2018), when the weather is pleasant (Brandenbur & Arnberger, 2001; Böcker et al., 2013) and in the middle of the day (Böcker et al., 2013; Pęksa & Ciach, 2018). This study aims to find correlations between these environmental predictors for levels of recreational use and the response of ungulates in their antipredator behaviour. The grey wolf (*Canis lupus*) recently returned to the area after an absence of approximately 150 years (Wolven in Nederland, n.d.), which brings interesting opportunities for research. Whether the ungulate population in this area has kept its antipredator response to wolves is debatable. Some studies indicate that the disappearance of predators can lead to a rapid loss of antipredator behaviour of prey (Blumstein et al., 2004), but others argue that the antipredator response on a previously extinct predator depends on whether prey had experience with other predators in the meantime ("Multipredator Hypothesis"; Blumstein, 2006). If prey animals still perceived predation risk prompted by another predator after the first predator disappeared, the antipredator response to the first predator was generally still existent after its reappearance. From this, we can argue that if ungulates in this area perceived humans as predators, they might have kept their antipredator response to wolves. To gain insight in the perception of ungulates of humans and human disturbance could therefore bring valuable information on the effects of the reappearance of this ancestral predator.

Based on previous research, we can expect ungulates to avoid risky areas during risky periods (Lima & Bednekoff, 1999; Laundre et al., 2010), which would be during the opening hours of the park (the daytime) and close to paths for ungulates in the Veluwe area. Since mule deer, who also follow a crepuscular rhythm, were highly influenced by the day of the week (reduced activity during the weekend) and it is hypothesized that this is due to the high temporal overlap (Nix et al., 2018), the same can be hypothesized for ungulates in the Veluwe. Behavioural responses of ungulates are expected to correspond to spatial (distance to the closest human path; Pęksa & Ciach, 2018) and temporal (hour of the day, day or night, weather and day of the week; Brandenburg & Arnberger, 2001; van Doormaal et al., 2015; Nix et al., 2018) variation in human disturbance. We therefore observed ungulates with cameratraps in a human-dominated natural area in the Netherlands, the Veluwe. We placed two cameras on twenty-five locations in a paired design: one camera close to the path (< 20 meters) and one camera further from the path (> 100 meters), to observe to what extent ungulates were influenced by human paths. However, human disturbance can vary on a temporal as well as a spatial scale, as recreational

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pressure can be influenced by the weather and the day of the week (Brandenburg & Arnberger, 2001; Böcker et al., 2013). We therefore compare different days in the observational period to each other and try to predict human disturbance as a correlate of the weather-comfort, day of the week, time of observation (day or night and hour of the day) and distance to the path. We strive to assess to what extent ungulates are able to respond to variation in human disturbance, on both a spatial (distance to paths) and a temporal scale, where we make a distinction between variation within a day and variation between days. Gaining knowledge on how ungulates respond to human disturbance in an anthropogenic landscape is not only valuable for management of these areas, but also offers valuable insights for future studies on antipredator behaviour responses to perceived predation risks in prey species.

Method

Study area and population

This study was conducted at the Veluwe, Gelderland, the Netherlands, a natural area that is part of the European Natura 2000 infrastructure plan. The areas used (Leuvenumse bos (837 ha), Het Loo Royal Estate (10400 ha), Boswachterij Nunspeet (2388 ha) and Elspeeterstruiken (part of an area of 1100 ha), see Figure 1) are managed by four different organisations (resp. Natuurmonumenten, the Royal family, municipality Nunspeet, Staatsbosbeheer). The areas are fairly connected through agricultural and cultivated areas, and only separated in some places by roads and paths. The main habitats in the areas are heathland and open grassland and mixed deciduous and coniferous forest. All areas are open to visitors from sunrise to sunset. Multiple hiking and bicycle paths run through the area, though visitors are not allowed outside of these paths. All
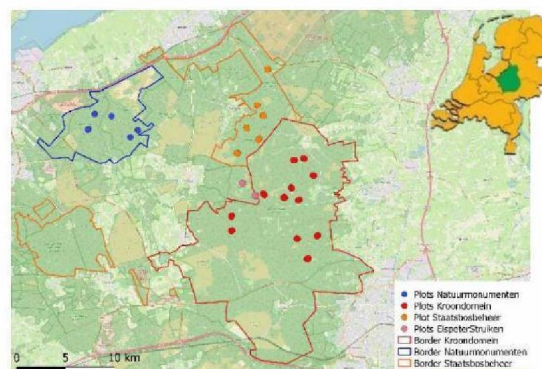

Figure 1: overview of the study areas used. The blue border shows the area of Leuvenumse bos, managed by Natuurmonumenten. Red represents the area of the Kroondomein het Loo, managed by the Royal Family. Orange represents the area of forestry Nunspeet, managed by Staatsbosbeheer. Dots with corresponding colours represent the different locations used for two plots. The pink dots represent the locations used in Elspeeterstruiken, the area managed by the municipality of Nunspeet.

areas are relatively crowded, since the Veluwe is one of the most popular natural areas of the Netherlands (Visit Veluwe, 2017), especially during summer (Ensing et al., 2014). Hunting season is in autumn and winter and mainly done in designated areas, depending on the management. The main ungulate species that occur in the study area are roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), wild boar (*Sus scrofa*; hereafter referred to as boar), and red deer (*Cervus elaphus*) and are therefore chosen as the focus species for this study.

Data collection

Data were collected between the 16th of July and the 27th of September 2020, using three types of Bushnell Camera-traps ("A": Bushnell Aggressor Trophy Cam 2017, "B": Bushnell Aggressor Trophy Cam 2017 No Glow & "C": Bushnell Core DS No Glow). The cameras were placed in pairs on 25 locations attached to a tree at approximately one meter height, on two different distances to human paths (within 20 metres and further than 100 metres from paths), which resulted in a total of 50 plots with cameras. All cameras were placed in comparable locations, with European blueberry bushes (*Vaccinium myrtillus*) and coniferous trees as main vegetation. Canopy openness and visibility were comparable between plots to minimize differences between plots. All camera types had a trigger speed of 0.2 seconds and a recovery rate (between triggers) of 0.5 seconds. After being triggered, the cameras first took a picture and immediately after made a video of 15 seconds. Either 1 (camera type "A") or 0.6 seconds (camera type "B" and "C") after this video was taken, the camera made another picture and afterwards again a video of 15 seconds if the motion detector was still being triggered. Data of the cameras were collected approximately every month, so batteries could be swapped and the cameras were able to

