What makes an ecosystem tick?

Indirect effects on ticks and dung beetles of altered ungulate behavior from human disturbance around hiking tracks in a landscape of fear.

Joseph Eric Churchill, s3788849

Primary supervisor: Chris Smit

Daily supervisor: Bjorn Mols

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Abstract

Predators are essential in regulating deer habitat-use and space movement. This can cause deer to avoid areas they perceive as more dangerous than others to avoid predation. This has the potential to cause indirect effects on lower trophic levels. In human dominated landscapes it is known that humans can replace the non-lethal effects of predators by triggering fear responses in deer. However, it is unclear if other species are affected by fear responses seen in deer. We investigated two invertebrate species as biological indicators to assess the extent of indirect behavioural mediated effects. We used a forest which had hiking tracks of both high and low levels of human activity. We investigated deer droppings across 150m transects at 20m and 100m into the forest from a hiking track of high and low human activity, as a proxy of deer space use. We then tested the differences of tick and dung beetle abundances at 20m and 100m into the forest from the same hiking tracks. Alongside this, dung removal experiments were placed on the same transects as a proxy of nutrient cycling. We found more deer droppings and more ticks in areas of low human activity. Whilst beetles and dung removal rates were unaffected. Our results suggest human activity causes an avoidance behaviour in deer, and this avoidance behaviour causes a decrease in tick abundance. The consequences of this inter-trophic link is important as it has implications into conservation management and Lyme disease prevalence, which will allow better management of our wildlife, public safety and disease control in forested areas.

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Introduction

It is crucial in conservation to understand the effects of human disturbance on our ecosystems to develop and practice effective management. The Anthropocene has had and is continuing to have a destructive global scale effect on our wildlife and ecosystems (Tilman and Lehman, 2001; Tabarelli, Da Silva and Gascon, 2004; Tuomainen and Candolin, 2011). But what is less-well documented are the smaller impacts and the effects that low levels of human activity has on our wildlife and ecosystems.

Human activity is widely accepted to have a wide scope of direct and indirect effects on organisms on lower trophic levels (Azlan, 2006; Kuijper *et al.,* 2016; Mohd-Azlan, Kaicheen, and Yoong, 2018). Indirect effects offer more subtle changes to our ecosystems because most direct effects are associated with destruction, removal or degradation of whole systems. The first study of these subtle indirect effects was by Walther (1969) who found that humans could cause indirect fear responses in Thomson's gazelles (*Eudorcas thomsonii)*; he did this by recording their behaviour when he approached them by vehicle or on foot under different circumstances. This phenomena later became known as the "landscape of fear", which was first described in the reintroduction of gray wolves (*Lupus lupus)* to Yellowstone National Park in the 1980s (Brown, Laundré and Gurung, 1999). We now know that human presence causes fear responses in many large herbivores, strong enough to cause changes in their grazing, vigilance and space-use behaviour (Frid and Dill, 2002; Stankowich, 2008; Krishna, Kumar and Isvaran, 2016). This interaction causes further effects on species of lower trophic levels and ecosystem functioning, which is known as trophic cascade effects (Hebblewhite *et al.,* 2005; Laundré *et al.,* 2010; Stark, Männistö and Smolander, 2010).

A clear example of a cascading effect through the landscape of fear can be found in a study in the Białostocka Czarna region in Poland. This study looked at ungulate browsing on European oak (*Quercus robur)* saplings in forested areas at different distances away from roads and found; ungulates spent less time closer to roads because of human activity and found more undamaged oak tree saplings closer to roads as a result of reduced browsing (Mathisen, Adam and Zbigniew, 2018). The strength of a cascade effect of this nature is widely accepted to be mediated by a trade-off between resource quality and predation risk (Wright, 1983; Schmitz, Krivan and Ovadia, 2004; Dupke *et al.,* 2017). This is an indirect non-lethal effect where deer avoid areas that they associate with greater predator danger, even if richer resources are available. This is a key reason why cascade effects from humans to ungulates have varying impacts and a different range of effects (Kays *et al.,* 2017).

Biological indicator species are useful in assessing cascade effects as they can reveal biological patterns which are indicative of a cascading effect (Carignan and Villard, 2002). For example, measuring different sized algal blooms in waterbodies caused by different levels of Nitrogen pollution can be used to assess the impact on ecosystem processes below the surface, which inevitably impacts other species (Clark *et al.,* 2017). One biological indicator species used in our study is sheep ticks (*Ixodes ricinus).* These are the most common hard tick in Europe and are important in many temperate ecosystems (McGeoch, 1998). One reason for this is that they are the main vector of the bacteria which causes Lyme disease (*Borrelia* *burgdorferi)*. Ticks have 3 hosts in their life cycles but require large bodied hosts for reproduction, so larger hosts like deer and sheep are considered essential in the tick life cycle (Bishopp and Trembley 1945; Hoogstraal, Trapido, and Kohls, 1965; Gray, 1998). It is widely accepted that tick survival is dictated by climate, host space-use, host availability and vegetation structure (Ostfeld *et al.,* 1995; Steigedal *et al.,* 2013). This is what makes them a useful indicator species, as patterns in their distribution can be attributed to one of these influencing factors and then investigated to narrow down the potential causes.

Literature is clear that tick numbers decrease when their hosts are removed from an area (Gray *et al.,* 1992; Gilbert *et al.,* 2012), but it is unclear if different densities of hosts causes different densities of ticks (Perkins *et al.,* 2005; Hofmeester *et al.,* 2017). Rand *et al* (2003) showed that ticks and white-tailed deer (*Odocoileus virginianus)* correlated over a gradient of abundance, finding that tick numbers increased exponentially up to 40 deer per km^2 and found significantly less ticks below 10 deer per km^2. This gives a potential threshold for tick densities, however other factors like vegetation, scale and alternative hosts varied when compared to other studies which concluded there was weak evidence for a correlative relationship between ticks and herbivore hosts (Perkins *et al.,* 2005; Hofmeester *et al.,* 2017). Yet, thus far it is unclear how spatial scale, the incidence of alternative hosts and vegetation can influence the gradients of tick and deer association.

Dung beetles are also well-known biological indicators because of their roles in nutrient cycling by dispersing and burying dung (Spector, 2006; Tixier, Bloor and Lumaret, 2015). Investigating dung removal rates is commonly conducted alongside pitfall trapping to confirm the link between nutrient cycling and dung beetle abundance (Gollan *et al.,* 2013). Herbivores and dung beetles are explicitly linked as beetles rely on dung for feeding, shelter and reproduction. It is therefore a reasonable assumption that the presence or absence of deer will affect patterns in dung beetle distribution and nutrient cycling. One study by Lumaret, Kadiri and Bertrand (1992) found an extreme effect of introducing red deer (*Cervus elaphus)* to a forest patch; it gave dung beetle abundance a three-fold increase and boosted diversity from 38 to 42 different dung beetle species in just 5 years. This study did not assess deer and beetles over a gradient of abundance, nor did it investigate the effects on nutrient cycling, but this study illustrates the influence that deer are able to have on dung beetles. Dramatic changes like these are likely to cause farther reaching effects on nutrient cycling and other biological patterns. One study where this gradient was examined by Iida *et al.* (2016a) found a mixed species response amongst dung beetles. In high densities of deer, larger beetle species were more abundant and in lower densities of deer, smaller species were more abundant, although there were no changes in overall abundance on dung beetles, measured in this case in biomass (mg). However, the link of human influence on deer and to nutrient cycling in this study is still lacking. Studies which consider a three link interaction from humans to deer to dung beetles and consider nutrient cycling are rare (Raine and Slade, 2019). To our knowledge, no study considers all these factors simultaneously.

The aim of this study was to assess if high human activity on hiking tracks could cause a behavioural shift in deer, which in-turn could cause an indirect effect on ticks, dung beetles and dung removal rates. Our expectations are to find less deer droppings around tracks of high human activtiy, and less deer droppings at 20m away from these tracks compared to 100m away. We expect to find less ticks and less dung beetles in the same areas as a negative correlative relationship with deer droppings. As an extension of reduced dung beetle abundances we also expect to find lower dung removal rates in the same areas.

