

ORIGINAL RESEARCH

Red deer behavioural response to hiking activity: a study using camera traps

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anthropogenic disturbance; behavioural responses; camera traps; hiking; human–wildlife interactions; outdoor recreation; ungulates; vigilance behaviour.

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Abstract

With increasing levels of outdoor recreation activities, consequences for wildlife through interactions with recreationists are highly variable. Behavioural changes in wildlife are one potential consequence of interactions with outdoor recreationists. In ungulate populations, vigilance and flight responses are well-known antipredator behaviours, and an increase in their level indicates a more intense stress level which, ultimately, can have consequences for animal fitness. In Scotland, the geographical distribution of red deer (*Cervus elaphus*) overlaps greatly with areas used for popular outdoor activities such as hill walking. In this piece of research, we studied red deer time allocation, vigilance, and flight behaviours near a popular hiking path using camera traps. We positioned the cameras in transects at different distances (25, 75, and 150 m) from the path and recorded hiking activity using an automated people counter. Red deer behaviour was categorized from photo analysis as (1) no response (e.g. feeding and resting), (2) vigilant (i.e. upright head position), and (3) flight response. We also investigated demographic variables (group size and sex) and the direction of red deer movement relative to the trail. We used generalised linear mixed models to analyse behaviour in relation to the distance from the hiking track, hiking activity, time of the day, demographic, and environmental variables. We did not find an increase in vigilance or flight behaviour in relation to the distance from the hiking path or the hiking activity. These results suggest that red deer, in our study area, are habituated to the presence of hikers and may spatially avoid areas close to the hiking path instead of displaying cost-intensive behaviour (i.e. flight or vigilance behaviour).

Introduction

Non-consumptive outdoor recreation activities such as biking, riding, and hiking can impact wildlife in the same way as predation (Frid & Dill, 2002). The interaction between outdoor activities and wildlife can lead to, a change in animal habitat selection (Filla et al., 2017), spatial and temporal displacement (Marion et al., 2021), change in parental investment (Gill et al., 2001), and change in behaviour (Langbein & Putman, 1992; Ydenberg & Dill, 1986). In the latter case, vigilance and flight behaviour are widely studied to understand foragers' anti-predator responses (Brown, 1999; Hopewell et al., 2005; Lima, 1995).

The interaction between wildlife and recreationists can cause different levels of behavioural response in wildlife, which can be classified as no response, vigilance, or flight, and this order

of response usually corresponds with an increase in the intensity of the stimulus (Jiang et al., 2013). Among ungulates and vertebrates, vigilance behaviour is often characterised by an animal's head position, where a raised position allows the detection of a predator by scanning the surroundings (Hopewell et al., 2005). Similar to vigilance, flight behaviour aims to reduce predation risk by spatially avoiding the predator (Borkowski, 2001; Stankowich, 2008). An increase in the level of vigilance is commonly used as a first indicator of disturbance (Jiang et al., 2013). Flight behaviour is a more intense response than vigilance, where an animal interrupts its current activity, for example, feeding to spatially avoid a perceived threat. While reducing predation risk, these behaviours come at a cost for the animal, as they reduce its feeding and mating time, and increase the amount of time spent being vigilant and

taking evasive behaviour. A prey species' time allocation varies amongst its different activities: the animal's goal is to optimise feeding time and, at the same time, limit predation risk (i.e. by being vigilant or by fleeing). Thus, the animal carries out a risk assessment and performs a behavioural trade-off between the different behaviours. In the long-term, and with repeated disturbance, an increase in the level of vigilance and flight behaviour can impact the general welfare of the animal, and ultimately its fitness (i.e. survival and reproduction success; Frid & Dill, 2002). Likewise, vigilance and flight behaviour are short-term (i.e. immediate) responses to a disturbance, but the relative amounts of each behaviour type can reveal a longer-term adaptation to a non-lethal disturbance such as habituation (Villanueva *et al.*, 2012). These trade-offs and anti-predator responses are highly variable depending on multiple factors.