continue filming for the entire session. The cameras automatically switched to a night mode when light conditions were too low for normal filming. The videos were analysed by three trained observers (B, K & J) in BORIS v. 7.9.7, by scoring the behaviour of the first individual that came into view. However, if an individual that first came into view was visible for less than 5 seconds and a second individual within the same observation stayed longer than 5 seconds, the second individual was used as focal individual, and so on. If no individual stayed for longer than 5 seconds, the first animal that came into view was used as focal individual. Different videos were considered one observation if they were recorded within 5 minutes of each other and the same species was visible. Only one focal individual was chosen for every observation, to avoid pseudoreplication. For all videos the time, date, location of the plot, day or night mode of the camera and species, sex and whether the focal individual was an adult, an adult with a juvenile or a juvenile were recorded. Furthermore, all behaviours (e.g. foraging, walking, laying, scratching, running; see Ethogram in Appendix) that a focal individual showed during the observation were recorded in BORIS. Vigilant behaviour was scored when an individual raised its head above its shoulders, looked around and/or showed twitching ears (Winnie & Creel, 2007). A distinction was made between vigilance while chewing (only visual) and when an individual stopped chewing (also audial), as auditory vigilance might have different fitness implications than just visual vigilance (Lynch et al., 2015). Running was also considered as vigilant behaviour. Since this study does not look at fitness implications that might come from antipredator behaviours, all vigilant behaviours were grouped together, as well as the non-vigilant behaviours, to be able to calculate the percentage of time spent on vigilance per observation. Videos where the focal individual looked into the camera or was startled by the camera were excluded from the analyses, which happened in a total of 11.4% of all observations, as their behaviour might be influenced by the camera and can therefore show non-natural biases towards vigilant or non-vigilant behaviour.

Data analyses

Data was analysed in R v. 3.6.3. In this study, three response variables were analysed to assess ungulate behavioural responses: (i) the duration of the visit, (ii) the vigilance level (i.e. percentage of time spent on vigilance per visit), and (iii) the number of visits per plot. For the duration of the visit, the total number of seconds an ungulate was visible in front of the camera, showing any type of behaviour, were added up. This gave a total duration per visit. For the vigilance level, the duration of vigilant behaviours (see Ethogram in Appendix) was divided by the total duration of the observation, which gave a value between zero and one. The number of visits was calculated by adding all observations per plot, weather score and per species. For the first two variables we made a distinction between whether the focal individual of an observation was a deer species (fallow, roe or red deer) or boar, as boar can differ in their general antipredator behaviour from deer (Marini et al., 2009; Kuijper et al., 2014). However, because the number of visits was calculated per plot, both species groups were included in this model (iii). Since all three response variables showed different distributions and types of data, different models were performed accordingly (also: see Table 1):

i.   The duration of a visit was expressed in seconds and gave a continuous scale. To make it normally distributed, a log transformation was performed. Since this was a gaussian distribution, a linear mixed model was performed.
ii. The vigilance level was a continuous value between zero and one. It was therefore treated with a beta regression.
iii. The number of visits per plot/weather score/species was a count value, with a bias on a value of one. It showed overdispersion when performing simulations on models that used a generalized mixed model with a Poisson distribution. To account for this overdispersion, a Quasipoisson distribution was used.

Proxies for temporal variation in human disturbance used in this study were: a weather score, based on the percentage of sun hours, wind speed and duration of rainfall (calculation method gained from Ton van Gelder of the "Vereniging voor Weerkunde en Klimatologie",

, and adjusted to fit this study; climatologic data was obtained from weather station De Bilt, owned by The Royal Netherlands Meteorological Institute; see Appendix for precise formula of the weather score), the day of the week (Monday to Sunday; Brandenburg & Arnberger, 2001; Nix et al., 2018), time of the observation and whether the observation was during the night or day (van Doormaal et al., 2015). The proxy used for spatial variation in human disturbance was the distance to the closest human path (< 20 meters or > 100 meters; Pęksa & Ciach, 2018). These were used as fixed factors in all three models. We ran a paired design with two path distances per location and therefore included the location as a factor in the statistical models. It was included in models (i) and (iii) as a random factor and included in model (ii) as a fixed factor, since beta regression models cannot take random factors into account. The duration of the visit (i) and the vigilance level (ii) were performed on both the dataset with all deer species, and with just wild boar. The species was added as a fixed factor for the models performed on the deer dataset, to account for any differences in behaviour between the deer species. The number of visits model (iii) had species incorporated as a fixed effect, to account for differences in number of visits of deer and boar. All models were tested for goodness of fit by either visually checking residual plots for the beta regression model or modelling the simulations using the "DHARMA" package for the mixed regression models (Hartig & Lohse, 2020). A correlation matrix was made to test for any correlations between predictor variables by either using a Cramer's V correlation test (for predictors that were considered as factors), or by performing a one-way ANOVA between a factor predictor variable and a continuous predictor variable (Akoglu, 2018).

Model selection was performed by stepwise exclusion and comparing AIC values between models (Xin & Zhu, 2012). We tested for significant improvements of models by using a likelihood ratio test from the "lmtest" package (Hothorn et al., 2020). When a model was significantly better than the previous, that model was preferred over the previous. When a model was not significantly better, the model with the lowest AIC value was preferred (Xin & Zhu, 2012). See Table 1 for an overview of the used models per response variable and see the Appendix – Model selection for the tested models. Since most observations that were shorter than five seconds were observations of individuals running past the camera, observations with durations shorter than 5 seconds were excluded for the analyses of the vigilance level (14,06 % of all observations). These observations did not only bring little behavioural insights because of their length, they were also mainly of animals running in front of the camera, and therefore might cause a bias towards vigilant behaviour.

To test for any differences between observers (3) and camera types (3), a Kruskal Wallis test was performed on all three response variables (duration of a visit, vigilance level and the number of visits) and observer and camera type. This showed a significant difference between the three camera types for all response variables, where camera type Bushnell Core DS ("C") showed a higher vigilance level (A-B: $p = 0.16$; A-C: $p = 0.002$; B-C: $p < 0.001$), and all three camera types differed in the duration of a visit (A-B: $p = 0.002$; A-C: $p = 0.05$; B-C: $p = 0.009$) and weakly differed in the number of visits (A-B: $p = 0.07$; A-C: $p = 0.09$; B-C: $p = 0.07$). A significant difference between the observed vigilance level was also found between two observers (B-J: $p = 0.24$; B-K: $p = 0.24$; J-K: $p = 0.03$). Therefore, observer was included in the vigilance model, and camera type was included in all models as a random effect to see if they improved the models. AIC scores for all models went up with the inclusion of observer or camera type however, so observer and camera type were not included in any of the final models.