Methods

Study sites

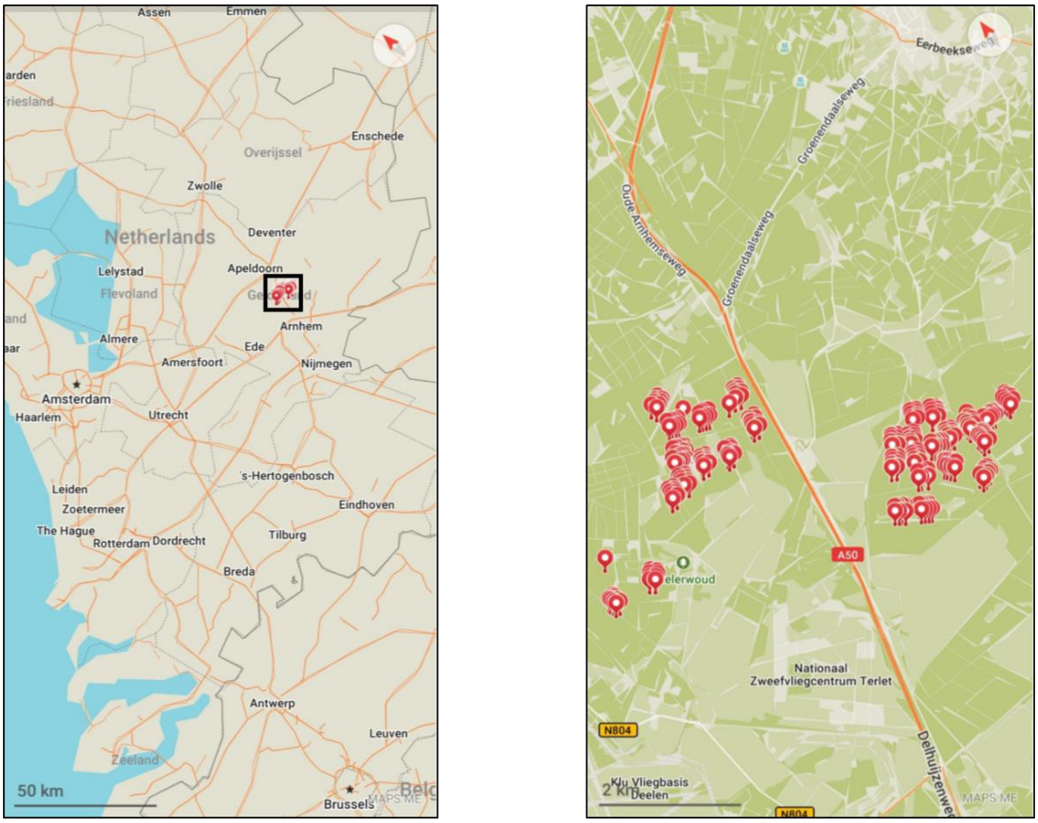


Figure 1 shows a map of the Netherlands (left) with our forest highlighted in the black box (left). The right hand photo shows two clusters of datapoints; the left cluster is the Deelerwoud forest and the right cluster in the Veluwezoom forest.

Our study was conducted across two areas of the Veluwe forest in the central Netherlands (52.2388°N, 5.8323°E); the Deelerwoud (DW) and the Veluwezoom (VZ), located ~40km from the west-German border. The Deelerwoud is 1230ha in size and the Veluwezoom is 5000ha. The two areas are separated by a busy highway but are connected by an eco-bridge which allows movement between areas. Both areas have coniferous, deciduous and heather areas, but our transects are in coniferous forest, dominated by Scots pine (*Pinus sylvestris)* with sparsely scattered European beech (*Fagus sylvaticus)* and silver birch (*Betula pendula)*, whilst the understory is homogenously dominated by wild bilberry (*Vaccinium myrtillus)*. Both areas are managed by Natuurmonumenten and are accessible to cyclers and hikers, but not by vehicle, except for park managers. Both sites have restricted areas which act as refuges for wildlife, giving them naturally higher abundances of red (*Cervus elaphus)* and fallow deer (*Dama dama)*, combined at ~35 individuals per km^2 (Natuurmonumenten, 2018, *unpublished data*). The Veluwezoom is thought to have slightly lower abundances of deer than the Deelerwoud (Natuuromonumenten, 2018, *unpublished data*). Our transects on hiking tracks coincide with designated hunting zones which are active between 1st August and 15th February depending on the species; these are focused on red deer, fallow deer, and wild boar (*Sus scrofa)*. The only other large herbivores present are small populations of roe deer (*Capreolus capreolus)* and Highland cattle (*Bos taurus)* which are not hunted.

Study design

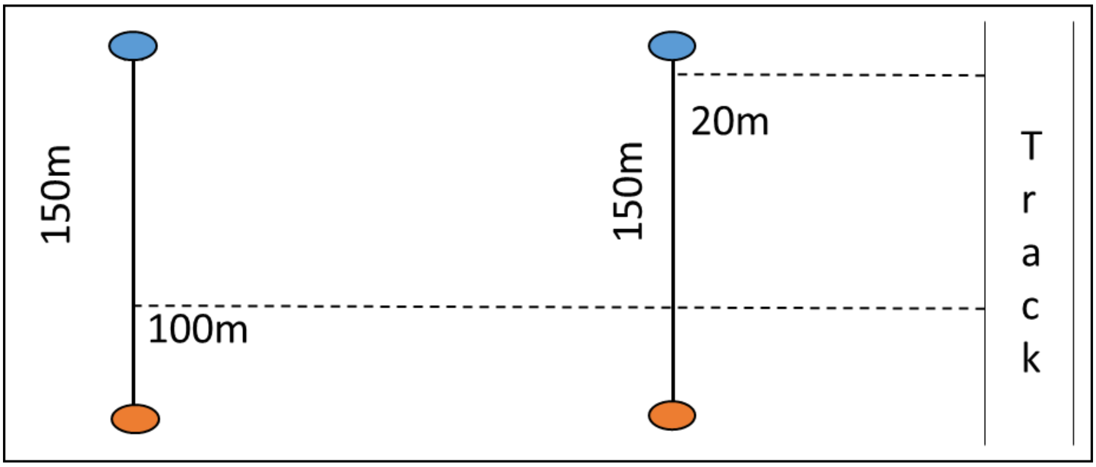


Figure 2 Shows the layout of each plot with 150m transects which are 20m and 100m away from a hiking track. The blue represents the pitfall traps and the orange represents the decomposition experiments. These were only placed at sites after tick, vegetation and dung event recordings had taken place.

Our study design involved transects at 20m and 100m away from hiking tracks in areas of high and low human activity. Levels of ´high´ and ´low´ use were determined using Strava heat map data (*see appendix supp. Fig.7).* Plots were measured with a tape measure up to 150m per plot. All data was collected at the same plots but ticks, vegetation and deer droppings were sampled before dung beetles and dung removal rates to avoid interference. After one week, pitfall traps and dung removal experiments (Fig.3) were placed to sample dung beetles and dung removal rate data. Pitfall traps and experiments were kept 150m apart (one at each end) to avoid interference. Each plot was at least 100m away from the next plot and at least 100m away from the nearest hiking track and were always at least 200m away from a forest edge.

Deer droppings and vegetation

Deer droppings were recorded at 62 paired plots, 31 plots evenly split between 20m and 100m away. Droppings were used as a proxy to represent deer space use (Ellis and Bernard, 2005; Alves *et al.,* 2013; Franca *et al.,* 2016). Droppings were observed over the 150m transect by scanning a meter either side of the tape measure for deer droppings by 2 people. If the observers who scanned for droppings changed, it was paired to ensure the same observers had scanned an equal number of plots to minimize observer bias. Dropping events were recorded when either whole piles or individual droppings were found. Each event was decided if piles and/or droppings belonged to the same individual based on size, shape, age and location. Vegetation was measured using the disk (40cm radius) and stick (1m) method over the same 62 plots as deer droppings (Stewart, Bourn and Thomas, 2001). This was because vegetation height is important in tick questing behaviour and abundance (Steigedal *et al.,* 2013). The vegetation was recorded from the height given at the top of the stick and was recorded every 1m over a 50m transect and then averaged.

Tick abundance

The same 62 paired plots were sampled for tick abundance between April – May 2019. Tick sampling was only conducted on dry days on dry vegetation, when the air temperature was 10 degrees Celsius or above as conditions below this range has been shown to significantly reduce tick questing behavior (Mejlon and Jaenson, 1997; Vail and Smith, 1998; Alonso-Carné *et al.,* 2016). All plots were sampled for ticks by dragging a 1m^2 white cotton cloth, attached to a bamboo pole and string through 50m long transects at 20m and 100m away from the hiking track (Vassallo *et al.,* 2002; Steigedal *et al*., 2013). Ticks were removed, counted and classified as either an adult or nymph after every 5m of dragging, ticks were then flicked off behind or to the side of the cloth to avoid re-attaching (Tack *et al.,* 2011). We assumed all ticks collected were of the species *Ixodes ricinus* based on previous findings in the Netherlands (Hofmeester *et al.,* 2017; Takken *et al.,* 2017). Larvae were ignored because of their extremely high abundance and clustered occurrence which gave them a disproportionate distribution across plots and difficulty to count accurately. Larvae are also not carriers of the Lyme disease bacteria.

Dung beetle abundance and dung removal rates

Figure 3 - pictured left is the dung removal rate experiment set-up and pictured right is the pitfall trap used to collect dung beetles.

Dung beetles were collected using 16 non-lethal pitfall traps (Fig. 3). Pitfall traps were made of a 20cm width x 14cm depth metal bucket and wrapped in wire fencing with holes that were 5cm wide, to avoid accidental by-catch of amphibians, reptiles and small mammals. Dung was suspended from the bucket handle in a small plastic bag which had 25 holes poked into it on both sides of the bag to aid the diffusion of the dungs smell. A plastic plate was used as shelter which was held in place by 4 sharpened sticks which were piled into the ground. Wooden pegs were used to steady the bucket handle from which the dung was suspended. The top of the container was made sure to be level with the ground to make falling into the trap easier for investigating beetles. The dung was replaced once with new dung of the same criteria as the original bait, when beetles were collected after 5 days. This was conducted in the Deelerwoud between the 4th June 2019 – 13th June 2019 (9 days) and the Veluwezoom between the 5th June 2019 – 14th June 2019 (9 days), with traps being emptied every 5 days. Any by-catch was released alive and dung beetles were counted, then removed from the field for species classification. This also prevented re-capturing individuals. Every trap was placed no more than 1m away from the nearest tree with canopy openness approximately similar where each trap was set (da Silva *et al.,* 2019).

