

Landscape of relaxation

On the effect of humans on fallow deer spatiotemporal behaviour and distribution



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Abstract

Apex predators are theorised to be able to shape ecosystems via changing the distribution and behaviour of their prey, this is called the ecology of fear. This change can lead to a cascading effect, impacting the whole ecosystem. In human dominated areas, humans have often taken over the role of apex predators and are theorised to play a similar role in the ecosystem. Recently, whether cascading effects often follow from a change in the ecology of fear has come under discussion, with studies showing that this not always takes place. One major critique is that prey species can compensate for predator activity by varying their distribution and behaviour temporally and spatially, allowing little overall effect. In this study, we evaluated the effect of five different factors and their interactions on fallow deer distribution and vigilant behaviour in the human dominated areas of Veluwezoom and Deelerwoud in the Netherlands. The factors we evaluate are path distance (20m, 100m), zonation (hunting and recreation, only recreation, no hunting and recreation), habitat (forest, heather), time of day (day, night) and season (hunting, non-hunting). We expected the perceived risk to be higher close to the path, in zones with hunting and recreation, on the heather, during the day and in the hunting season. In places and during times which are perceived as highly risky, we expected fallow deer presence to be low and vigilance to be high. We installed cameras on 20m and 100m from tracks, equally divided between the zones and habitats. On the videos derived from the cameras, we scored the total time present and ratio of vigilant behaviour of fallow deer. We found a higher presence in the refuge zone when compared to the hunting zone and a higher presence outside the hunting season compared to during the hunting season when analysing these factors individually without interactions. There was no single factor effect on vigilance. The full models revealed a large amount of interactions however for both measurements. These interactions showed that deer rather avoid perceived to be risky areas in perceived to be risky periods and largely compensate in periods they consider less risky. Instead of adapting their vigilance, fallow deer select places where they perceive low risk, creating a landscape of relaxation rather than fear. Overall, we conclude that micro-compensation negates strong overall effects but leaves windows of opportunity for cascading effects to still take place.

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Introduction

Apex predators are theorised to be able to shape ecosystems. Both the removal and reintroduction of apex predators often has large effects. The reintroduction of wolves in Yellowstone National Park is classically used as an example. Due to this reintroduction, the number of elk and bison was significantly reduced (Laundré, Hernández and Altendorf, 2001; Smith, Peterson and Houston, 2003; Dobson, 2014). This reduction is theorised to be both density-mediated, with predators preying upon prey directly, and behaviourally-mediated, with prey avoiding places with predators and changing their behaviour by being more vigilant (Terborgh and Estes, 2010). This change in distribution and behaviour leads to a lowered fitness and reproduction in prey. As they experience more stress and fear in places they perceive to be dangerous, they spatially avoid them or exhibit more vigilant behaviour in them. These behaviourally-mediated effects can cause trophic cascades. Moreover, this can lead to less effectively foraging and to lower prey numbers. This indirect effect on prey abundance and behaviour can be as strong as the direct effect of predator hunting (Schmitz, Beckerman and O'Brien, 1997). This is described by the landscape of fear and ecology of fear theories (Laundré, Hernández and Altendorf, 2001; Laundré, Hernández and Ripple, 2010; Kuijper *et al.*, 2013; Bleicher, 2017).

The landscape of fear theory states that prey species perceive a landscape of predation risk, with risk peaks and valleys. These spatial differences create a range of cost-benefit analyses in terms of foraging versus safety trade-offs (Charnov, 1976; Barnier *et al.*, 2014; Kuijper *et al.*, 2015; Bleicher, 2017). Prey behaviour is adaptive to the different outcomes of these analyses (Laundré, Hernández and Altendorf, 2001). This adaption can be via avoiding risky areas or by being more vigilant while foraging in these areas, leading to a decrease in browsing efficiency (Hernández and Laundré, 2009). Next to spatial effects, there can also be temporal effects of a landscape of fear. Prey species can shift their foraging periods to minimize overlapping activity with predator species. This is shown in roe deer, which shift their foraging period towards night-time when exposed to a daytime predator (Sönnichsen *et al.*, 2013). Also, prey can alter their habitat choice to spend high-risk times in low-risk habitats and vice versa. Elk, for instance, have been shown to spend more time near forest edges when wolves are present than when wolves are absent (Hernández and Laundré, 2009).

The ecology of fear is theorised to be able to have strong cascading effects on other trophic levels (Ripple and Beschta, 2006). In the case of Yellowstone, the effect wolves had on their prey, not only had an indirect effect on coyote populations, but also on sapling recruitment and forest rejuvenation (Ripple *et al.*, 2001; Ripple and Beschta, 2003). The carcasses left after wolf hunting also proved to affect scavenger birds, such as golden eagles and ravens, increasing their numbers (Smith and Ferguson, 2012). However, whether a change in the ecology of fear leads to cascading effects is subject to scientific debate. In the case of Yellowstone, it has been argued that, rather than wolf reintroduction, change of water availability might have been the main driver of vegetation change (Kauffman, Brodie and Jules, 2010). This study showed no difference in elk browsing levels on aspen regardless of wolf predation risk. Another study argued that willow and aspen recovery has been due to climate change extending their growth season, rather than trophic cascades created by wolf reintroduction (David Mech, 2012).

If prey behaviour takes place in a landscape of fear, this landscape has both temporal and spatial elements. This opens up the opportunity for prey to avoid fearful places at fearful times, to return to those places at less fearful times, possibly cancelling out the effects of the initial avoidance (Tolon *et al.*, 2009). If this is the case, prey would not show more fearfulness as they would rather avoid fearful places. So instead of perceiving landscape of fear, they would select for places where they would not need to be afraid. If risks are spatiotemporally heterogeneous and predictable up to a certain extent, this opens up the window for spatiotemporally compensation.

If this compensation exists the relation between predation risk and the cascading effects that follows, is questionable at best. Most of the studies done in behavioural ecology, focus on that the effect a single factor has on a behavioural response. These types of studies fail to take the complexity of behaviour into account. Although some researchers might hold that behaviour is not that complex and rather caused by a few simple rules, ecologists researching the ecology of fear cannot do so. This whole theory explicitly assumes the complexity of behaviour, by assuming that prey species perceive gradients of risk across a spatial and temporal landscape and adjust their behaviour to this gradient.

This complexity opens up the possibility that the factors which cause these gradients, might interact with another. Recently, more studies have stressed this fact (Bonnot *et al.*, 2013; Padié *et al.*, 2015). There have been studies showing that daytime avoidance of paths is compensated at night (Coppes *et al.*, 2017). Without taking diel differences into account, it is well possible that they would not have found any results. This does not only hold for difference between daytime and night-time. There can be multiple spatial and temporal factors involved in behavioural compensation for predation risk, such as distance to predators, area foraging quality, diel rhythms and seasonality.

Risks and rewards shape behaviour (Charnov, 1976; Searle, Stokes and Gordon, 2008). Therefore, in both conservation ecology and behavioural ecology, it is vital that studies take into account multiple factors. It is easier to quantify the effects of a single factor without evaluating the context, making it tempting to do so. However, without investigating the interactions that this factor has with the environment, one cannot conclude much about the effects of this factor in a natural system. In studies on the ecology of fear, both spatial and temporal factors influence another.

The majority of research on the ecology of fear has taken place in regions with little human impact, even though human presence in natural systems has been increasing for the last centuries (Vitousek *et al.*, 1997). Although this does not always cause local extinction of large predators, as is shown by Chapron *et al.*, this does occasionally happen, leading to changes in the landscape of fear (Chapron *et al.*, 2014). The Netherlands' largest predator species, the wolf (*Canis lupus*) has been absent for over a century. Without a controlling predator, ungulate numbers have been increasing rapidly. This may prevent forest rejuvenation due to few tree saplings surviving until they reach a height where ungulates are prevented from browsing large portions of their leaves. It is hypothesized that this could result in the loss of oak-beech forests in the long term (Kuiters, 1998). The increasing number of ungulates might also threaten other rare plant species and damage crops (Mysterud, 2006). Due to this, hunting quota were established to regulate ungulate numbers. This effectively caused humans to become the apex predator in the Netherlands, replacing the wolf. Whereas wolves are pursuit-predators, humans can be considered ambush predators. This affects deer behaviour due to a change in the landscape of fear (Ciuti, Muhly, *et al.*, 2012). Deer show higher level of vigilance in open areas under hunting pressure, while they show a preference for these areas when under predation pressure from wolves (Benhaïem *et al.*, 2008). The effect of hunting can be so strong, that even in areas where wolves are still present, deer change behaviour to avoid human hunting rather than wolf predation (Ciuti, Northrup, *et al.*, 2012).

Human hunting is seasonal, and typically takes place outside the breeding season. This seasonality causes a temporal change in the landscape of fear to which some species of deer are known to react (Benhaïem *et al.*, 2008; Sönnichsen *et al.*, 2013). As humans tend to hunt during daytime, deer also shift their activity to twilight and night (Sönnichsen *et al.*, 2013). Also, deer increase their group-size when faced with hunting (Spaedtke *et al.*, 2006). Other than via hunting, other forms of human presence can influence deer behaviour. On a temporal scale, human recreation, such as hiking and mountain biking, mainly takes place during daytime as many parks are closed off for visitors between dusk and dawn. Recreation is likely to be higher during summer than

winter. Spatially, human recreation will be more frequently close to large roads and villages, from which trails start. As trails and nature reserves often have a limited number of entrances and starting points, the number of humans is highest here and then dilutes as they disperse over the trails. Humans also have the tendency to stay on the roads, this is often even enforced by law. As such humans are spatially rather predictable. It is shown that deer tend to avoid humans and trails, especially with no other predators present which can cause the “human shield effect” where humans deter predators and thereby provide safety for prey species (Kuijper *et al.*, 2016; Coppes *et al.*, 2017; Mathisen, Wójcicki and Borowski, 2018; Scholten, Moe and Hegland, 2018). This tendency to avoid humans can have implications for wildlife conservation and nature management. Especially in countries such as the Netherlands, which lack apex-predators to control ungulate populations, the danger associated with humans is a main driver for ungulate behaviour. Clever use of ungulate fear for humans might be used as a management tool to deter ungulates from regions where they are undesirable, such as places where they damage agriculture, cause traffic accidents or where forest rejuvenation and sapling recruitment is wanted (Cromsigt *et al.*, 2013).

