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Red deer exhibit spatial and temporal responses to hiking activity

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Outdoor recreation has the potential to impact the spatial and temporal distribution of animals. We explore interactions between red deer *Cervus elaphus* and hikers along a popular hiking path in the Scottish Highlands. We placed camera traps in transects at different distances (25, 75 and 150 m) from the path to study whether distance from hiker activity influences the number of deer detected. We compared this with the detection of red deer in an additional, spatially isolated area (one km away from any other transects and the hiking path). We collected count data on hikers at the start of the path and explored hourly (red deer detection during daytime), daily, diurnal (day versus night) and monthly spatial distributions of red deer. Using generalized linear mixed models with forward model selection, we found that the distribution of deer changed with the hiking activity. We found that fewer red deer were detected during busy hourly hiking periods. We found that during daytime, more red deer were detected at 150 m than at 25 m. Moreover, during the day, red deer were detected at a greater rate in the isolated area than around the transects close to the path and more likely to be found close to the path at night. This suggests that avoidance of hikers by red deer, in this study area, takes place over distances greater than 75 m and that red deer are displaced into less disturbed areas when the hiking path is busy. Our results suggest that the impact of hikers is short-term, as deer return to the disturbed areas during the night.

Keywords: camera traps, outdoor activity, recreation interaction, spatio-temporal distribution, ungulate

Non-consumptive outdoor recreation activities such as hiking, biking and skiing are increasing in popularity globally (Cordell 2008) and can have unintended impacts on animals. The consequences of outdoor recreation activity depend on the taxon, the type of recreation and its intensity (Monz et al. 2013, Larson et al. 2016). An avoidance response is one of the consequences of recreation activity and can be defined as a change in animal residency patterns, such as change in home range or change in movement behaviour, to reduce interaction with human activity (spatial avoidance) (Wakefield and Attum 2006, Bateman and Fleming 2017, Coppes et al. 2017). Avoidance responses can also be defined as a change in the animal's activity patterns in disturbed areas, such as spending less time in these areas or avoiding periods during which the disturbance takes place (temporal avoidance) (Neuhaus and Mainini 1998, Bateman and Fleming 2017, Fuglei et al. 2017).

Spatial avoidance of human recreation can induce various animal's responses such as increased stress levels (Barja et al. 2007), reduced population size (Wolfe et al. 2000) and increased energy consumption (Cassirer et al. 1992). These responses depend on whether an animal is displaced into equivalent or less suitable habitats (Gill et al. 2001) and whether displaced animals expend more energy moving to avoid human outdoor recreation (Cassirer et al. 1992, Nellemann et al. 2010). This spatial avoidance behaviour represents a trade-off between the risk from the disturbance versus the cost of movement (Lima and Dill 1990, Gill et al. 2001).

Temporal avoidance of outdoor recreation, especially in ungulates, can also co-occur with spatial avoidance and can be observed at a range of timescales: hourly, diurnal (day versus night), daily or seasonal. Hourly avoidance implies the return of an animal to its pre-disturbance location in the short term (Reilly et al. 2017). Outdoor recreation activity can also cause diurnal changes in animal activities (Fuglei et al. 2017, Reilly et al. 2017), affecting the different activities that animals undertake during day and night, which are essential for maintaining species' feeding and sleeping patterns (Fuglei et al. 2017), and mating practices (Frey et al. 2017). Finally, seasonal avoidance reflects the

avoidance of an area during a specific period of the year, for instance, as a result of variations in recreation intensity (e.g. winter sports; Olson et al. 2017).

To study the different spatial and temporal scales of avoidance, we focused on the interaction between red deer *Cervus elaphus* and hikers in Scotland. In this country, red deer hunting (done through stalking and in Scotland often referred to as such) is culturally important to some sectors of society and is an economic asset for some land managers (Macmillan and Phillip 2008). The culling of red deer is also necessary to manage grazing and browsing impacts on vegetation (Albon et al. 2007) due to absence of natural predators. Furthermore, mountains, moors and woodlands that are red deer habitat, are also attractive for hiking in Scotland. Indeed, the Land Access Reform (Scotland) Act 2003 provides rights to access Scotland's countryside to anyone engaged in outdoor recreation. With a popular hiking culture in the country, especially in the Highlands where most of the red deer are located, there is potential for increased human–wildlife interaction with consequences for the temporal and spatial distribution of red deer (Sibbald et al. 2011). Our study complements previous studies in Scotland (Sibbald et al. 2011, O'Neill 2016) which used GPS tracking and direct observation to monitor red deer interactions with hikers at a very fine spatio-temporal scale. Here, camera traps are used to capture the impact of hikers on red deer spatio-temporal distribution over a much longer period of time and across a larger sample of hiking activities.

We first explore how hiker activity impacts red deer presence at four temporal scales: hourly (red deer temporal detection during a quiet or a busy hiking hour), daily (red deer temporal detection during a quiet or a busy hiking day) and diurnal (detection during day versus during night), and across five months. At the same time, we explore how hikers may influence red deer presence at two spatial scales: first, we compare red deer numbers at three distances from a hiking path, and second, red deer presence in areas near the path (less than 150 m) versus in an isolated area (more than one km away from the path). We test three hypotheses related to the spatio-temporal behaviour of red deer. The first hypothesis is whether red deer avoid higher-intensity recreation; here we expect that red deer will be observed less frequently close to the path during a busy hour and a busy day (avoidance hypothesis). The second hypothesis is whether red deer appear more frequently near the path during the night than during the day; we expect to detect more red deer during the night near the path (diurnal hypothesis). Our third hypothesis is that hiking activity influences red deer detection at a larger spatio-temporal scale (displacement hypothesis). The expectation is that red deer detection will be greater in the isolated area (distant from the hiking path) compared to areas in closer proximity to the hiking path.

Material and methods

Study area

The study area was a 2746 ha land holding (estate) in Glen Lyon, Perthshire, Scotland (56°37′04.5″N, 4°10′50.7″W) (Fig. 1). This area is managed for red deer hunting, which occurs every year from the end of August to mid-October for the male (stag) season and from mid-October to mid-February for the female (hind) season. During our period of data collection (below), the number of hunting days was 10 in 2017, 24 in 2018 and 18 in 2019. The number of people involved generally varied between 2 and 5 people and the location of the hunt is typically targeted at specific parts of the estate which vary depending on the weather conditions. In this area, hunters are the main predators of red deer. In 2019, the population of red deer on this estate was approximatively 382 (13.91 deer km^{-2}; Deer Management Plan, Breadalbane DMG). The estate is not fenced, so deer can roam freely across the landscape and across neighbouring properties. Red deer are not fed in this area, but mineral (salt) licks are present in various locations. The estate is also used for summer sheep *Ovis aries* grazing. Other terrestrial resident animals include, for example, small populations of badgers *Meles meles*, red foxes *Vulpes vulpes* and pine martens *Martes martes*.