Dung removal rates were investigated by setting out 28 paired decomposition experiments (Fig. 3). This was conducted on the Deelerwoud with 14 set-ups between 30th May 2019 – 13th June 2019 (14 days) and on the Veluwezoom with 14 set-ups from 5th June 2019 – 12th June 2019 (7 days). The data was converted using the equation *(control dung dry weight – exposed dung dry weight / exposure time = dung removal rate per day)*. Each trap consisted of an equally cut white cotton cloth (~60cmx60cm) and was baited with 100g fresh homogenised red and fallow deer dung. Some small beetles remained in the dung at the start of the experiment as it was not frozen prior to trap setting (O'hea, Kirwan and Finn, 2010). The dung was homogenized, making any small beetles left inside the dung spread across plots to control for bias (Horgan, 2005). Dung removal experiments (Fig.3) were set at 20m and 100m away from hiking tracks. All experiments were placed approximately in the same canopy openness and tree density conditions to reduce variation between plots (da Silva *et al.* 2019). Both were placed at least 1m from the nearest tree and always set up in bilberry cover. One set-up at each distance was accessible to all dung beetles and another covered by a metal cage with holes of 3mm diameter, to allow sun exposure and to exclude larger dung beetles. This did not exclude beetles <3mm from the control cages. After the set time periods, all dung was labelled and collected, then transported to the University of Groningen where the dung was dried at 60 degrees Celsius for 48 hours and weighed to obtain dry weight (g).

Statistical analysis

All statistical analyses were conducted in Rstudio 3.4.3. Boxplots were made to assess the relationship between droppings over the interaction of zone (high vs low human activity) and distance from tracks (20m-100m). Deer dropping data was tested for normality using histograms and the shapiro-wilks test. It showed a poisson distribution so initially these were placed into glmer models with a poisson distribution. However, these models returned convergence and overfitting errors, so were converted and instead placed in lmer models, (Bates, 2005; Stroup, 2012). The deer dropping data was log converted to achieve normal distribution for linear mixed effect models. Pearson's correlation coefficient was then carried out with deer droppings and vegetation, dung removal rates and dung beetle abundance to assess if our variables influenced finding deer droppings.

We made 3 different linear mixed multiple effect models for each response variable of interest (Tab.1). These models used the predictors; zones (low *vs* high human activity) and distance (20m *vs* 100m) with plotID and vegetation height (cm) as random factors. The lowest AIC score was used to determine the model of best fit for the data from the 3 models (Tab.1) and then the qqplots were plotted to assess margins of error (*see appendix supp. Fig.1-6)*. If other models were within 2 AIC points of the best model, these were also checked for significances (*see appendix supp. Tab.1-5*) (Arnold, 2010). Significances in the model (if any) were followed-up with a post-hoc analysis using the 'lsmeans' function with a Tukey test to pinpoint significance in the data. The 'lsmeans' function works by comparing the means of the subgroups of interactions specified by the model. A qqplot was then made of the residuals of the model of best fit to determine the margins of error and overall reliability of the model.

The total number of ticks were analysed first and then nymphs and adults were analysed afterwards separately. The normality of these variables were tested (poisson distribution) and placed in glmer models initially. However, when converted to multivariate normality and placed in lmer's, these fit the data better so were selected over glmer models (Bates, 2005; Stroup, 2012). Tick total and adults were cube converted and nymphs were log10 link converted. Pearson's correlation coefficient was carried out on nymphs, adults and total number of ticks with dropping counts and vegetation height; this will indicate if ticks are influenced by deer movement and if vegetation height influences tick distribution. Appropriate predictors in our models included distance and zone (with interactions) and random factors included vegetation and PlotID. PlotID was used instead of area (VZ/DW) as a random factor as plotID accounts for more of the variation, including the variation between areas. Tick total, nymphs and adults were tested separately in 3 different models, giving 9 models in total. Then, the models were compared using their AIC scores to determine the best fit, with the lowest AIC being the best fit. Models within 2 AIC points of the lowest scoring model were also checked for significances (Arnold, 2010). When the best model was selected and if a significance was found, a post-hoc analysis was conducted using the ‘lsmeans’ function. The residuals of the best model were then plotted in a qqplot to determine acceptable margins of error and overall reliability of our model (*see appendix supp. Fig.1-6)*.

Dung beetle abundances were log converted and placed in 3 different linear mixed effect models (Tab.4). A Pearson’s correlation coefficient was conducted between beetle abundance and dung removal rates as more beetles may indicate higher removal rates. Using appropriately selected variables these were then placed in 3 different linear mixed effect models (lmer’s), giving 6 models in total. Different models were built using the predictor variables; zone and distance, with plotID and deer droppings as random factors. The AIC score was then determined for the model of best fit. Models within 2 AIC points were also checked for significance (*see appendix supp. Tab.1-5)* (Arnold, 2010). This was followed by post-hoc analysis with the ‘lsmeans’ function in a Tukey test. The residuals of the best model were then plotted to determine the acceptable margins of error and overall reliability (*see appendix, supp. Fig.1-6).*

Results

Deer droppings and vegetation

Table 1 Shows the formula’s of the lmer models from analysing deer space movement (droppings). The lowest AIC is highlighted in bold. Zo = Zone, Di = Distance, V = Vegetation, P=

Plot. The random factors are shown in brackets ().

Model	Formula	Deer space movement AIC
1	Zo * Di + (P)	131.6462
2	Zo * Di + (V)	140.3780
3	**Zo * Di + (V) + (P)**	**123.2909**

Post-hoc analysis of model 3

Subgroup	Estimate	Standard Error	Df	P-value
Low,20 vs High,20	**1.0261**	**0.302**	**33.0**	**0.0093 ****
Low,20 vs Low,100	-0.0964	0.183	23.7	0.9514
Low,20 vs High,100	0.5394	0.312	32.6	0.3260
High,20 vs Low,100	**-1.1225**	**0.314**	**32.5**	**0.0058 ****
High,20 vs High,100	**-0.4867**	**0.175**	**24.0**	**0.0470 ***
Low,100 vs High,100	0.6359	0.340	26.1	0.2648

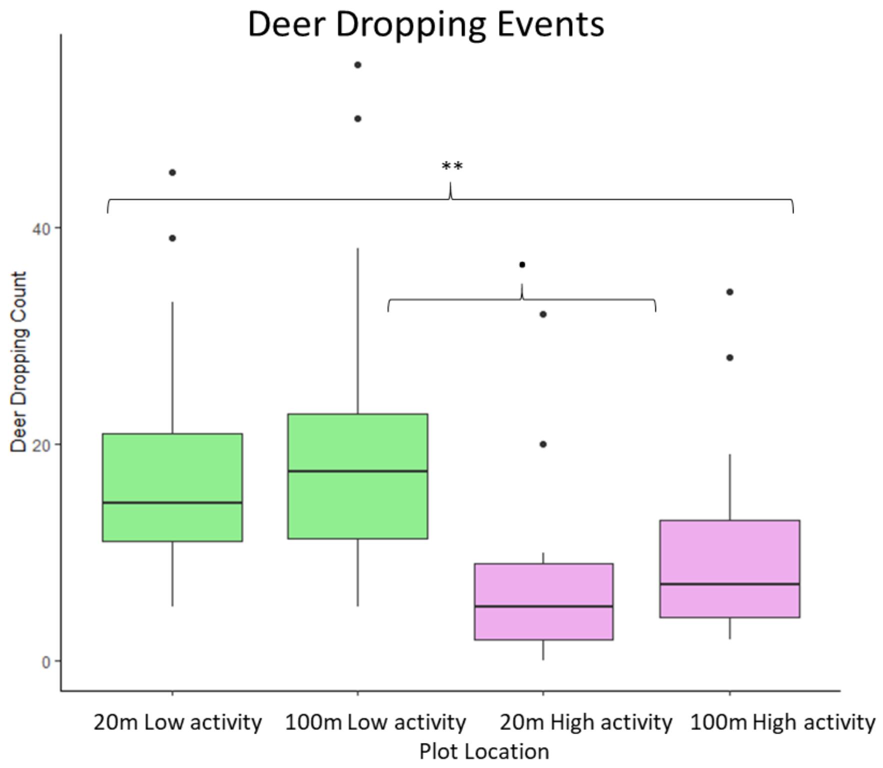


*Figure 4 -Significances are indicated with '**' very significant (p=<0.001), significant '*' (p=<0.01) and (•) marginal significance. The top bar (**) shows the difference in deer droppings between low and high human activity. The bottom bar (•) shows the effect of an interaction on deer droppings between zone*distance (high vs low * 20m vs 100m)*

The boxplot (Fig. 4) reveals an effect of human activity on deer droppings, with more droppings in areas of low human activity (P = .00181******). Independently, distance (20m vs 100m) did not have an effect on deer droppings (P = .55165) but a trend was seen in the interaction zone * distance (P = .08). The outcome of the best model (model 3) was determined by the lowest AIC, a qqplot gave acceptable margins of error (*see appendix supp. Fig.4)*. Importantly, within the interaction which showed a trend, there were significantly more deer dropping events at 100m than at 20m in areas of high human activity (high 20m vs high 100m) (P = .04) but not between 20m and 100m in areas of low human activity (low 20m vs low 100m), which shows an effect of human activity on deer droppings.

Tick abundances

Table 2 Shows the formula of the lmer models from analysing total tick, nymph and adult abundance. The lowest AIC is highlighted in bold. Zo = Zone, Di = Distance, V = Vegetation, P = PlotID . The random factors are in brackets().

