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Thesis Title - The Effects of Human Activity on Large
Herbivore
Temporal Behaviour Within a Rewilded Landscape

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Abstract

Aim: The present study seeks to ascertain the effects of human recreational activity on large herbivore temporal behaviour within a rewilded landscape. **Method:** Between the 20th May - 14th June 2019 research was conducted within the southern block (470 ha) of Knepp Estate, West Sussex. Using a combination of a Garmin eTrex GPS device and ArcGis, 18 camera traps were deployed around main trails, footpaths and bridleways as well as points 50 and 100 metres perpendicular from the initial trap deployment. The total camera trap sampling effort equated to 288 days. Anthropogenic infrastructure variables were also determined by measuring trail width 5 times at random intervals over a 50-metre stretch. A GLMM model was implemented to examine the significance between trail width and herbivore activity. Statistical software packages (e.g. ‘Circular’, ‘Overlap’ & ‘Activity’) were also applied in R Studio to estimate the coefficient of overlap and infer statistical significance between human & herbivore activity patterns. **Results:** On trails all cervids displayed significantly low temporal overlap with human activity (Fallow deer $\Delta 4 = 0.25$, CI = 0.19 – 0.31, $p = 0.001$; Red deer $\Delta 1 = 0.31$, CI = 0.14 – 0.50, $p = 0.03$; Roe deer $\Delta 1 = 0.28$, CI 0.13 – 0.42, $p = 0.001$), whilst long horn cattle had high temporal overlap ($\Delta 4 = 0.64$, CI = 0.34 - 0.82, $p = 0.64$). However, with increasing distance from the trail this overlap varied greatly between all herbivores. Cervids were also significantly ($p<0.05$) more active on trails during nocturnal hours when human activity was low. However, again this varied greatly with increased distance away from trails. Finally, with regards to the influence of human infrastructure only Roe deer displayed a significant negative correlation with an increase in trail width during the day ($R^2 = 0.17 \pm 0.08$, $p =0.04$). **Conclusion:** Based on the results obtained it would appear that human activity is having a behavioural impact on cervids but not Long horn cattle within the southern block of Knepp. However, due to the limit extent of sampling, and other temporal/ environmental factors not measured in the present study, it cannot be said with confidence that the trends observed are in fact a direct consequence of anthropogenic activity. To consider the multiple interspecific variables at play, further repeated longitudinal research comparing different seasons and applying appropriate models (e.g. occupancy model) are needed before reliable inferences and conclusions can be drawn.

Keywords: Human, Herbivores, Activity, Overlap, Circular, Rewilding

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1.0 Introduction

1.1 Rewilding

Rapid environmental change, population growth and the rising worldwide exploitation of natural resources, have led to global degradation and loss of ecosystems (Matthews and Hammond., 1999; Sih, Ferrari & Harris, 2011; Peacock 2018). Due to such pervasive anthropogenic impacts, wildland managers are now progressively switching their attention away from traditional attitudes of preservation and conservation towards a more proactive restoration of ecosystem services and biodiversity (Schweiger et al., 2019).

Whereas the perception of rewilding has had a long-standing and controversial history due to being associated with various land-management practices, theories, concepts and loose definitions (Nogués-Bravo et al., 2016; Rubenstein & Rubenstein 2016), it has recently been summarised and accepted as a method to increase ecosystem resilience by promoting interaction among ecological processes whilst trying to (re)connect people with nature (Pettorelli et al., 2018; Perino et al., 2019). Whereas the majority of conventional methods of managing natural ecosystems concentrate on the conservation of specific ecosystem states or a single species (Pereira & Navarro, 2015; Schweiger et al., 2019), rewilding focusses on the restoration of natural processes, whilst attempting to achieve the predetermined renewal of self-regulating, sustainable ecosystems by gradually reducing or minimising human interventions (Sandom et al., 2013; Svenning et al., 2016; Perino et al., 2019).

Since the original definition of rewilding, the concept has been on an evolving quest to include a wide range of diverse approaches (Fernández, Navarro, & Pereira, 2017; Perino et al., 2019). One of these approaches, known as trophic rewilding, is conceivably the closest to the original notion, as it advocates the reintroduction of lost keystone species such as large herbivores and carnivores. These non-native large-bodied species are thought to act as fundamental replacements promoting a self-regulating biodiverse ecosystem by acting as ecological proxies for species that became extinct centuries or millennia ago (Jepson, 2016; Svenning et al., 2016; Perino et al., 2019).

1.2 Knepp Wildland Project

Knepp estate, located to the south of Horsham, West Sussex, was predominately given over to intensive dairy and arable farming practices. However, after the estate struggled to be financially and practically viable, the owners introduced the ‘Knepp Wildland Project’; a rewilding ecotourism venture, in a bid to allow more natural processes to take place, create a way of managing the land and (re)connect people with nature (Tree, 2017).

The ‘Grazing Ecology’ and ‘Forest History’ work and research of Frans Vera (Vera, 1997; Vera, 2000) has been identified as the inspiration and stimulus behind the Wildland project. Vera proposed that the pre-agricultural landscapes of Western Europe were not just closed forest, but a mosaic of closed forest, open grassland, scrub and wood pasture. This system was a dynamic one, with the mosaic habitat shifting over time, and driven by the grazing and browsing activities of the formerly present large herbivores such as the tarpan (wild horse - *Equus ferus*), aurochs (wild ox - *Bos taurus primigenius*), deer (Cervidae) and wild boar (*Sus scrofa*) (Vera, 2000).

Therefore, the aim of the Wildland project was to reintroduce replacement ecosystem drivers to produce this dynamic, shifting landscape. A low density of English longhorn cattle (*Bos primigenius)*, Exmoor ponies (*Equus ferus caballus)*, Tamworth pigs (Sus scrofa domesticus), Fallow deer (*Dama dama)* and Red deer (*Cervus elaphus)*, were introduced into different parts of the estate (known as blocks) at varying times, whilst wild Roe deer (Capreolus capreolus) and rabbits (Sylvilagus spp.) already occurred naturally in the wider landscape. The Southern Block (470 hectares) received these herbivores last in 2009.

The time given to the Southern Block to “scrub up” naturally before herbivores were introduced facilitated an unambiguously different landscape character, as the flora structure and diversity varies significantly from field to field (Bottone, 2016). This has led to the estate (but particularly the Southern Block) from benefitting immensely in terms of biodiversity; with 90 species of breeding bird (22 of which are Red List Species and 18 Amber List Species), 33 species of butterfly, 19 species of earthworm, 13 out of the UK’s 17 breeding species of bats, all 5 main UK species of owl, 558 vascular plants and 119 bryophyte species (Tree, 2018). Furthermore, Knepp is now also the largest breeding hotspot for purple emperor butterflies in the UK, and the number of nightingale territories has nearly quadrupled from 9 in 1999 (prior to the rewilding scheme) to 34 (Tree, 2018).

1.3 Activity

An essential element of successfully managing ecological communities is attaining a basic understanding of their inherent composition across an area and over time (Kraft et al., 2007). Failing to understand this spatiotemporal variation within a population structure can reduce the validity of any conservation data (Sun et al., 2015). Information on whether various species within a community are present or absent over time is essential for temporal and spatial patterns within habitats to be interpreted (Escalona et al., 2009). This is particularly pertinent when applying survey data gathered over extensive sampling periods at the same locations. Having a comprehensive understanding of how a species activity may vary over time is of utmost importance for conservation efforts as this informs managers as to whether any conservation effort is warranted for a particular area (Martín-López et al., 2009). It should be noted that within the literature human activity and disturbance has many definitions, ranging from habitat displacement/ destruction (mining, logging etc) to human recreation (walking, cycling etc). The current study will be using the term 'human activity' to mean the latter classification.

Daily activity patterns can be defined as adaptive sequences of temporal routines and habits, shaped by evolution, that meet the time structure of the environment and fine-tuned to the condition of the present environment (Halle, 2000; Diaz-Ruiz et al., 2016). It recognised that in ungulates such temporal patterns are regulated by internal species-specific endogenous clocks (Gwinner, 2012) as well as external aspects such as dietary necessities (Pagon et al.,2013), habitat selection (Beier, 1990) and intraguild interaction or predation risk (Gaynor et al., 2018). However, it is also thought that ungulates, as well as other classes of animals, display behavioural changes and responses to environmental shifts brought about by human activities (Nix et al, 2018; Wisdom et al., 2018).

The global expansion of human presence into natural environments is well understood to be having profound consequences for wildlife, with research demonstrating the effects of habitat defaunation and destruction on species and ecosystems (Dirzo et al., 2014; Scanes, 2018). However, the nonlethal or indirect effects through which humans alter natural areas have largely avoided scientific quantification (George & Crooks, 2006; Van Doormaal et al., 2015). The presence of humans can still impart substantial fear responses in wild animals, which can cause adjustments in their activity levels to evade human interaction, creating a landscape of fear (Frid and Dill, 2002). As in natural predator-prey systems it has been suggested that such risk avoidance can have significant nonlethal effects on animals' psychology and physiology, potentially affecting the demography of entire species triggering trophic cascades (Preisser, Bolnick & Benard, 2005; Gaynor et al., 2018).

Within the literature, other reported effects of recreational activities on wildlife are wide ranging and varied. In response to human activity, Jayakody et al (2011) reported that Red deer were forced to feed in sub-optimal habitat, which affected their diets and overall health. Stankowich (2008) also established that ungulates demonstrated other behavioural effects such as altered habitat-use and vigilance behaviour, whilst Phillips and Alldredge (2000) showed how anthropogenic-induced recreation can have distinct biological impacts on cervids, such as increased stress and energy expenditure as well as reduced fertility. Other studies have also revealed how an increase in human activity over time leads to reduced detection rates of Sika deer and Wild boar in Japan and Roe deer in California (Van Doormaal et al., 2015; George & Crooks, 2006).

Notably, several studies have also demonstrated that cervids are not just impacted by human recreational activities, but also the infrastructures associated with them. For example, several cervid species adjust their space-use behaviour to avoid close proximity to recreational trails (Rogala et al. 2011, Coppes et al. 2017, Scholten, Moe & Hegland, 2018), especially during times of high human use, such as during the day or during weekends (Sibbald et al. 2011, Nix et al. 2018). As well as avoiding trails during the day, Gaynor et al., (2018) conducted a meta-analysis on the influence of human activity on wildlife nocturnality. The authors concluded that animals increased their nocturnality by an average factor of 1.36 in response to human disturbance.

1.4 Telemetry

In recent years camera trap surveys have been utilised as an invaluable technology within the field of conservation and ecology for investigating species' abundance, density, distribution, diversity as well as highlighting the direct effects humans are having on ecosystems (Rowcliffe et al., 2008; Liu et al., 2013). However, it is the indirect impacts of anthropogenic presence, facilitating interactions among species in shifting communities, which do not feature extensively within the literature and are of need of further investigation. (Frid & Dill, 2002; Frey et al., 2017).