Vegetation in the area consists of a mixture of open heather *Calluna vulgaris*, grassland (e.g. *Agrostis capillaris*, *Anthoxanthum odoratum* or *Muhlenbergia rigens*) and peat (e.g. *Sphagnum compactum* or *Eriophorum vaginatum*), typical of the Scottish Highlands, with some plantation (commercial conifer plantation) and semi-natural broadleaf woodland cover confined to low-lying areas. The estate includes a 17 km circular hiking route that takes in four Munros (mountains with summits over 914 m). Climbing as many of the 282 Munros as possible is popular with Scottish hikers. The recreation trail in our study area and the four Munros to which it gives access, are therefore very attractive to hikers.

Data collection

Data collection occurred over three periods: from the beginning of August to mid-November 2017, from mid-June to the end of October 2018 and from the end of May to end of October 2019, for a total of 7077 camera trap survey effort days. We chose these three periods of data collection to represent intensive times for hiking activity which overlap with the calving season and hunting period. Thus, this busy time represents the period where the hiking activity can potentially interfere with red deer movement and consequently affect red deer management on the estate.

The spatio–temporal distribution of red deer along the hiking path was quantified using transects of three camera traps at distances of 25, 75 and 150 m on one side of the hiking path (the transects were perpendicular to the path). The choice of these distances was informed by two previous studies in Scotland which suggested that red deer maintain a distance of 100 m (O'Neill 2016) to 250 m from hiking paths (Sibbald et al. 2011). However, these studies were carried out in low elevation areas with limited topographic variation, higher recreational visitor numbers (as high as 300 tourists per day) and in landscapes with more forest cover (Sibbald et al. 2011). In contrast, our study area usually sees only dozens of hikers on a busy day in a landscape characterised by relatively low-growing vegetation and more marked changes in elevation. Furthermore, in the case of our study, we expected that the hiking activity was largely associated with the hiking path and this study design aimed to capture

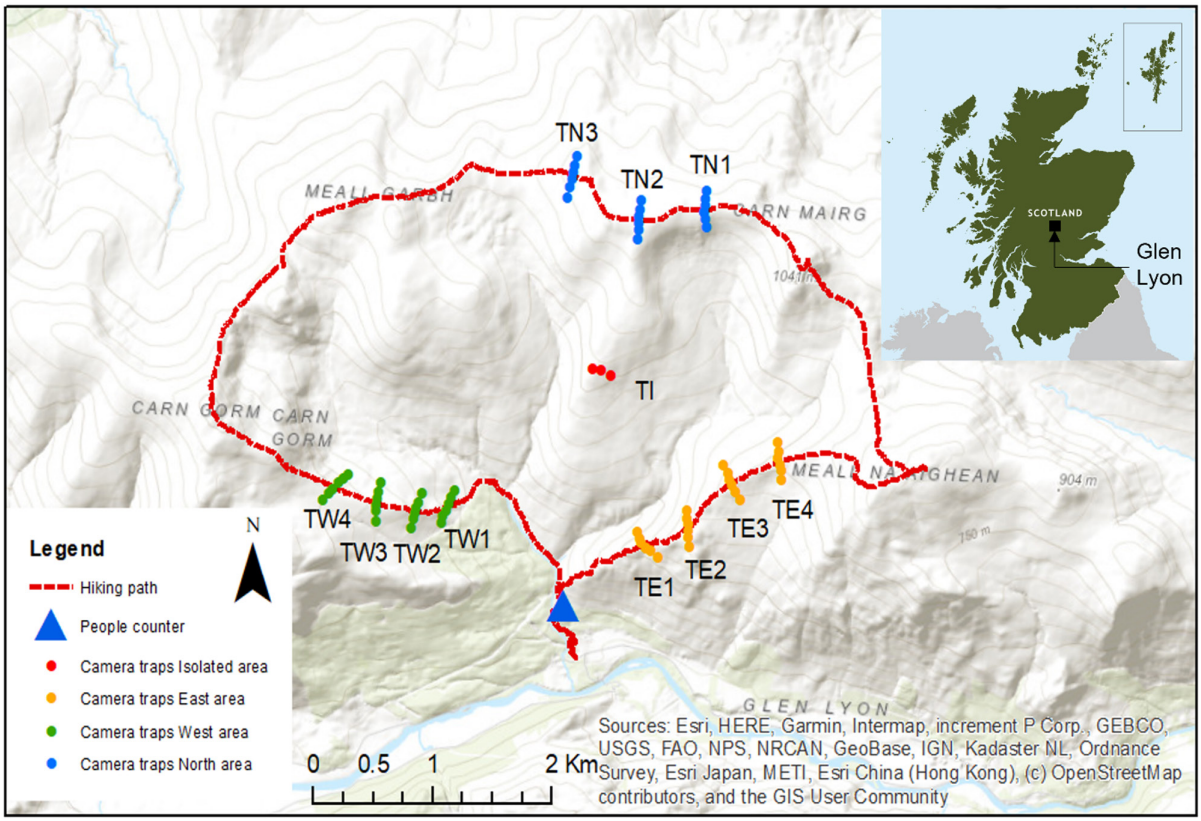

Figure 1. Study area in Scotland, with locations of camera trap transects grouped in three areas close to the hiking path (red dashed line) and a fourth transect in an isolated area. The blue triangle shows the people counter location near the start of the hiking trail.

the finer scale response of red deer along the hiking path. We therefore designed the study to detect the response of red deer at a higher resolution up of to 150 m (i.e. being able to detect red deer at multiple points from 0 to 150 m) as we expected the hikers to impact red deer distribution at a finer scale.

The transects were set up in three different points along the hiking path: East (TE), West (TW) and North (TN) in all three years (2017–2018–2019) (Fig. 1). The locations of these transects were chosen to be close to the hiking path but separated from one another (by more than 3 km along the hiking path). A separate transect (in 2019 only) was set up in an isolated area of the landscape with no path nearby (the closest distance to the hiking path was 1 km). The location of this isolated transect was chosen for its general landscape similarity to the other areas; that is, the presence of a high elevation ridge (such as in TE, TW and TN) with vegetation similar to that of the East and West areas. The north transects and the isolated transect are similar due to the presence of a ridge, but the vegetation is not identical nor is the amount of hiking activity.