Table 1: Overview of the used models with their fixed and random effects per response variable.

Response variable	Duration of a visit	Vigilance level	Number of visits
Type of data	Continuous	Percentage (bound 0-1)	Count
Model	Linear mixed model	Beta regression model	Generalized linear mixed model
Distribution	Gaussian	Beta distribution	Quasipoisson

Fixed factors	- Weather score - Distance to path - Weekday - Day/night - Hour of observation - (Species for deer)	- Weather score - Distance to path - Weekday - Day/night - Hour of observation - Location - (Species for deer)	- Weather score - Distance to path - Weekday - Day/night - Hour of observation - Species
Random factors	Location	NA	Location
Best model	*Deer:* Log(duration) ~ distance to path + (1|location) *Boar:* Log(duration) ~ day/night + (1|location)	*Deer:* Percentage of vigilance ~ day/night *Boar:* Percentage of vigilance ~ time slot	*Deer + boar:* Number of visits/plot ~ weather score + distance to path + species + (1|location)

Results

During the 73-day observational period, we collected a total of 902 observations. The majority of these observations were captured during the day (534 during the day vs. 368 during the night) and further from paths (565 observations > 100 meters from paths vs. 337 observations < 20 meters from paths). In these 902 observations, 77 fallow deer, 105 roe deer, 288 red deer, 383 wild boar and 49 unknown individuals were used as focal individuals (one focal individual per observation). The mean duration of a visit of deer was 22.36 seconds (sd: 32.56 s, median: 14.06 s, range: 0.05-307.89 s) and the mean duration of a visit of boar was 22.63 seconds (sd: 40.39 s, median: 14.77 s, range: 0.14-533.64 s). The mean vigilance level by deer was 19.4 % (sd: 29.4 %, median: 0 %, range: 0-100 %) and the mean vigilance level by boar was 4.1 % (sd: 15.6 %, median: 0 %, range: 0-100 %). The mean number of visits per plot over the observational period was 18.0 visits (sd: 15.5 visits, median: 13.0 visits, range: 0-71 visits) for deer and boar together. The mean number of visits per plot for deer was 9.4 visits (sd: 9.3 visits, median: 6 visits, range: 0-49 visits) and the mean number of visits per plot for boar was 7.7 visits (sd: 9.9 visits, median: 6 visits, range: 0-60 visits).

Correlation matrix

A correlation matrix was performed on all possible predictor variables to check for any correlations. On two predictor variables that were considered factors, a Cramers V correlation was performed (marked with a ˅; see Table 2). On a predictor variable that was considered a continuous variable and a predictor variable that was considered a factor, an ANOVA was performed (marked with a [a]; see Table 2). A very strong positive correlation was found between the location of the observation and the observer, the camera type ("Camtype"), the observation period ("Day/night") and the focal species, and a strong correlation was found between the location and the distance to the path, and between the focal species and the camera type and the observation period (see Table 2).

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Table 2: Correlation matrix on all predictor variables. Correlations between predictor variables that were considered as factors were calculated by using a Cramer's V correlation and are marked with a ᵛ. Correlations between predictor variables where one was considered a factor and the other a continuous variable were calculated by using a one-way ANOVA and are marked with a ᵃ. Very strong correlations, interpreted according to Akoglu (2018), are shown in bold, strong correlations are shown in italic.

	TimeSlot	Location	Weekday	Species	Distance	Day/night	Camtype	Observer
Observer	0.04ᵃ	**0.51**ᵛ	0.01ᵛ	0.13ᵛ	0.00ᵛ	0.08ᵛ	0.13ᵛ	1
Camtype	0.03ᵃ	**0.85**ᵛ	0.02ᵛ	*0.16*ᵛ	0.00ᵛ	0.05ᵛ	1	
Day/night	0.03ᵃ	**0.29**ᵛ	0.00ᵛ	*0.23*ᵛ	0.10ᵛ	1		
Distance	0.01ᵃ	*0.21*ᵛ	0.03ᵛ	0.15ᵛ	1			
Species	0.16ᵃ	**0.35**ᵛ	0.05	1				
Weekday	0.11ᵃ	0.10ᵛ	1					
Location	0.27ᵃ	1						
TimeSlot	1							

Duration of visit

The duration of a visit of deer was significantly affected by the distance to the path (p < 0.001, estimate = 0.38, n = 470), where the duration of a visit was longer further from the path (> 100 meters) than closer to paths (< 20 meters). However, the statistical model with an interaction between the day or night and the distance to the path was almost as good as the model with just the path (see Table 3). We therefore compared the effect of the distance to the path on the duration of a visit by deer between the day and night, and found that there is a strong effect of the path during the day (p < 0.001, estimate = 0.62, n = 270), but not during the night (p = 0.50, estimate = 0.10, n = 200) (see Figure 2). The day or night itself was found to slightly affect the duration of a visit of deer in the model including the interaction between the day or night and the distance to the path (p = 0.06, estimate = 0.32, n = 470).

Table 3: model selection table on the duration of a visit of deer as the response variable. All models have the location included as a random factor. Full model: duration of visit ~ weather score + distance + species + day/night + (1|location). The Full model with Timeslot is the same as the Full model, only is the day/night replaced by the timeslot (i.e. the hour of the day). K is the number of parameters in the model (default is 2), AICc is the information score of the model, Delta_AICc is the difference in AIC score between the best model and the model being compared, AICcWt is the AICc weight, which is the proportion of the total amount of predictive power provided by the full set of models contained in the model being assessed, Cum.Wt is the sum of the AICc weights, and Res.LL is the restricted maximum-likelihood. A difference in AICc scores bigger than 2 is considered a lesser model.