While research using camera-traps has historically focused on the numerical and spatial characteristics of population and species ecology (e.g. Karanth, 1995; Trolle & Kery, 2003) they have less frequently studied species' interactions and behaviours and the related significance for their community structure (Frey et al., 2017). Only within the last decade or so have studies focused on the finer spatiotemporal information provided by time-stamped camera-trap video and images (Frey et al., 2017). Even though such spatiotemporal datasets can present statistical and analytical challenges, they are, and undoubtedly will be, vital for developing a more complete understanding of wildlife community and population dynamics in the face of global change and uncertainty (Frey et al., 2017; Ladle et al., 2018). Through the analysis of activity patterns and partitioning along the temporal niche axis, spatiotemporal camera-trap data can now give researchers the chance to address some of these unanswered inquiries with regards to community interactions and species ecology in response to anthropogenic activity (Oberosler et al., 2017). Such temporal data is not only invaluable from an ecological perspective, but it also provides critical information into any potential human-induced changes to species interactions and behaviours as well as the consequential impacts on community structure and niche partitioning (Van Berkel, 2014; Frey et al., 2017). Recent statistical and software developments such as the "Activity", "Circular" and "Overlap" packages in R studio (Team, R., 2019) have made significant steps in addressing the challenges posed by such complicated telemetry data (Agostinelli, & Lund, 2013), thereby allowing for the characterisation of activity patterns and temporal niche overlap (Frey et al., 2017).

1.5 Rationale

Outdoor human led recreation is typically assumed and accepted to be compatible with biodiversity conservation (Briffett, 2001; Oberosler et al., 2017) and allowed in some of the most protected areas around the globe, but its effect is still a relatively unknown topic in the conservation science literature and completely unexplored within a rewilding context. As discussed, rewilding is presented as an optimistic strategy for conservation seeking to restore natural processes through a minimum intervention approach, benefitting biodiversity and ecosystem services. Furthermore, the ecological importance of large-bodied herbivores acting as proxies for both habitats connectively and ecosystem health is increasingly being acknowledged within the conservation-biology literature.

However, it is also recognised that rewilding should be focusing, not only on the prominence of wild spaces and natural processes, but also on the opportunities to (re)connect society to nature. Tourism has also been established as an important factor in the practical implementation of Rewilding (Cerqueira et al., 2015). Whilst there is no doubt that the promotion of recreational activities will be an important factor for maintaining public support for rewilding areas (Pereira and Navarro, 2015), such activities may present nonlethal and indirect effects which could have significant ecological implications for wildlife and the surrounding community structure (George & Crooks, 2006; Van Doormal et al., 2015). With the pressure of increasing visitor numbers into rewilding areas, it is crucial to understand the effect this is having on animal interactions and behaviour. Assessing any impact of anthropogenic disturbance requires data on distribution and activity patterns of target species in relation to human presence (Frey et al., 2017; Gaynor et al., 2018; Amspacher et al., 2019).

Aim

To assess the effects of human activity on large herbivore temporal behaviour within a rewilded landscape

Hypotheses

1. Herbivores will display a low activity of overlap with humans on trails but a high activity of overlap away from trails
2. Herbivores will display greater nocturnal activity on trails and greater diurnal activity away from the trails
3. Herbivore activity will decrease with an increase in trail width during diurnal hours but increase during nocturnal hours.

2.0 Materials & Methods

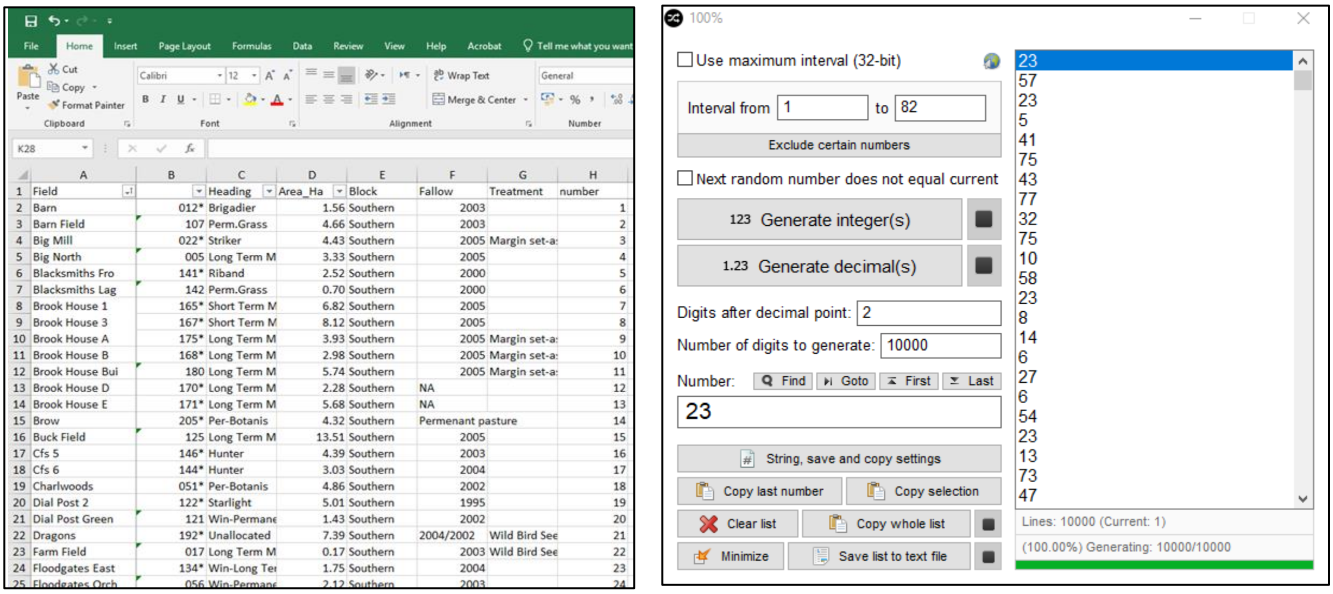
2.1 Study Site

Data collection took place between 20th May to the 14th June 2019 at Knepp Estate; a pioneering rewilding project located to the south of Horsham, West Sussex. The estate encompasses 1417 hectares of heavy Low Weald clay soil covering a bedrock of limestone. This landscape has been divided into 3 blocks, each under a unique vegetation regeneration strategy. First in 2001, the middle block was taken out of agricultural production and reseeded with a grassland mix. Then in 2003, the northern block followed and was reseeded with wildflowers and native grasses. The southern block, being the largest out of the three had a different approach. Between 2001 and 2006, individual fields were removed gradually out of production and left fallow so that the flora could grow back naturally. This particular research took place within the Southern Block of the estate.

2.2 Site Selection

Before camera trap sites could be selected within the southern block, the data was randomised. Fields from the southern block were organised into an excel spreadsheet and numbered 1 – 82. These numbers were then put into a random number generator using the software ‘Softpedia’ and generated 10,000 times until the first 6 numbers could be taken from the top line of the results (see figure 1). This procedure was repeated until it was apparent camera traps would an appropriate distance away from one another, allowing for a broad representation of the southern block whilst avoiding any potential confounding effects and to ensure site independence (Van Berkel, 2014).

Once fields had been selected, the software ‘ArcMap’ (the main component of Esri's ArcGIS suite of geospatial processing programs) was used to plot the GPS coordinates of camera trap placements. A point was arbitrarily selected, approximately in the middle of main trails, permissive footpaths and bridleways of each selected site and GPS coordinates were plotted. The ‘Measure tool’ in ArcMap was then used to select points perpendicular at 50 and 100 metres to the preliminary point from the tracks (see figure 2). The distance variable can therefore be viewed as independent, with limited influence of any subjective choices (Scholten et al., 2018).



	A	B	C	D	E	F	G	H
1	Field		Heading	Area_Ha	Block	Fallow	Treatment	number
2	Barn	012*	Brigadier	1.56	Southern	2003		1
3	Barn Field	107	Perm.Grass	4.66	Southern	2003		2
4	Big Mill	022*	Striker	4.43	Southern	2005	Margin set-a:	3
5	Big North	005	Long Term M	3.33	Southern	2005		4
6	Blacksmiths Fro	141*	Riband	2.52	Southern	2000		5
7	Blacksmiths Lag	142	Perm.Grass	0.70	Southern	2000		6
8	Brook House 1	165*	Short Term M	6.82	Southern	2005		7
9	Brook House 3	167*	Short Term M	8.12	Southern	2005		8
10	Brook House A	175*	Long Term M	3.93	Southern	2005	Margin set-a:	9
11	Brook House B	168*	Long Term M	2.98	Southern	2005	Margin set-a:	10
12	Brook House Bui	180	Long Term M	5.74	Southern	2005	Margin set-a:	11
13	Brook House D	170*	Long Term M	2.28	Southern	NA		12
14	Brook House E	171*	Long Term M	5.68	Southern	NA		13
15	Brow	205*	Per-Botanis	4.32	Southern	Permenant pasture		14
16	Buck Field	125	Long Term M	13.51	Southern	2005		15
17	Cfs 5	146*	Hunter	4.39	Southern	2003		16
18	Cfs 6	144*	Hunter	3.03	Southern	2004		17
19	Charlwoods	051*	Per-Botanis	4.86	Southern	2002		18
20	Dial Post 2	122*	Starlight	5.01	Southern	1995		19
21	Dial Post Green	121	Win-Permane	1.43	Southern	2002		20
22	Dragons	192*	Unallocated	7.39	Southern	2004/2002	Wild Bird See	21
23	Farm Field	017	Long Term M	0.17	Southern	2003	Wild Bird See	22
24	Floodgates East	134*	Win-Long Ter	1.75	Southern	2004		23
25	Floodgates Orch	056	Win-Permane	2.12	Southern	2003		24

☐ Use maximum interval (32-bit)

Interval from 1 to 82

☐ Next random number does not equal current

Digits after decimal point: 2

Number of digits to generate: 10000

Number: 23

23
57
23
5
41
75
43
77
32
75
10
58
23
8
14
6
27
6
54
23
13
73
47

Lines: 10000 (Current: 1)

(100.00%) Generating: 10000/10000

Figure 1: Randomisation of fields using software from ‘Softpedia’.

2.3 Data Collection

9 ‘Busnell DS Low Glow’ and 9 ‘Busnell Essential E3’ camera traps were used in total across

6 fields. Using a combination of a ‘Garmin eTrex 10 Handheld GPS’ device and the mobile application ‘Mapit GIS’, camera traps were placed at the positions previously assigned in ‘ArcMap’. All camera traps were placed approximately 1 metre above ground level and padlocked to stakes, trees and fences for security purposes. Prior to deployment, time (BST/UTC/GMT +1hr) and date was set within the menu settings of each camera trap. Furthermore, because temporal and behavioural data was being collected, camera traps were set to record for 30 seconds of each trigger with 20 second intervals between captures in order to acquire a sufficient amount of data.

To prevent accidental triggers and glare, a ‘Trekrite Explorer Compass’ was used to have camera traps either facing north or south. Additionally, markers were placed at 5 and 10 metres of each camera trap to consider distance sampling. Cameras were active for a total of 16 trap days, which amounted to a sampling effort totalling 288 days. Cameras were checked daily and every trap ran consistently for 24 hours each day as the batteries did not need to be replaced/recharged for the entire study period. Furthermore, to consider anthropogenic infrastructure variables, at each preselected site using a “30 metre Stanley tape measurer”, trail width was measured 5 times at random intervals over a 50-metre stretch. The average width (cm) of the trail could then be calculated for later analysis.