Model	Formula	Tick total AIC	Adult AIC	Nymph AIC
1	**Zo * Di + (P)**	**154.1512**	**108.3890**	**38.80366**
2	Zo * Di + (V)	158.9258	108.6717	46.38397
3	Zo * Di + (P) + (V)	156.1512	109.8143	40.80366

Post-hoc analysis of model 3

Sub-groups	Estimates	Standard errors	Degrees of freedom	P-value
Tick Total				
Low,20 - High,20	**1.275**	**0.394**	**40.7**	**0.0124 ***
Low,20 - Low,100	-0.298	0.299	24.0	0.7519
Low,20 - High,100	0.133	0.394	40.7	0.9866
High,20 - Low,100	**-1.574**	**0.394**	**40.7**	**0.0015 ****
High,20 - High,100	-1.142	**0.299**	**24.0**	**0.0043 ****
Low,100 - High,100	0.431	0.431	40.7	0.6948
Nymphs				
Low,20 - High,20	**0.4086**	**0.1220**	**37.8**	**0.0096 ****
Low,20 - Low,100	-0.0768	0.0845	24.0	0.8001
Low,20 - High,100	0.0340	0.1220	37.8	0.9923
High,20 - Low,100	**-0.4854**	**0.1220**	**37.8**	**0.0017 ****
High,20 - High,100	**-0.3745**	**0.0845**	**24.0**	**0.0009 *****
Low,100 - High,100	0.1109	0.1220	37.8	0.8004
Adults				
Low,20 - High,20	0.1804	0.236	45.3	0.8706
Low,20 - Low,100	-0.3148	0.205	24.0	0.4349
Low,20 - High,100	-0.2484	0.236	45.3	0.7207
High,20 - Low,100	-0.4952	0.236	45.3	0.1703
High,20 - High,100	-0.4287	0.205	24.0	0.1861
Low,100 - High,100	0.0664	0.236	45.3	0.9922

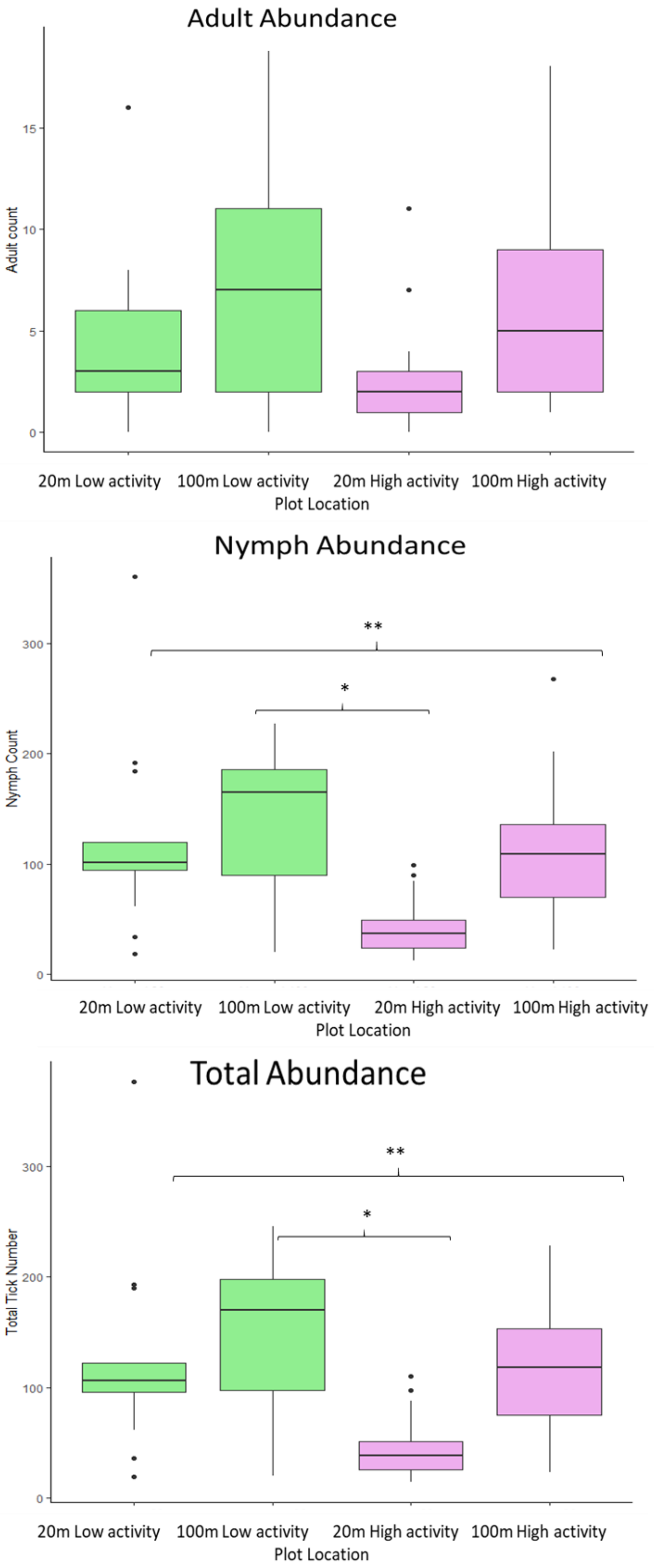


Figure 5 *shows the adult, nymph and total tick densities split between zone (high/low) and distance (20m/100m). The top bar on the nymph and total tick abundance graphs show the independent effect of zone ie. high and low levels of human activity (large scales). The bar below it on these graphs show an interaction effect of zone*distance.*

In total, 5,098 ticks were caught, 291 of these were adults and 4,807 were nymphs. Although the sample size was 62, only 52 of these were carried forward into further analysis because 10 plots were too wet to be dragged, this is known to affect tick questing behaviour (Vassallo *et al.,* 2000; Tack *et al.,* 2011). The total number of ticks in model 1 (Tab.2) showed that human activity independently has an effect on total tick abundance (low 20m vs high 20m & high 20m vs low 100m, P = .0124* & P = .0015**, respectively). Independently, distance overall (20m vs 100m) did not have an effect on tick abundance (P = .328). There was a significant (*) interaction effect on tick abundance (P = .05*). Within this interaction (Tab.2) less ticks were found at 20m compared to 100m from a hiking track in areas of high human activity (high 20m vs high 100m) (P = .0043**).

When nymphs were analysed separately they showed that human activity independently had an effect on their distribution (low 20m vs high 20m), (high 20m vs low 100m) (P = .0096** & .0017** respectively). Distance from a track did not independently have an effect on nymph numbers (P = .372). There was an interaction effect of zone * distance on nymph numbers (P = .02005*). Within this interaction (Tab.2) it was found that similarly to total number of ticks there were less nymphs at 20m compared to 100m away from a hiking track in areas of high human activity (Tab.2 – high 20m vs high 100m, P = .0009***).

When adult ticks were analysed separately they showed trends which were found in nymph and total number of ticks, but were not significant (Fig.5). Although adult ticks showed the same trend as nymphs, they were not significantly affected by human activity, distance from tracks or as an interaction of zone * distance. Within this interaction (Tab.2) although it is not significant, there is still a trend in adult tick distribution with less adults found at 20m compared to 100m from a hiking track in areas of high human activity. Additionally, total number of ticks and nymphs were significantly negatively correlated with deer droppings overall ($r^2 = -0.3050046$, P = .02953* & $r^2 = -0.3125191$, P = .02557*). All models which were within 2 AIC points in the nymphs, adults and the total number of ticks were checked but were indifferent from the model with the lowest AIC. The simplest models which also had the lowest AIC score were the models of best fit and overall the most reliable (Matuschek *et al.,* 2017).

Dung Beetles and dung removal rates

Table 4 Shows the formula's of the glmer models from analysing beetle abundance and dung removal rate. The lowest AIC is highlighted in bold. Zo = Zone, Di = Distance, De = Droppings. The random factors are in brackets ().

Model	Formula	Beetle AIC	Dropping Removal AIC
1	**Zo * Di + (P)**	**27.46594**	**35.07849**
2	Zo * Di + (De)	30.72875	**35.28115**
3	Zo * Di + (P) + (De)	**29.30071**	**37.07849**

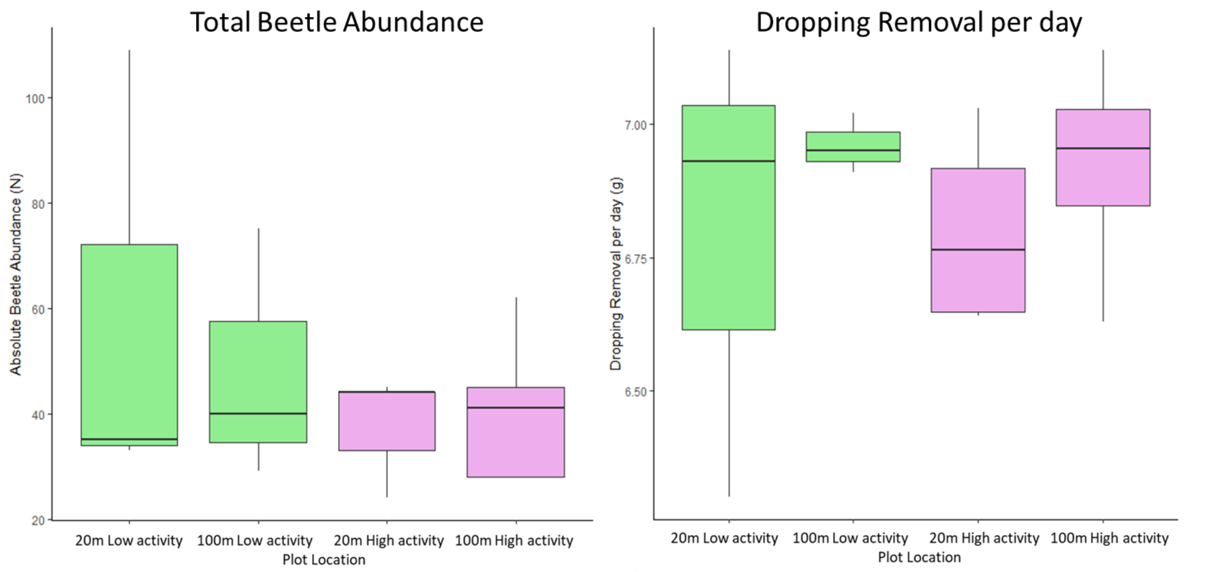


*Figure 6 - Boxplots of beetle abundance and dung removal rate between subgroups of high vs low use hiking tracks and 20m/100m. As seen, there is no effect of human activity (high/low use tracks), distance from tracks (20m/100m) or an interaction effect zone * distance on beetle abundance or dung removal rates.*