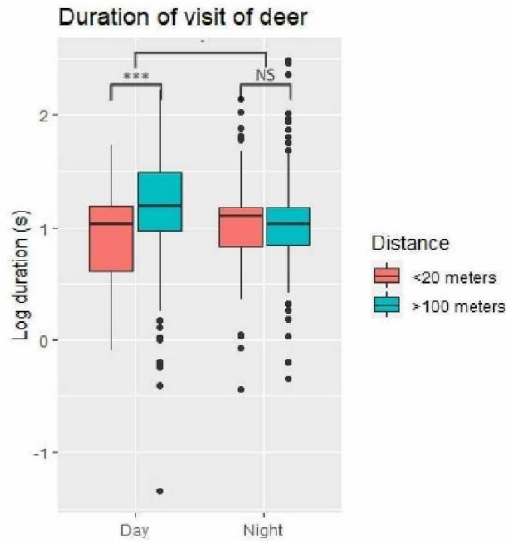| Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	Res.LL
Distance	4	1463.42	0.00	0.70	0.70	-727.67
Day/night * Distance	6	1466.10	2.69	0.18	0.88	-726.96
Distance + Camtype	6	1468.07	4.65	0.07	0.94	-727.94
Distance + Observer	6	1469.76	6.34	0.03	0.97	-728.79
Day/night * Distance + Camtype	8	1470.85	7.43	0.02	0.99	-727.27
Day/night + Distance	7	1472.61	9.19	0.01	1.00	-729.18
Day/night	4	1475.02	11.60	0.00	1.00	-733.47
Full model	8	1479.73	16.31	0.00	1.00	-731.71
Full model with Timeslot	8	1484.76	21.34	0.00	1.00	-734.22

Figure 2: the duration of a visit of deer species compared to day or night observations. Red boxplots represent observations made in plots within 20 meters of a path, blue represent plots further than 100 meters from paths. The duration in seconds is plotted in a log transformation. A significant positive effect was found on the duration of a visit of the observational period (i.e. "day or night": $p < 0.001$, estimate = 0.38, n = 470). This effect is strong during the day ($p < 0.001$, estimate = 0.62, n = 270) but not visible during the night ($p = 0.50$, estimate = 0.10, n = 200).
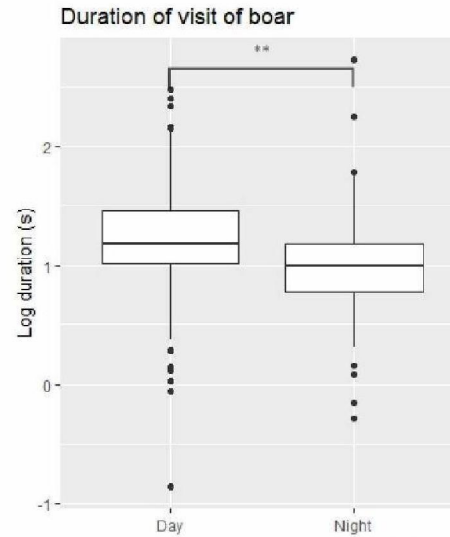

Figure 3: the duration of a visit of wild boar compared between day or night observations. The duration in seconds is plotted in a log transformation. A significant negative effect was found between the duration of a visit and the observational period ($p = 0.002$, estimate = -0.37, n = 383).

The duration of a visit of boar was significantly negatively affected by the day or night ($p = 0.004$, estimate = -0.34, n = 383), where the duration of a visit was higher during the day than during the night (see Figure 3). The model with only day/night was not significantly better than the model with day/night and camtype (see Table 4). The duration of a visit of boar was furthermore influenced by the camtype ($p = 0.05$, n = 383), where camera type "A" had a significantly higher duration of visit than cameratype "B" and "C". We found no effect of other predictors, which suggests that the duration of a visit of boar is not influenced by the weather, the distance to the path, the day of the week or the hour of the day.

Table 4: model selection table on the duration of a visit of boar as the response variable. All models have the location included as a random factor. Full model: duration of visit ~ weather score + distance + day/night + (1|location). The Full model with Timeslot is the same as the Full model, only is the day/night replaced by the timeslot (i.e. the hour of the day). K is the number of parameters in the model (default is 2), AICc is the information score of the model, Delta_AICc is the difference in AIC score between the best model and the model being compared, AICcWt is the AICc weight, which is the proportion of the total amount of predictive power provided by the full set of models contained in the model being assessed, Cum.Wt is the sum of the AICc weights, and Res.LL is the restricted maximum-likelihood. A difference in AICc scores bigger than 2 is considered a lesser model.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	Res.LL
Day/night	4	1103.61	0.00	0.53	0.53	-547.75
Day/night + Camtype	6	1103.92	0.31	0.45	0.97	-545.85
Day/night + Weekday	5	1110.46	6.86	0.02	0.99	-550.15
Day/night + Observer	6	1112.11	8.50	0.01	1.00	-549.94
Weather score + Day/night + Weekday	6	1117.21	13.61	0.00	1.00	-552.49
Full model	7	1121.85	18.25	0.00	1.00	-553.78
Full model with Timeslot	7	1135.91	32.30	0.00	1.00	-560.81

Vigilance level

The vigilance level of deer was significantly affected by the day or night (p < 0.001, estimate = -0.58, n = 390), where deer spent relatively more time on vigilance during the day than during the night (see Figure 4). We found no effect of the weather score (p = 0.44, estimate = -0.03, n = 390), the distance to the path (p = 0.67, estimate = -0.06, n = 390), species (fallow deer – red deer: p = 0.37, estimate = 0.17; fallow deer – roe deer: p = 0.16, estimate = 0.30, n = 390) or location (p = 0.84, estimate = 0.00, n = 390).
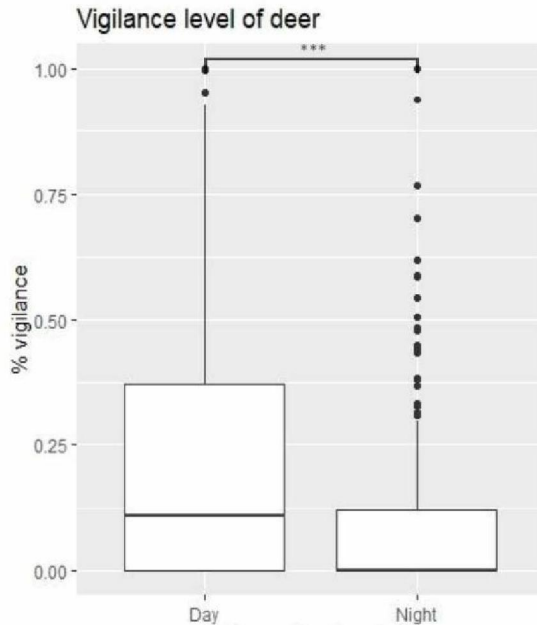

Figure 4: the vigilance level of deer compared to the observational period. A significant negative effect was found between the percentage of time spent on vigilance and the observational period (p < 0.001, estimate = -0.58, n = 390).