2.4 Video Processing

After the completion of trap sampling, cameras were recovered, and videos were extracted from the memory cards and put into an excel spreadsheet. After all videos were annotated, the entire data set was exported as a comma-separated values (.csv) file used for later analysis in R Studio (Team, R., 2019). Unless it was clear and obvious that the footage observed were of two separate individuals, videos that were captured within 15 minutes of an earlier recording which presented the same species and at the same camera-trap assignment were not used. This is because they were not deemed to be independent samples (Massara et al., 2018). This time-interval is shorter than is usually found in the literature (30 minutes to 1 hour being the most popular timeframe: e.g Diaz-Ruiz et al., 2016; Cruz et al., 2018). However, both Kays and Parsons (2014) and Oberosler et al., (2017) found that reliable independent captures can be obtained even after a few minutes between captures.

Using this timeframe, the remaining data could be viewed as a random sample from the underlying distribution that describes the probability of a video being taken within any particular interval of the day (Ridout and Linkie 2009). The probability density function of this distribution was treated as the activity pattern, which presupposes that the animal is equally likely to be videoed at all times when it is active (Ridout and Linkie 2009; Linkie & Ridout 2011).

Figure 2. *Map of the southern block at Knepp estate, showing the distribution of camera traps around the reserve (on trails, 50 and 100 metres).*

2.5 Statistical Analysis

Statistical analyses were conducted utilising the R software and using the R Studio interface (R Statistical Development Core Team, 2019). Initially by applying the ‘Circular package’ (Lund et al., 2017) a ‘Mardia Watson Wheeler’ test was implemented to compare the 24-hour distribution records of all large herbivores recorded among all sites. However, due to lack of convergence of the test statistics, this function can only be conducted with >10 registers of each recorded species (Massara et al., 2018); therefore, data from each site and distance was pooled in the subsequent analysis (Frey et al., 2017). Activity of all species was categorised into diurnal (species observed between 1 hour after sunrise and 1 hour before sunset) and nocturnal (species observed between 1 hour after the sunset and 1 hour before sunrise) (Sassa, 2010). The density of activity of each species was estimated using kernel density through the ‘Overlap package’ (Meredith and Ridout, 2014). This is a non-parametric statistical test for assessing the probability density-function of random moving variables in space and time (Meredith and Ridout, 2014). Using this information, the most suitable coefficient of overlap was calculated. This overlap varies from 0 (no overlap) to 1 (complete overlap), between herbivore and human activity. The Δ_1 (Dhat1) estimator was used when the number of registers of at least one species had <75 video recordings, whilst the Δ_4 (Dhat 4) estimator was implemented for sample sizes >75. Δ <0.50 was interpreted as low overlap values, > 0.50 Δ < 0.60 as moderate overlap values and Δ >0.60 as high overlap values (Massara et al., 2018). 95% confidence intervals were calculated for Δ from 10,000 bootstrap samples (Efron, 2012; Meredith & Ridout, 2014,). To enhance the coefficient of overlap, the activity package (Rowcliffe, 2019) was used to conduct a ‘Wald test’ (W) for the statistical difference between human and large herbivore activity level estimates for each distance (Rowcliffe et al., 2014). A Wald test was also implemented to test whether large herbivores activity patterns were significantly different between nocturnal and diurnal time periods. Finally, to test the prediction that herbivore activity would decrease on trails with a greater width and that this effect would be more pronounced during daytime a binomial generalised mixed model was adopted.

$$W = \frac{(E_1 - E_2)^2}{s_1^2 + s_2^2}$$

where E_i are the estimates to be compared, s_i their standard errors and the statistic W is χ^2 distributed on one degree of freedom (Rowcliffe et al., 2014).

3.0 Results

3.1 Camera Trapping

The sampling effort over 288 days (mean ± SE: 48 ± 2.5 trap days per site) resulted in 5 out of 6 large herbivore species being recorded (Exmoor ponies were not detected, n = 0). Camera trapping led to 2708 independent detections (see table 1 for full analysis) of humans (n=2097), Fallow deer (n = 311), Long horn cattle (n = 195), Red deer (n = 46), Roe deer (n = 39) and Tamworth pig (n = 2) (see figure 3). 1.15% of recordings could not be identified, either due to light under/over exposure or poor animal angle. The number of independent detections of Tamworth pig was too low (n = 2) to do any sufficient analysis and therefore was removed from the overall sample. There were 7 different types of recreational activities/disturbances that people participated in (summarised in figure 4). Of all the recreational activities, people Walking/ Hiking & Dog walking were most prominent (54% & 23%).

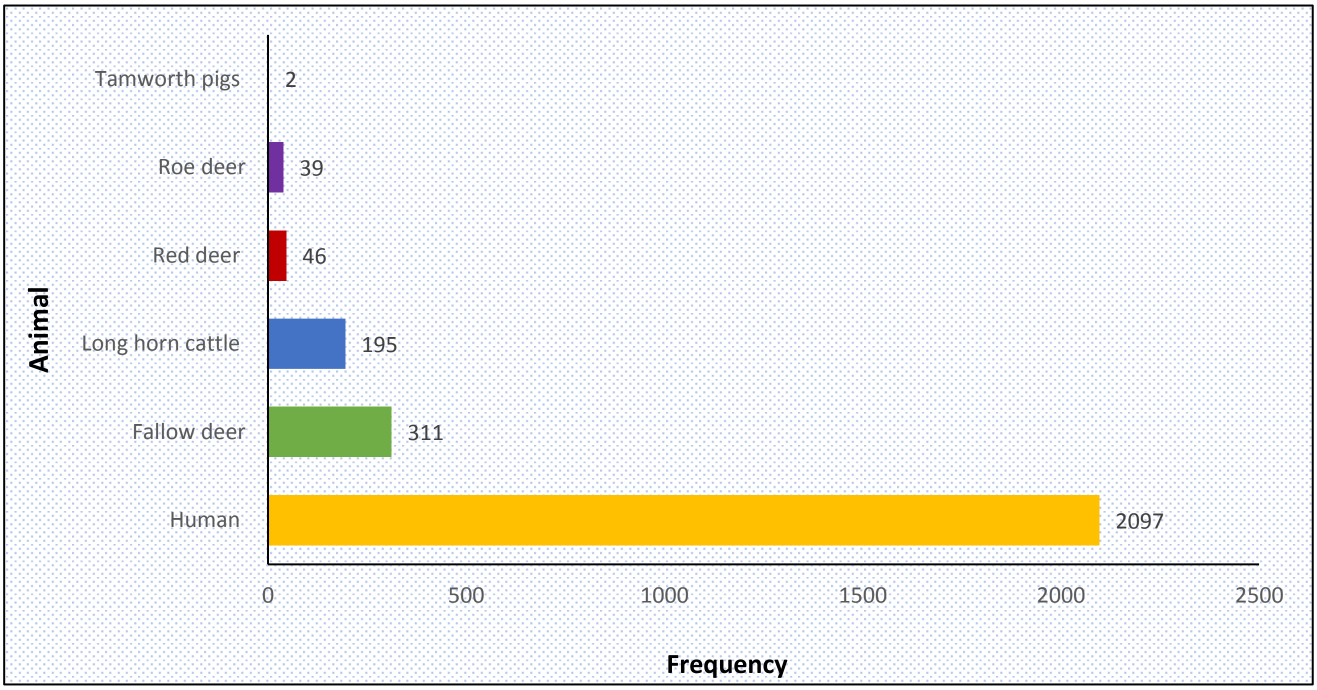


Figure 3. *Frequency of all large herbivores and Humans captured on camera traps across all study sites*

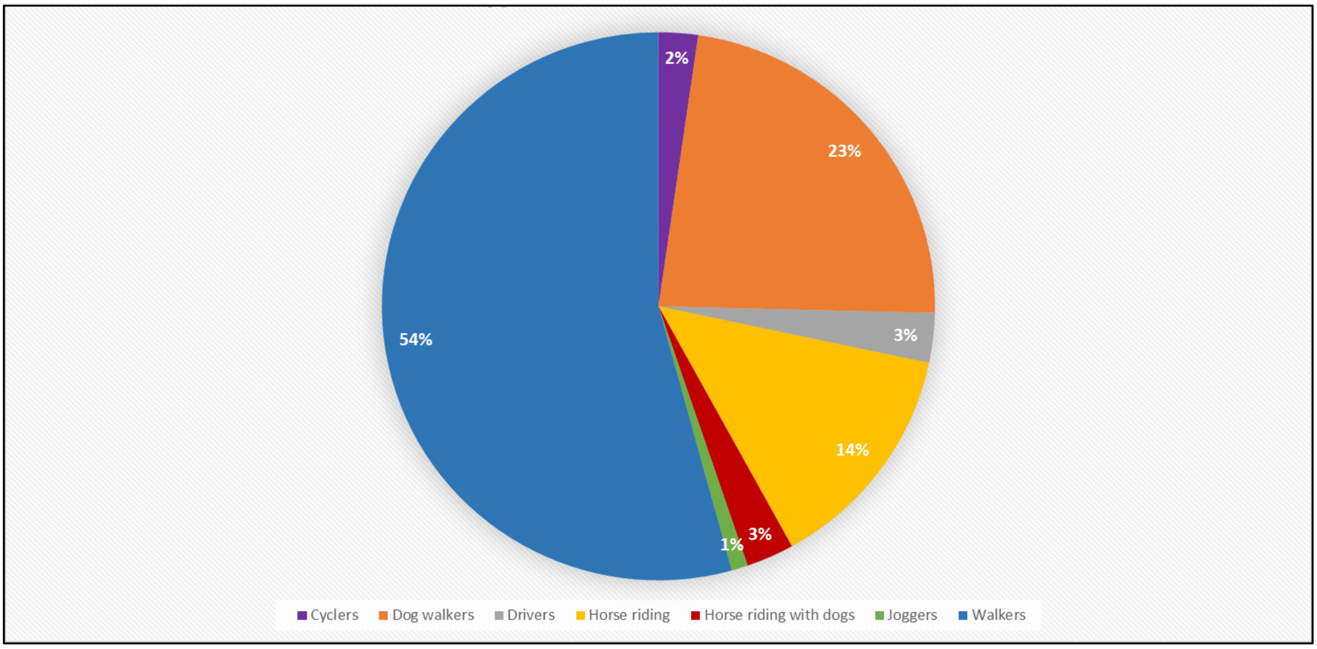


Figure 4. *Type of human disturbance, 54% of the 2097 people captured were walkers, 23% Dog walkers, 14% Horse riders, 3% Horse riders with dogs and 3% people driving vehicles, 2% cycling and 1% Jogging.*

Table 1

2.2 Activity Overlap & Nocturnality

On trails (a) the coefficient of overlap between the activity of all three deer species (see figures 5, 6, 7) and humans was low (Fallow deer Δ_4 = 0.25, CI = 0.19 – 0.31; Red deer Δ_1 = 0.31, CI = 0.14 – 0.50; Roe deer Δ_1 = 0.28, CI 0.13 – 0.42), whereas the coefficient of overlap between Long horn cattle and humans was high (Long horn cattle Δ_4 = 0.64, CI = 0.34 - 0.82). The Wald test also corroborated this result, as significantly different activity levels ($p<0.05$) were observed between humans and deer but not between humans and long horn cattle (see table 2). Furthermore, on trails all cervids were significantly more active over nocturnal time periods, whilst long horn cattle displayed significantly greater diurnal activity (see figure 5a,6a,7a,8a. & table 3).