Here, we focus on behavioural responses of red deer (*Cervus elaphus*) to hikers and study this using various disturbance metrics such as the distance from the disturbance and intensity of the disturbance. Our study takes place in a unique system, in Scotland, where no natural predators of red deer have been present for more than 250 years when the last occurrence of the wolf was recorded. Since then, red deer prey–predator interaction is only due to human hunting. Human contact for long periods of time and over multiple generations can have an impact on ungulates risk perception, (Reimers *et al.*, 2011), and ultimately they become habituated to the presence of humans (Stankowich & Blumstein, 2005). This can have an impact on red deer-specific responses to humans such as flight responses which vary depending on if the risk is lethal (i.e. hunting) or not (i.e. outdoor recreation activities). Moreover, the risk assessment is affected by the predator's behaviour, the awareness of the prey, and the distance at which they detect the predator (Stankowich & Coss, 2007). Similarly, in ungulate populations, group size impacts the level of vigilance (Hopewell *et al.*, 2005; Matson *et al.*, 2005). An individual animal's level of vigilance conflicts with other activities (trade-off) while animals that are aggregated rely on other group members to scan their environment (Treves, 2000). It allows an individuals' vigilance rate to be lessened when the animals are in groups and reduce the trade-off between vigilance versus other activities (Roberts, 1996; Treves, 2000). This is also known as the 'group-size effect on vigilance' (Elgar, 1989). Group size is also important to studying flight behaviour response in prey populations, for example, Matson *et al.* (2005) and Recarte *et al.* (1998) found that large groups of ungulates are more tolerant to risk predation, than are ungulates in small groups. Ultimately, these effects will have a positive impact on animal fitness. The impact of outdoor activities depending on the animal group size has been previously studied but with most of the focus on the impact on the flight distance (e.g. Recarte *et al.*, 1998; Taylor & Knight, 2003). However, Jayakody *et al.* (2008) studied the impact of hikers on red deer vigilance and did not find that group size influenced the animal response to this outdoor activity. Finally, the characteristics of the local environment, such as the vegetation available, have been demonstrated to influence the animal vigilance risk response (Bonnot *et al.*, 2017). As the impact of outdoor activities on wildlife is highly variable (Bateman & Fleming, 2017) more study is necessary.

Previous studies have quantified flight and vigilance behaviours in response to a disturbance (e.g. Jayakody *et al.*, 2008; Reimers *et al.*, 2011), these behaviours have not been extensively studied at different distances from the source of disturbance and at the different intensity of disturbance. Similarly, the interaction of ungulate populations with outdoor recreation has been widely studied (Stankowich, 2008), but various behavioural responses to recreationists have been found. Thus, there is a need to further explore different behavioural responses of the ungulate population (here red deer) to recreationists (here hikers) using various disturbance metrics such as the distance from the disturbance and intensity of the disturbance. To detect changes in these behaviours due to the variable intensity of hiking activity at our site, we further focus on small spatial distances.

Historically, animal vigilance, flight behaviour, and the trade-off between them have been studied using direct observation (Borkowski, 2001; Gander & Ingold, 1997; Malo *et al.*, 2011) which limits the observation to situations where the researcher is in close proximity to the animal (Marion *et al.*, 2020). Conversely, camera traps are less invasive and allow the monitoring of wildlife behaviour over long periods of time (Caravaggi *et al.*, 2017). Therefore, we use camera traps placed in perpendicular transects to a well-defined hiking path to detect red deer and categorize the time they allocate to vigilance or flight behaviour as well as the direction of movement. We further consider the distance from the path as well as demographic information (e.g. group size) and environmental variables (e.g. hunting season) which may affect vigilance and flight behaviour. We hypothesize that the time allocated to the different behaviours will change depending on the distance from the hiking path and the level of hiking activity (Trade-off hypothesis). We also hypothesize an increase in the level of vigilance at shorter distances from the hiking path and increased vigilance associated with higher levels of hiking activity (Vigilance hypothesis). We hypothesize that red deer will exhibit flight behaviour more often when they are close to the hiking path (Flight hypothesis) and we predict that before and during intense hiking periods the animals' direction of movement will be away from the hiking path (Movement hypothesis).

Materials and methods

Study area

Data collection occurred over three fieldwork seasons from early July to early November 2017, from mid-June to the end of October 2018, and from early June to the end of October 2019. The study site was the mountainous terrain of a landholding (estate) in Glen Lyon, Perthshire, Scotland centred on 56°37'04.5"N 4°10'50.7"W (Fig. 1). The observations spanned the most intensive period of hiking activity, which occurs during the summer and autumn, and is an important period for the management of red deer in this area. The estate is managed for red deer stalking (hunting), which occurs from the end of August to the end of October for shooting stags (adult male red deer) and onwards to the end of February for the control