The number of cameras and their set up in each year varied due to availability of functioning equipment (Supporting information) and insufficient cameras were available to deploy at every position in every year. However, we ensured that the camera distribution among the transects provided us with an overview of the spatial distribution of the red deer on both sides of the hiking path (south and north part of the hiking path) and aimed to limit effects that different camera brands might have at different locations of the path and thus we rotated our camera trap locations each year. Therefore, in 2017, the east and the west areas each consisted of four transects for a total of 12 camera traps per area and the north transect consisted of three transects for a total of nine camera traps. These transects of cameras were alternated between the north and south side of the hiking path approximatively every two weeks. In 2018 and 2019, the east and the west areas comprised two transects each for total of six camera traps per area (south side of the trails used) and the north area consisted of one transect of three camera traps (south side in 2018 and north side in 2019) (see the Supporting information for details).

We used wooden poles to position each camera trap at a height of approximatively 1.10 m and, as dictated by terrain (i.e. field of view not running up slope), facing either away from or parallel to the hiking path. We calibrated every camera trap to trigger as many photos as possible per detection to increase the chance of clear photos to more accurately estimate (i.e. count) red deer numbers from camera images. This depended on the individual camera model; three for the Bushnell, eight for the Browning and 10 for the Reconyx cameras. Cameras were calibrated to re-trigger with minimal delay. We visited each camera trap at least once a month to collect SD memory cards, change batteries and perform general maintenance.

We recorded the dominant vegetation type at each camera location, focusing on the direction that the camera was facing. For this we used an existing vegetation classification protocol (JNCC 2010) and identified the following five vegetation types: wet dwarf shrub heath, dry dwarf shrub heath, montane vegetation, bare peat and blanket bog.

To count how many people entered the path we used a Chambers RadioBeam People Counter RBX_EB, which allowed us to record the number of hikers passing by the counter every hour and every day (Fig. 1). This counter was present for all camera trap periods of activity. This single counter was placed at the start of the circular hiking path. To account for the fact that our counter was positioned to double-count hikers (i.e. when they entered and when they exited the path), we first took the total number of hikers the counter captured per day and divided this by two. The number obtained was the maximum of hikers present in the area during a day. For each hour of this day, we added the hourly number of hikers detected in that hour to the number of hikers detected in the previous hour until the daily maximum number of hikers was reached. After this, we subtracted the hourly counts until we reached 0 (typically later in the evening). The counter is an efficient way to record the overall number of hikers present on the study area but the direct link with camera traps detections is limited due to the counter's distance from the camera traps and the individual behaviour of the hikers (speed and navigation choice). Due to an interference problem with the automated counter (false detections triggered by vegetation growing in the detection zone), three brief periods were removed from our analysis (18 Jun 2018 to 24 Jun 2018, 7 Jul 2018 to 9 Jul 2018 and 3 Aug 2019 to 15 Aug 2019). Camera trap photos taken during these periods were also removed from all analyses involving the number of hikers (i.e. the avoidance hypothesis).

To assess whether most of the hikers stayed on the track and whether the hiking intensity was similar amongst the different camera traps, we collected GPS tracking data from hikers. During the three-year period of our study, we sampled 60 days of hiking activity using GPS tracking. These days were evenly distributed between weekday and weekend days. We approached hikers starting their walk between 07:00 and 13:00 and asked them to carry a GPS tracker (i-Blue 747proS GPS Trip Recorder) after explaining the aim of the project. If they agreed, one GPS tracker was given to each group of hikers. Hikers were asked to leave their GPS tracker in a drop box located at the end of the path. We used GPS data to estimate the percentages of hikers performing the full hiking loop, passing the counter on their way in, and out of the upland portion of the trail, and next to each of our camera traps transects. We performed a kernel density estimation of all the GPS tracks using a 10 m kernel bandwidth.

Data processing and analysis

Red deer can stay in the same area, including in front of a camera, for long periods of time, resulting in a large number of images for the same detection event (e.g. when foraging in front of a camera). Thus, to avoid counting the same animal multiple times, we specified red deer observations as being independent when more than 10 min elapsed between two consecutive detections. Previous studies have used different times to determine independent camera trap observations (e.g. 30 min; Sollmann 2018) but we decided to use 10 min due to the small size of the study area and the relatively large number of animals.

We separated the statistical analysis by hourly and daily levels of hiking activity and night versus day. This separation made it possible to focus on specific temporal scales: during the day only for the impact of the level of hiking activity, at hourly and daily temporal scales (avoidance hypothesis), and at a broader temporal scale with the comparison between night and day (i.e. the period 'day' as a proxy of hiking activity; diurnal hypothesis).

We used the people counter data to assess the overall number of hikers present on the path for each hour, each day and each month (Fig. 2, Supporting information). We classified the level of hiking activity for each hour and each day as 'quiet' or 'busy'. The level of activity 'quiet' was when the number of hikers was below the hourly mean number of hikers (8) and 'busy' when above this mean (8) (Fig. 2a). We also used this number to classify quiet versus busy days. We used this categorization as a proxy for hiking activity instead of the raw number of hikers as we did not expect a linear relationship between the number of hikers and red deer spatio-temporal avoidance, and to limit uncertainty due to the counter itself. However, to assess the impact of different levels of hiking activity, we also calculated quartiles of the total number of hikers per day: 25%: 0; 50%: 4; 75%: 11 (Supporting information). We used the sunset and sunrise times of each day as delimiters of night and daytime. As the location of the study area is at 56.6° latitude, sunrise and sunset times vary substantially across the observational period, from 04:23 to 07:15 and 16:35 to 22:11 respectively. We obtained the exact sunset and sunrise times for each day using the function sunriset from the package maptools (1.0-2; Bivand and Lewin-Koh 2015) in R ver. 3.5.2 (<www.r-project.org>).

Detection rate (DR)

For the purpose of our analysis, we defined the level of survey effort associated with each camera trap location as the number of days when that camera trap was working. The survey effort took into consideration that some cameras were working only during busy days or only during quiet days. We calculate the average detections per camera day. This average was called the detection rate (hereafter DR) of each camera.

We resampled many of the same locations more than once over the course of our study (Supporting information). Thus, we summed the number of detections and the number of working days for each camera trap location. We first visually compared the DR of each camera for each distance from the hiking path during different periods of hiking activity: hourly (quiet versus busy), daily (quiet versus busy) and during day and night using comparative boxplots. In the next section, we used the statistical modelling to further explore these results.