To better understand the mechanisms that drive deer behaviour and how factors can influence another, this study looks at large and small scale temporal and spatial effects of human hunting and recreation on presence and vigilance of fallow deer (*Dama dama*) via camera traps. We studied large scale spatial effects of human recreation and hunting and habitat type, the small scale spatial effects of path distances, the large scale temporal effects of hunting seasonality and the small scale temporal effects of time of day. We expect that fallow deer perceive humans as dangerous and thus avoid them spatial-temporally. However, since most human presence is both temporally and spatially restricted, we expect no overall effects. Rather, we expect large compensation via interactions, with fallow deer avoiding dangerous areas in dangerous times, and compensating this in less dangerous times and vice versa.

Methods

Study area

The study was done in the National park Veluwezoom and nature reserve Deelerwoud in the Netherlands (Figure 1). Both regions contain mixed forests, of which the coniferous parts mainly consist of Scots pine (*Pinus sylvestris*) with an undergrowth of European blueberry (*Vaccinium myrtillus*) and heather patches, consisting mainly of common heather (*Calluna vulgaris*). Several hiking trails and bicycle paths run through the parks. The areas are split by a highway, which is crossed by an ecoduct, allowing animal movement between the two regions. The Veluwezoom region has a surface area of around 5000 hectares and is, with a yearly total of around 1,5 million visitors, often crowded (*Wat zijn de bezoekerijfers aan ‘attractie’ natuur? - Pretwerk*, no date). Deelerwoud is smaller, with 1230 hectares of surface area, and also receives less visitors. Both regions are managed by “Natuurmonumenten”, a Dutch nature conservation

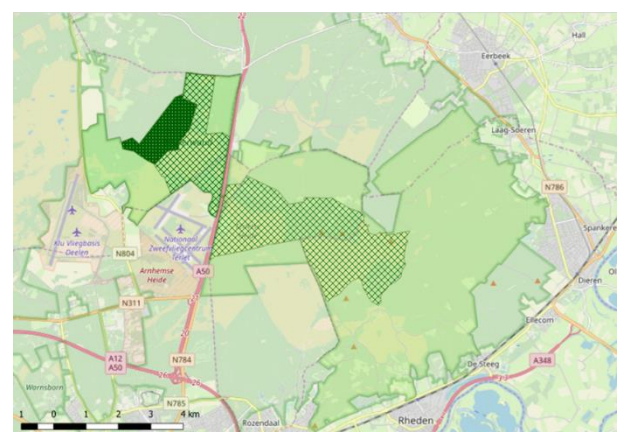


Figure 1: Overview of the study area. On the left of the highway is the Deelerwoud and on the right is the Veluwezoom. The dark-green part is the refuge area, hatched is the hunting area with recreation and light green is recreation only.

organisation. The regions are divided into recreational areas, where visitors are allowed, and refuge areas, prohibited for visitors. The recreational area can further be divided into a hunting area, where apart from recreation, hunting is also allowed, and a recreational area, where hunting is prohibited. Several large ungulates inhabit both regions, namely red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), highland cattle (*Bos Taurus*), and wild boar (*Sus scrofa*). Hunting takes place from around August until March, depending on the hunting quota for that year and is mainly focussed on red deer and fallow deer.

Study species

This study focussed on fallow deer, as this species is most abundant (*Dama dama*, 28 ind. km⁻¹) in both regions and as such it was most feasible to obtain enough reliable data from them. Secondly, as they are most abundant, hunting quota for this species are the highest. This creates a higher incentive for the fallow deer to seasonally adapt their behaviour to hunting. Lastly, as these deer have the highest abundance, we estimated them to be the main browsers of sapling trees, possibly preventing rejuvenation of the forests.

Global plot selection and camera installation

Data was obtained from April 2018 until April 2019. Cameras (Bushnell Trophy Cam HD) were installed both outside and inside the hunting season. The cameras were placed at hip height. In the forest, they were locked to a tree whereas on the heather, they were locked onto a wooden pole. On the heather, the cameras were facing north, ensuring video visibility. The cameras were set up with high contrast, automatic day/night switching and sensitivity on normal, as high sensitivity gave too many false positives. Sixty seconds of video and a photograph were taken if the camera was triggered during daytime, and after a 0,6 second latency the camera could be triggered again. During night time, only 15 seconds of video and a photograph were taken. As more energy is used to generate clear contrasted videos during the night, this created the risk that the camera overheated if it records longer videos. This limitation is built-in in the camera and could not be overridden. The same latency was used during night time. The SD card was formatted and a check was done to verify whether the camera registers movement at a distance of at least 10 meters. Then, the camera was turned on and triggered by the installer. The camera was again triggered at the retrieval, so that we could ensure that the camera had been functioning from the start until the end of the session. This was to check whether when there were no deer on the videos, this was due to malfunctioning of the camera or that there were actually no deer present.

A total of 48 cameras were installed outside the hunting season, from May to August 2018. Inside the hunting season the same 48 plots were repeated, together with several new plots for a total of 108 cameras from November 2018 to April 2019, to examine the effect of the hunting season. Each camera took videos for between 14 and 55 days, after which the camera was moved to a new sample location. In total we did three sessions outside the hunting season and six sessions within the hunting season. The total number of plots was equally distributed over Deelerwoud and Veluwezoom, after which it was further divided between the refuge area, the recreational and hunting area (Figure 1). As there is no refuge area in Veluwezoom, we selected areas with old, unused paths where access is prohibited, which we then classified as refuge areas. We chose these three types of area to examine the effects of human hunting and recreation. To investigate the effect of different habitats, the plots in these areas were then equally divided between heather and forest patches. For both sessions, the requirements were the same. For Veluwezoom, the most crowded places were avoided, as the managers of the parks preferred no research in these areas.

We selected tracks with similar use intensity based on Strava, an app used by both professional and amateur outdoor athletes to track their performance.

Local plot selection

To determine the influence of paths on deer behaviour, the cameras were placed perpendicular to paths at distances of 20m and at 100m to the path. To prevent interference from another path, we required each plot to be at least 100m from other paths. Also, where possible, wildlife tracks were avoided to avoid a bias in behaviour type. Finally, the camera pairs were placed at least 100 meters from another, to minimize pseudo-replication. In the forests, the cameras were placed in either patches of Scots pines with an undergrowth of European blueberry or in patches of common heather in patches of common heather, as these are most representative of the region.

Video scoring method

To analyse the video-samples, we used Boris (Friard and Gamba, 2016). This is a software that allows an observer to code behaviour via the keypad of his computer. As routine vigilance is hard to observe, only active vigilance was scored. This behaviour results in the loss of foraging opportunities and is as such more costly (Blanchard and Fritz, 2007). We defined this vigilance as when the deer had its head above its shoulders, stopped rummaging and twitched its ears (Winnie and Creel, 2007). The videos are scored via the protocol found in Appendix A.

To stratify the measurements, we excluded all fallow deer does with calves and the calves themselves, as these are mainly present outside the hunting season and might bias the results since does with calves are suspected to show a higher risk aversion.

This study focussed on two indicators of how fearful fallow deer are of a place; deer presence and deer vigilance. As it was possible that deer avoid places where they need to be more vigilant, it was necessary to take both the vigilance level and the amount of time present into consideration to create a good picture of how humans shape deer behaviour and distribution.

For presence, we measured the amount of seconds a deer was present in front of a camera. For this amount of time, all behaviours performed were included. This amount of time has afterwards been corrected for the amount of days that the cameras had functioned by dividing the total amount of time by the days the camera was active. Also, we divided the camera records into day time and night time to see whether there is an effect of the time of day. So each individual camera yielded both a day result and a night result. The exact moment on which the data was divided, depended on the dates on which the cameras had functioned. We took the median sunrise and sunset of each camera session as the cut-off point by which we divided the two times of day.

The level of vigilance is a ratio calculated by dividing the total amount of time spent actively vigilant by the total amount of time a deer was present on the camera, except for the behaviour of "looking into the camera". This behaviour was caused by our cameras and more prevalent on heather than in the forest, as here we used poles which makes the cameras more noticeable. As this was not a natural behaviour which would have taken place without our cameras present, we decided not to include this measurement in the calculation. It was taken into account for presence, as presence did not look at the behaviour of the deer but rather only the time it was present.

Statistical method

Statistical analyses were done in R version 3.6.0. To compare the effects of the five factors, generalized linear mixed effect models were deployed. This enabled us to look at interaction-effects,

such as the effect of the hunting season in the different types of area (refuge, recreation and hunting). It also allowed us to pair the observations where necessary, via random effects.

Fallow deer presence

The data best fitted a generalized linear mixed effects model with a Gamma(log) link. As some cameras did not capture any deer, we had data points where the number of seconds was zero. Since log-links cannot handle zero values, an extra second was added up to each of the data points. With this corrected fallow deer presence as our response variable, we constructed several models. These models were compared with another by using the AIC value to determine which model best explained our data. The model we selected as our best model was the most complex model within a 2 points difference of the lowest AIC score (Burnham and Anderson, 2002). Due to the complexity of our models, we had to choose a non-default optimizer. We used the optimizer “*nlminbwrap*”, as it converged our models fastest and without convergence errors.

The five fixed factors we included in our most complex model were zonation (categories: refuge, recreation, hunting), habitat (heather, forest), path distance (20m, 100m), season (hunting-, non-hunting season), and daytime (day, night). We allowed these five factors to interact up until three-way interactions, to prevent too much overdispersion of our data and to somewhat simplify our interpretation. To account for the pairs in our design, we added random factors to link the season pairs, the path distance pairs and the day and night pairs. As the two study-areas differ in both the number of fallow deer present and the number of human activity present, we included area as a random factor (categories: Veluwezoom and Deelerwoud), to correct for differences between these areas. For a summary of these factors, see Table 1.