The vigilance level of boar was better explained by the hour of the day than the day or night (see Table 5). It was however not significantly correlated to the hour of the day (p = 0.61, estimate = - 0.01, n = 330). All other predictor variables also did not affect the vigilance level of boar and were excluded from the used model (weather score: p = 0.65, estimate = -0.02, n = 330; distance to the path: p = 0.95, estimate = 0.01, n = 330; location: p = 0.95, estimate = 0.00, n = 330; day or night: p = 0.75, estimate = 0.04, n = 330; day of the week: p = 0.79, estimate = -0.01, n = 330).

Table 5: model selection table on the vigilance level of boar as the response variable. K is the number of parameters in the model (default is 2), AICc is the information score of the model, Delta_AICc is the difference in AIC score between the best model and the model being compared, AICcWt is the AICc weight, which is the proportion of the total amount of predictive power provided by the full set of models contained in the model being assessed, Cum.Wt is the sum of the AICc weights, and LL is the Log-likelihood. A difference in AICc scores bigger than 2 is considered a lesser model.

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Timeslot	3	-5943.68	0.00	0.19	0.19	2974.88
Weather score	3	-5943.57	0.11	0.18	0.37	2974.82
Day/night	3	-5943.50	0.18	0.17	0.54	2974.79
Weekday	3	-5943.49	0.19	0.14	0.58	2974.78

Timeslot + Camtype	4	-5942.54	1.15	0.11	0.65	2975.33
Weather score + Timeslot	4	-5941.77	1.91	0.07	0.72	2974.95
Timeslot + Location	4	-5941.64	2.04	0.07	0.79	2974.88
Day/night + Observer	4	-5941.52	2.16	0.06	0.85	2974.82
Day/night + Camtype	5	-5940.54	3.14	0.04	0.89	2975.36
Weather score * Timeslot	5	-5939.76	3.92	0.03	0.92	2974.97
Weather score + Timeslot + Distance	5	-5939.71	3.97	0.03	0.94	2974.95
Weather score + Day/night + Location	5	-5939.56	4.12	0.02	0.97	2974.87
Weather score + Day/night + Distance	5	-5939.56	4.12	0.02	0.99	2974.87
Weather score + Distance + Day/night + Location	6	-5937.49	6.20	0.01	1.00	2974.87

Number of visits

The number of visits of both boar and deer combined per plot was significantly affected by the distance to the path ($p < 0.001$, estimate = 0.33, n = 467), where the number of visits per plot was higher further from the path (> 100 meters) than closer to the path (< 20 meters). The number of visits was also significantly affected by the weather score ($p = 0.02$, estimate = 0.05, n = 467; see Figure 5) and boar had a significantly higher number of visits than other species ($p = 0.006$, estimate = 0.41, n = 467). This effect was however independent of species, as the effect of the distance to the path stayed significant when testing deer and boar separately (deer: $p = 0.001$, estimate = 0.33, n = 264; boar: $p = 0.02$, estimate = 0.37, n = 164), but the effect of the weather score lost some statistical power due to the smaller sample size (deer: $p = 0.10$, estimate = 0.04, n = 264; boar: $p = 0.10$, estimate = 0.07, n = 164).
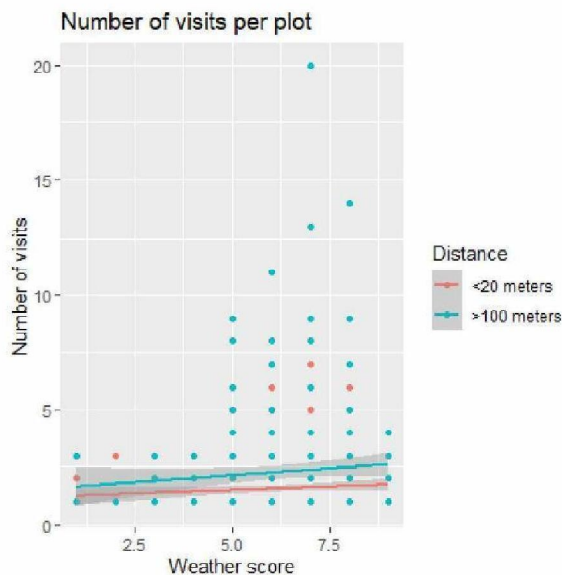

Figure 5: the number of visits per plot compared to the weather score for two distances to paths. Red dots represent observations in plots within 20 meters of a path, blue dots represent observations further than 100 meters from paths. A linear regression line in corresponding colours is shown to visualize the direction of the correlation. The shading around the regression line shows the standard error. A significant positive effect was found by the weather score on the number of visits ($p = 0.02$, estimate = 0.05, n = 467), and by the distance to the path on the number of visits ($p < 0.001$, estimate = 0.33, n = 467).

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Discussion

We analysed behavioural camera data of deer (fallow –, roe – and red deer) and wild boar in a natural area in the Netherlands to gain insights in how ungulates respond to variation in human disturbance on both a spatial and temporal scale. We found that deer were affected by the distance to the path in their duration of a visit during the day, but not during the night (see Figure 2). Deer also had a higher vigilance level during the day than during the night (Figure 4). They were however not affected by the weather, day of the week or hour of the day, which were expected to be proxies of human disturbance (Brandenburg & Arnberger, 2001; Böcker et al., 2013). Boar had a longer duration of a visit in a plot during the day than during the night (Figure 3) but were not affected by the distance to the path, like deer were. Boar were also not affected in their vigilance level by any of the predictors (weather score, hour of the day, day of the week, day or night or distance to the path). The number of visits increased for both deer and boar with a higher weather score (i.e. more pleasant weather), and was overall higher further from paths than closer to them.

Since deer species stayed longer in plots further from paths during the day and showed an increased amount of time spent on vigilance during the day (i.e., during opening hours of the park), we can suggest that deer species adjust their behaviour to temporal (difference between opening hours of the park) and spatial (closer and further from paths) variation in (human) disturbance, effectively forming a landscape of fear. The increase in number of visits and duration of visits of deer further from paths than close to paths could indicate that not only do deer stay longer in these places, but that these plots are also more regularly visited. This is in line with our hypothesis, which stated that the areas and moments with the highest risks were during the daytime and close to paths, and shows support for the risk allocation hypothesis (Lima & Bednekoff, 1999). The behavioural response to human disturbance by deer found in this study suggests that deer try to avoid humans by staying away from paths during the day and adjusting their vigilance accordingly. This response to variating risk was also found in previous studies (for example Winnie & Creel, 2007; Sönnichsen et al., 2013), where ungulates responded to anthropogenic or natural predators with the same (antipredator) behaviours. Since the behavioural response of deer in this study is the same as the behavioural response observed in previous studies to natural predators, our results suggest that deer in the Veluwe area respond to human disturbance as they would to actual predation risk.