At 50 metres away from the trail the coefficient of overlap between the activity of Red deer, Roe deer, Long horn cattle and humans was low (Red deer Δ_1 = 0.21, CI = 0.04 - 0.40; Roe Δ_1 deer = 0.21, CI = 0.06 - 0.29; Long horn cattle Δ_1 = 0.18, CI = 0.11 - 0.25), whilst high activity overlap was observed for Fallow deer (Fallow deer Δ_1 = 0.72, CI = 0.60 - 0.82). For this distance the Wald test displayed significant results for all animals apart from Fallow deer (W = 2.48, p = 0.11). Additionally, at this distance both Red and Roe deer displayed greater nocturnal activity, whilst Fallow and Long horn cattle demonstrated diurnal activity. However only Roe and Fallow deer produced significant results (see figures 5b ,6b ,7b ,8b & table 3).

Finally, 100 metres away from the trail both Fallow and Long horn cattle displayed a high coefficient of overlap with humans (Fallow deer Δ_4 =0.66 CI = 0.58 - 0.73; Long horn cattle Δ_1 = 0.60 CI = 0.35 0.82), whilst Red deer presented a moderate coefficient of overlap and Roe Deer presented a low degree of activity overlap (Red deer Δ_1 = 0.51, CI = 0.33 - 0.61; Roe deer Δ_1 = 0.30, CI= 0.12 - 0.51. The Wald test revealed significant activity differences between humans and Roe deer (W = 10.4, p = 0.001) but not for any other animal (see table 2). At this distance all animals apart from Roe deer displayed greater diurnal activity, though the Wald test revealed that this was only significant for Fallow and Red deer (see figures 5c ,6c ,7c ,8c & table 3).

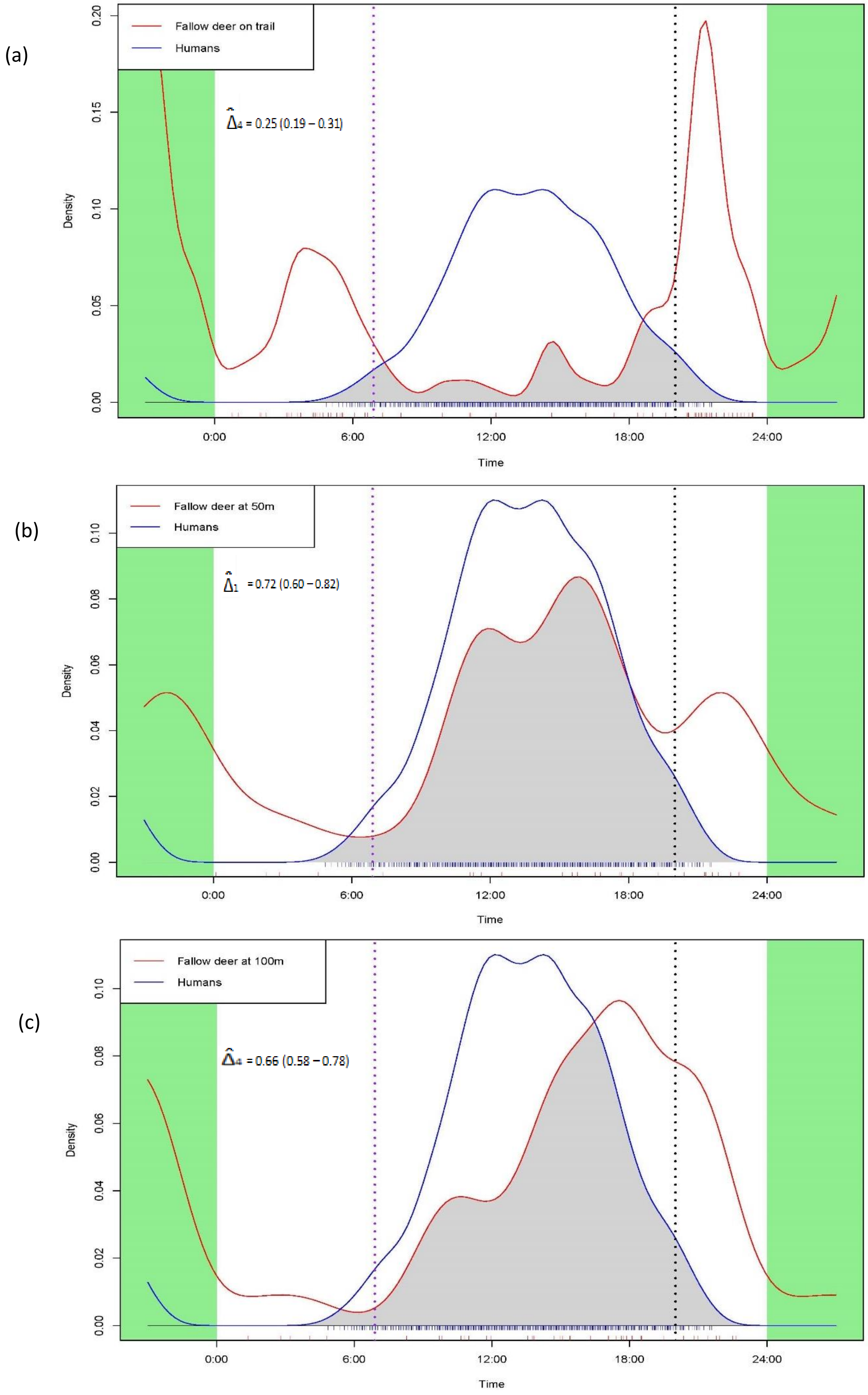


Figure 5. *Low temporal overlap between Humans and Fallow Deer on trails (**a:** $\hat{\Delta}_4$ = 0.25 with 95% CI 0.19 - 0.31) however, there is high temporal overlap at both 50 (**b**: $\hat{\Delta}_1$ = 0.72 with 95% CI 0.60 – 0.82) and 100 metres (**c:** $\hat{\Delta}_4$ = 0.66 with 95% CI 0.58 – 0.78). Overlap between activity periods is represented by the shaded area. The x-axis represents the time of day (hr) and the y-axis represents the kernel density (density of temporal activity). (....)* represents sunrise and (....) represents sunset.

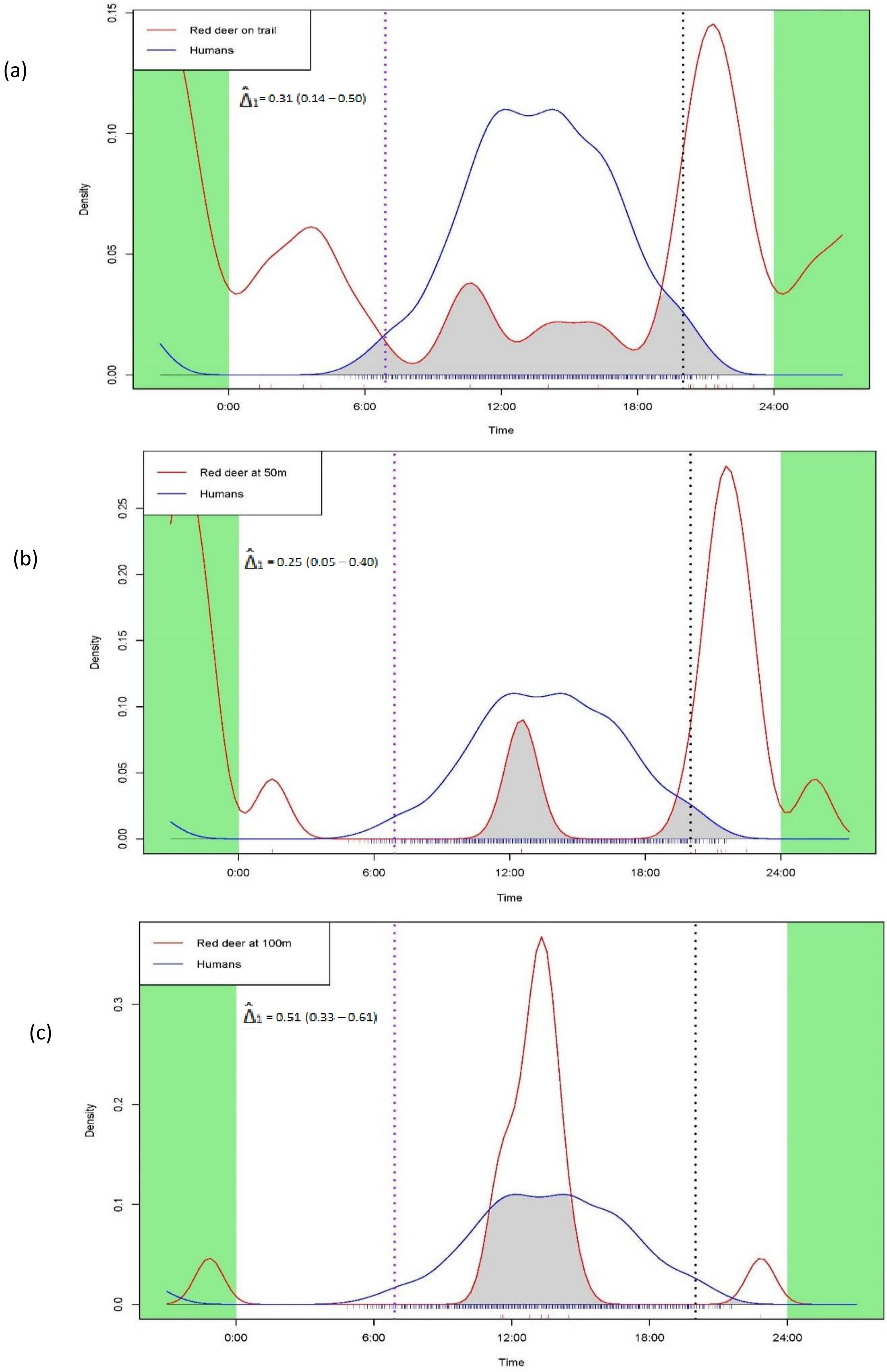


Figure 6. *Low temporal overlap between Humans and Red Deer on trails (**a:** $\hat{\Delta}_1$= 0.31 with 95% CI 0.14 - 0.50) & at 50 metres (**b**: $\hat{\Delta}_1$ = 0.25 with 95% CI 0.05 – 0.40) however, there is moderate overlap at 100 metres (**c:** $\hat{\Delta}_1$ = 0.51 with 95% CI 0.33 – 0.61). Overlap between activity periods is represented by the shaded area. The x-axis represents the time of day (hr) and the y-axis represents the kernel density (density of temporal activity). (••••)* represents sunrise and (••••) represents sunset.