Drivers of red deer detection

To incorporate additional environmental variables (e.g. elevation and vegetation) into our hourly and daily hiking activity (busy versus quiet) and time of day analyses (day versus night), we used three generalized linear mixed models (GLMMs) with a negative binomial distribution for the dependent variable (detection counts; Table 1). Our study site is characterized by low-lying vegetation and an open landscape; thus topography is the main factor influencing red deer detectability. Cameras were placed so that they faced either parallel to or away from the direction of the hiking

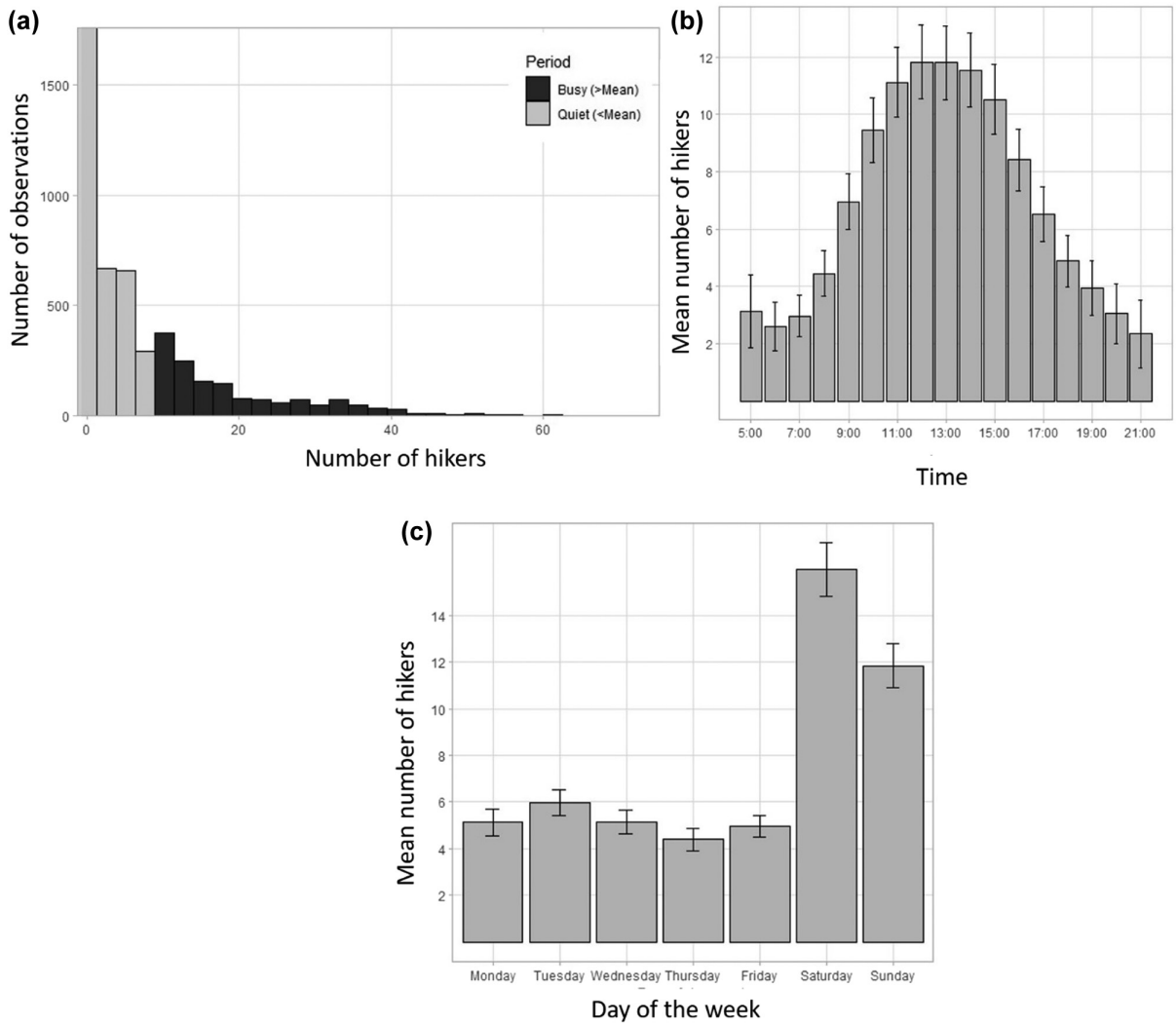

Figure 2. Number of hikers over the periods of camera trap deployment. (a) Distribution of the cumulative number of hours classified as quiet (≤ 8) or busy (> 8) from the automatic counter. (b) Mean number of hikers per hour and (c) per day. In both panels, error bars indicate the standard deviation.

trail. We therefore expect relatively uniform detectability amongst the different camera trap locations, which warrants use of a GLMM rather than a model that explicitly models the detection process (Gorosito et al. 2016). For the hiking activity (only during daytime), the dependent variables were the sum of the detections per camera for each hour or each day. For the time of day analysis, the dependent variable was the sum of the detections per camera during night or day of each day the camera trap was working. Four fixed effects were included in our models: three class variables (factors) which included distance from the path (close (25 m), moderate (75 m) or far (150 m)), vegetation type (five classes listed above), and the level of hiking activity (busy versus quiet) or the time of the day (day versus night) and one continuous variable: elevation (in metres). We used an interaction term between the distance and level of hiking activity for the

Table 1. Generalized linear mixed model (GLMMs) dependent variables and model covariates. Two separate models with a negative binomial distribution were used: one for the hiking activity (daytime data only), one for the time of the day (all data). (×) indicates an interaction term (**) indicates the category used as a reference.

GLMM analysis	Dependent variables	Model covariates	Type of variables and number of levels
a) Hiking activity	Sum of the detections per camera o during quiet or busy periods	Distances from hiking path	Categorical: 3 levels (25**, 75 and 150 m)
		Elevation (in meters)	Continuous
		Level of hiking activity	Categorical: 2 levels (quiet versus busy**)
		Distances × level of hiking activity	Interaction term
b) Period of day	Sum of the detections per camera during the night or the day	Distances from hiking path	Categorical: 3 levels (25**, 75 and 150 m)
		Elevation	Continuous
		Time of the day	Categorical: 2 levels (day versus night**)
		Distances × time of the day	Interaction term

first model and between the distance and the time of the day for the second model. After testing for collinearity amongst the potential variables, we removed vegetation from the saturated model to avoid correlation (i.e. vegetation varies with elevation; Zuur et al. 2017). The transect ID and the camera trap location ID were used as nested random effects. We used the packages glmmTMB (1.0.2.1, Brooks et al. 2017) to fit the most complex model. Then, we fit different models using the 'dredge' function in the R package MuMIn (1.43.17, Bartoń 2020). This function fit models of all the possible combinations of the above covariates, presented in Table 1. We then selected models using the Akaike information criterion corrected for small sample sizes (AICc) (Akaike et al. 1973). Following Richards et al. (2011), we retained for inference all models with $\Delta AICc < 6$, except those that were more complicated versions of any model with a lower AIC.