Table 1: Overview of the fixed effects and random effects in the model

Fixed effects	Categories	Random effects	Categories
Zonation	Refuge, recreation & hunting	Area	Veluwezoom & Deelerwoud
Habitat	Heather & forest		
Distance to path	20m & 100m	Pair of paths	Unique number for each pair
Season	Non-hunting & hunting	Pair of seasons	Each plot number as a category
Time of day	Day & night	Pair of day & night	Unique number for each camera

We used stepwise exclusion via the lowest AIC of interactions and fixed effects to reduce our model to the best model. This best model was reached if dropping any interaction or effect would result in a higher AIC than the current model. As three-way interactions cover all two-way interactions and one-way factor effects, if the initial best model was reached, we continued to exclude these interactions until a new best model was reached. Of these best models the AIC was compared and the most complex model within 2 AIC was accepted. A QQ-plot was constructed to test for the normality of the residuals. The interactions and variables within the best model were analysed with a post hoc Tukey test. Also, the effects of each fixed factor in itself were tested with Wilcoxon rank sum tests.

Fallow deer vigilance

The vigilance score we used is the ratio of vigilant behaviour divided by the total natural behaviour. This ratio is always between 0 and 1. We had to exclude the cameras on which no deer was

captured, as we cannot calculate a ratio without any behaviours. The vigilance scores best fitted an GLMER with a binomial family and a logit link. We used the same optimizer as during our modelling of presence, “nlminbwrap”, which gave us again no convergence errors. As the vigilance scores were based on equations of different scales, with some vigilance scores being based on less than a minute of behaviour and others being based on more than an hour of behaviour, there is a difference in certainty of these scores. To allow our model to reflect this difference in certainty, we weighed our results by the total number of seconds of video per data point.

We proceeded in the same way as when constructing presence models and used the same fixed and random factors. For these factors and their categories, see Table 1. Again, we created several best models, and finally selected the most complex best model within 2 AIC of the model with the lowest AIC. We constructed a QQ-plot to check for normality of the residuals. After this we firstly tested each fixed factor in itself via Wilcoxon rank sum tests, after which we analysed the interactions and variables within the best model with a post hoc Tukey test.

Results

Presence

Of the various models that we evaluated, the best model fitting fallow deer presence included three three-way interactions. Firstly, between season, path distance and time of day, secondly, between season, time of day and zonation and thirdly, between habitat, distance to path and time of day. This model also included every two-way interaction and individual factor underneath these three-way interactions. This model was model31b (Table 2). The model with the lowest AIC, model31d, included only the three-way interaction between season, time of day and zonation. Path distance was completely dropped from this model. Table 3 shows the estimates of the best model. The QQ-plot displaying the residuals of this model is found in Appendix B.

When only taking a single factor in account, Wilcoxon rank sum tests revealed that path distance did not significantly affect presence (p-value = 0.645), nor did habitat (p-value = 0.114) or time of day (p-value = 0.481). However, a significant higher presence was found outside the hunting season (p-value = 0.442). A pairwise Wilcoxon rank sum test done on zonation showed a significantly higher presence in the refuge zone compared to the hunting zone (p-value = 0.023) but not in the refuge zone compared to the recreation zone (p-value = 0.244). There is also no difference between recreation and hunting zones (p-value = 0.244).

Table 2: The four models that were built for corrected fallow deer presence, sorted by their Δ AIC. The model depicted in bold is the best model.

Model	Δ AIC	df
model31d	0.0	19
model31c	0.9	23
model31b	1.6	25
model31a	27.9	42

Table 3: Estimates of the best model for fallow deer presence. The estimates, standard errors (SD), t-values and p-values are displayed. Significant effects ($\alpha, 0.05$) are in bold. Se-NH is non-hunting season, Ha-Hea is heather habitat, Path-20 is 20m path distance, Time-Ni is night time, Zone-Rec is the recreation zone where no hunting is allowed and Zone-Ref is the refuge where recreation nor hunting is allowed

	Estimate	SE	t-value	p-value
(Intercept)	1.374	0.594	2.315	0.021
Se-NH	-0.306	0.493	-0.620	0.535
Ha-Hea	-1.082	0.483	-2.240	0.025
Path-20	-0.438	0.378	-1.159	0.246
Time-Ni	-0.457	0.565	-0.808	0.419
Zone-Rec	0.218	0.531	0.410	0.681
Zone-Ref	0.962	0.573	1.678	0.093
Se-NH:Path-20	0.033	0.398	0.084	0.933
Se-NH:Time-Ni	0.807	0.477	1.691	0.091
Se-NH:Zone-Rec	1.278	0.708	1.807	0.071
Se-NH:Zone-Ref	1.242	0.772	1.610	0.107
Ha-Hea:Path-20	0.205	0.558	0.368	0.713
Ha-Hea:Time-Ni	2.175	0.563	3.861	<0.001
Path-20:Time-Ni	0.883	0.394	2.244	0.025
Time-Ni:Zone-Rec	-0.110	0.638	-0.173	0.863
Time-Ni:Zone-Ref	-1.029	0.686	-1.501	0.133
Se-NH:Path-20:Time-Ni	0.341	0.193	1.767	0.077
Se-NH:Time-Ni:Zone-Rec	-2.128	0.715	-2.978	0.003
Se-NH:Time-Ni:Zone-Ref	-2.192	0.742	-2.953	0.003
Ha-Hea:Path-20:Time-Ni	-1.146	0.578	-1.982	0.047

The post hoc comparisons revealed a large number of significant interactions. Most of these are time of day interactions. Therefore we split them into time of day interactions and other interactions. There were no significant interactions for season or path distance. The results are displayed in Table 4.

Time of day

Comparison of day and night presence revealed several interactions. Firstly, there was a higher presence during day time in the forest in the refuge zone. This effect was significant for both distances and seasons, with the exception of at 20m in the hunting season. Secondly, there was more day-than night-presence in the recreation zone, during the non-hunting season at 100m in the forest. Thirdly, there was more night presence during the hunting season on heather. This effect was significant for both path distances in both the recreation zone and hunting zone (Figure 2). Finally, there was more night presence in the hunting zone, during the non-hunting season. This effect held for both distances and habitats, except for at 100m in the forest.

Other interactions

Firstly, comparing zones, we found a higher presence in the refuge zone than in the hunting zone during the day in the non-hunting season. This was for both 20 and 100 meter and in both heather and forest. Secondly, for habitat types, we found a higher presence on the heather during the night at 100m. This effect was found both inside and outside the hunting season in all zones. Thirdly, also comparing habitats, we found a higher presence in the forest during the day at 100m. This effect was found in both seasons and in all zones (Figure 3).

Table 4: The significant interactions when looking at fallow deer presence. On the left are the categories of the factors which show a higher presence compared to the other categories. On the right are the categories of the other factors for which this higher presence is found. So if on the left "Day" is displayed, that means that within the factors on the right, there is more presence during the day than during the night.

Higher presence	Zone	Season	Path distance	Habitat	Daytime
Refuge - hunting	-	Non-hunting	Both	Both	Day
Day	Refuge	Non-hunting	Both	Forest	-
Day	Refuge	Hunting	100m	Forest	-
Day	Recreation	Non-hunting	100m	Forest	-
Night	Recreation	Hunting	Both	Heather	-
Night	Hunting	Non-hunting	Both	Heather	-
Night	Hunting	Non-hunting	20m	Forest	-
Night	Hunting	Hunting	Both	Heather	-
Heather	All	Both	100m	-	Night
Forest	All	Both	100m	-	Day

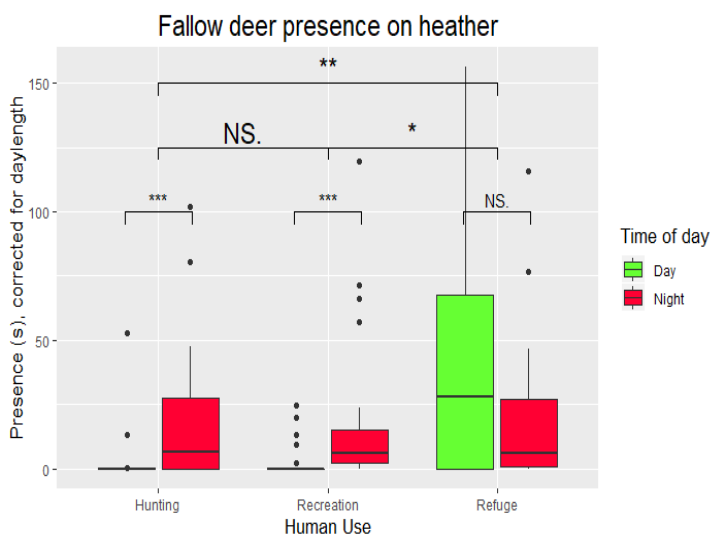


Figure 2: Fallow deer presence on heather for each combination of zones and time of day.

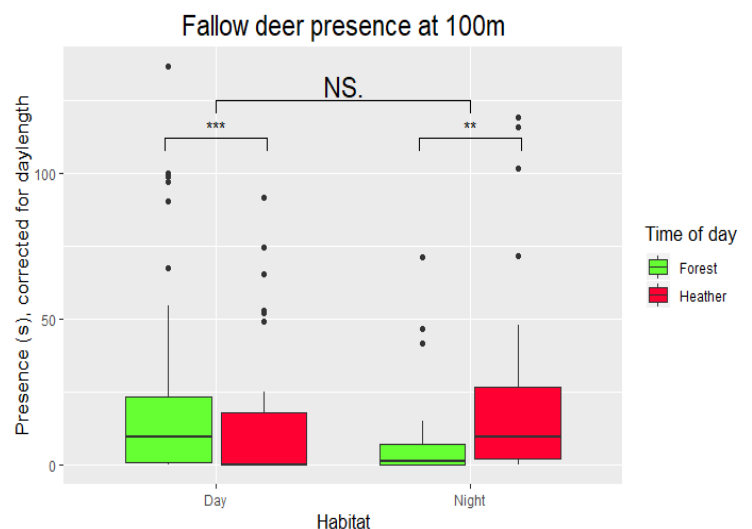


Figure 3: Fallow deer presence at 100m for each combination of time of day and habitat.

Vigilance

The best model fitting fallow deer vigilance includes three three-way interactions: between season, path distance and habitat, between habitat, path distance and time of day, and between path distance, time of day and zonation. The model also includes every two-way interaction and individual factor underneath these three-way interactions. The best model is model41d (Table 5). The model with the lowest AIC, model41e, lost the interaction between habitat, path distance and time of day. The estimates of the best model are displayed in Table 6. The QQ-plot displaying the residuals of this model is found in Appendix B.