In total, 715 beetles were collected from all 16 traps with 696 belonging to the species *Geotrupes stercorarius*, the remaining 19 individuals which covered 7 different species were removed from analysis. In total, from the 28 original traps, 4 traps were destroyed by wild boar on the Deelerwoud. There was a 2-fold difference in removal rate per day between dung removal in the Deelerwoud and Veluwezoom, despite the removal rate per day equation. This was mainly because regardless of exposure time, dung was almost completely removed in all cases. Because of this, only the Veluwezoom data was carried forward as no traps were destroyed at this location and exposure time was the same (7 days). There was no correlation found between dung beetles, dung removal rates or deer dropping counts. The model analysis revealed that the simplest models was the best fit in both cases for dung beetle abundance and dung removal rates. The model did not show any independent trends in zone, distances or in an interaction (zone * distance) with dung removal rates or dung beetle abundance. Post-hoc analysis was carried out on the models of best fit but no significances were found (*see appendix, supp. Tab.1).* Models within 2 AIC points were also checked for significances but were not significantly different from the model of best fit (*see appendix, supp. Tab.2)*.

Discussion

We looked at the abundances of ticks and dung beetles, deer dropping counts and dropping removal rates per day by dung beetles at two distances from hiking tracks of high and low human activity in a forest in the central Netherlands. We found that distances from track and levels of human activity has a strong negative effect on tick distribution and dropping counts. Whilst distances from tracks and zone have no significant effect on dung beetle distribution and dropping removal rates. These results are discussed in the context of human activity and how hiking can indirectly effect organisms on lower trophic levels.

Deer droppings

Deer droppings are widely agreed to be an accurate proxy of deer space use (Jay-Robert *et al.,* 2008; Kays *et al.,* 2017; Pfeffer *et al.,* 2018). Our data shows that there are more droppings in areas of low human activity than areas of high human activity, which shows that deer avoid human activity on larger scales. Our data also shows there are less droppings closer to tracks in areas of high human activity than further away. This indicates that deer avoid human presence on small scales in forested areas.

Many studies have reached similar conclusions on small local scales that humans are capable of influencing deer behaviour and as a result, cause cascading effects on lower trophic levels (Eisen *et al.,* 2008; Tinoco-Torres *et al.,* 2011; Marie, Adam and Zbigniew, 2018). One example by Mathisen, Wojcicki and Borowski,. (2018) investigated deer browsing on oak tree saplings and deer presence around small unpaved roads in Poland at 20m up to 250m away from forest roads, collecting data every 20m into the forest from the road. They also used droppings as a proxy of deer space use and found that deer presence is higher, further away from roads; significant differences in deer droppings became apparent between 20m and 120m away from the road, which are closely in line with our findings. This study had several environmental differences; different deer abundances and different proxy of human use (roads vs hiking tracks) but the effect on deer remained the same. This is not only in line with our findings but shows that our findings are not limited to hiking as a low level human activity.

It has also been commonly found that humans are able to alter deer behaviour and cause cascade effects on larger scales, similar to those found in our study (Nichols *et al.,* 2008; Coppes *et al.,* 2017; Barretto, Cultid-Medina and Escobar, 2019). One clear example of this effect on large scales from Ciuti et al. (2012) investigated elk

(*Cervus canadensis)* behaviour over a year in Canada across different sections of forest which differed in; human activity, natural predators and habitat quality. This study identified that human activity was the key governing factor in elk space movement, vigilance and browsing. Elk were most vigilant when on public land which caused the biggest reduction in feeding time in comparison with other factors like natural predators, habitat quality and circadian rhythms. This study is in line with our results and demonstrates that low level human disturbance can heavily impact deer behaviours like feeding and vigilance.

Other findings in our study found a strong negative relationship between vegetation height and deer droppings; as droppings increased, vegetation height decreased. This may have occurred for two reasons; firstly, this may be that deer droppings became more difficult to find in taller vegetation (Gilbert *et al.,* 2012), or this is an effect of deer browsing; shorter vegetation may infer more browsing by deer (Eisen *et al.,* 2008). However, vegetation height alone is not a reliable proxy of deer browsing because vegetation height is different from vegetation density and diversity, which can both be used to measure deer browsing intensity (Williams, Mosbacher and Moriarity, 2000; Iijima and Nagaike, 2015). In addition, deer favour specific plant/tree species over others when browsing (Mathisen, Wojcicki, Borowski, 2018) and when using the disk and stick method (measuring the tallest point of a sward) is non-species specific so is unlikely representative of grazing intensity. For these reasons, observer bias in this case is more likely than the latter. Although, this did not influence the results or significance when included in the models, so this observer bias can be considered negligible.

Interestingly, the impact of human activity seems to fade at 100m from hiking tracks;

there is a clear difference in droppings at 20m between low and high human activity on hiking tracks but no difference at 100m between low and high human activity (Tab.1). Our findings suggest that deer do not perceive a difference in danger when at 100m away from a hiking track of high or low human activity but do when at 20m from any given track. This shows that tracks themselves may cause deer avoidance, but stronger avoidance behaviours on tracks of high human activity compared to low. These results are supported by other similar studies that investigate deer presence at different distances from hiking tracks (Mathisen, Wojcicki and Borowski,, 2018; Marie, Adam and Zbigniew, 2018). An example study in line with our findings by Wisdom *et al. (*2018) GPS tagged 35 adult elk females and monitored their movement to different types of recreation. It was found that elk on average stay 276m away from a hiking track when in use, in real time. So although this is further away than in our observations, it is in line with the hypothesis that low level human activity causes avoidance in deer from hiking tracks. However, we must carefully consider the differences in track density, visibility, vegetation differences and deer population differences that may have led to the same conclusions. Unfortunately, these cannot be compared as the data for such comparisons is not available. Studies which compare low and high use hiking tracks are rare because this is a unique example with specific circumstances allowing us to have high and low activity in hiking tracks, but in principle the findings are coherent. Overall, many studies have found empirical evidence that hiking influences deer space-use (as discussed). Our study also supports this, showing clearly that deer dropping counts respond over different spatial scales to human hiking activity, which supports our initial hypothesis.

Tick abundance

Our data shows that high and low use tracks (large scales) and distances from single hiking tracks (small scales) strongly affected nymph abundances, which is in line with most previous studies (Eisen *et al.,* 2008, Hofmeester *et al.,* 2017). However, adult tick abundances appear unchanged regardless of spatial scales. We analysed adults and nymphs together as "total number of ticks" and found a negative effect of hiking tracks both between zones (low vs high human activity) and distances (20m vs 100m from tracks).

Firstly, nymphs were more abundant overall around hiking tracks of low human activity than busy ones, showing a large scale effect (Gray *et al.,* 1992; Lindsay *et al.,* 1999; Gilbert *et al.,* 2012). One study on similarly large scales by Rand *et al.* (2003) compared isolated forest areas with known densities of deer and found that ticks increase over a gradient of 10 deer per km^2 up to 40 deer per km^2, showing a clear link between deer and tick abundance, which supports our findings.

The total number of ticks were also less abundant at 20m than at 100m away on a hiking track with high human activity, but not on hiking tracks of low human activity. This shows that the total number of ticks are affected by human activity over short distances. Studies similar to ours which sample ticks alongside different densities of deer, in plot sizes within 1ha are rare, to our knowledge no such published literature exists, so a direct comparison is impossible. The inclusion of small scales (<1ha) is what makes our study unique from previous studies on tick abundance. For example, similar observations in tick abundances which excluded deer in small plot sizes (>1ha), found that tick populations remain stable or even increase in some cases. This was due to the increase in alternative hosts like rodents, enabled by reduced competition for space and resources with deer (Perkins *et al.,* 2006; Kugeler *et al.,* 2016). Studies which exclude deer from small plots and find no change in tick abundance are primarily caused by alternative host availability (Eisen and Eisen, 2018). As our areas lack alternative mammal hosts and we did not exclude deer we cannot come to similar conclusions. Yearly monitoring on pine martens *(Martes martes)* and wood mice (*Apodemus sylvaticus)* suggest that these are in low abundance across the forested areas of the park (Zoogdier vereniging, 2018). In addition, other small mammals like hedgehogs (*Erinaceus europaeus)*, badgers (*Meles meles)*, foxes (*Vulpes vulpes)* and *Leoprids* are rarely observed and are not currently monitored. Therefore, it is highly likely that deer abundance is the main driver of tick abundance on different spatial scales in our areas, because the lack of alternative hosts strains the alternative possibilities for the observed differences. Our results strongly support a relationship between human activity, deer space use and total tick abundances over different spatial scales and previous studies support our findings on broader scales (Alverson, Waller and Solheim, 1988; Cilek and Olson, 2000; Pfäffle *et al.,* 2013).