Overall, boar might be less influenced by human presence/disturbance than deer species, as they did not seem to adjust their vigilance or behaviour to variation in proxies related to human disturbance. Marini and colleagues (2009) found that boar had a later fleeing response to humans approaching, and suggest that his might be due to the differences in size between the two species groups. Since boar are generally lower to the ground and it is therefore easier for them to hide, boar can stay undetected for a longer time than deer and therefore respond later to humans (Marini et al., 2009). Boar did have a longer duration of a visit during the day, but also accounted for a generally higher number of visits than the deer species separately in our study. This indicates that there are relatively more boar than the separate deer species in this natural area, which we also found in our observations (77 fallow deer, 105 roe deer, 288 red deer and 383 wild boar). Boar, like deer, did visit plots further from paths more regularly than plots close to paths, which could indicate that boar do have a perception of a spatial landscape of fear. It could also be due to differences in food availability over the proximity to the paths, as human trails have been found to influence species richness (Bhuju & Ohsawa, 1998; Root-Bernstein & Svenning, 2018). It is still debatable if boar are able to adjust their behavioural responses on a temporal scale, as the effect of time, day or night or day of the week was less pronounced in boar than in deer. It can be argued that boar, due to differences in physiological needs and diet from deer (Dannenberger et al., 2013; Spitzer et al., 2020), have to make different cost-benefit trade-offs to the perception of risk, resulting in exhibiting no or a less easily to detect behavioural response when they do perceive risk (Gaynor et al., 2019).

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Ungulates in this area now also need to respond to predation risks by wolves. It can be expected that wolves in this area show hunting activity peaks during dawn and dusk, when hunting is most successful (Theuerkauf et al., 2003). We generally did not find an effect of the hour of the day on the behavioural responses of the ungulates however, which could have shown antipredator peaks during these crepuscular moments. Especially deer showed most behavioural responses during the day, which would be the highest risk moment of humans. Because wolves in this anthropogenic landscape can be expected to not hunt during the day, the predation risk by wolves is relatively higher during the night than during the day. During the night, deer did show lower vigilance levels. Because deer also actively seemed to avoid paths resulting in a lower number of visits, it can be suggested that deer still perceive humans as a greater risk (Proffitt et al., 2009; Nicholson et al., 2014; Clinchy et al., 2016; Darimont et al., 2015; Smith et al., 2017). However, since the wolf has only recently settled in the area, it can be interesting to observe whether this perception changes over time. Whether ungulates in this area have lost their antipredator response after the wolves went extinct (Blumstein et al., 2004), or whether ungulates still need time to adjust their perception of risk and their antipredator behaviour remains because of their experience with humans as predators (Blumstein, 2006) remains elusive (van Ginkel et al., 2019).

The number of visits was affected by the weather score, but this effect was the same for plots close to paths and further from paths. The weather itself might influence ungulate behaviour (Brivio et al., 2016; Pęksa & Ciach, 2018; Herfindal et al., 2019), and only when an interaction between the weather score and the distance to the path would have been observed it can be said that ungulates respond to the weather as a predictor for human disturbance. If the weather conditions were a strong predictor for levels of human disturbance, we would expect to find an interaction between the distance to the path and the weather condition, which we did not. This interaction was for example found in Tatra chamois (*Rupicapra rupicapra tatrica*), an Alpine ungulate, which were influenced in the amount of time spent on moving around by the weather, the distance to the trail and the time of the day (Pęksa & Ciach, 2018). An interaction was found between the distance to the trail (which was used as a proxy for human disturbance) and between the hour of the day, where hikers were already present from early hours in the morning and therefore cause more disturbance during the early hours of the day (Frid & Dill, 2002; Pęksa & Ciach, 2018). This interaction between a proxy for human disturbance (distance to the trail) and a predictor that might influence animal behaviour itself, indicates that Tatra chamois adjust their behaviour over the day for different levels of human disturbance. The weather score used in this study, however, was calculated over one summer season, which resulted in a relative weather score with weather conditions relatively similar between days. This gave a limited range for weather conditions as a predictor for the level of human disturbance, as most days in the sampling period were quite pleasant. This could explain why the weather score did not affect behavioural responses in ungulates, as it did not necessarily represent the recreational pressure. Furthermore, most of the sampling was done during Dutch summer holidays. This might have eliminated for a large part the day of the week and the weekend-effect (Nix et al., 2018). To get a clearer observation on the effect of the day of the week and of the weather score, behavioural observations outside of the summer season should be considered, preferably year-round.

An explanation for the fact that the statistical models did not improve with the inclusion of observer and camera type, despite of the significant effects found in the Kruskal Wallis tests, could be that the variation found in the response variables was better explained by other effects already included in the model. For instance, camera type and observer were both highly correlated to the location. This makes sense, since all camera types were always paired over one location (the two plots in the same location but on different path distances always had the same camera type). Location was mostly already included in the model, since it could explain other random variation found in the response variables. In general, camera types were seldom switched during the sampling period. Also, the effect found by the Kruskal Wallis test could just be because of the location since this test did not adjust for this variable. This may mainly indicate that there are differences between locations that explain some of the variation, rather than the observer or the camera type. Another interesting correlation was between location and species,

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distance to the path and the day or night. These correlations suggest that there is spatial variation in the distribution of species across the locations, as well as differences in recreational pressure. In our analysis, we only treated locations separately, but did not take the actual location into account. Since some areas are more regularly visited than others and management between areas differs, the effect of the path distance, the day or night, and species distribution is very likely to differ between locations. However, locations were not considered in respect of each other or of the area they were situated in, which might have resulted in the correlations between location and the other predictor variables. The area was not considered in this study however as the level of replication was limited, which would have negatively influenced the statistical power. Especially plots that were closer to residential areas or borders of the parks could have influenced responses to human activity (Hettena et al., 2014), resulting in differences in human-induced responses between different locations.