Looking at individual factors in isolation, Wilcoxon rank sum tests revealed that path distance did not significantly affect presence (p-value = 0.087). Neither did habitat (p-value = 0.775) nor time of day (p-value = 0.562). Different from presence, season did also not affect vigilance (p-value = 0.562). Also differing from presence, a pairwise Wilcoxon rank sum test done on zonation showed no significant difference between zones (Recreation – Hunting p-value = 0.33, Refuge – Hunting p-value = 0.65 & Recreation – Refuge p-value = 0.13).

The post hoc comparisons again revealed a large number of significant interactions. Most of these are path distance interactions. Therefore, we split them into path distance interactions and other interactions. The results are displayed in Table 7.

Path distance

This yielded several significant interactions. First of all, in the refuge zone, in the forest during the day, vigilance is higher at 100m than at 20m. This holds for both seasons. Second of all, in the recreation zone, on the heather during the night in the hunting season, vigilance was also higher at 100m. Thirdly, in the recreation zone on the heather during the day outside the hunting season, vigilance was higher at 20m (Figure 4). Fourthly, in the hunting zone, on the heather during the day in both seasons, vigilance was also higher at 20m. Finally, in the hunting zone, in the forest during the day in the hunting season, vigilance was higher at 20m as well.

Table 5: The models that were built for fallow deer vigilance, sorted by their Δ AIC. The best model is in bold

	Δ AIC	df
model41e	0	22
model41d	0.5	24
model41c	3.8	32
model41b	4.6	35
model41f	4.7	19
model41a	12.1	41

Table 6: Estimates of the best model for fallow deer vigilance.. The estimates, standard errors (SD), z-values and p-values are displayed. Significant effects ($\alpha < 0.05$) are in bold. Abbreviations are as previously.

	Estimate	SE	z-value	p-value
(Intercept)	-2.124	0.378	-5.614	<0.001
Se-NH	-0.529	0.348	-1.522	0.128
Ha-Hea	-0.744	0.423	-1.760	0.078
Path-20	1.559	0.584	2.667	0.008
Time-Ni	0.047	0.468	0.101	0.920
Zone-Rec	0.766	0.433	1.771	0.077
Zone-Ref	0.435	0.436	0.996	0.319
Se-NH:HaHea	0.449	0.543	0.826	0.409
Se-NH:Path-20	-0.333	0.540	-0.616	0.538
HaHea:Path-20	0.834	0.654	1.275	0.202
Ha-Hea:Time-Ni	0.544	0.469	1.160	0.246
Path-20:Time-Ni	-1.533	0.675	-2.270	0.023
Path-20:Zone-Rec	-1.991	0.680	-2.927	0.003
Path-20:Zone-Ref	-3.104	0.712	-4.362	<0.001
Time-Ni:Zone-Rec	-0.213	0.528	-0.404	0.686
Time-Ni:Zone-Ref	-0.880	0.600	-1.468	0.142
Se-NH:Ha-Hea:Path-20	2.140	0.869	2.464	0.014
Ha-Hea:Path-20:Time-Ni	-1.317	0.722	-1.824	0.068
Path-20:Time-Ni:Zone-Rec	1.157	0.803	1.440	0.150
Path-20:Time-Ni:Zone-Ref	3.141	0.884	3.553	<0.001

Other interactions

Firstly, comparing zones, there was a significantly higher vigilance at 20 meters, during the day in the recreation and hunting zones compared to the refuge zone. This effect was in both habitats and seasons. Secondly, between seasons, there was a higher vigilance outside the hunting season at 20m on heather in all zones and throughout the day. Thirdly, looking at the time of day, in both seasons and habitats, vigilance was higher during the day in the recreation and hunting zones at 20m. Lastly, comparing habitat types, there was a higher vigilance on heather outside the hunting season at 20m. This was found in each zone at every time of day (Figure 5).

Table 7: The significant interactions when looking at fallow deer vigilance. On the left are the categories of the factors which show a higher presence compared to the other categories. On the right are the categories of the other factors for which this higher present in found. So if on the left "Day" is displayed, that means that within the factors on the right, there is more presence during the day than during the night. Rec is recreation zone, Hunt is hunting zone and Ref is the refuge zone.

Higher vigilance	Zone	Season	Path distance	Habitat	Daytime
Rec & Hunt - Ref	-	Both	20m	Both	Day
Non-hunting	All	-	20m	Heather	Both
Day	Rec & hunt	Both	20m	Heather	-
100m	Hunt	Both	20m	Forest	-
100m	Ref	Both	-	Forest	Day
20m	Rec	Hunting	-	Heather	Night
	Rec	Non-hunting	-	Heather	Day
20m	Hunt	Both	-	Heather	Day
20m	Hunt	Hunting	-	Forest	Day
Heather	All	Non-hunting	20	-	Both

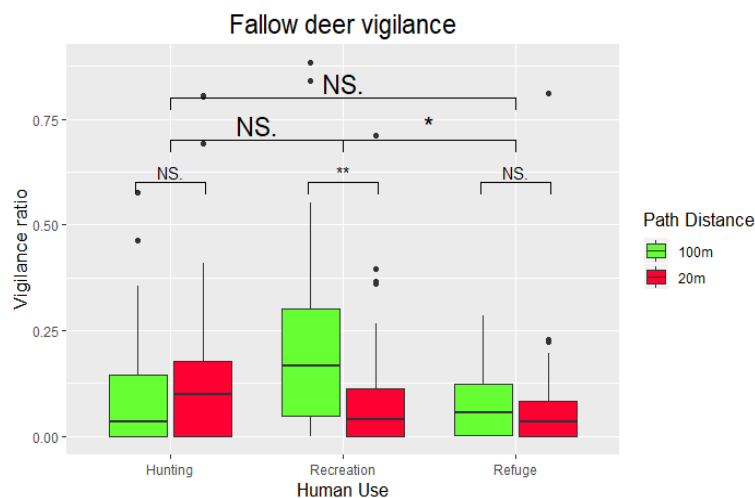


Figure 4: Fallow deer vigilance for each combination of zones and distance to path.

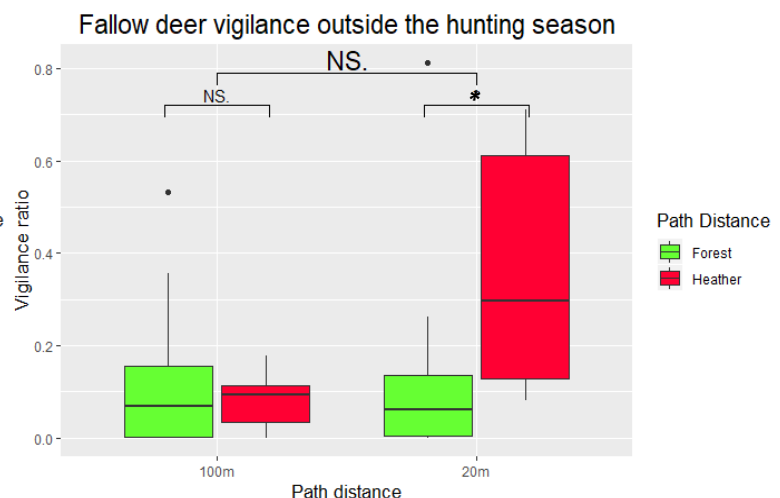


Figure 5: Fallow deer vigilance outside the hunting season for each combination of habitat and distance to path.

Discussion

We studied fallow deer distribution and vigilance in a natural system, with several factors interacting with another. On a spatial macroscale, we looked at differences between forest and heather and refuge-, recreation- and hunting-zones, while on a spatial microscale, we compared 20m and 100m from a path. On a temporal microscale, we looked at the effects of the hunting season, while on a temporal macroscale, we evaluated at the influence of day and night.

When only taking a single factor into account, we found a higher deer presence in the refuge zone than in the hunting zone but no difference between the recreation zone and the other two zones. We also found a higher deer presence outside the hunting season when compared with inside the hunting season. However, these results were meagre when compared with all the interactions that were present. This is visible in Figure 2 and Figure 3, which show lot of significant interactions and but few significance overall effects. Also, even though we found some differences in presence

on single factors, we found no differences on vigilance levels for the different factors. Although fewer than for presence, there were several interactions which influenced the vigilance levels. This is visible in Figure 4 and Figure 5, which show some significant interactions but no large scale interaction.

Distribution

Corresponding with literature, we found an overall higher presence in the refuge area than in the hunting area. Previous studies have shown that deer avoid humans in areas with hunting (Benhaiem *et al.*, 2008). Also, they found a lower presence during the hunting season than outside the hunting season, which we also found. As the fallow deer are not able to migrate out of the area in the winter, there has to be a different reason as to why we have less videos of them. There are several possible reasons. Firstly, there are less deer in the hunting season than outside it. As hunting takes place in the winter and just before the deer reproduce, deer abundance can be expected to be lower than outside the hunting season. Secondly, deer might be less likely to be captured on the camera. As the days are shorter in the winter, there is a large difference in the time that cameras are on night-mode. During this night-mode, the cameras might have a lower chance of successfully capturing deer presence. That camera-trap studies have some limitations in this aspect is known (Newey *et al.*, 2015). We also had the issue that our night-videos were only 15 seconds, after which a latency time of 0.6 seconds was used. That might also have caused a lower presence score in the hunting season. Thirdly, although not univocally, red deer are known to be less active during the winter and it is likely that the same holds for fallow deer (Georgii, 1981; Ensing *et al.*, 2014). As the food availability is lowered and the temperatures are lowered, deer might conserve energy by lowering their activity, making it harder for us to capture them on camera.

We did not find any difference between path distances, neither main effects nor interactions, which does not correspond with some of the literature (Scholten, Moe and Hegland, 2018). This study was done on red deer, which might be more frightful than fallow deer. Also, when looking at the interaction effects that we found, we see a large night compensation in the hunting area, especially on the heather. As the other study did not take diel rhythm into account, we can conclude that the effect that they found might only be during the day, or that the effect during the day is so large, that deer cannot compensate for this effect during the night. This is generally a problem with studies based on dung counts. They can only show net-effects as this method of measuring deer abundance cannot take diel rhythm into account.