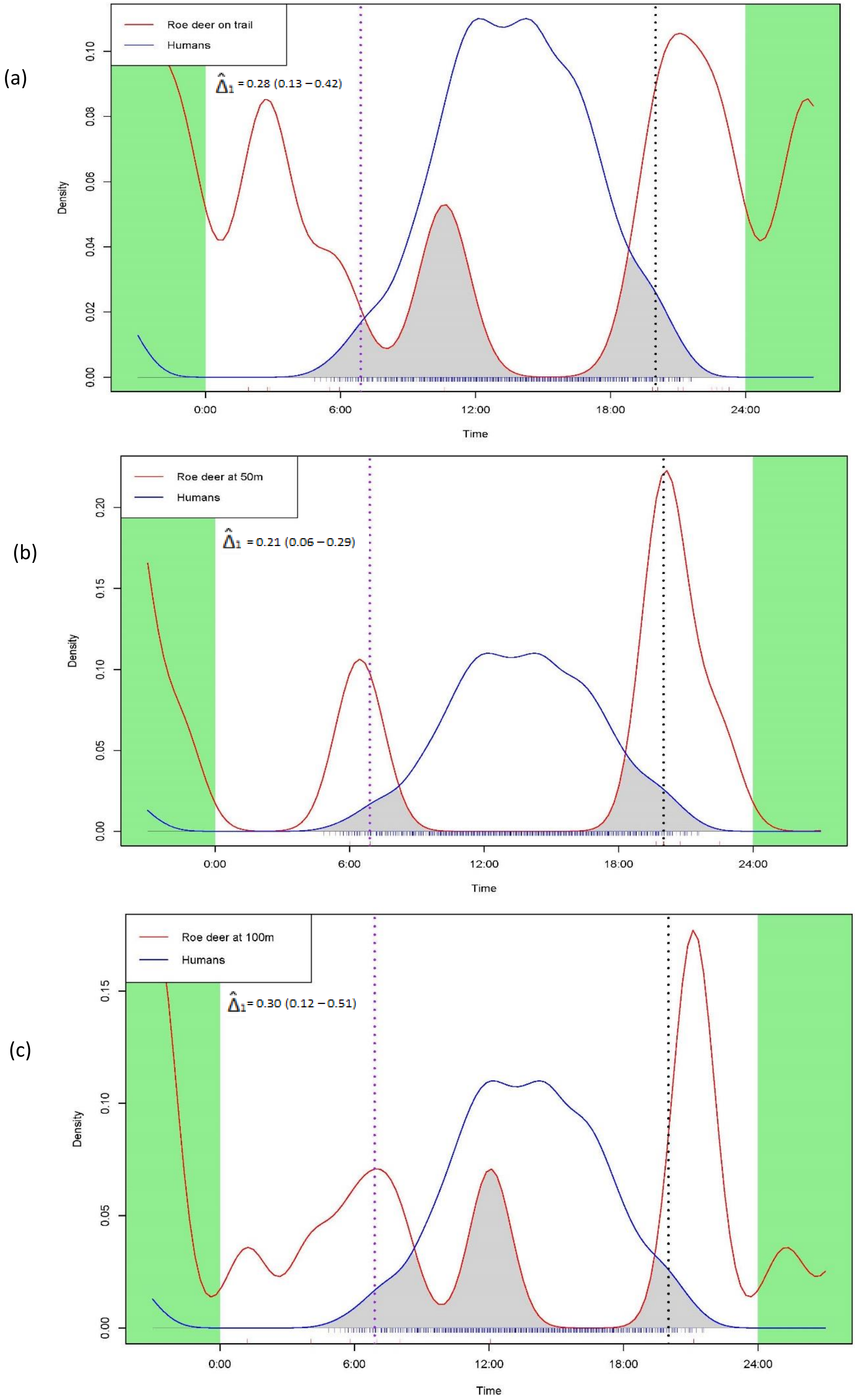


Figure 7. *Low temporal overlap between Humans and Roe Deer on trails, (**a:** $\hat{\Delta}_1$ = 0.28 with 95% CI 0.13 - 0.42) at 50 metres (**b:** $\hat{\Delta}_1$ = 0.21 with 95% CI 0.06 – 0.29) & at 100 metres (**c:** $\hat{\Delta}_1$ = 0.30 with 95% CI 0.12 – 0.51). Overlap between activity periods is represented by the shaded area. The x-axis represents the time of day (hr) and the y-axis represents the kernel density (density of temporal activity). (**••••**)* represents sunrise and (**••••**) represents sunset.

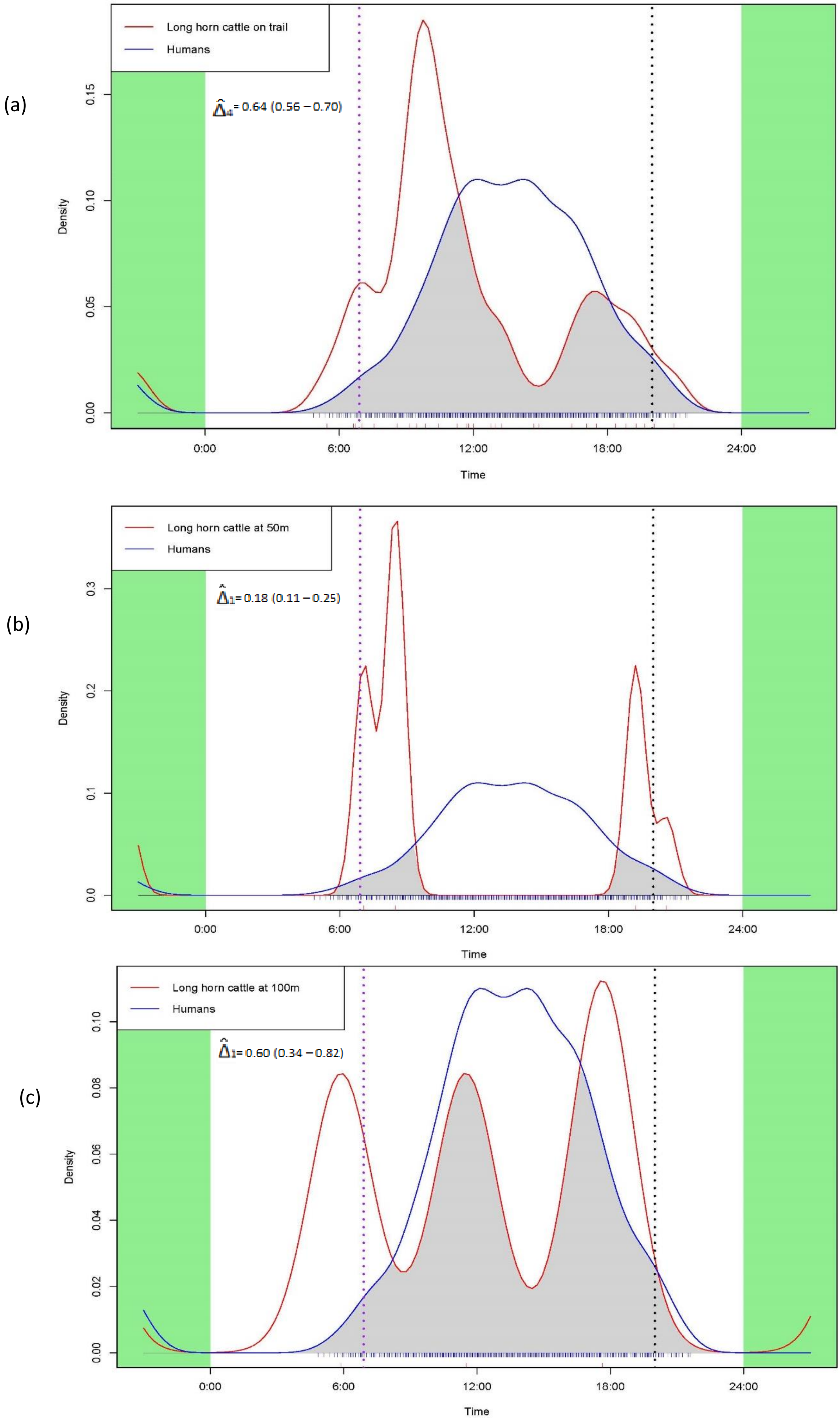


Figure 8. *High temporal overlap between Humans and Long horn cattle on trails (**a:** $\hat{\Delta}_4$= 0.64 with 95% CI 0.56 - 0.70) and at 100 metres (**c:** $\hat{\Delta}_1$ = 0.60 with 95% CI 0.34 – 0.82). However, there is no temporal overlap at 50 metres (**b**: $\hat{\Delta}_1$= 0.18 with 95% CI 0.11 – 0.25). Overlap between activity periods is represented by the shaded area. The x-axis represents the time of day (hr) and the y-axis represents the kernel density (density of temporal activity). (****••••****)* represents sunrise and (**••••**) represents sunset.

Table 2

Table 3

2.3 Trail Width

The binomial GLMM revealed that all herbivores except Roe deer (R^2 = 0.006, 1/Slope = 0.23) showed a positive association with an increase in trail width during nocturnal hours, whilst all herbivores excect Long horn cattle (R^2 = 0.34, 1/Slope = 0.16) displayed a negative association with an increase in trail width during diurnal hours (see figures 9, 10, 11, 12 & table 4). Even though correlations were established, only Roe deer showed a significantly negative correlation with an increase in trail width during the day (see figure 11 & table 4).

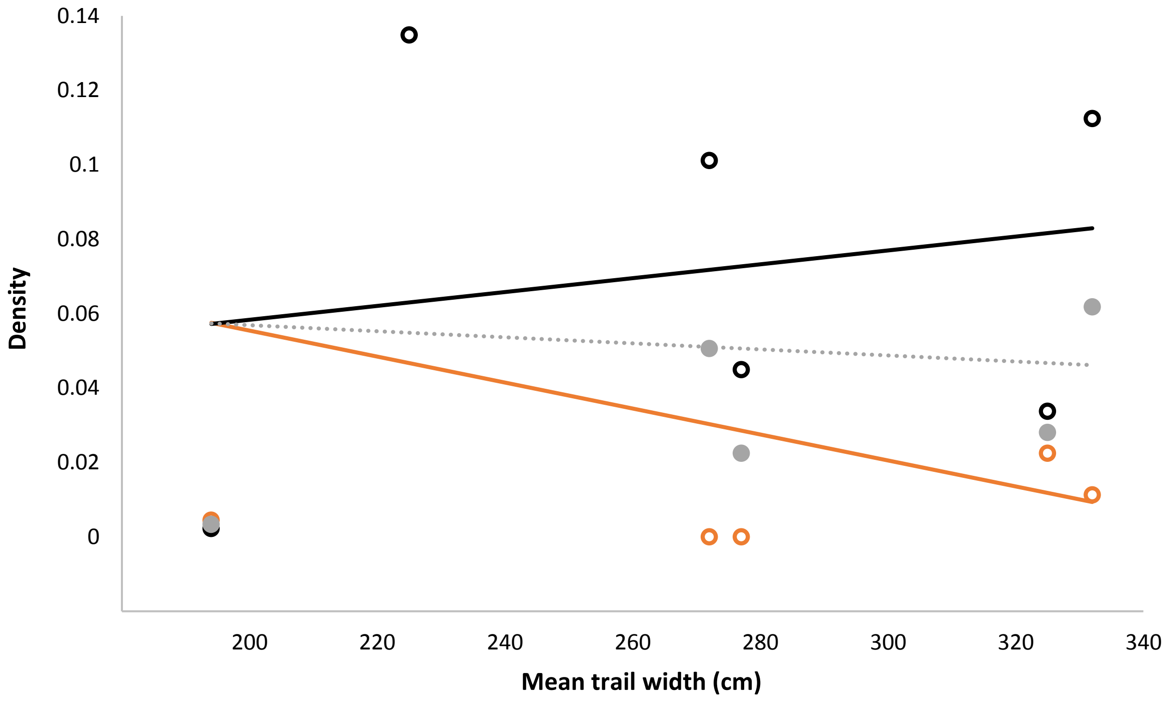


Figure 9. Scatter plot displaying the relationship between Fallow deer activity and trail width. The black linear line (▬) represents night-time and orange linear line (▬) represents daytime. The average is represented by the grey dotted line (……..).