The consequences of this inter-trophic link around hiking tracks are as such. One is the effect on Lyme disease prevalence. A reduction in tick abundance because of its main host may put more people at risk of the disease in forested areas (Levi *et al.,* 2016; Huang *et al.,* 2019). Ticks are also an important food source for Amphibians, Reptiles and Birds whom consume thousands of these organisms. A reduction of a key food source poses an obvious threat, as this may put excessive dependence on other food sources and force stronger competition, both of which could result in decreased biodiversity of those dependent on ticks as a food source.

As mentioned, our data showed that there was no effect of human activity on deer movement at 100m away from tracks of high human activity, this is also true for total tick abundances. There was no difference in tick abundances at 100m away between high and low use hiking tracks, but there was an effect at 20m away from high/low use hiking tracks. This shows that 100m away from a track is far enough to prevent an indirect effect on tick abundance by human activity. Total tick abundance correlates with deer space use, supporting our hypothesis that deer space use is essential for tick distribution.

Our results show that adult tick numbers were unaffected by human activity on hiking tracks, unlike nymphs. Although, when combined "the total number of ticks" did show an effect. This was likely due to the relatively large number of nymphs compared to the number of adults. Some studies completely exclude adult ticks because of their lack of importance in Lyme disease risk and naturally low abundances (Perkins *et al.,* 2006; Gilbert *et al.,* 2012). Although, some studies do include adults and find that they are more resistant than nymphs, however sample sizes in many studies are often too low to make strong conclusions (Hofmeester *et al.,* 2017).

Overall, our findings support the hypotheses of a negative indirect effect on ticks from altered deer behavior caused by high human activity on hiking tracks. An important next step is to investigate the effect that reduced tick numbers and deer presence around hiking tracks has on Lyme disease prevalence (Ripoche *et al.,* 2018). Our study provides important evidence towards forest management and public health. With this information hiking tracks can be more carefully planned to reduce human interaction with ticks. This may allow forest managers to predict "hotspots' of tick abundances based on deer abundances and previous human activity which may indicate Lyme disease risk (Paddock and Yabsley, 2007), but this should be carefully considered as in some circumstances, more hosts can act as dilution hosts and reduce Lyme disease risk (Huang *et al.,* 2019). This information may also prove useful in forest management and public safety. This information could be used to convince park managers and private owners to invest into effective communication with the general public about the importance of staying on hiking tracks. This could be in the form of sign posting around activity hotspots to stay on the provided hiking paths or through utilizing social media.

Dung beetle abundance

Dung beetle abundance was unaffected by hiking tracks of different human activity levels and the distances from said hiking tracks. As deer droppings were affected by these factors, we can infer that deer dropping distribution and human activity have little effect on dung beetle abundance.

This is in line with previous studies at both small and large scales that found weak or no evidence that dung beetle abundance is mediated by deer dropping distribution (Kadiri, Lobo and Lumaret, 1997; Iida *et al.,* 2016b; Van Klink, Ruifrok and Smit, 2016). One specific study in Poland (Mroczyński *et al.,* 2018) also found no effect of deer distribution on dung beetle abundance across 3 different forest types, including a Scots pine forest with a homogenous understory, similar to our forest type. This study instead found that habitat structure and understory vegetation were key drivers of beetle abundance, although dung beetle diversity was correlated with deer abundance. Our study found no correlations between vegetation height and beetle abundance but unlike the previous study we did not collect variables like vegetation density which may explain the lack of correlation. Some studies have correlated specific dung beetle species and deer on large scales and over long time periods

(Hanski and Koskela, 1977; Ridsdill-Smith, 1986; Koike *et al.,* 2014), studies only find that diversity or the abundance of specific species correlate with deer abundance (Hutton and Giller, 2003; Iida *et al.,* 2016b). The differences in conclusions about dung beetle abundance variation are mainly explained by the size, function and species of beetle (Iida *et al.,* 2016a). A study in Japan by Iida *et al.* (2016b) between two sites with naturally different Sika Deer *Cervus nippon* populations had one forested site with 50 deer per km^2 and another forested site with 10 deer per km^2. This study, like ours, found no differences in overall dung beetle abundance between sites, but did find differences within specific types of dung beetles. We cannot delve into this possibility as our sample lacked diversity, with *G. stercorarius* accounting for 97.3% of all individuals. Our study had a disproportionate dominance of one large dung beetle over others. This could have been due to our relatively short sampling period (Akaba, Takafumi and Yoshida, 2014). However, the large amount of individuals collected in a short time period is likely representative of our overall population of dung beetles, based on previous studies' sample sizes and sampling periods (Hosaka *et al.,* 2014; Martínez-Falcón *et al.,* 2018). Alternatively, other species of dung beetles may not have been active at this point in the season, as different species of beetle have different breeding cycles (Hanski, 1991)**.** Thus, pitfall trapping could have been conducted over the course of May, June, July and August to capture between-generation and species differences in dung beetle activity (Mroczyński *et al.,* 2018). For this reason, it may be difficult to assume that other species are this overwhelmingly outcompeted. Further investigations into between-generation differences in dung beetle abundances may provide some clarity.

Studies which specifically investigate small scale differences in beetle abundance are rare, so the effect of deer on beetles on small scales are largely unexplored (Raine and Slade, 2019). There is one study by Nichols *et al.* (2013) whom looked at the effect of human presence on deer space use and the effect of this on dung beetles, which supports our findings. They found that deer avoided human presence and that smaller beetle species (<0.1g) were less abundant closer to human settlements than further away, whilst larger species (>0.1g) were unaffected, over distances of 400m away from settlements. This suggests that larger species are more resistant to human activity, which may explain why at our site, large species (*G. stercorarius*) were in high abundance and smaller species were almost non-existent. Our study cannot confirm that smaller species are affected by human activity or deer presence because of our small sample sizes. The lack of differences in abundance of dung beetles over different spatial scales is likely because large dung beetles are highly mobile and more likely to reach dung piles first (Frank *et al.,* 2017). This reduces the potential effect of spatial scale when measuring dung beetle abundance and would likely need to be on larger scales than our study proposes to detect a difference, or with more contrasting environmental differences (da Silva *et al.,* 2019).

Another factor which may have influenced our results is sporadic climate. Prior to pitfall trapping, sporadic weather conditions of high temperatures during the day and low temperatures at night caused many beetles to freeze to death. This was widely observed across our plots. It is difficult to conclude if this affected our sampling or altered the balance of diversity prior to the extreme weather, but should be carefully considered as larger dung beetles are known to be more resistant than smaller ones (Hanski, 1991). It is likely that more beetle larvae had not yet hatched as numbers evidently recovered. Beetle larvae can spend prolonged periods of time buried beneath the soil and extreme weather events will only slow development (Eggert and Muller, 1997). Our results clearly demonstrate that human activity and deer presence have little effect on dung beetle abundance. Further investigation is warranted into the structure of the dung beetle community in the Veluwe National Forest. This will confirm that our sample was representative of the whole population and that there is weak evidence for a link between human activity and deer space use on dung beetle abundance.