We found that diel rhythm is a large explanatory force in our models, with day and night often significantly differing in presence for a combination of our other factors. This was also found in Germany, where deer show more night activity in places with high human pressure (Coppes *et al.*, 2017). Interestingly, this difference in presence works both ways. It might be somewhat logical that deer spend a larger amount of time on areas which experience a small amount of human presence. However, that deer actively leave the area where they spent the day to move to other areas during the night, significantly lowering the amount of presence in these first areas, is interesting. This shows that not only fear affects deer presence but also foraging qualities. This is in accordance with literature (Charnov, 1976) and suggests night-time compensation for the day-time avoidance, which is so strong that we measure little effect if we don't take diel rhythm into account. We still found a higher presence in the refuge zone when compared to the hunting zone, showing that there is no full compensation for the daytime presence of humans. The importance of diel rhythm is stressed by other studies as well (Lima and Dill, 1990; Kohl *et al.*, 2018).

This same compensation takes place on the heather. We have shown that deer are

significantly more present on the heather during the night. Seeing as visibility and, thus, perceived risk is higher on the heather when compared to the forest, it seems logical that deer avoid the heather during the day, when humans are present. This has been shown in a previous study as well (Benhaïem *et al.*, 2008). Looking at the forest, the opposite pattern is visible. Deer are significantly more present in the forest during the day, showing that they actively switch the forest for heather during the night. This compensation is actually so strong, that we measure no difference between the two habitats if we do not split them for diel rhythm and path distance. That we only measured a significantly higher daytime presence in the forest at 100m could be due to that the areas close to the paths are also largely avoided during daytime in the forest, though not as strongly as on the heather. This avoidance of paths has been shown previously (Coppes *et al.*, 2017; Scholten, Moe and Hegland, 2018).

Whether or not deer are aware of hunting is not something we can give a definitive answer to. Deer do avoid zones in which there is hunting when compared to refuge zones, but not when compared with recreation zones. Due to these having a similar deer presence, with recreation being a bit lower, it is hard to tell whether deer avoid hunting. There is also not a lower presence or higher vigilance in the hunting zone during the hunting season than outside, which one would expect if deer were actually temporally aware of hunting. It could also be that the deer are temporally aware of hunting but that the reaction is so short that we don't measure an effect. This does not mean that there is no overall effect of hunting, as there could still be a higher vigilance throughout the areas and seasons.

All in all, we see much micro-compensation, due to which strong single-factor effects are largely mitigated. However, if the effect of a factor is strong enough, such as the effect of the different zones, this effect cannot fully be alleviated.

Vigilance

We found no differences on a single factor level for vigilance. Previous studies did find an increase in vigilance in zones with human activity and in areas with bad cover, such as heather (Jayakody *et al.*, 2008). Although we did not find an overall effect in our study, we did find a higher vigilance in zones with human activity but only during the day at 20m from the path. As the other study only measured during the day, this might explain the difference with our findings. This again suggests a strong diel compensation, where overall vigilance is strongly alleviated during the night. We did also find an increase of vigilance on heather on 20m outside the hunting season, which corresponds with the previous study. We suggest that we find this effect outside the hunting season due to a higher recreation pressure in this period. This, in turn, might suggest that the amount of human activity has a stronger effect than the type of activity (recreation vs hunting) on fallow deer vigilance.

Most of the increases in vigilance are found solely at 20m from a path during the day. This is expected to be due to the proximity to humans, where risky areas are perceived to be extra risky. Due to this, there is a large difference in risk between 20m and 100m at areas with a high human presence, while in areas with a low human presence this difference in risk is much smaller.

We also found a higher vigilance during the day in both the recreation and hunting zones at 20m. This was in every habitat except for forest in the recreation zone. As these specific areas and times are the places and time where human activity is highest, we conclude that this difference in vigilance is mainly caused by human activity.

When comparing path distances, we obtained mixed results. In general we see a higher vigilance at 20m than at 100m during the day. One surprising result was that there was a higher vigilance at 100m during the day in the forest in the refuge zone. This was hypothesised to be the

place where there was least human activity during the day and as such the safest place to be. This could be because they move to the refuge forest in large numbers, and maintain a large distance from paths but still consider daytime as a risky period, leading to an increased vigilance at the 100m refuge forest. The difference observed could also be due to individual differences between deer. More risk averse deer might all move to the forest in the refuge zone during the day, and stay away from the paths as much as possible, while retaining a high level of vigilance. Less risk averse deer might maintain a lower level of vigilance while staying at 20 meter from the path in the same area. These animal personalities have long been thought to be evolutionary unstable but more recently this theory is increasingly getting attention and now theories have argued that it can be evolutionary viable (Bell, 2007). These differences in personality are mainly studied in birds (Quinn *et al.*, 2012; Cole and Quinn, 2014). However, there is no reason to assume that this mechanism could not take place in ungulates (Bergvall *et al.*, 2011).

Concluding, although we observed some variation in vigilance, we measured no overall increase of vigilance in a single factor. We conclude that this is due to deer avoiding the places where they need to be vigilant and instead select the places where they can maintain a low level of vigilance.

Ecology of fear

Our research has found few large overall effects of human pressure on fallow deer distribution and behaviour. We have shown that micro-scale temporal and spatial compensation cause large overall effects to be largely nullified. This does not disprove the ecology of fear framework though. Instead, it shows that there is a behavioural change in deer due to fear, as these compensations are done to minimize risk while keeping a high foraging efficiency. This is an addition to the optimal foraging theorem, again showing the complexity of natural systems (Charnov, 1976; Searle, Stokes and Gordon, 2008). That this behavioural change does not manifest itself in an increase of fearfulness but rather in a shift of presence to less risky areas is underpinned by a study which incorporated multiple scales to predict habitat selection (Padié *et al.*, 2015). Although we found an effect of fear, we found little evidence for consistent behavioural and distributional change. Due to the deer being able to compensate for temporal and spatial risk variation, the net effect of this can be marginal at best. Although this weakens the possibility of cascading effects taking place, this does not mean that it is impossible. In our study, human presence was both temporally and spatially predictable, creating both spatial and temporal opportunities for the fallow deer to compensate. If risk was constantly higher in a specific area, then this could create cascading effects as fallow deer would be less present in that area. We see an inverse version of this, with such a strong attraction of the refuge zone during the day that this cannot be fully compensated during the night. Also, this only holds for animal-vegetation interactions, as for vegetation temporal differences in browsing matter little. Instead, the total amount of browsing matters. When it comes to animal-animal interactions, micro-scale spatial or temporal behavioural and distributional change in one species might create windows of opportunity for other species to fill this niche. Overall, we found that the relation between the ecology of fear and cascading effects is more complex than often depicted. This does not disapprove either the ecology of fear nor the existence of cascading effects but rather shows that the effects of a change in fear perception are not straightforward and that fear-effects can often largely be compensated for, lowering the opportunities for cascades.

Importance of including multiple variables

The importance of multi-factor analysis has been shown by our research. Without taking into account the interactions between factors, we would have concluded that the ecology of fear theory is bogus, and that fallow deer are not influenced by humans. We would have only found an increase of presence in the refuge area and an increase of presence outside the hunting season, without any changes in vigilance. As such, we would have had to conclude that deer are largely unaffected by human presence, as they do not avoid heather or paths. With the interactions included, the whole view changes, we observe a complexity with many micro-scale interactions, negating large scale effects. Also, without proper understanding of these different factors, one might draw the wrong conclusion from their findings. The importance of using multiple factors when investigating natural systems is stressed by multiple researches (Bonnot *et al.*, 2013; Padié *et al.*, 2015; Moll *et al.*, 2017). Many studies still rely on live observations, which mostly are done during the day (Laundré, Hernández and Altendorf, 2001; Jayakody *et al.*, 2008). If they fail to take into account that behaviour and distribution may be different in the night, these studies might falsely hypothesize cascading effects. Instead, the effects they observe are likely to be mitigated at night. These interactions also highlight the importance of in vivo studies. Without taking a factor into its natural context, it is hard to predict the effects of this factor. This does not mean that experimental and laboratory research have no use. It is valuable to investigate the effects of a factor outside its natural context as well so as to compare it with the effects in its context. This way we can better understand the interactions between factors, which would be hard to grasp without single-factor analysis.

Conservation implications

As we found little differences between inside and outside the hunting season, we hypothesize that hunting itself cannot be used to guide deer behaviour and presence in its current form and in a system with this high deer densities. With higher densities, food availability might be a more limiting factor, which can cause larger compensating behaviour of daytime fear-effects. This, however, does not mean that hunting cannot be used as such. Novel ways of hunting, with as a goal to induce fear, might be more potent in conservation management (Cromsigt *et al.*, 2013). It also appears from our study that fallow deer generally avoid humans rather than make a distinction between hunters and recreationists. This does not prove that there is no effect of hunting. As hunting took place in both areas that we investigated, fallow deer might show stronger human avoidance due to this hunting than in an area without hunting. This would be an interesting follow-up of this research. The current way in which the parks are managed likely causes the chance of spotting deer for visitors to be low (despite high densities). Depending on whether increasing this chance is the goal the park management, they could remove the refuge zones. This would remove a safe place for the deer to stay at during the day, increasing the chance of visitors spotting the deer. Another way to increase this chance, is by decreasing human predictability. Doing night tours through the hunting and recreation zones would likely force the deer to either avoid these zones completely or make less distinction between night and day, likely increasing the day presence of fallow deer in these zones. Another interesting follow-up would be by starting to hunt in the refuge. Although we found little effect of hunting in itself, our hunting always took place in the same zones as recreation. If hunting does have an effect, then by moving hunting to the refuge-zone, one forces the deer to the recreation zones as these would be in fact safer. This would again increase the chance for visitors to spot deer.

Future research

Apart from the above-mentioned recommendations, there are some interesting follow-ups that we would like to suggest. Firstly, instead of using zones as we have done in this study, a future study might incorporate continuous data for both hunting and recreation. In our research, a hunting event might have been closer to a camera in the refuge or recreation zone, than to a camera in the hunting zone. As such, instead of these zones, a distance to the nearest hunting event would likely be a better scale to observe the effects of hunting. The same holds for recreation. There are likely large differences between the intensity of path usage in all zones, including the refuge zone. As it stands now, we took paths as a proxy for this presence and zones as a proxy for intensity. Making this variable continuous, by counting the number of humans using the path for example, would allow one to actually look at the effect of the intensity of human presence.