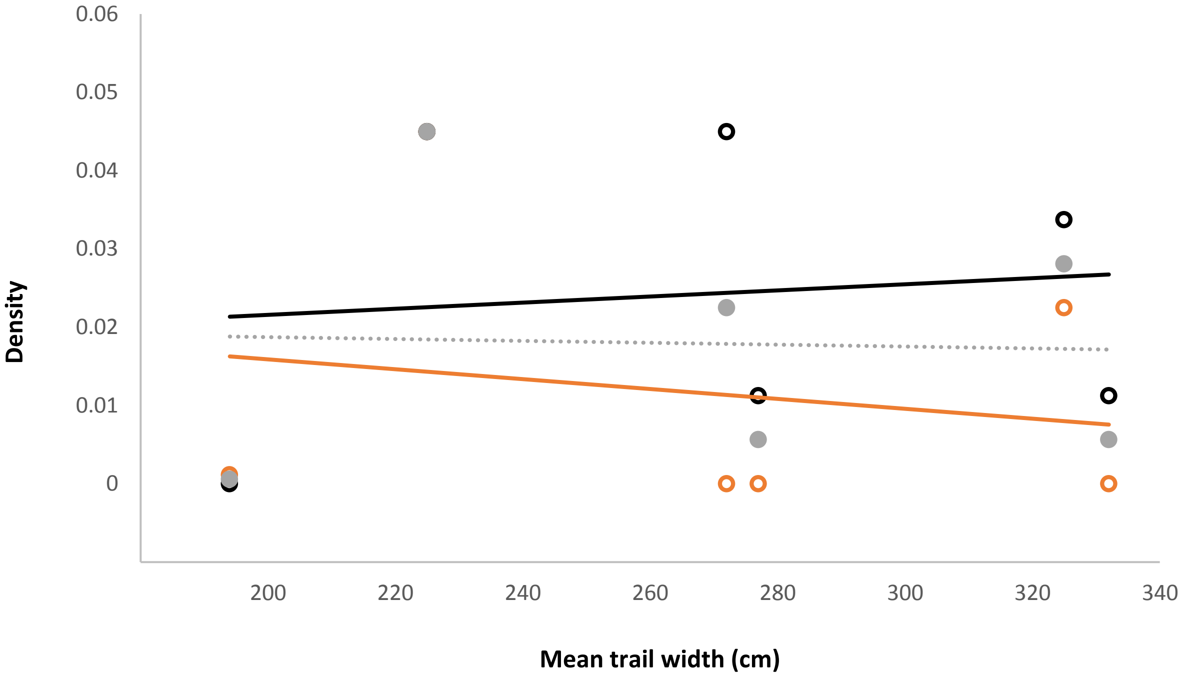


Figure 10. Scatter plot displaying the relationship between Red deer activity and trail width. The black linear line (——) represents night-time and orange linear line (——) represents daytime. The average is represented by the grey dotted line (········).

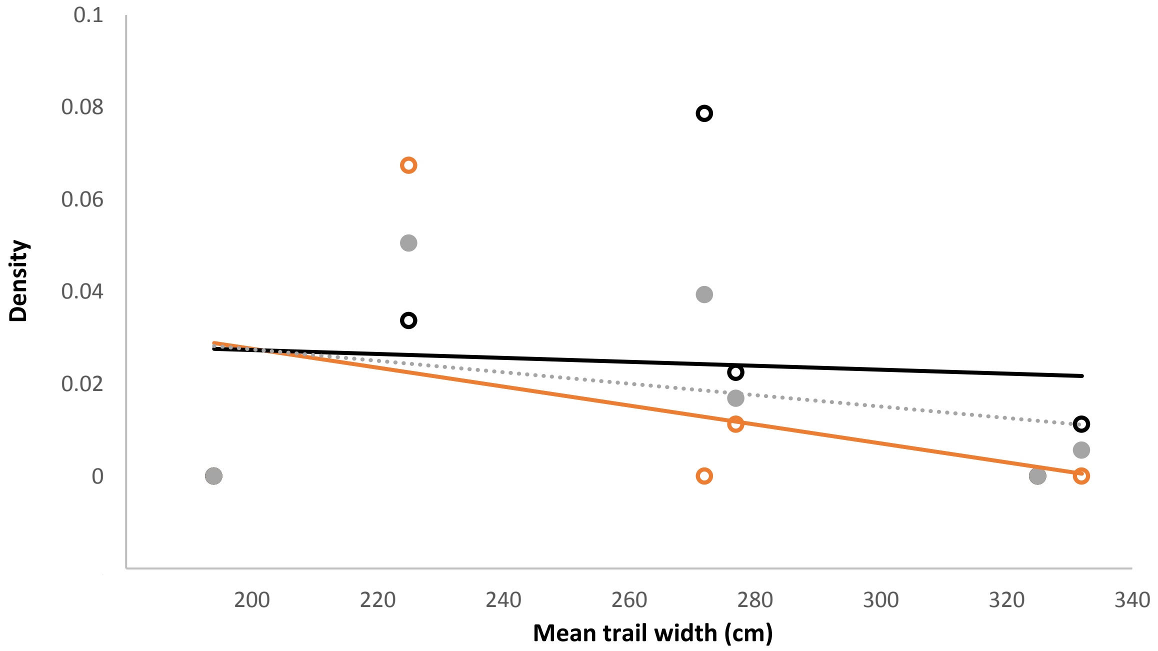


Figure 11. Scatter plot displaying the relationship between Roe deer activity and trail width. The black linear line (——) represents night-time and orange linear line (——) represents daytime. The average is represented by the grey dotted line (········).

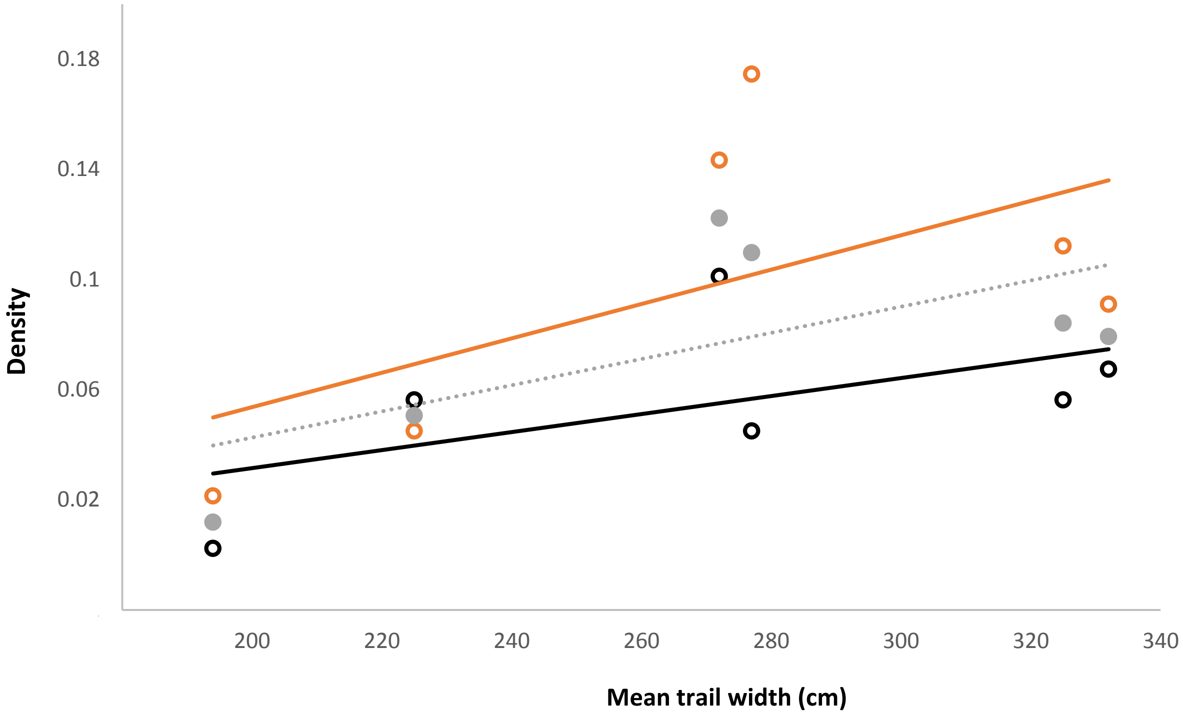


Figure 12. Scatter plot displaying the relationship between horn cattle activity and trail width. The black linear line (——) represents night-time and orange linear line (——) represents daytime. The average is represented by the grey dotted line (⋯⋯).

Table 4

4.0 Discussion

4.1 Overlap

All cervids in the present study displayed significantly low temporal overlap with human activity on trails, whilst long horn cattle presented significantly high temporal activity overlap. However, with increasing distance from the trail this overlap varied greatly between all herbivores and therefore the first hypothesis must be rejected. There are several possible reasons for the variation observed in the present study. The fact that both Roe and Red deer both demonstrated low - moderate activity overlap, even with increasing distance away from trails fits their behavioural description and traits as being an elusive ungulate which is sensitive and shies away from human activity, even at distances >100 metres (Scholten et al., 2018).

The results from Fallow deer indicate that they are still avoiding trail use during high human activity (Δ4 = 0.25, CI = 0.19 – 0.31). However, compared to both Red and Roe deer, Fallow deer are more content displaying non-vigilant routine behaviours (foraging, roaming, grooming) 50 and 100 metres away from the trail (Δ1 = 0.72, CI = 0.60 - 0.82; Δ4 =0.66 CI = 0.58 - 0.73). Long horn cattle on the other hand displayed a random assortment of overlap with human activity, with high overlap being presented on the trails and at 100 metres (Δ4 = 0.64, CI = 0.34 - 0.82; Δ1 = 0.60 CI = 0.35 0.82). The behaviours observed could be an indication that because of the relatively high density of both Fallow deer and Long horn cattle compared to that of the other ungulates, both these animals have become more tolerant and potentially desensitised to human recreational activity (Malo et al., 2011; Skarin and Ahman, 2014). However, non-uniform activity overlap observed by all herbivores could also be due to the relatively low sample size (n =39, n = 46) detected in the current study. Although their exact population size is unknown, it is recognised that Roe deer occur in the southern block in relatively small densities whilst the last recorded stocking number for Red deer in the southern block was also small (n = 48) (Overend and Lorimer, 2018; Tree, 2018).

Even with the low Dhat1 sample estimator, such small sample sizes could give an underrepresentation of the temporal activity overlap observed in the current study, making it challenging to infer whether such variation was due to human recreation or other environmental factors (Pigeon et al., 2016; Ladle et al., 2018). The current study was conducted over a short sampling period (n = 16 days), with limited site selection (n = 6) and lack of seasonal variation (Summer) and this may have influenced the trends observed. Such fine-scale inferential analysis requires a robust sampling design as well as large amounts of data for capturing the effect of multiple explanatory variables across a spatial gradient (Frey et al., 2017). Srbek-Araujo and Chiarello (2013) demonstrated that presence or non-detection as well as capture rates vary significantly among the different sampling lengths and designs.