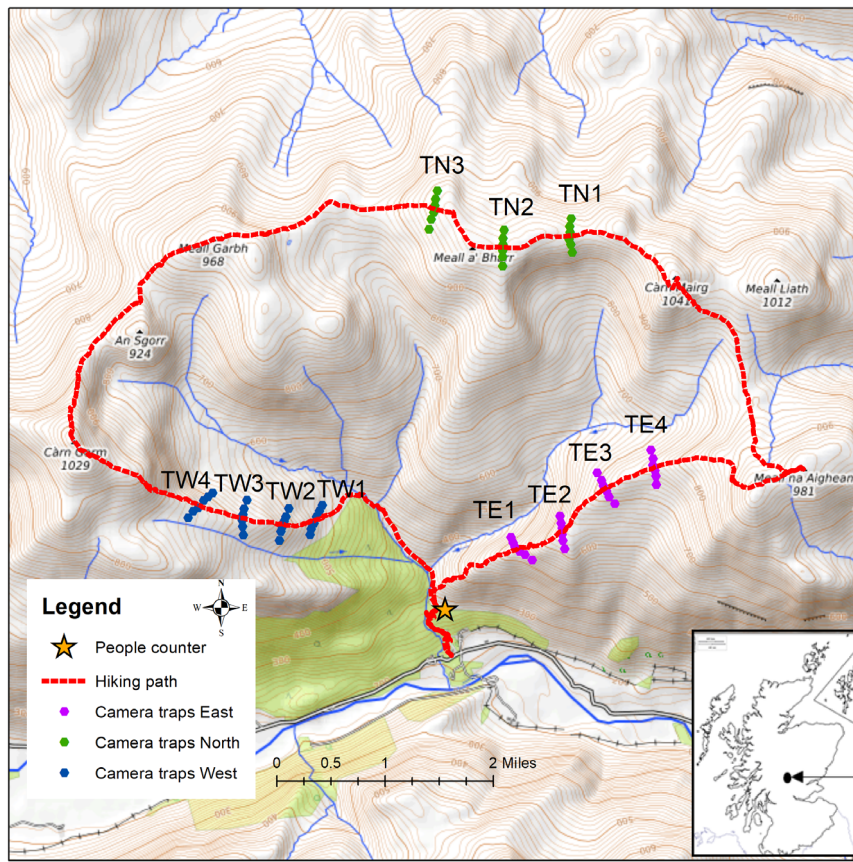


Figure 1 Study area in Glen Lyon (Scotland) with the location of each camera positioned as transects at different distances from the hiking path. The star shows the location of the people counter.

of hind (adult female red deer) numbers. The stag seasons overlapped with our study and the number of hunting days varied every year, comprising 28 days in 2017 (between the 31/08 and the 20/10), 24 days in 2018 (between the 30/08 and the 20/10), and 18 days in 2019 (between the 30/09 and the 19/10). The landholding is not fenced and, thus, red deer can move freely from this estate to neighbouring areas. In 2019, the red deer population was estimated at around 380 animals in the area (13.91 deer/km²; Deer Management Plan, Breadalbane Deer Management Group). Red deer are not given supplementary feeding on this estate, but mineral (salt) licks are used throughout. No natural predators are present in the area and, during the summer, sheep graze in the same landscape. Vegetation on the estate consists of a combination of open heather moorland, grassland, and peat communities, typical of this part of Scotland with some fenced plantation forestry close to the valley bottom.

The study area includes a popular 17 km circular hiking path which makes it possible to reach four Munros in one day. Munros are Scottish mountains over 3000 ft, and ‘Munro bagging’ is a popular activity that consists of climbing all 282 Scottish peaks above this height. Since the path in our study area crosses four of these mountains, it is relatively popular among hikers and, as such, provides a good site to study how

deer react to hikers. Furthermore, the terrain in this area constrains the path to one entry/exit point (even the rare hikers who do not complete the full loop and who use one of the southward facing gullies are forced to return to the start point). This allows the intensity of hiker activity to be monitored at only one location (at the start/end of the trail, see Section 2.2: [Hiking activity](#)), through the people counter placed before the path splits into two (Fig. 1).

Hiking activity

To count how many people entered the path, we used a Chambers Radio Beam People Counter RBX_EB, which allowed us to record the number of hikers passing the counter every hour (Fig. 1). This single counter was placed at the start of the circular hiking path—almost all people enter the path at this point where a forestry gate gives access to the area. Hikers tend to complete the trail clockwise from west to east to ascend all four Munros and then return to this starting point (Marion *et al.*, 2021). For each day we calculated when the maximum number of hikers was reached by summing the number of hikers every hour. When this maximum was reached, we estimated that the number of hikers was decreasing from then onward (people exiting the path). Due to an interference problem with the automated

counter caused by the movement of tall vegetation, three brief periods were removed from our analysis (18-Jun-2018 to 24-Jun-2018, 07-Jul-2018 to 09-Jul-2018, and 03-Aug-2019 to 15-Aug-2019). Camera trap photos (see Section 2.3: **Camera traps**) taken during these periods were also removed from all analyses involving the number of hikers.