We found a surprising increase of vigilance in the refuge zone at 100m during the day. We suspect that this might be caused by individual deer personalities. An interesting future continuation of this research, could combine camera data with GPS-collaring deer, hereby combining individual deer movement patterns with detailed information about their behaviour. This would allow us to find new insights in differences between individual deer.

A final interesting continuation of this study would be taking the factors to an even smaller scale. Instead of treating day and night differently, it would be interesting to look at the time it takes for deer to return to a place after a human disturbance. It might be that, instead of hiding in the refuge zone the whole day, fallow deer return close to the path minutes after a disturbance.

Landscape of relaxation

Deer vigilance is highly linked to deer presence. Fallow deer spent more time at places where they need to be less vigilant. During the day, this risk is the main driver for the fallow deer to move towards areas with little human presence. We also explained how this has led to an increase of vigilance in the refuge forest at 100m during the day. During the night, due to the lack of human presence, food availability drives an exodus out of the deep forest and refuge area onto the heather and other areas closer to paths.

We did find little effect of the hunting season on presence, and even a decrease of vigilance outside the hunting area on heather close to paths. As such, we conclude that deer do not seasonally adapt to hunting and rather focus on avoiding humans in general. This does not fully match previous literature, which found that deer become more vigilant and show stronger avoidance towards humans during the hunting season, although these findings are not univocal (Benhaïem *et al.*, 2008; Jayakody *et al.*, 2008; Bonnot *et al.*, 2013). That we do not find such a difference, might be because of the way in which hunting is done in our research area. It is done in a way which avoids deer suffering, so each shot has a large chance to kill a deer. Also, it is done in a way which avoids the creation of an association between humans and hunting, as the park management does not want to increase human avoidance in the deer.

All in all, fallow deer spatially and temporally avoid human activity, considering humans risky. This does not affect overall deer distribution, as fallow deer manage to largely compensate their avoidance by moving to areas which were avoided during periods with low human activity. This results in strong diel patterns. Due to the ability to avoid dangerous places in dangerous times, there is little effect on vigilance. By altering their distribution to minimize the overlap with humans, fallow deer essentially create a landscape of relaxation instead of a landscape of fear.

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Appendices

Appendix A: Behaviour scoring protocol

BEHAVIOUR PROTOCOL - CAMERA TRAP DATA BEHAVIOURAL ANALYSIS

Program

Behavioural Observation Research Interactive Software (BORIS).

Scoring Order

When scoring a video, firstly the subject is defined (see list of subjects below) by pressing the corresponding key. At this point, the focal subject is set. After this, the parameters for the background information (except for the number of individuals) are set by pressing their corresponding keys. After this, the behaviour of the focal subject is scored on the behaviours found below. To start scoring this behaviour, press it's corresponding key. Once the focal subject finishes the behaviour, either press this key again to stop scoring this behaviour or press the key of another type of behaviour to automatically stop the first type of behaviour. Just before the end of the video, when the number of individuals does not increase anymore, this parameter has to be scored as well. Each video is 15 to 60 seconds long, and even if the same subject remains in the next video, each of the background parameters needs to be set again. One does not need to redefine the focal subject, unless a different type of subject needs to be assessed.

Creating an ethogram

File > New Project > Ethogram

For each behaviour, one can assign a specific key. Furthermore behaviours can be excluded by each other with the exclusion matrix, so when pressing the key of another type of behaviour the program automatically stops scoring the first behaviour.

Behaviors exclusion matrix

Check behaviors excluded by

	Browsing Other	Scratching	Browsing Tree	Running	Vigilant
Looking into camera	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Walking	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Browsing Other		<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Scratching	<input checked="" type="checkbox"/>		<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Browsing Tree	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>		<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
Running	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>		<input checked="" type="checkbox"/>
Vigilant	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	

Also parameters can be extended with modifiers. An example:

Set modifiers for "Dag/Nacht" behavior

Modifier

Key code

Key code is case insensitive. Type one character or a function key (F1, F2... F12)

Set #1

Set name

Day/Night

Modifier type

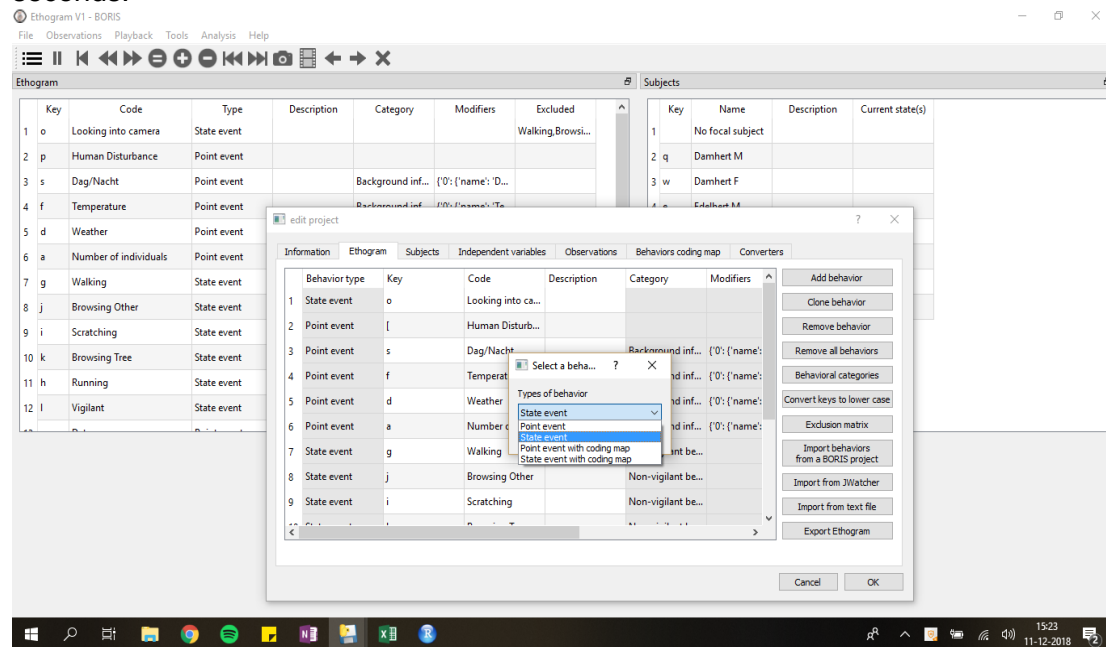
Multiple selection

Values

Day (1)

Night (2)

Lastly, the behaviour can be set as an point event and state event. A point event records an event at a single time-point. This is used to indicate a single, instant event. A state event is used to record a behaviour which last longer than an instant. It is used to score behaviours such as browsing and vigilance, as these behaviours often last for several seconds.



Background information

No. of individuals:

How many individuals are there present in the video?

Best scored in the end of the video, as more animals can enter the video later on.

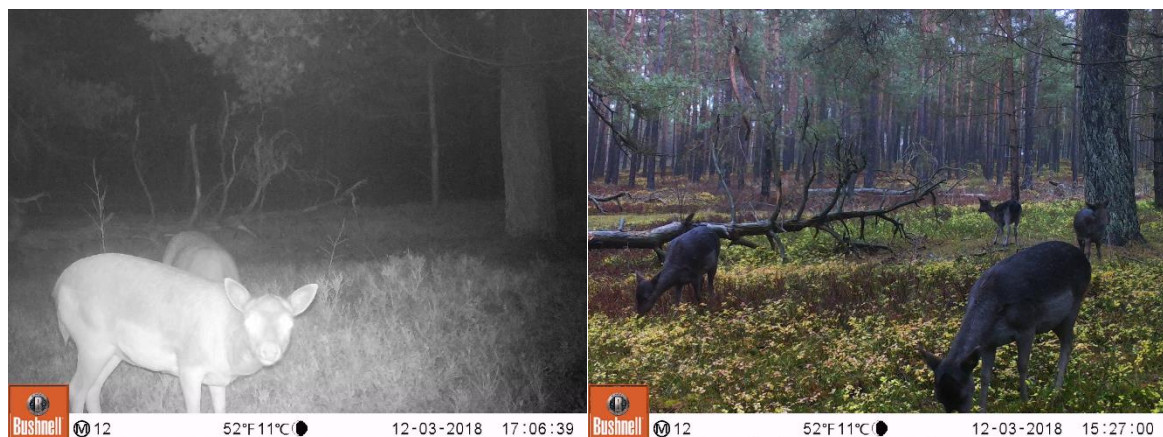
→ point event, modifiers set as numeric.

Day/Night

Is the video made in day mode or in night mode?

Best scored in the beginning of the video.

→ point event, modifiers set with multiple selection (Day (1), Night (2)).



Temperature

What is the temperature the video information bar shows?

Best scored in the beginning of the video.

→ point event, modifiers set as numeric.



Weather

How is the weather on the video?

Best scored in the beginning of the video. However, when unknown (e.g. in night mode) leave it empty.

→ point event, modifiers set with multiple selection (Rain (1), Cloudy (2), Clear (3), Snow (4)).

Vigilant behaviour

Auditory vigilance (induced vigilance)

Is the animal showing vigilant behaviour?

Scored when the animal has the head above the shoulder and is not chewing (first the animal freezes then it starts scanning) → *induced vigilance*.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour → *meaning that this behaviour is stopped when other behaviour is started by pressing that particular button*

Visitory vigilance (routine vigilance)

Is the animal showing vigilant behaviour?

Scored when the animal has the head above the shoulder and is chewing (first the animal freezes then it starts scanning) → *routine vigilance*.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour → *meaning that this behaviour is stopped when other behaviour is started by pressing that particular button*

Unknown vigilance

Is the animal showing vigilant behaviour?

Scored when the animal has the head above the shoulder, but it is unknown if the animal is chewing or not (first the animal freezes then it starts scanning).

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour → *meaning that this behaviour is stopped when other behaviour is started by pressing that particular button*

Running

Is the animal running?

Scored when the animal is moving fast on foot, by taking quick steps in which each hoof is lifted before the next hoof touches the ground.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour.

Looking into the camera

Is the animal looking into the camera?

Scored when the animal seems to see the camera, looks right into the camera.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour.