4.2 Nocturnality

The current study was able to demonstrate how all deer species were significantly ($p<0.05$) more active on the trail during nocturnal hours when human activity was low. However only Fallow deer displayed greater diurnal activity away from the trails (50m = (W) 4.70, SE ± 0.02, p = 0.04; 100m = (W) 7.16, SE ± 0.04, p = 0.05), therefore the second hypothesis must be rejected. Nevertheless, with regards to trail activity, such findings have been consistently repeated by numerous authors. Coppes et al (2017) also found that during both winter and summer seasons Red deer actively avoided human trails during the day but were positively associated with them during the night. Similar results were also demonstrated by Sibbald et al (2011), who found that deer moved away from the source of disturbance when trails were active with hill walkers. However, this effect lasted for the entire 24-hour period even when the trails were quiet again. Herbivores that become progressively nocturnal may radically modify their diets toward forage and nutrition that are more available at night, thereby rearranging lower trophic levels (Ordiz et al., 2017; Gaynor et al., 2018).

Deer are not exclusively nocturnal but become more nocturnal during the hunting season and when it otherwise protects them (Ensing et al., 2014). Crepuscular is sometimes a better term for deer and as highlighted by the present study’s activity overlap analysis, may have been a more appropriate classification to use to describe the cervids activity pattern. Animals which are known to display crepuscular activity are thought to be active between twilight hours (the period approximately before dusk and immediately after dawn) (Pagon et al., 2013). The appropriate application of the term is also debated as some crepuscular species display activity throughout an overcast day or during a moonlit night (Meiswinkel & Elbers, 2016). Roe and White-tailed deer (*Odocoileus virginianus*) have been shown to exhibit crepuscular activity patterns that is shaped by their natural predators as well as human activity (Olson, Squibb, and Gilbert, 1998; Pan et al., 2011). Furthermore, the time of day cervids are active also relies on additional factors: prey may attempt to evade times when their primary predators are roaming (Beier and McCullough 1990), whilst predators try to link their activities to times at when their prey are active (Sih, Englund, & Wooster, 1998). Additionally, cervids may need to adjust their activity levels based on whether the temperature during the day is too high or too low at night, meaning the compromise of crepuscular periods may be the best activity-hours that meet their everyday requirements (Scheibe et al., 2009).

Anthropogenic-induced alterations in wildlife diel activity is a growing field of inquiry. Nevertheless, very limited studies have examined the population, community or individual level significance of these behavioural alterations (Gaynor et al., 2018). Given the extensive evidence of amplified night-time activity presented in the literature, there is a need to research not just the implications for species interactions, habitat selection and the physiological effects but also its magnitude, not just in terms of rewilding but ecological conservation as a whole. This extends to a requirement for additional synthetic analyses and competent research to look into whether ungulates as well as nonmammalian taxa within Knepp are exhibiting diel shifts in response to human activity (Atickem, Loe & Stenseth., 2014; Gaynor et al., 2018).

4.3 Trail Width

Even though trends were established, only Roe deer displayed a significant negative correlation with an increase in trail width during the day ($R^2 = 0.17 \pm 0.08$, $p = 0.04$). Thus, it cannot be said with confiendence that trail width influences herbivore activity and therefore the third hypothesis must be rejected. Considering how significant results were found for both of the previous hypotheses, with regards to cervid temporal activity being different from human on trails, it is surprising that more significant results were not found. Scholten et al (2018) only found a marginal effect between Red deer activity and trail width. However, this was not significant for their pellet counts nor camera trap analysis. The authors put the results down to the trails being significantly smaller (<177cm) than trails found in more populated areas. However, this was not the case for the current study, as the average trail width ranged from 194 – 332 cm respectively.

The limited number of trails used (n=6), sampling duration, as well as herbivore sample size could be the explanations for the results observed here. Even though a bionomial GLMM was established as being the most appropriate test to show the interaction between herbivore diurnal/ nocturnal activity and trail width, both standard error and significancy can be profoundly affected by small sample sizes when conducting this statistical test (Bolker et al., 2009). Furthermore, the current study only chose sites (main trails, bridleways, footpaths) that were permissive to human recreationists. Knepp have adopted a system of spatial zonation, whereby refuges have been created in-order to separate human activity and wildlife. Comparing the permissive pathways to these wildlife refuges would be an interesting aspect to explore in the future, as studies have demonstrated how animals, sensitive to human activity, tend to retreat to such sancturies (Milner et al., 2006; Coppes et al., 2017).

4.4 Limitations & Future Research

The present study used camera-trapping technology to attain an innovative understanding into how human activity affects the herbivore behaviour within a rewilded landscape. However, the current study has caveats that impact on the validity and reliability of similarly conducted non-systematic methodological procedures (Azevedo et al., 2018). For example, due to the insufficient herbivore sample size across all sites and distances, data was pooled for the subsequent activity pattern analysis. Therefore, it is conceded that there might be other inter-site-specific variables at play (Ridout & Linkie, 2009). Further longitudinal studies into the variances between study sites would undoubtedly be of interest and importance in enhancing the understanding of how anthropogenic and biophysical landscape aspects influence spatiotemporal activity patterns of herbivores within Knepp (Linkie & Ridout, 2011; Bowler et al., 2017; Azevedo et al., 2018).

Even though the current study only looked at human activity, interspecific interactions and other ecological and/or environmental variables play an essential part in moulding species' behaviours and demography (Araújo & Luoto, 2007; Ladle et al., 2018). For example, interspecific competition has been demonstrated to cause resource-partitioning which permits numerous species that are ecologically similar to coincide within the same area (Amarasekare, 2002), thus ensuring sympatry with niche-divergence (Rosenzweig, 1991; Ladle et al., 2018). Current statistical procedures now allow for occurrences of multiple species to be modelled as a function of both conditional and habitat variables in relation to the presence of other species (Rota et al., 2016). Ignoring such biotic and abiotic interactions and relationships between species and associated environment can cause inaccurate and biased conclusions regarding an animal's changes in behaviour or habitat selection (Rota et al., 2016). Even though integrating such interactions into species-distribution modelling can be logistically complicated, and challenging, occupancy-models are statistical frameworks that allow researchers to examine relationships between habitat characteristics of a particular area and the presence/absence of a community or individual species (Ladle et al., 2018; Massara et al., 2018). Such a framework could be incorporated into future studies looking into herbivore/human temporal segregation and niche divergence within rewilded landscapes.

Despite the fact that the current study was able to establish a low overlap between human and deer activity at varying distances, it did not identify the exact drivers that may be causing this avoidance (ie. The type of human activity taking place at the time of low herbivore activity). Lenth et al (2008) studied mammal activity close to and far from trails in parks where leashed dogs were permitted on trails as well as in parks where dogs were prohibited. They found lower signs of activity of mule deer (*O. hemionus*), rabbits (*Sylvilagus spp.*), prairie dogs (*Cynomys ludovicianus*), and other small mammals on trails where dogs were permitted, compared to dog-free trails. Other studies have demonstrated how dogs off leashes can have even more detrimental effects on wildlife, with some injuring and even killing animals in reserves (Holderness-Roddam and McQuillan 2014). Dog walking was the second most popular recreational activity observed around the southern block (23%), with 80% of the dogs observed being off their lead. Knepp try to enforce a strict rule of having dogs on leashes at all times whilst walking in the reserve. Exploring such fine scale interactions could have important management implications for the project in the future.

5.0 Conclusion

Based on the results gathered from the present study it would appear that human activity is having a behavioural impact on cervids within the southern block of Knepp. However, due to the limited extent in sampling, and other temporal/ environmental factors, it cannot be said with confidence that the trends observed in the present study are of a direct consequence of anthropogenic activity. Like many other rewilding projects, the majority of Knepp’s income comes from ecotourism; as they currently offer camping, glamping as well as a variety of wildlife safaris. Furthermore, to be taken into account are the psychological and physiological benefits that are associated with individuals of all ages being exposed to natural or green spaces. However, in the context of rewilding and conservation in general there are multiple cumulative effects of anthropogenic impacts as well as interacting ecological processes yet to unravel.

Examining the human-induced fine and extensive scale temporal behavioural changes amongst wildlife will undoubtedly be an essential area of future research, as the indirect impacts of environmental (including human activity) stressors on species interactions and activity may be as significant as the direct effects (Frey et al., 2017). However, given the high geological and topographical variation that exists across the United Kingdom and in rewilding areas in particular, a more accurate methodology to consider in the future when examining spatial and temporal behaviour change within a landscape, may be one that incorporates different modelling frameworks (e.g. occupancy model) as there is likely to be several disturbance factors (season, sex, temperature, grazing-intensity, forage type, flood, fire, disease, wind & human activity), all driving change to differing extents, the significance of which could also vary over time (Hodder et al., 2009; Pagon et al., 2013; Ladle et al., 2018).