We have estimated the number of hikers per day to be around 7, with more hiking activity during the weekends and around lunchtime (Marion *et al.*, 2021). This number was constant from May to November, with a slight decrease in frequency from October (Marion *et al.*, 2021). Using the hourly information from the people counter, we classified hiking activities as quiet or busy. We classified each hour as quiet or busy using the mean number of hikers per hour (mean ~ 8) as the threshold between quiet and busy hiking activity (Fig 2a). This threshold had previously been found to be a relevant separator to studying hiking activity in this area (Marion *et al.*, 2021).

To assess whether hikers were staying on the hiking path or taking detours, and to support the use of the counter as an indicator of hiking activity in the area, we asked hikers to carry GPS trackers (Fig 2b). We sampled 60 days of hiking activity using GPS trackers. These days were evenly distributed over our 3-year periods of data collection, including weekdays and weekends. We approached hikers between 7:00 AM and 13:00 at the entrance to the hiking path and, after explaining the aim of our project, we asked them to carry a GPS tracker (i-Blue 747proS GPS Trip Recorders). One GPS tracker was given per hiking group and we asked the group to drop off the tracker in a box at the end of their route. From these GPS tracks, we estimated the percentages of hikers completing the full hiking loop, passing our camera trap transects and the counter twice. We used a kernel density estimation with 10 m kernel bandwidth for all GPS tracks combined.

Camera traps

To study red deer behaviour at different distances from the hiking path we used camera traps laid out in transects (Fig. 1). We used three different camera trap models: Bushnell (Trophy Cam Trail 119456C), Reconyx (UltraFire), and Browning (Strike Force HD Pro). To investigate small distances avoidance of hiking activity, we set up these camera traps in transects at 25, 75, and 150 m from the path. Previous studies in Scotland suggested that avoidance behaviour occurs at relatively fine distances from hiking paths [i.e. within 100 m (O'Neill, 2016) to 250 m (Sibbald *et al.* 2011)]. In 2017, 27 camera traps were deployed in 11 transects; in 2018 and 2019, 15 camera traps were deployed in 6 transects (see Table S1). Each transect consisted of three cameras and was set up on one side of the hiking path (North or South) at a time. The location of the transects was selected to represent three portions of the hiking trail, most of which occurs along a natural ridge in the upland section of the route (Fig. 2b).

All camera traps were set at a height of 1.10 m and angled away from the hiking path to limit captures of human hikers. We calibrated camera traps to take multiple photos per detection event (which varied depending on camera make and

model: 3 for Bushnell, 8 for Browning, and 10 for Reconyx) and they were set to re-trigger with no delay. The cameras were deployed across a range of different types of vegetation, elevation, and visibility present in the area. We classified the predominant vegetation in front of the camera into one of five vegetation types: wet dwarf shrub heath, dry dwarf shrub heath, mountain vegetation, bare peat, and blanket bog, based on an existing vegetation classification scheme (JNCC 2010).

This camera traps design was previously used in Marion *et al.* (2021) to study red deer spatio-temporal avoidance of areas close to the hiking path. They found that the red deer detection rate did not vary seasonally but more red deer were detected during the night-time than during the daytime in the areas close to the hiking path. The detection rate of red deer was also changed by the hiking activity intensity with fewer red deer detection in areas close to the hiking path during the busy hiking period (Marion *et al.*, 2021).

Photo processing

For each photo, we manually recorded demographic, behaviour, and movement direction data using the photo processing software Exifpro 2.1 (<https://exifpro.informer.com>). We identified the number of red deer observed for each sex (Fig. 3a). We classified the number of deer in each image into categories: one, two, three to six, and more than 6. This aims to reflect the social aggregation behaviour of red deer as hinds aggregate in groups of 6 (a group of hinds consisting of a grandmother, her daughters, and granddaughters) while stag groups vary in size (Clutton-Brock & Albon, 1989). For each photo, we categorised the deer behaviour following the categories from Kuijper *et al.* (2014) and added one category to their list ('Lying down'). This generated nine categories: eating (masticating or grazing), standing (still), walking (not eating), running, lying down, sudden rush (from still to running), sniffing, interaction (two animals interacting), and mixed behaviour (Fig. 3b). From this, we classified an animal as 'Vigilant', when the animal was 'Standing' or 'Lying down' and had its 'Head up' at the same time (Schuttler *et al.*, 2017). When the main behaviour was walking or running, we categorised the direction of the movement of the animal with respect to the path (Fig. 3d). When more than one animal was detected, we manually counted the number of behaviour observed for each category and attributed to the photo a dominant behaviour of the group.