Conclusion

Gaining understanding of how prey perceive risk in regards to human disturbance should make mitigation of this risk more effective and increase generality of predictions of antipredator behaviour as a response to perceived predation risk (Frid & Dill, 2002). Deer species (fallow -, roe -, and red deer) in the natural area the Veluwe, the Netherlands, seem to adjust their behavioural responses on both a temporal and a spatial scale regarding human disturbance. During opening hours of the park, deer showed an effect of the distance to the nearest path in their duration of their visit. Deer also showed an increased vigilance level during the day compared to the night. This indicates a behavioural response of deer to variation in human disturbance on a temporal scale within a day. Deer also visited plots further from paths more often, which indicates a perception of spatial predation risk derived from the distance to the path. These two findings suggest that deer are able to perceive variation in risk on both a temporal and a spatial scale, possibly resulting in the formation of a landscape of fear created by human disturbance. Boar however seemed to be less influenced by the tested predictors of human disturbance. This might be due to having to make different trade-offs in antipredator behaviour between deer and boar, because of for example differing diets (Spitzer et al., 2020). We found no indication in both species of responding to variation in human disturbance between days, using the weather score and the day of the week as proxies for human disturbance. Since we found most behavioural responses during the day and influenced by path distance, we suggest that ungulates in this area might perceive humans as a greater risk than their newly returned natural predator, the wolf, who are expected to mainly hunt during twilight or at night. We therefore encourage future studies to further study whether the fear of the anthropogenic predator overrides fear of prey animals for their natural predators in anthropogenic landscapes and how human recreation influences prey's antipredator behaviours.

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Appendix

Ethogram:

Behaviour	Description
Foraging	Non-vigilant behaviour where the individual is browsing either the ground or higher vegetation
Walking	Non-vigilant behaviour where the individual walks in a striding gait
Scratching	Non-vigilant behaviour where the individual uses either its hindlegs or their mouths to scratch their body
Lying	Non-vigilant behaviour where the individual lies on the ground
Social interaction	Non-vigilant behaviour where the individual interacts with another individual by touching or calling
Rutting	Non-vigilant behaviour where a male individual runs after a female individual in heat
Walking while vigilant	Vigilant behaviour where the individual walk in a striding gait while looking around, twitching it's ears or walking "tip-toe" (carefully placing it's feet)
Other non-vigilant	Non-vigilant behaviour that was not included in the ethogram
Visual vigilant	Vigilant behaviour where the individual is looking around while chewing
Auditory vigilant	Vigilant behaviour where the individual is looking around and stops/is not chewing
Running	Vigilant behaviour where the individual runs from point A to point B
Looking into camera	Vigilant behaviour where the individual looks straight into the camera or approaches the camera
Unknown vigilant	Vigilant behaviour where it is unclear if the individual is chewing or not
Other vigilant	Vigilant behaviour that was not included in the ethogram
Sudden rush	Vigilant behaviour where an individual was startled by something and suddenly ran away
Sudden rush by camera	Vigilant behaviour where an individual was startled by the camera and suddenly ran away
Unknown behaviour	When an individual is not clearly visible or only partly in sight and it is not certain what type of behaviour they are performing

Examples of behaviours from observational videos:

Auditory vigilant

54°F 12°C   07-27-2020   06:47:31

Foraging

Looking into camera

Walking while vigilant

Running

Formula for calculating the weather score:

$$Weather\ score = 6.45 + (0.04 * percentage\ of\ sun\ hours\ of\ total\ daylight\ hours) - (0.35 * number\ of\ hours\ when\ in\ rains\ if\ there\ is\ more\ than\ 0.3\ mm\ of\ rain) - (0.07 * average\ windspeed\ in\ 0.1\ m/s)$$

Model selection

All models always include location as a random factor, except the models used for the vigilance level, as beta regression can not take random factors into account. The same full model with either day/night or hour of the day (i.e. "Timeslot") are compared to check which predictor explains most of the variation.

Duration deer:

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	Res.LL
Distance	4	1463.42	0.00	0.70	0.70	-727.67
Day/night * Distance	6	1466.10	2.69	0.18	0.88	-726.96
Distance + Camtype	6	1468.07	4.65	0.07	0.94	-727.94
Distance + Observer	6	1469.76	6.34	0.03	0.97	-728.79
Day/night * Distance + Camtype	8	1470.85	7.43	0.02	0.99	-727.27
Day/night + Distance	7	1472.61	9.19	0.01	1.00	-729.18
Day/night	4	1475.02	11.60	0.00	1.00	-733.47
Full model	8	1479.73	16.31	0.00	1.00	-731.71
Full model with Timeslot	8	1484.76	21.34	0.00	1.00	-734.22

Full model: duration of visit ~ weather score + distance + species + day/night + (1|location)

Duration boar:

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	Res.LL
Day/night	4	1103.61	0.00	0.53	0.53	-547.75
Day/night + Camtype	6	1103.92	0.31	0.45	0.97	-545.85
Day/night + Weekday	5	1110.46	6.86	0.02	0.99	-550.15
Day/night + Observer	6	1112.11	8.50	0.01	1.00	-549.94
Weather score + Day/night + Weekday	6	1117.21	13.61	0.00	1.00	-552.49
Full model	7	1121.85	18.25	0.00	1.00	-553.78
Full model with Timeslot	7	1135.91	32.30	0.00	1.00	-560.81

Full model: duration of visit ~ weather score + distance + day/night + (1|location)

Vigilance deer:

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Day/night	3	-3951.00	0.00	0.17	0.17	1978.53
Day/night + Observer	5	-3950.67	0.33	0.15	0.32	1980.41
Day/night + Weekday	4	-3950.53	0.47	0.14	0.45	1979.32
Day/night + Camtype	5	-3950.33	0.67	0.12	0.58	1980.24
Day/night + Weather score	4	-3949.52	1.48	0.08	0.66	1978.81
Day/night + Location	4	-3948.97	2.03	0.06	0.72	1978.54
Weather score + Day/night + Weekday	5	-3948.91	2.09	0.06	0.78	1979.53
Day/night * weekday	5	-3948.49	2.51	0.05	0.83	1979.32

Day/night + Weekday + Location	5	-3948.48	2.52	0.05	0.88 1979.32
Day/night + Weekday + Species	6	-3948.34	2.66	0.05	0.92 1980.28
Weather score + Distance + Day/night + Species	6	-3947.13	3.87	0.02	0.95 1979.67
Weather score + Location + Day/night + Weekday	6	-3946.85	4.15	0.02	0.97 1979.53
Weather score + Species + Day/night + Weekday	7	-3946.71	4.29	0.02	0.99 1980.50
Weather score + Distance + Day/night + Weekday	7	-3945.52	5.48	0.01	1.00 1979.90
Timeslot	3	-3932.89	18.11	0.00	1.00 1969.48