Hourly and monthly variations: area comparison

To test if daily red deer detection differed between the isolated area and areas within 150 m of the hiking path, we compared daily detection patterns using kernel density curves of the temporal records from each area (east, west, north and isolated). For this, we used the non-parametric approach suggested by Ridout and Linkie (2009) where camera trap detections are considered as random samples from a continuous distribution over 24 h and used to estimate a probability density function (Lashley et al. 2018). We also calculated the hikers' kernel density curves using the automatic counter information. From the two daily activity curves for red deer and hikers, we calculated the coefficient of overlap Δ which estimates the temporal overlap in activity between two species: red deer and hikers (Ridout and Linkie 2009, Niedballa et al. 2019). This coefficient ranges from 0 (no temporal overlap) to 1 (full temporal overlap) and is the joint area under the probability density functions of the estimated daily activity density curves for both species. Three different methods can be used to estimate Δ and we used the estimator Δ_4 as it is the most appropriate for sample sizes larger than 50 (Ridout and Linkie 2009). It uses vectors of densities estimated at the time of observation of the two species. We calculated the 95% confidence interval of these estimates from 1000 bootstrap samples (of red deer and hikers). Finally, to incorporate seasonal variations in red deer detection, we also examined the monthly coefficient of overlaps for each area. For this, we used the R package overlap (0.3.3, Meredith and Ridout 2014).

Results

Hiking activity

The peak in hiking activity occurred during the middle of the day with a mean of 12 hikers at 12:00 (Fig. 2b), with a mean of 13 hikers during the weekend and five hikers during weekdays (Fig. 2c). The hourly mean number of hikers was constant between May and November with a slight decrease over time (highest hiking activity in June and lowest in October) (Supporting information).

We collected 252 hikers' GPS tracks from which 83% of the hikers completed the full delimited hiking loop and 90% of the hikers tracked did not went go track (Fig. 3); some hikers only completed some part of the hiking loop but did not went off track (i.e. they walked the same way in and out). Hikers were entering and exiting the area by going through the laser counter 98% of the times. The percentages of hikers walking on the hiking path close to our camera traps were 87% in the east area, 94% in the west area and 86% in the north area. We did not record any hikers walking close to our isolated transect. Thus, the percentage of hikers visiting each area is comparable to each other and the counter information can be use as indicator of the hiking intensity in the study area.

Detection rates

We obtained 3054 independent detections of red deer from 7077 camera trap survey effort days. For each distance, the DR (sum of detections per survey effort (sum of days)) was higher during quieter hiking hours (avoidance hypothesis, Fig. 4a) and lower closer to the path than further away (Fig. 4a–b). At the day scale, we did not detect more red deer during quiet hiking days than during busy days (Fig. 4b). There were more detections of red deer during night than day at close and moderate distances (Fig. 4c) (diurnal hypothesis).

To ensure that these results are not dependent on the choice of the point at which to separate quiet and busy hours and days we used different quantiles of the total hourly number of hikers as separators (Supporting information). The results were similar to the mean when the median and the quantile were used as separators, with more detection during quiet hours than during busy hours and no difference between quiet and busy days.

Drivers of red deer detection

To identify determinants of red deer detection, we focused on the difference between busy versus quiet hours and days (hiking activity; avoidance hypothesis) and night versus day (diurnal hypothesis), also taking account of the elevation as an environmental covariate (Table 2). We found that the hourly detection of red deer was well explained by the hiking activity, the distance from the path and the elevation (as they were covariates of the best model in Table 2a). Hiking activity and elevation activity were the only variables retained in each model of the confidence set ($\Delta AICc < 6$). We found that more deer were detected during quiet hiking hours and more frequently far 150 m from the hiking path than near, at 25 m (Avoidance hypothesis) (Table 3a). At the day scale, we found that the detection of red deer was well explained by the distance from the hiking path and the elevation (Table 2b). We also found that more red deer were detected further away from the hiking path than at 25 m (Table 3b). Moreover, we also found that more red deer were detected during night than during days (diurnal hypothesis, Table 3c) with more red deer detected further away from the path than at 25 m during the day (Table 3c). Finally, we found that fewer red deer were detected in lower elevation (Table 2, 3).

Hourly and monthly variations: comparison of areas

We explored the detection patterns of deer and hikers in each of the four transect groups separately (displacement