Red deer can spend a large amount of time in the same location, for example, while eating or lying down. We categorised a sequence of photos as independent if more than 10 min elapsed between two photos. The 10-min threshold is lower than previous studies (see Sollmann, 2018) but we chose this to take into consideration the large group sizes relative to the small size of our study area. The classification at the photo level was used to obtain the classification at the sequence level. For each sequence of photos, we calculated the percentage of each behaviour and the total length of the sequence in seconds using the time of the first and last photos of the sequence. If, in a sequence, the number of animals varied amongst photos, we attributed to this sequence the maximum

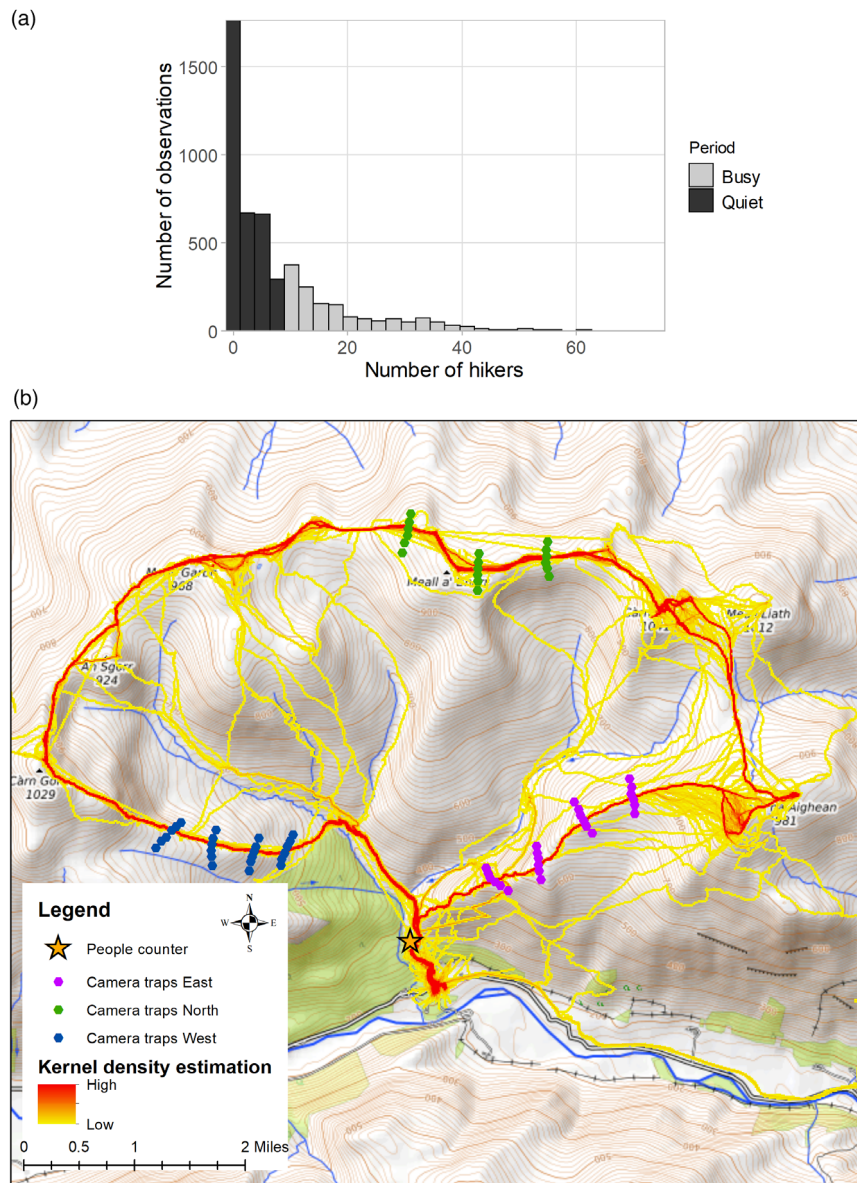


Figure 2 Hiking activities over periods of camera trap deployment. (a) Distribution of the cumulative number of hikers per hour classified as quiet (≤ 8) or busy (> 8) from the automatic counter. (b) Map of hiker GPS tracks relative to the terrain and location of camera traps. We estimated hiking density values using kernel density estimation with a bandwidth of 10 m.

number of animals. For the sex of the animal, if two animals of different sex were recorded on two photos of the same sequence, we associated the sequence with a combination of these two animals (e.g. one photo with a ‘hind’ and one photo with a ‘stag’ gave ‘hind and stag’ at the sequence level).