Non-vigilant behaviour

Walking

Is the animal walking?

Scored when the animal is moving while allowing each hoof to touch the ground before lifting the next.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour.

Browsing Tree

Is the animal browsing one of the two trees that were planted for previous research?

Scored when the animal is eating from or browsing through one of the two trees.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour.

Browsing Other

Is the animal browsing any vegetation other than the planted trees?

Scored when the animal is eating from or browsing through vegetation other than the trees mentioned previously.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour.

Scratching

Is the animal scratching its own body with one of its legs or with its mouth?

Scored when the animal is scratching itself.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour.

Sitting

Is the animal sitting on the ground?

Scored when the animal's belly touches the ground and its hoofs are tucked in beneath itself.

→ state event, exclusion matrix with all the other variables from vigilant behaviour and non-vigilant behaviour, except for looking into the camera.

Human disturbance

When a video contains one or multiple human persons, score this as human disturbance. This might influence the following videos.

→ point event.

Creating subjects

File > New Project > Subjects

For each subject, one can assign a specific key.

Human

Homo sapiens

Red deer

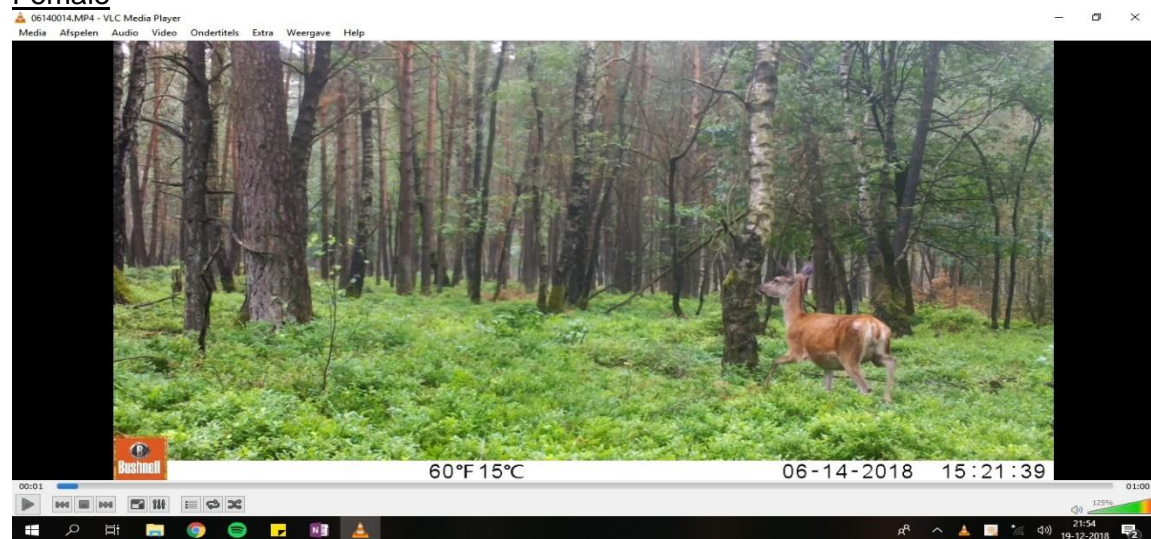


Cervus elaphus (red-brown)

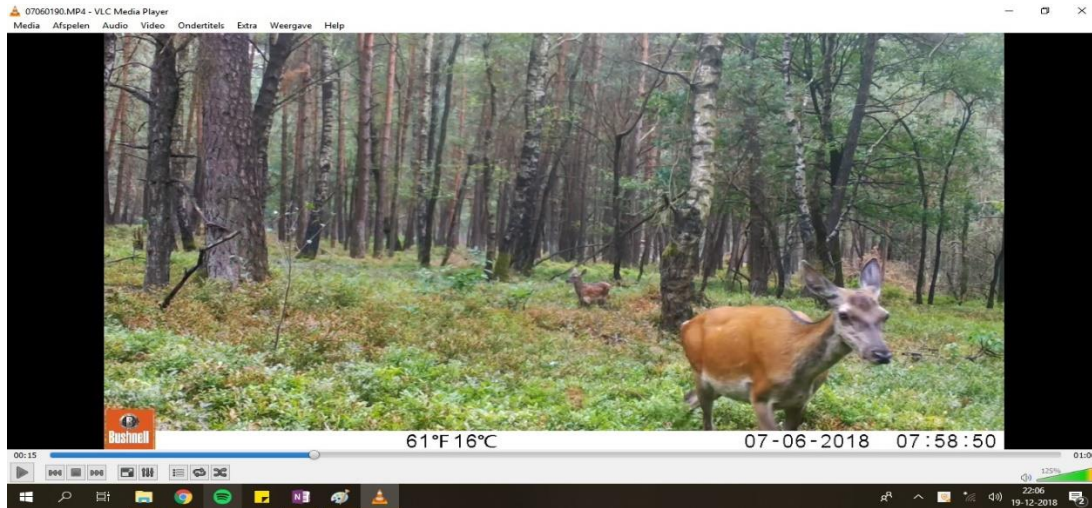
Male

- Shoulder height of 140cm.
- Loses the antler in march, new antler is full-grown in july.

Female

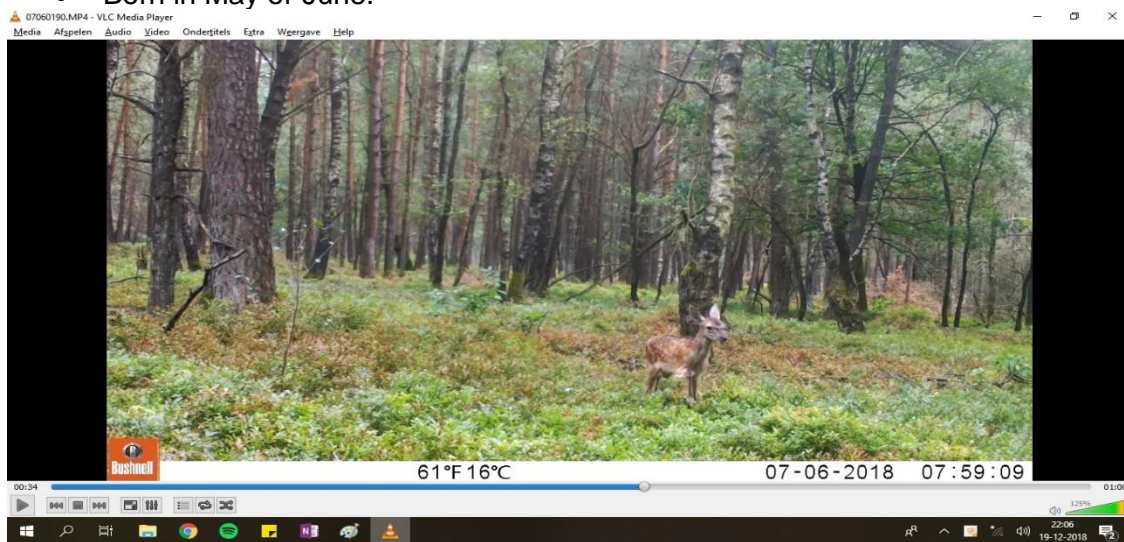


Female with calf



Calf

- Born in May or June.



Fallow deer




Dama dama (brown with white dots or black)

Male

- Shoulder height of 75cm till 100 cm.
- Loses the antler in april, new antler is full-grown in august.

Female



60°F 15°C 

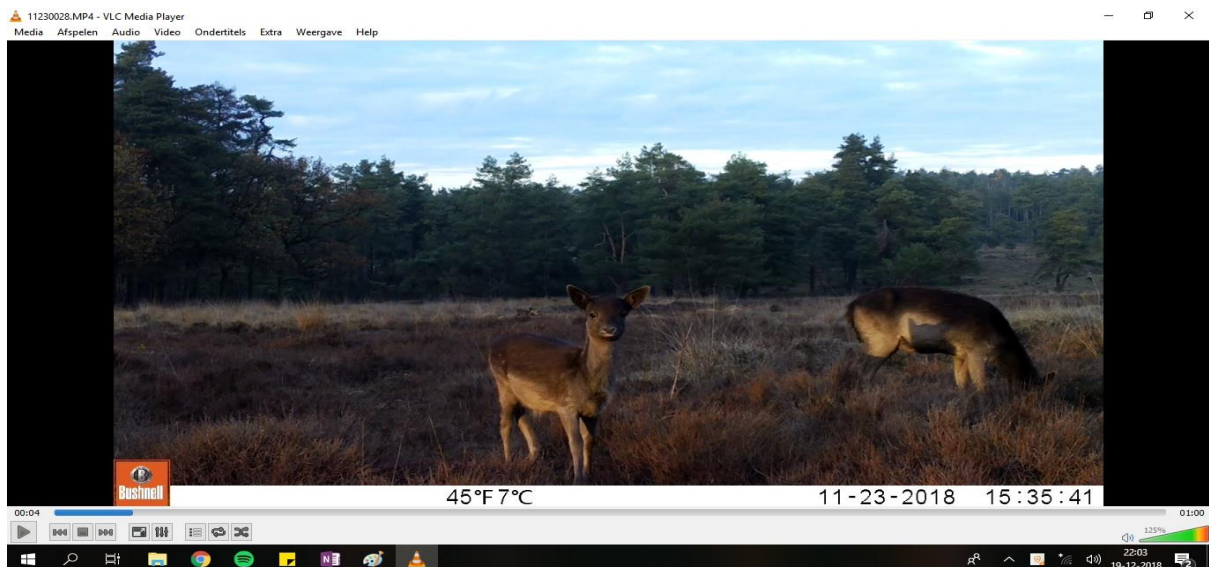
05-19-2018 11:58:44

Female with calf



Calf

- Born in May or June.



Unknown deer

When it is difficult to see if the deer is a Fallow or a Red deer, score this as unknown.

Creating independent variables

File > New Project > Independent variables

Where?

Area

Veluwezoom, Deelerwoud.

Zone

Hunting, refuge, recreation.

Vegetation

Forest, heather.