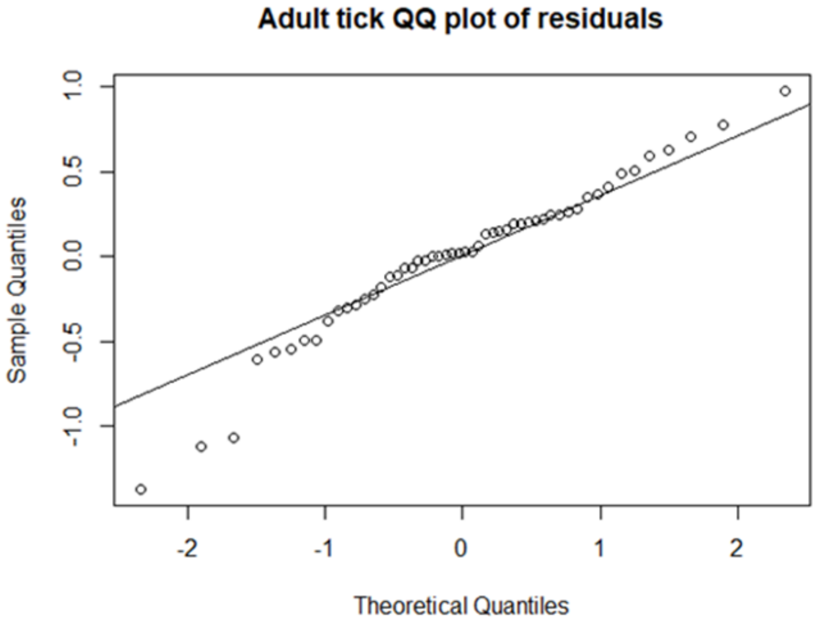
Dung removal rates

We found no evidence that dung removal rates were different between areas of high and low human activity, or different between 20m and 100m from tracks in either areas. But because deer droppings and dung beetle abundance was not related in our study, these results are expected, in this light the results are consistent. Other studies have also found no relation between dung beetle abundance and dung removal rates within forested sites in field experiments (Slade *et al.,* 2007; Slade, Mann and Lewis, 2011; Iida *et al.,* 2016b; Frank *et al.,* 2017). One specific study by Milotić *et al.* (2019) conducted 17 separate studies in 10 different countries across the western-Paleoarctic on dung removal rates, dung beetle abundance, diversity and functional groups of dung beetles. In their models of overall differences in removal rates, out of 8 different predictor variables to predict dung removal rates, beetle abundance was the only insignificant predictor with; temperature, rainfall, dwellers, tunnellers, rollers, small and large soil macro-invertebrates all significantly influencing dung removal rates. This demonstrated how environmental and physiological factors are likely more important in predicting dung removal rates in the field. When dung removal rates are predicted by dung beetle abundance, these appear under specific circumstances such as; comparisons between two different habitat types (ie woodland vs grassland), between fragmented habitats or in tropical systems with richer diversity (Herrick and Lal, 1996; Horgan, 2005; Bustamante-Sánchez *et al.,* 2004; Hosaka *et al.,* 2014; Batilani-Filho and Hernandez, 2017). Our site does not fit any of these descriptors so perhaps the environments of our comparative areas are too similar to warrant significant changes in dung removal rates by dung beetles. Dung beetle types and decomposition rates have been linked before, but it seems most commonly in mesocosm experiments, where competition and environmental factors are controlled for (O'hea, Kirwan and Finn, 2010; Tixier, Bloor and Lumaret, 2015). As our experiment was in the field, it was vulnerable to potential confounding factors which may have influenced the results. But as shown, our findings are consistent with other field experiments under similar circumstances, which leads us to conclude that deer dropping distribution and as an extension, human disturbance do not affect dung removal rates by dung beetles.

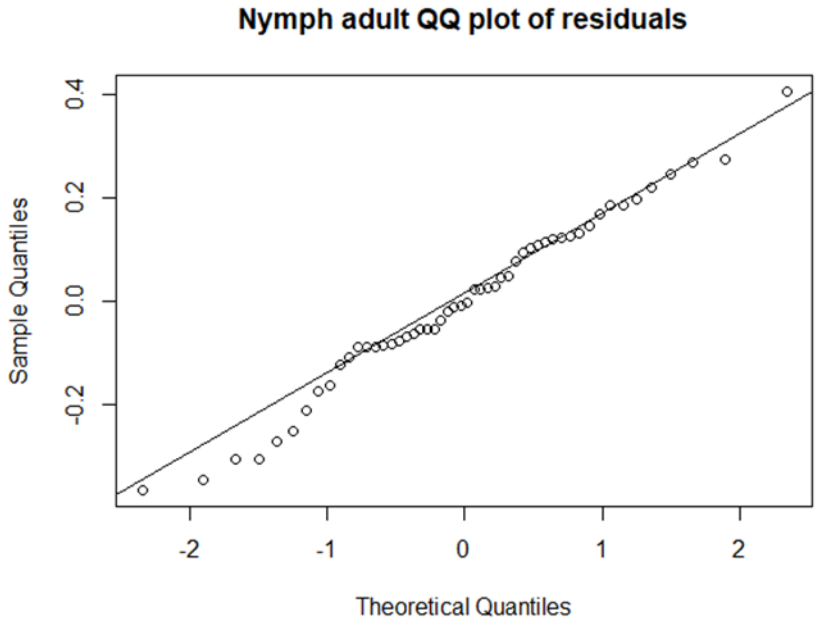
Concluding remarks

It has been observed that high human activity on hiking tracks causes a decline in deer droppings on different spatial scales, which infers that deer avoid areas of high human activity. This effect correlates with the number of ticks which were also found to decrease in areas of high human activity, because of deer avoidance. This effect is not seen in beetles or in dung removal rates, suspected to be because of a number of confounding factors like diversity, environmental conditions, habitat quality and time of season. The implications of our findings is widely applicable in forest management and public health. The prevalence of Lyme disease is increasingly important as climate change is causing a global rise in tick-borne diseases (Dumic and Severmini, 2018). Forest managers must be able to effectively mitigate tick-borne diseases, which from our evidence would be most effective by staying on established hiking paths. Clearer warnings to tourists in our national parks about the dangers of off track hiking must be more effectively communicated to help mitigate the rise in tick-borne diseases. Furthermore, this study provides evidence that even low levels of human disturbance like hiking can cause unforeseen effects in forest ecosystems on different species. This is useful when establishing new hiking tracks or new national parks. It allows us to predict the effects on wildlife of new hiking tracks and where wildlife will be more concentrated because of lower human presence.

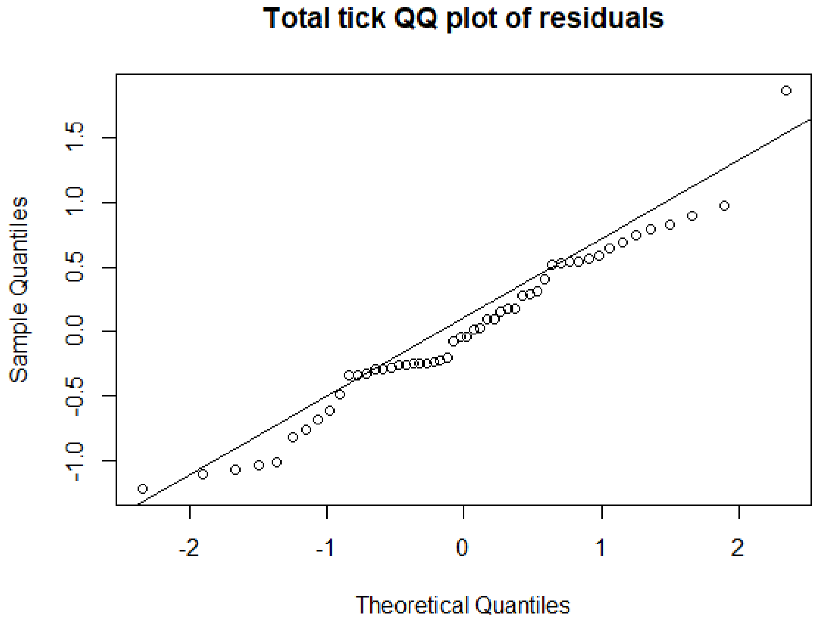
Appendix



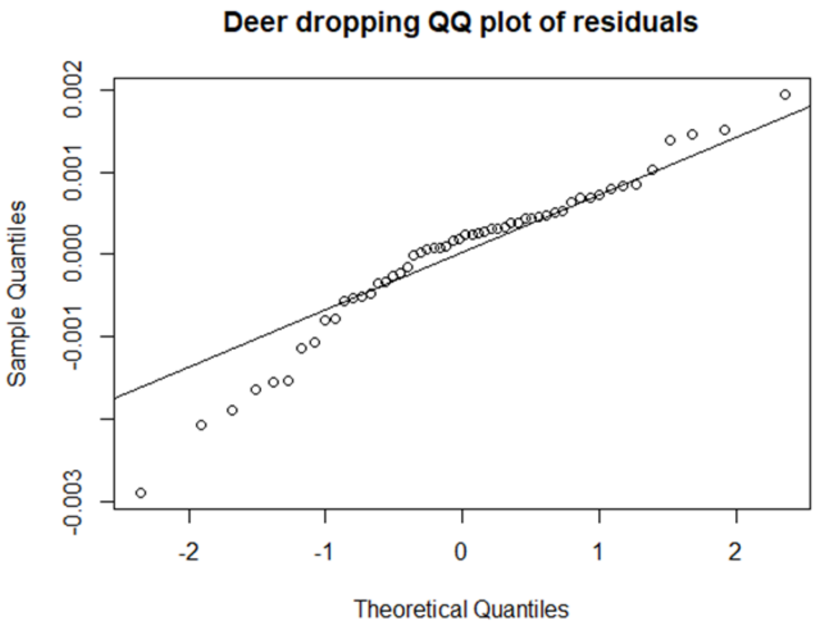
Supplementary figure 1 – qqplot of the residuals of the model of best fit for *predicting adult tick abundances over different plots.*



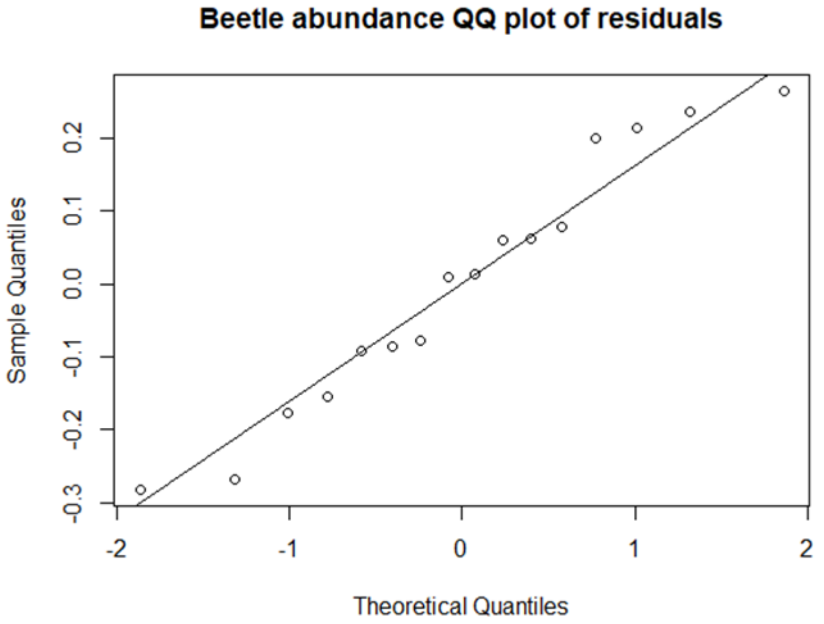
Supplementary figure 2 – qqplot of the residuals of the model of best fit for predicting nymph tick abundances over different plots.