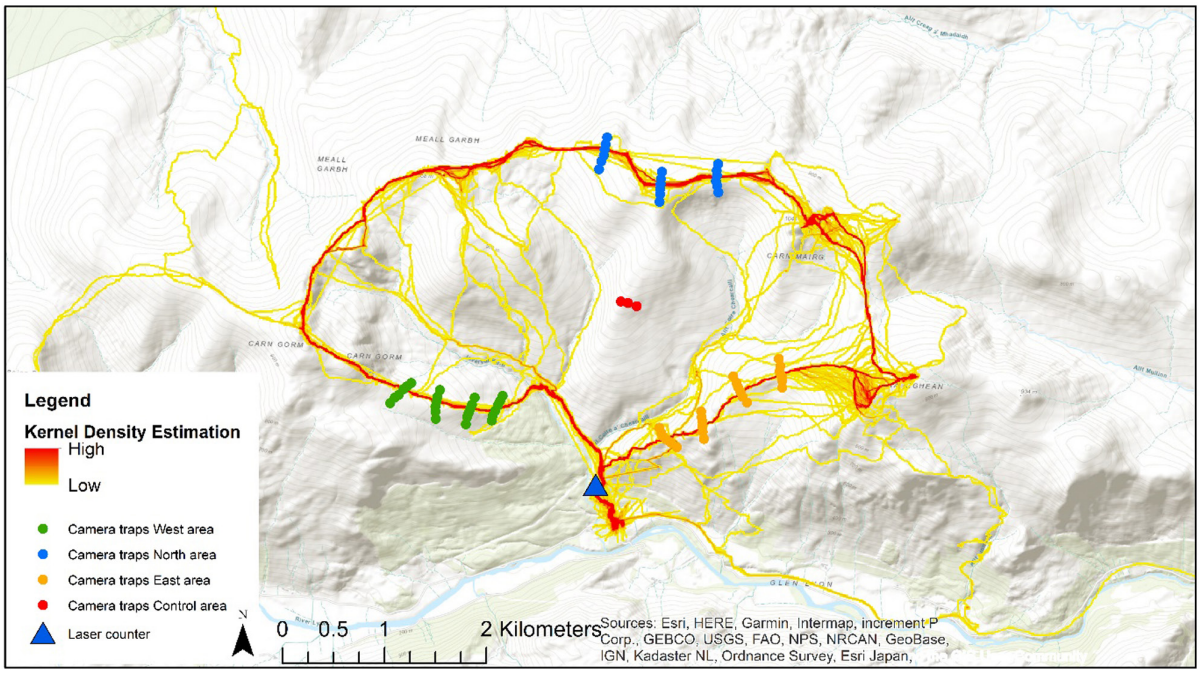

Figure 3. Density of hiking activity derived from GPS tracks (n = 252) and camera trap transects in our study area in Glen Lyon, Scotland. The density values were calculated using kernel density estimation with a bandwidth of 10 m. This shows that the majority of GPS hikers kept to the hiking trail (which corresponds to the areas with high density – in red) with only occasional individuals exiting the trail and crossing the area through the gullies.

hypothesis; Fig. 5). For both the East and West groups, we observed highest deer presence from around 18:00 until 06:00 (respective DR between 0.06 and 0.04), with low red deer presence (near 0) outside this period (Fig. 5a). In the North group, red deer were mainly detected between 18:00 and 22:00 (DR around 0.01), with a few detections between midnight and 9:00 (DR between 0 and 0.05). As in the east and west groups, fewer animals were detected in the middle (DR close to 0) of the day. Red deer detections at the isolated site show a peak in the morning around sunrise (DR around 0.02) with a second detection peak around 21:00 or around sunset (DR between 0.02 and 0.04). During daytime, red deer were more detected in the isolated area than in other locations at the same time (DR around 0.01).

The percentage of temporal overlap between red deer and hikers for the east and west groups was 30.8% and 33.6%, respectively (Fig. 5b). In the north area, this percentage was 46.8%. In the isolated area, the percentage of temporal overlap was 67.8%, representing a large difference over the three transect areas. The bootstrap CI between the isolated area and path areas did not overlap which showed that red deer detection in the isolated area and in areas close to the hiking path differed significantly. We also compared the detection patterns and the coefficient of overlap for each month separately and found similar overlap patterns in each area (Supporting information).

Discussion

Our study focused on how hiking activity influences the spatial and temporal distribution of red deer in an area of the Scottish Highlands that includes a popular hiking path. We showed that red deer avoided areas within 150 m of the hiking path during busy hiking times (avoidance hypothesis) and during daylight more generally (diurnal hypothesis). We also showed that during daytime, more red deer were detected at 150 m than at 25 m. In contrast, there was no difference in detection at close distances to the path during night versus during day. We also showed that during busy hiking periods (daylight), red deer were more active in an isolated area (> 1 km away from the trail) than in areas adjacent to the path (displacement hypothesis).

Sibbald et al. (2011) also found differences in red deer use patterns between quiet and busy days. However, they detected this difference within 100 m of the path, whereas we found more deer at 150 m during the day. Red deer avoided the hiking path during busy hiking periods and seem to keep a distance greater than 75 m during quiet periods. The difference in results between Sibbald et al. (2011) and our study might be due to the more varied topography and generally open, low-growing vegetation, which increases visibility over longer distances. Specifically, the open landscape of our study area might increase the direct sighting of hikers by red deer. In this upland terrain, spatial avoidance of hikers by red deer appears to result in displacement of deer to distances greater than 75 m from the hiking path.

In our study, red deer were more frequently detected during night than during day in areas close to the path (< 150 m). This aligns with Coppes et al. (2017) who found that red deer occupy less disturbed areas during the day and move towards human recreational areas at night. To explore the effects of human activity on a broader spatial scale, we compared our transects along the hiking path with an isolated transect in a similar habitat situated remote from the hiking path (more than one km away). During day, and thus during period when hiking typically occurs, red deer were more fre-