Vigilance boar:

| Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Timeslot	3	-5943.68	0.00	0.19	0.19	2974.88
Weather score	3	-5943.57	0.11	0.18	0.37	2974.82
Day/night	3	-5943.50	0.18	0.17	0.54	2974.79
Weekday	3	-5943.49	0.19	0.14	0.58	2974.78
Timeslot + Camtype	4	-5942.54	1.15	0.11	0.65	2975.33
Weather score + Timeslot	4	-5941.77	1.91	0.07	0.72	2974.95
Timeslot + Location	4	-5941.64	2.04	0.07	0.79	2974.88
Day/night + Observer	4	-5941.52	2.16	0.06	0.85	2974.82
Day/night + Camtype	5	-5940.54	3.14	0.04	0.89	2975.36
Weather score * Timeslot	5	-5939.76	3.92	0.03	0.92	2974.97
Weather score + Timeslot + Distance	5	-5939.71	3.97	0.03	0.94	2974.95
Weather score + Day/night + Location	5	-5939.56	4.12	0.02	0.97	2974.87
Weather score + Day/night + Distance	5	-5939.56	4.12	0.02	0.99	2974.87
Weather score + Distance + Day/night + Location	6	-5937.49	6.20	0.01	1.00	2974.87

Number of visits

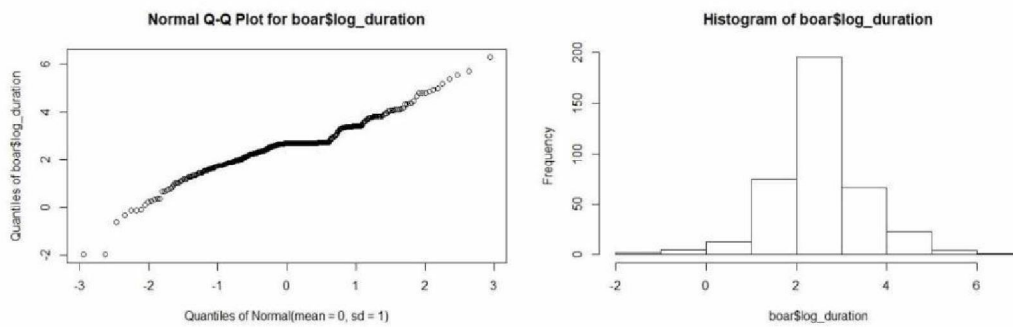| Model	K	QAIC	Delta_QAIC	QAICWt	Cum.Wt	Quasi.LL
Weather score + Distance + Species	8	1594.05	0.00	0.54	0.54	-789.03
Full model	9	1595.83	1.77	0.22	0.76	-788.91
Distance + Species + Day/night	8	1597.05	3.00	0.12	0.88	-790.53
Weather score + Distance	4	1598.71	4.65	0.05	0.93	-795.35
Distance	3	1600.25	6.20	0.02	0.96	-797.12
Weather score + Species * Distance	12	1600.59	6.53	0.02	0.98	-788.29
Weather score + Distance + Day/night	5	1600.67	6.62	0.02	1.00	-795.34
Weather score + Distance + Species + Camtype	8	1605.12	11.07	0.00	1.00	-794.56
Weather score + Distance + Species + Observer	8	1605.12	11.07	0.00	1.00	-794.56
Full model with Timeslot	9	1678.81	84.76	0.00	1.00	-830.40

Full model: # visits ~ weather score + distance + species + day/night + (1|location)
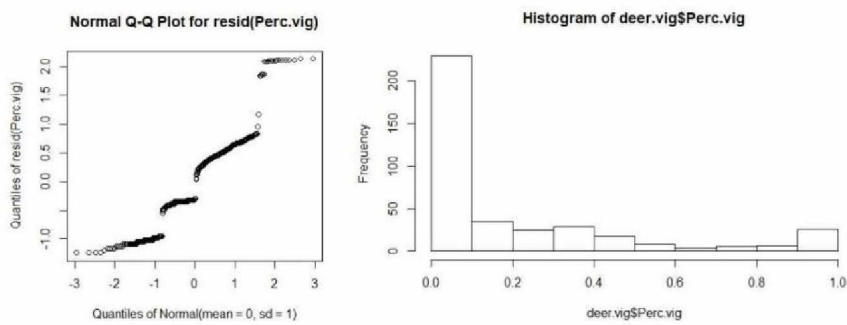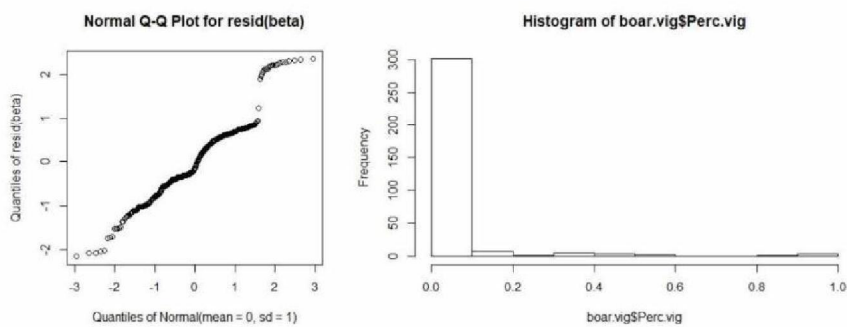
Normality

Duration of a visit of deer:
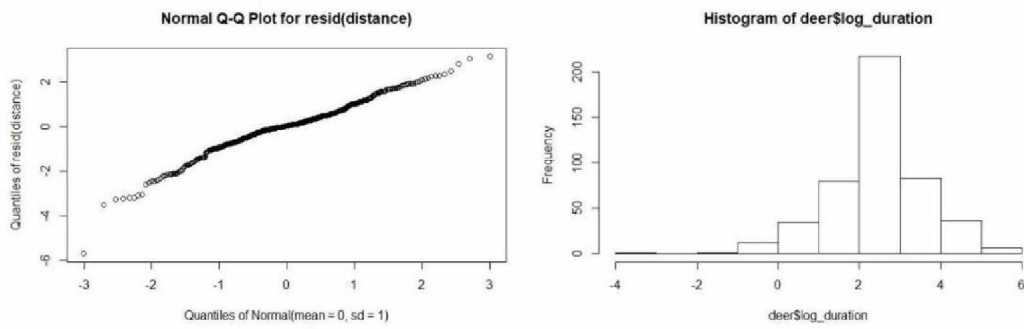
Duration of a visit of boar:

Vigilance level of deer:

Vigilance level of boar:

Number of visits:

Normal Q-Q Plot for resid(no_dn_q)

Histogram of visit.wc.sp.dn$visit