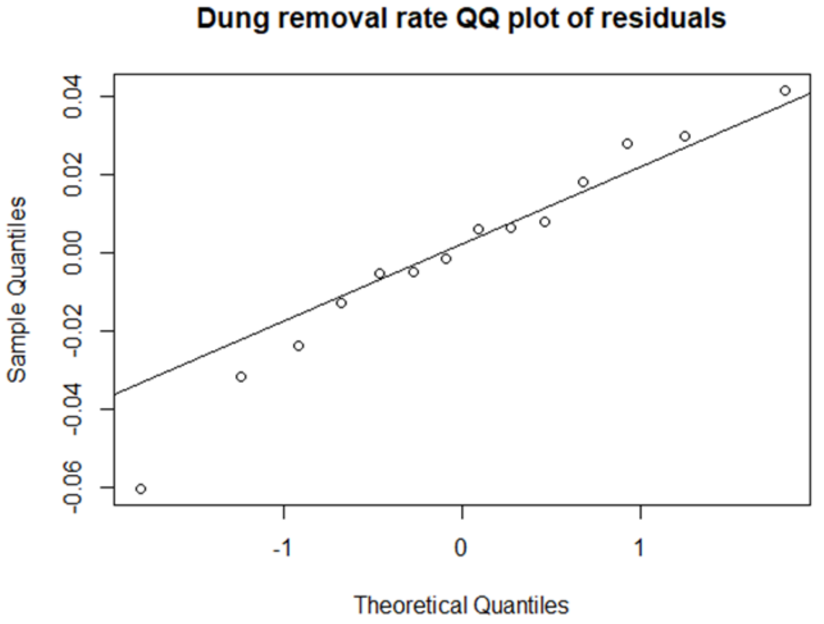
Supplementary figure 3 – qqplot of the residuals of the model of best fit for predicting total tick abundances over different plots.



Supplementary figure 4 – qqplot of the residuals of the model of best fit for predicting deer dropping counts over different plots.



Supplementary figure 5 – qqplot of the residuals of the model of best fit for predicting dung beetle abundance over different plots.



Supplementary figure 6 – qqplot of the residuals of the model of best fit for predicting dung removal rates over different plots.

Veluwezoom

Deelerwoud

`Veluwezoom - https://www.strava.com/heatmap#15.06/5.95724/52.07180/hot/all`

`Deelerwoud - https://www.strava.com/heatmap#15.15/5.92282/52.08467/hot/all`

Supplementary Figure 7 - Hiking tracks of high and low human activity were selected based on previous knowledge of the areas and Strava heat maps. Brighter coloured lines indicate more human activity and darker, more faded lines represent less human activity. These heat maps include only hiking ‘heat’ data collected between 2015-2017 from anyone using the app.

Dung beetle abundance models

```
d1 <- lmer(logbt ~ zone*distance + (1|PlotID), data=beetle)
```

```
Fixed effects:
                     Estimate Std. Error     df t value Pr(>|t|)    
(Intercept)            3.9144     0.2433 8.4539  16.090 1.23e-07 ***
zoneUsed              -0.3045     0.3077 8.4539  -0.989    0.350    
distance100           -0.1232     0.2042 6.0000  -0.603    0.568    
zoneUsed:distance100   0.1756     0.2583 6.0000   0.680    0.522    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
lsmeans(d1, pairwise~zone*distance, adjust="tukey")

$contrasts
 contrast                estimate    SE   df t.ratio p.value
 Unused,20 - Used,20       0.3045 0.308 8.45  0.989  0.7592
 Unused,20 - Unused,100    0.1232 0.204 6.00  0.603  0.9274
 Unused,20 - Used,100      0.2520 0.308 8.45  0.819  0.8441
 Used,20 - Unused,100     -0.1813 0.308 8.45 -0.589  0.9327
 Used,20 - Used,100       -0.0524 0.158 6.00 -0.331  0.9862
 Unused,100 - Used,100     0.1289 0.308 8.45  0.419  0.9738

Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 4 estimates
```

Supplementary table 1 – Dung beetle abundance model of best fit (model 1) output and post-hoc tukey test across plots which had no significant differences.

```
d3 <- lmer(logbt ~ zone*distance + (1|plotID) + (1|dung_events),
data=beetle)

Fixed effects:
                     Estimate Std. Error      df t value Pr(>|t|)
(Intercept)            3.9137     0.2416  8.1753  16.201 1.68e-07 ***
zoneUsed              -0.3037     0.3076  8.4065  -0.988    0.351
distance100           -0.1920     0.1481  0.5500  -1.296    0.523
zoneUsed:distance100   0.2444     0.2116  1.6386   1.155    0.389
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

lsmeans(d3, pairwise~zone*distance, adjust="tukey")

$contrasts
 contrast                estimate    SE   df t.ratio p.value
 Unused,20 - Used,20       0.3037 0.368 7.84  0.825  0.8412
 Unused,20 - Unused,100    0.1920 0.390 0.21  0.492     Na
 Unused,20 - Used,100      0.2513 0.368 7.84  0.683  0.9008
 Used,20 - Unused,100     -0.1118 0.368 7.84 -0.304  0.9895
 Used,20 - Used,100       -0.0524 0.151 5.91 -0.347  0.9843
 Unused,100 - Used,100     0.0593 0.368 7.84  0.161  0.9984

Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 4 estimates
```

Supplementary table 2 – Dung beetle abundance output of model within 2 AIC (model 3) and post-hoc tukey test across plots which had no significant differences.

Deer dropping removal models

```
lsmeans(r1, pairwise~zone*distance, adjust="tukey")

$contrasts
 contrast               estimate     SE   df t.ratio p.value
 Unused,20 - Used,20    -0.00259 0.0285 9.62 -0.091  0.9997
 Unused,20 - Unused,100 -0.02612 0.0272 5.00 -0.959  0.7775
 Unused,20 - Used,100   -0.02001 0.0285 9.62 -0.703  0.8936
 Used,20 - Unused,100   -0.02352 0.0285 9.62 -0.826  0.8409
 Used,20 - Used,100     -0.01742 0.0236 5.00 -0.738  0.8780
 Unused,100 - Used,100   0.00610 0.0285 9.62  0.214  0.9963

Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 4 estimates
```

Supplementary table 3 – Deer dropping removal post hoc test (model 1) across plots which had no significant differences.

```
r3 <- lmer(logvrem ~ zone + distance + zone*distance + (1|dung_events) +
(1|plotID), data=vrem)

Fixed effects:
                    Estimate Std. Error         df t value Pr(>|t|)
(Intercept)        1.9075114  0.0263654  9.6106185  72.349 1.77e-14 ***
zoneUsed           0.0047672  0.0348782  9.6106185   0.137    0.894
distance           0.0003265  0.0003406  5.0000063   0.959    0.382
zoneUsed:distance -0.0001087  0.0004505  5.0000063  -0.241    0.819
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

lsmeans(r3, pairwise~zone*distance, adjust="tukey")

$contrasts
 contrast               estimate     SE   df t.ratio p.value
 Unused,20 - Used,20    -0.00259 0.0299 9.57 -0.087  0.9998
 Unused,20 - Unused,100 -0.02612 0.0293 4.98 -0.892  0.8099
 Unused,20 - Used,100   -0.02001 0.0353 8.29 -0.567  0.9393
 Used,20 - Unused,100   -0.02352 0.0336 9.57 -0.701  0.8943
```

```
 Used,20 - Used,100     -0.01742 0.0295 4.29 -0.590  0.9304
 Unused,100 - Used,100   0.00610 0.0393 9.61  0.155  0.9986

Degrees-of-freedom method: kenward-roger
P value adjustment: tukey method for comparing a family of 4 estimates
```

Supplementary table 4 – Deer dropping removal model output and post hoc test of model 3 (within 2 AIC of model of best fit) across plots which had no significant differences.

```
r2 <- lmer(logvrem ~ zone + distance + zone*distance + (1|dung_events),
data=vrem)

Fixed effects:
                    Estimate Std. Error         df t value Pr(>|t|)    
(Intercept)        1.9075114  0.0274346 10.0000000  69.529 9.23e-15 ***
zoneUsed           0.0047672  0.0362926 10.0000000   0.131    0.898    
distance           0.0003265  0.0003805 10.0000000   0.858    0.411    
zoneUsed:distance -0.0001087  0.0005033 10.0000000  -0.216    0.833    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

lsmeans(r2, pairwise~zone*distance, adjust="tukey")

$contrasts
 contrast               estimate     SE   df t.ratio p.value
 Unused,20 - Used,20    -0.00259 0.0301 9.93 -0.086  0.9998
 Unused,20 - Unused,100 -0.02612 0.0324 9.93 -0.806  0.8503
 Unused,20 - Used,100   -0.02001 0.0353 8.42 -0.567  0.9393
 Used,20 - Unused,100   -0.02352 0.0339 9.93 -0.693  0.8975
 Used,20 - Used,100     -0.01742 0.0322 9.03 -0.541  0.9467
 Unused,100 - Used,100   0.00610 0.0387 9.99  0.158  0.9985
```

Supplementary table 5 – Deer dropping removal model output and post hoc test of model 2 (within 2 AIC of model of best fit) across plots which had no significant differences.

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