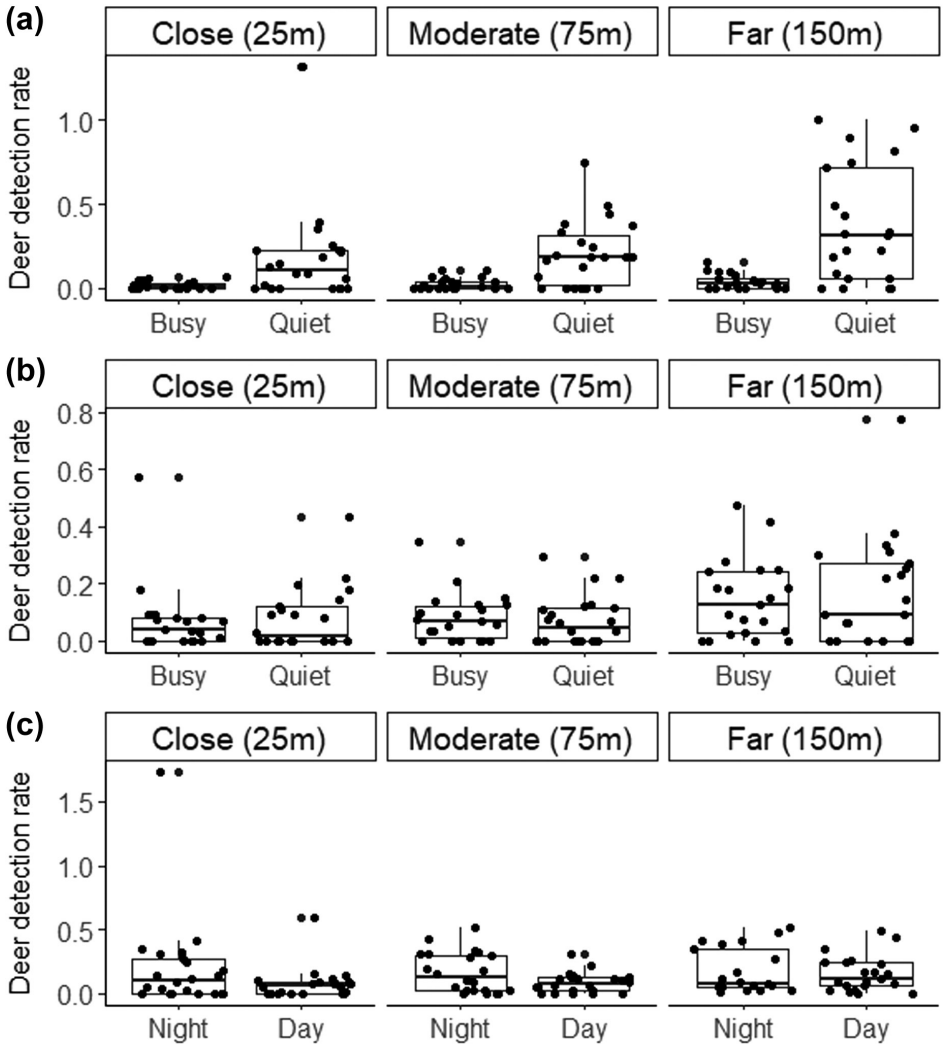

Figure 4. Detection rate (DRs; the ratio of the sum of the number of detections to the total number of working camera days) for red deer, where each point is a camera trap location. (a) DRs during busy versus quiet hours (the mean number of hikers every hour (mean = 8) was used as the separator) compared across the three distances. (b) DRs during busy versus quiet days. (c) DRs during night versus daytime (delimitated using the sunrise and sunset times of each day) compared across the three distances.

quently detected in the isolated area. Therefore, spatial patterns of avoidance have an important temporal component. The daily pattern of red deer detection in our study shows the expected crepuscular diurnal pattern of activity with a peak activity in the morning and in the evening (Georgii 1981). This is evident at both the isolated and path transects which might explain the difference in findings between the hourly and daily scales. At the daily scale, few deer were detected in the middle of the day when most of the hiking activity occurred, while the overall number of red deer can be high due to early and late detection. However, higher daylight detection in the isolated area may indicate that the deer moved from areas near the path to more distant terrain to avoid hikers. In Scotland, the home range of adult female

Table 2. Selected GLMMs (ΔAICc < 6) and variables retained for red deer detection depending on the hour hiking activity (a), the day hiking activity (b) or the period of the day (night versus day, c). The dependent variables were the number of detections per camera trap during each hour (a), each day (b) or during the day and night of each day (c). Each model was fitted using a negative binomial family and the transect ID and the camera trap location were used as a nested random effect.

Model retained	df	LogLik	AICc	ΔAIC	Weight
a) Hiking activity hour					
Hiking + distance + elevation	8	−4774.09	9564.2	0	0.76
Hiking + elevation	6	−4778.12	9568.2	4.06	0.1
b) Hiking activity day					
Distance + elevation	7	−2457.2	4928.4	0	0.629
Elevation	5	−2461.53	4933.1	4.64	0.062
c) Period of the day					
Period × distance + elevation	10	−6579.14	13 178.3	0	0.986

Table 3. Results of the best generalized linear mixed-effects models (GLMMs) of red deer detection depending on the hour hiking activity (a), the day hiking activity (b) or the period of the day (night versus day, c). In (b) we also presented the hiking pressure GLMM which correspond to our hypothesis as the hiking variable was not retained in the best model. Bolded rows show statistically significant variables (p-value < 0.05).

Covariates	Estimate	SE
a) Hiking activity hour		
Best model: hiking + distance + elevation		
Lognormal R^2: $R^2m = 0.09$, $R^2C = 0.17$		
Intercept	**−3.260**	**0.694**
Distance 25 m	Ref	Ref
Distance 75 m	0.230	0.254
Distance 150 m	**0.704**	**0.25**
Elevation	**−0.004**	**0.001**
Hiking (busy)	Ref	Ref
Hiking (quiet)	**0.793**	**0.093**
b) Hiking activity day		
Best model: distance + elevation		
Lognormal R^2: $R^2m = 0.17$, $R^2C = 0.27$		
Intercept	−0.114	0.699
Distance 25 m	Ref	Ref
Distance 75 m	0.244	0.266
Distance 150 m	**0.766**	**0.261**
Elevation	**−0.004**	**0.001**
Hiking pressure: distance × hiking		
Lognormal R^2: $R^2m = 0.09$, $R^2C = 0.35$		
Intercept	−3.031	0.330
Distance 25 m	Ref	Ref
Distance 75 m	0.310	0.279
Distance 150 m	**0.871**	**0.274**
Hiking (busy)	Ref	Ref
Hiking (quiet)	−0.074	0.179
Distance 25 m × hiking (quiet)	Ref	Ref
Distance 75 m × hiking (quiet)	−0.192	0.254
Distance 150 m × hiking (quiet)	−0.047	0.228
c) Period of the day		
Best model: period × distance + elevation		
Lognormal R^2: $R^2m = 0.19$, $R^2C = 0.42$		
Intercept	1.376	0.865
Distance 25 m	Ref	Ref
Distance 75 m	0.129	0.296
Distance 150 m	0.337	0.296
Elevation	**−0.005**	**0.001**
TOD (night)	Ref	Ref
TOD (day)	**−0.864**	**0.102**
Distance 25 m × period (day)	Ref	Ref
Distance 75 m × period (day)	**0.279**	**0.142**
Distance 150 m × period (day)	**0.625**	**0.132**

red deer varies from one to five km², while adult males range over greater distances and areas (Clutton-Brock and Albon 1989). The distance between our isolated site and the transects near the hiking path ranges from 1 km to 2.5 km and falls within these estimates of home range size, making daily travel between locations possible. Thus, disturbances resulting from hiking activity may have generated a consistent behavioural pattern where the deer favour less disturbed areas. The deer are not fenced in and are free to roam into neighbouring properties so comparing these findings with an area of lower human activity, such as a site outside our study area with no hiking activity, could improve understanding of this process of displacement.

We did not observe a difference in the hourly/daily temporal distribution of red deer detections during busy hiking months (e.g. June) compared with other months. Previous studies have identified a seasonal response to disturbance, relating to peak tourism months. For example, a study in Norway found a difference in reindeer escape distance behaviour in relation to annual tourism patterns (Reimers et al. 2006). This distinction may be due to large differences in the level of recreational activity between the summer and winter in some areas, which is perhaps less marked in our study area (i.e. the area is still accessed by hikers into October and November).