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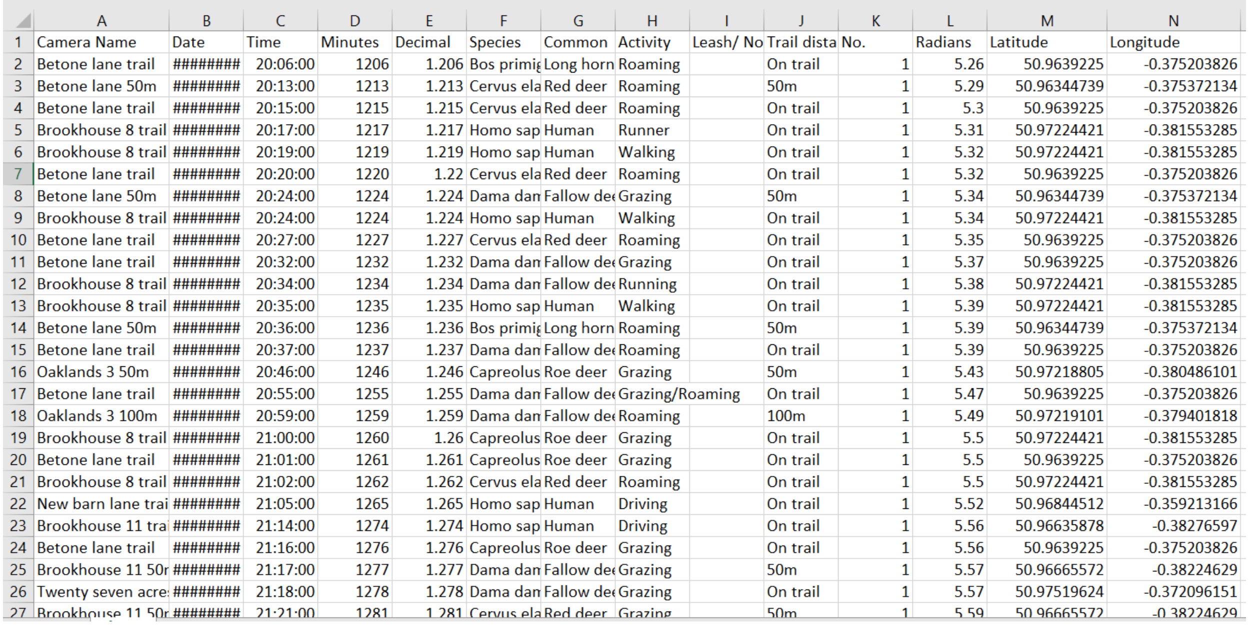
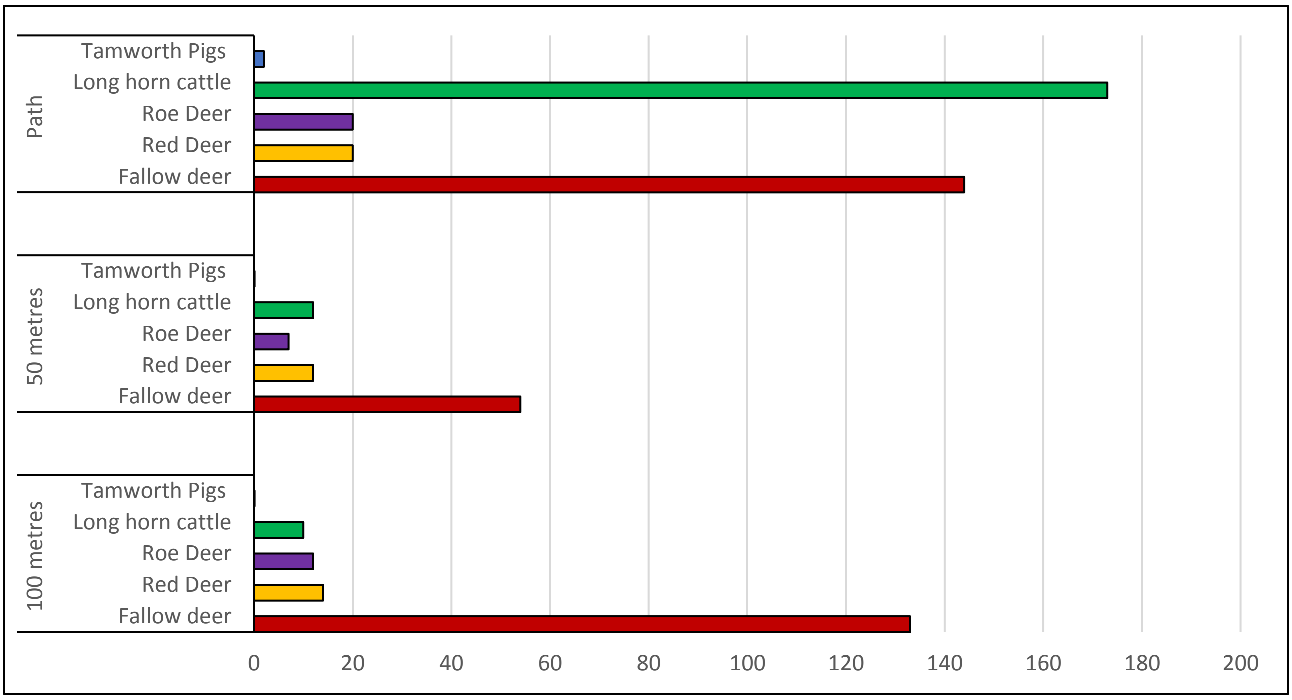
Appendix

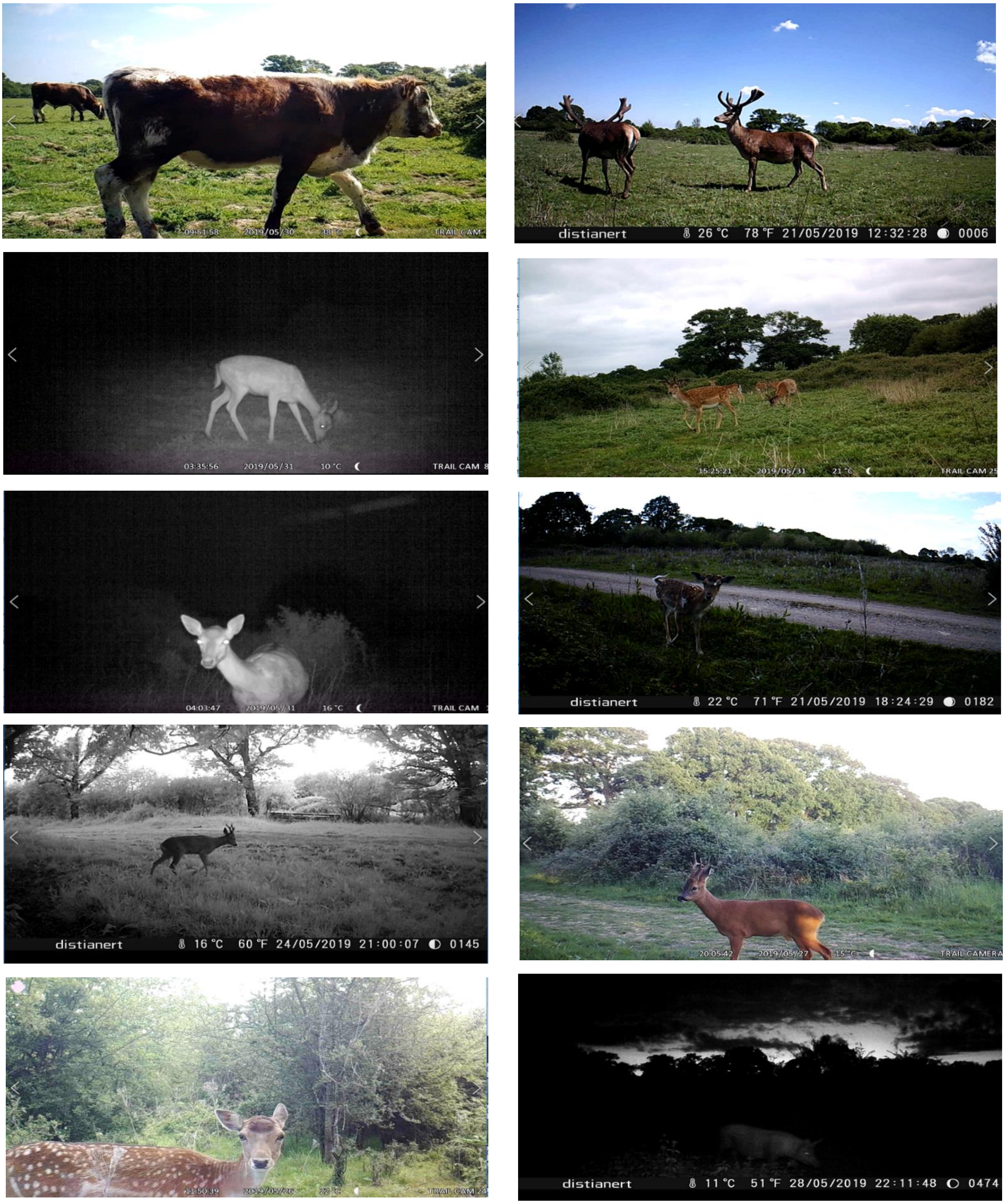
Appendix table A: *Sample of how data was processed in excel before being imported into R Studio.*



	A	B	C	D	E	F	G	H	I	J	K	L	M	N
1	Camera Name	Date	Time	Minutes	Decimal	Species	Common	Activity	Leash/ No	Trail dista	No.	Radians	Latitude	Longitude
2	Betone lane trail	########	20:06:00	1206	1.206	Bos primig	Long horn	Roaming		On trail	1	5.26	50.9639225	-0.375203826
3	Betone lane 50m	########	20:13:00	1213	1.213	Cervus ela	Red deer	Roaming		50m	1	5.29	50.96344739	-0.375372134
4	Betone lane trail	########	20:15:00	1215	1.215	Cervus ela	Red deer	Roaming		On trail	1	5.3	50.9639225	-0.375203826
5	Brookhouse 8 trail	########	20:17:00	1217	1.217	Homo sap	Human	Runner		On trail	1	5.31	50.97224421	-0.381553285
6	Brookhouse 8 trail	########	20:19:00	1219	1.219	Homo sap	Human	Walking		On trail	1	5.32	50.97224421	-0.381553285
7	Betone lane trail	########	20:20:00	1220	1.22	Cervus ela	Red deer	Roaming		On trail	1	5.32	50.9639225	-0.375203826
8	Betone lane 50m	########	20:24:00	1224	1.224	Dama dan	Fallow de	Grazing		50m	1	5.34	50.96344739	-0.375372134
9	Brookhouse 8 trail	########	20:24:00	1224	1.224	Homo sap	Human	Walking		On trail	1	5.34	50.97224421	-0.381553285
10	Betone lane trail	########	20:27:00	1227	1.227	Cervus ela	Red deer	Roaming		On trail	1	5.35	50.9639225	-0.375203826
11	Betone lane trail	########	20:32:00	1232	1.232	Dama dan	Fallow de	Grazing		On trail	1	5.37	50.9639225	-0.375203826
12	Brookhouse 8 trail	########	20:34:00	1234	1.234	Dama dan	Fallow de	Running		On trail	1	5.38	50.97224421	-0.381553285
13	Brookhouse 8 trail	########	20:35:00	1235	1.235	Homo sap	Human	Walking		On trail	1	5.39	50.97224421	-0.381553285
14	Betone lane 50m	########	20:36:00	1236	1.236	Bos primig	Long horn	Roaming		50m	1	5.39	50.96344739	-0.375372134
15	Betone lane trail	########	20:37:00	1237	1.237	Dama dan	Fallow de	Roaming		On trail	1	5.39	50.9639225	-0.375203826
16	Oaklands 3 50m	########	20:46:00	1246	1.246	Capreolus	Roe deer	Grazing		50m	1	5.43	50.97218805	-0.380486101
17	Betone lane trail	########	20:55:00	1255	1.255	Dama dan	Fallow de	Grazing/Roaming		On trail	1	5.47	50.9639225	-0.375203826
18	Oaklands 3 100m	########	20:59:00	1259	1.259	Dama dan	Fallow de	Roaming		100m	1	5.49	50.97219101	-0.379401818
19	Brookhouse 8 trail	########	21:00:00	1260	1.26	Capreolus	Roe deer	Grazing		On trail	1	5.5	50.97224421	-0.381553285
20	Betone lane trail	########	21:01:00	1261	1.261	Capreolus	Roe deer	Grazing		On trail	1	5.5	50.9639225	-0.375203826
21	Brookhouse 8 trail	########	21:02:00	1262	1.262	Cervus ela	Red deer	Roaming		On trail	1	5.5	50.97224421	-0.381553285
22	New barn lane trai	########	21:05:00	1265	1.265	Homo sap	Human	Driving		On trail	1	5.52	50.96844512	-0.359213166
23	Brookhouse 11 trai	########	21:14:00	1274	1.274	Homo sap	Human	Driving		On trail	1	5.56	50.96635878	-0.38276597
24	Betone lane trail	########	21:16:00	1276	1.276	Capreolus	Roe deer	Grazing		On trail	1	5.56	50.9639225	-0.375203826
25	Brookhouse 11 50r	########	21:17:00	1277	1.277	Dama dan	Fallow de	Grazing		50m	1	5.57	50.96665572	-0.38224629
26	Twenty seven acre	########	21:18:00	1278	1.278	Dama dan	Fallow de	Grazing		On trail	1	5.57	50.97519624	-0.372096151
27	Brookhouse 11 50r	########	21:21:00	1281	1.281	Cervus ela	Red deer	Grazing		50m	1	5.59	50.96665572	-0.38224629



Appendix figure A: *frequency of herbivore detections at varying distances.*



Appendix figure B: *Collage of various herbivores captured over the study period.*