Plotnr	Forest/Heather	Refuge/Recreation/Hunting	Deelerwoud/Veluwezoo
9	Heather	Recreation	Deelerwoud
10	Heather	Recreation	Deelerwoud
16	Forest	Recreation	Deelerwoud
18	Forest	Recreation	Deelerwoud
20	Forest	Hunting	Deelerwoud
24	Heather	Recreation	Deelerwoud
26	Heather	Recreation	Deelerwoud
28	Heather	Hunting	Deelerwoud
31	Heather	Hunting	Deelerwoud
32	Heather	Hunting	Deelerwoud
33	Heather	Recreation	Deelerwoud
34	Heather	Recreation	Deelerwoud
38	Forest	Refuge	Deelerwoud
39	Forest	Refuge	Deelerwoud
40	Forest	Refuge	Deelerwoud
43	Forest	Hunting	Deelerwoud
44	Forest	Hunting	Deelerwoud
45	Forest	Recreation	Deelerwoud
46	Forest	Recreation	Deelerwoud
48	Heather	Recreation	Deelerwoud
56	Forest	Refuge	Deelerwoud
59	Forest	Refuge	Deelerwoud
60	Forest	Refuge	Deelerwoud
63	Forest	Hunting	Veluwezoom
64	Forest	Hunting	Veluwezoom
69	Heather	Hunting	Veluwezoom
70	Heather	Hunting	Veluwezoom
70	Heather	Hunting	Veluwezoom
71	Forest	Hunting	Veluwezoom
72	Forest	Hunting	Veluwezoom
75	Forest	Recreation	Veluwezoom
78	Forest	Recreation	Veluwezoom
81	Forest	Recreation	Veluwezoom
82	Forest	Recreation	Veluwezoom
97	Heather	Recreation	Deelerwoud
98	Heather	Recreation	Deelerwoud
99	Heather	Hunting	Deelerwoud
100	Heather	Hunting	Deelerwoud
102	Forest	Hunting	Deelerwoud
108	Heather	Hunting	Veluwezoom
109	Heather	Hunting	Veluwezoom
110	Heather	Hunting	Veluwezoom
123	Forest	Hunting	Veluwezoom
124	Forest	Hunting	Veluwezoom
131	Heather	Refuge	Deelerwoud
132	Heather	Refuge	Deelerwoud

When?

What is the season? Is it hunting-season or not?

The videos made before October 2018 are in the non-hunting season. The ones made after this month are in the hunting season.

Notes

- If several deer are present: only score the adult individual who's first present video, if more than one deer is present at onset, score the centremost one.
- Ignore empty videos if there is still no animal present after 15 sec.
→ however, sound on! If you hear an animal, watch the video till the end, because the animal might come in front of the camera.
- When animal leaves the screen, stop scoring (so one more time push the button, e.g. STOP walking).

Comparing observers

We compared the results of scoring one hour of film from one camera between two observers. The values in this table are the total seconds the subjects spent on different actions per observer.

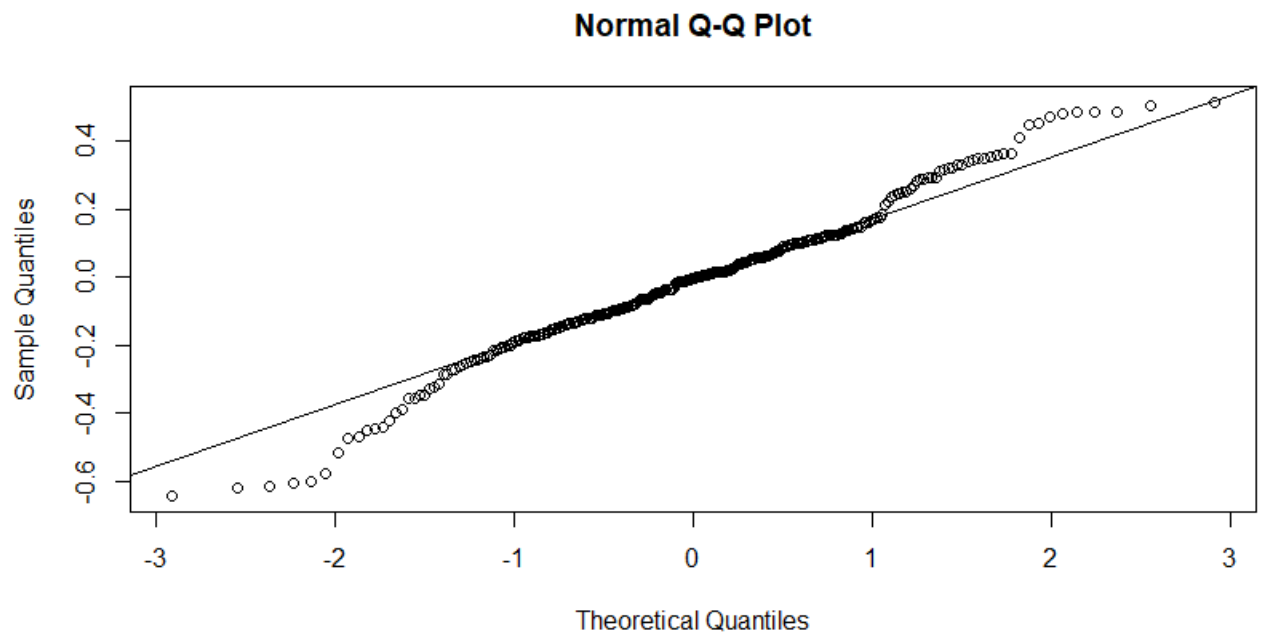
Subject	Action	Observer 1	Observer 2
Damhert F	Walking	241.755	204.977
Damhert M	Walking	8.743	25.472
Edelhert F	Walking	59.759	129.396
Edelhert M	Walking	7.498	4.771
Damhert Met jong	Walking	10.104	9.711
Edelhert Met jong	Walking	18.51	13.445
Damhert F	Running	5.377	13.781
Damhert M	Running	0	0.496
Edelhert F	Running	1.712	1.744
Edelhert M	Running	2.042	1.749
Damhert Met jong	Running	6.998	4.753
Edelhert Met jong	Running	1.543	2.441
Damhert F	Vigilant	212.241	116.019
Damhert M	Vigilant	3.5	55.478
Edelhert F	Vigilant	23.995	39.619
Edelhert M	Vigilant	0	0
Damhert Met jong	Vigilant	4.498	6.249
Edelhert Met jong	Vigilant	0	0
Damhert F	Browsing Other	856.897	600.472
Damhert M	Browsing Other	62.076	111.618
Edelhert F	Browsing Other	94.688	100.161
Edelhert M	Browsing Other	0	0
Damhert Met jong	Browsing Other	0	0
Edelhert Met jong	Browsing Other	0	0
Damhert F	Browsing Tree	74.714	70.599
Damhert M	Browsing Tree	0	29.233
Edelhert F	Browsing Tree	24.655	23.28
Edelhert M	Browsing Tree	0	0
Damhert Met jong	Browsing Tree	0	0
Edelhert Met jong	Browsing Tree	0	0
Damhert F	Scratching	33.094	303.742
Damhert M	Scratching	0	22.495
Edelhert F	Scratching	0	5.2
Edelhert M	Scratching	0	0
Damhert Met jong	Scratching	0	0
Edelhert Met jong	Scratching	0	0

With a Wilcoxon matched pairs test the results between the two observers was compared, to see if there is any significant difference.

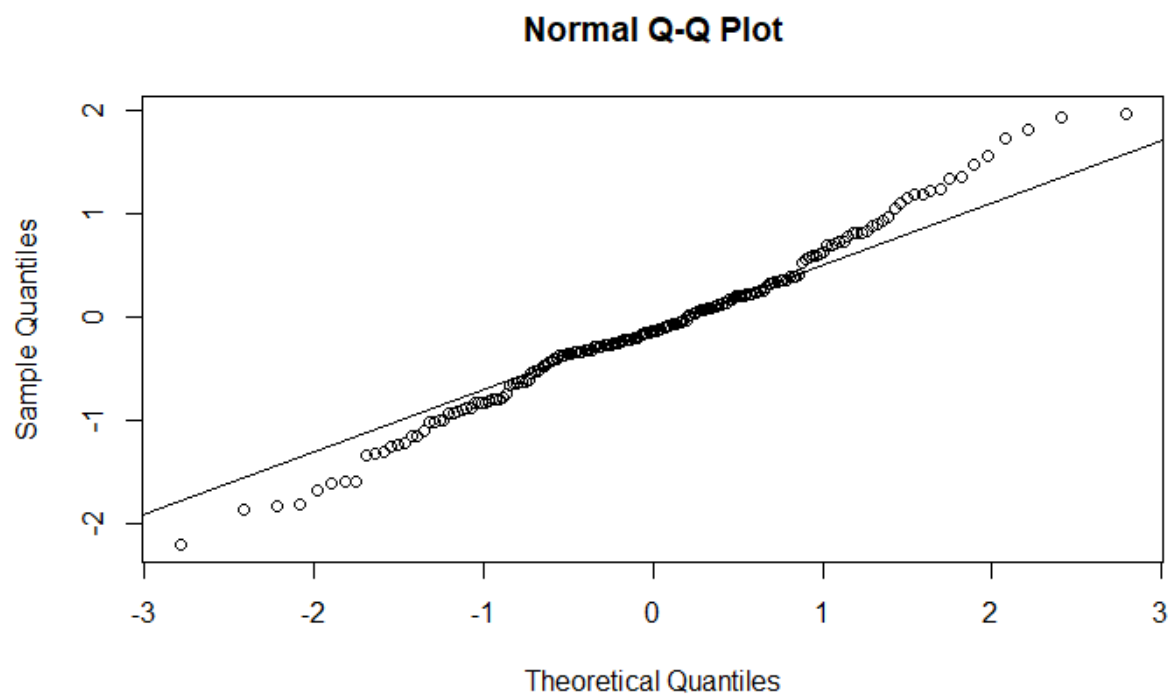
```
wilcoxon signed rank test  
data: d2$observer.1 and d2$observer.2  
V = 98, p-value = 0.5621  
alternative hypothesis: true location shift is not equal to 0
```

The p-value is 0.5621, so there is not significant difference between the two observers. This shows that this protocol of scoring in BORIS gives results independent of the observer for different videos.

Appendix B: QQ-plot fallow deer presence



QQ-plot of the best model predicting fallow deer presence.



QQ-plot of the best model predicting fallow deer vigilance