Some aspects of our approach could be considered for improvement in future work. First, due to technical limitations, we collected data in only one isolated area away from the path, and thus the presence of red deer during the day in this area – which differed from the areas next to the path – may be due to location specificity. Further studies using multiple isolated areas could be used to assess the differences in hourly detection of red deer. Second, our study lacks a before–after–control–impact design, so the long-term effect

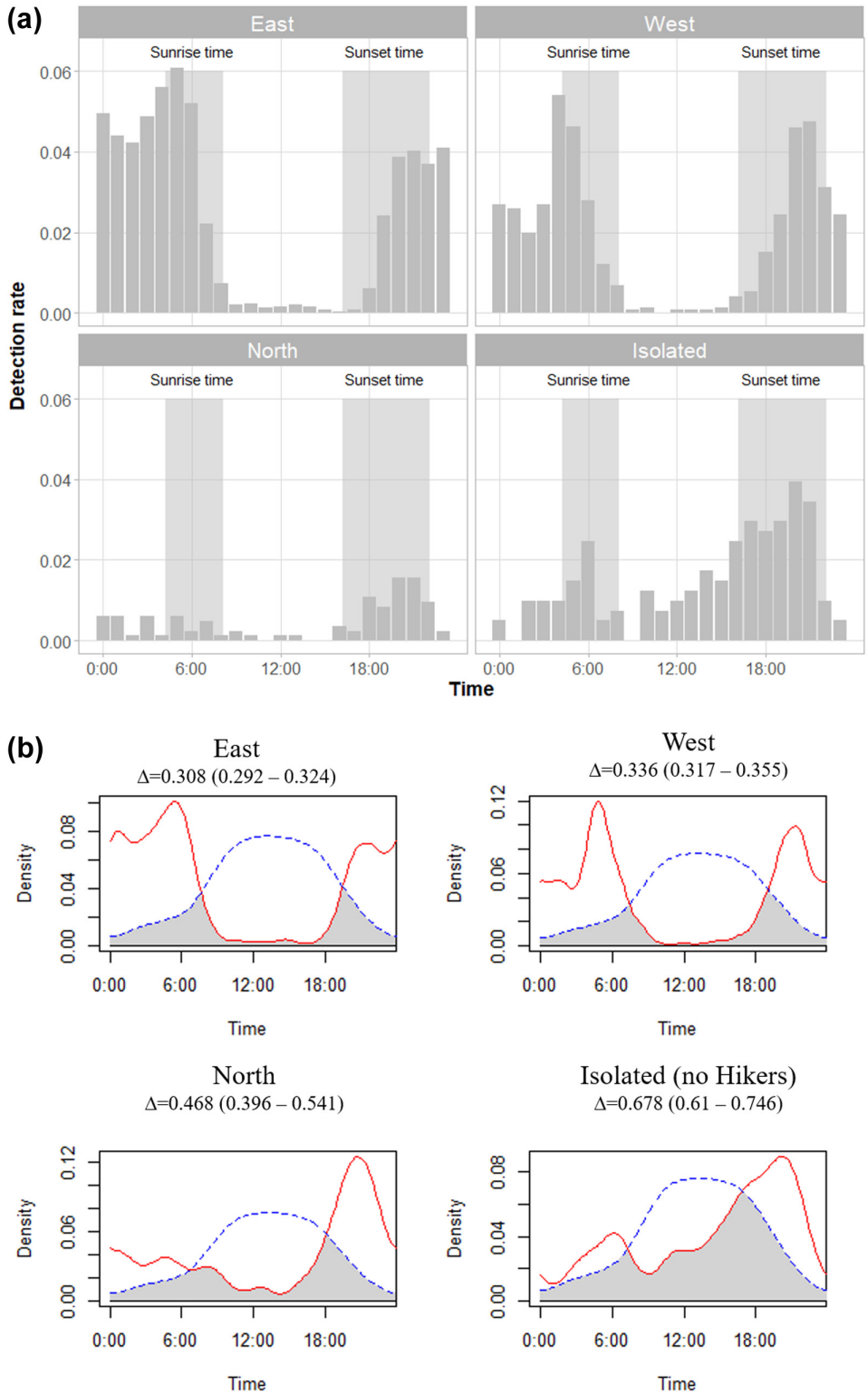

Figure 5. (a) Hourly total detection rates of red deer for each transect group (east, west, north and isolated). Cameras in the east, west and north groups are close to the path (< 150 m), while the isolated group is distant from the path (> 1 km). The grey area shows the period between the earliest and latest sunrise and sunset times. (b) Activity patterns of red deer (red lines) and hikers (blue dashed lines) for each transect group. The grey shading shows the overlap in activity between red deer and hikers in the study area at time of the day. Activity overlap was estimated from 1000 bootstrap samples of red deer camera trap detection and hikers counter information.

of hiking may have already resulted in a change to the spatial distribution of red deer, such that animals preferentially occupy surroundings areas (i.e. outside our focal area). A wider comparison, at a broader geographical scale, could help provide more insight into deer behavioural responses and how these change with varied levels of hiking. Finally, in this work, we assessed only the detection of red deer. Additional factors, such as the number of deer, their sex, the presence of forage competitors (e.g. sheep) and the presence of juveniles (Neuhaus and Mainini 1998) could also impact the spatio–temporal distribution of red deer and their interaction with hikers (i.e. increase or reduce interaction). Potential interactions between these factors would also benefit from further study.

Conclusion

Defining the spatial and temporal scales of interactions between outdoor recreation activities and animals is crucial to understand and manage these processes. We showed that the impacts of hiking activity on red deer detections are most likely occurring at an hourly scale, with more deer detected during quiet hiking hours. At the daily scale and at small distances (between 25 and 150 m), we observed more red deer at 150 m from the path during the day. We observed lower detection rates during the day than at night. However, these results did not appear to depend on time of year (within the times of year we studied). Our results align with previous studies but, by extending the evidence to more heterogeneous upland terrain, they provide new insights into the spatial and temporal scale of disturbance of red deer by outdoor recreation activity. The impact of this on the ability of deer managers to locate animals and carry out stalking or management culls will depend on how this displacement affects the ease of stalking access to the areas that red deer now occupy. A better understanding of how hiking influences deer detection within upland landscapes has the potential to reduce conflict between different users (e.g. land managers, sporting, recreation) and support social, economic and ecological elements of sustainable management.

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Conflict of interest – The authors declare that they have no conflict of interest.
Permit – The hikers' GPS tracking experiment was approved by the University Teaching and Research Ethics Committee (UTREC) of the University of St Andrews (approval no. GG13615). Participants were asked to give written informed consent and the consent form was approved by UTREC.

Author contributions

JAL, RJI and PAS conceived the original idea and obtained the funding. SM collected and analysed the data. SM performed the statistical analysis with contributions from JAL, UD, ALD and PAS. JAL, UD and ALD provided supervision at the different stages of the project. SM wrote the first version of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.v9s4mw6tz> (Marion et al. 2021).

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