Data analysis

Behavioural trade-off

For each behaviour, we calculated the sum of the length of every sequence with this specific behaviour and we divided

these sums by the total length of every sequence (i.e. all behaviour). We obtained the percentage of each behaviour for each distance (25, 75, and 150 m) and period of hiking activity (quiet vs. busy).

Drivers of vigilance and flight behaviour

To investigate which factors influence vigilance and flight behaviours, we used two generalized linear mixed models (GLMMs) with a binomial response function where we coded 1 for vigilance or flight and 0 for all other behaviours.

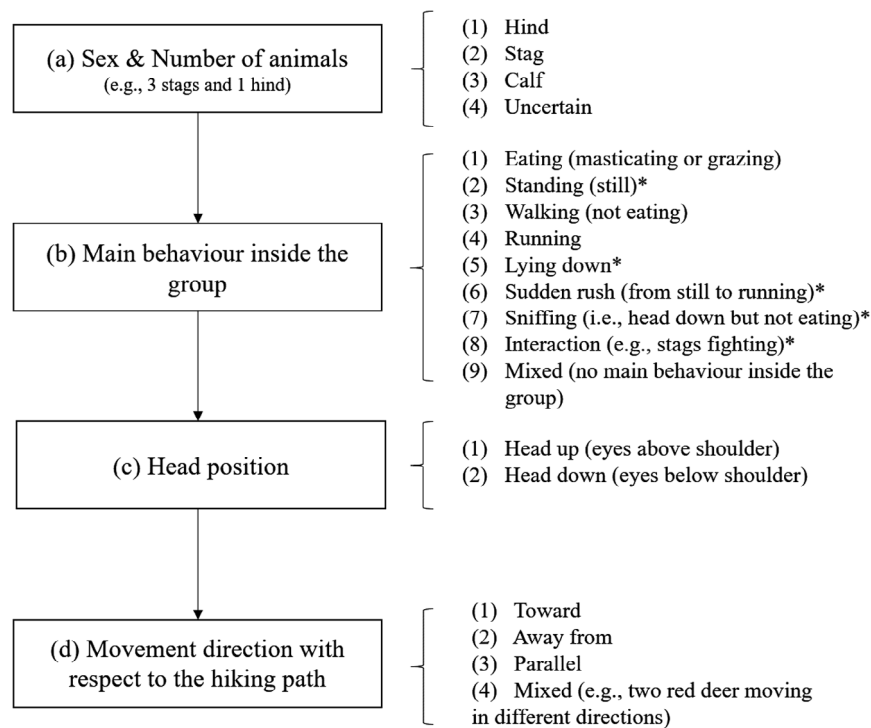


Figure 3 Image analysis to obtain the main behaviour of the red deer group in a photo and the corresponding option for each photo. *We grouped the behaviours (2) and (5) with “Head down” and (6), (7), (8) as “Other” behaviours due to very few observations of these behaviours (i.e. less than 5% of the overall number of observations).

We removed data with flight behaviour from the vigilance analysis, and vice-versa. We only included detection of these behaviours during the daytime. We choose to focus on the daytime periods as the quality of the photos during the night did not allow clear observation of the deer behaviour which could lead to some bias in the comparison with the behaviour observed during the day. Moreover, we focused our study on the immediate behavioural response to the hiking activity itself which occurred mostly during the daytime. We used the sunset and sunrise times of each day as delimiters of night and daytime. We obtained the exact sunset and sunrise times for each day using the function `sunriseset` from the package `Maptools` (Bivand and Lewin-Koh, 2015) in R version 3.5.2 (R Core Team 2018).

For the two models, we used eight fixed effects: distance from the hiking path (25, 75, or 150 m), hiking activity (quiet or busy as described above), the number of deer categorised in the image analysis, the sex (see Section 2.5.1: [Behavioural trade-off](#) about mixed-sex groups), hunting activity (classified as Yes or No depending on whether the detection occurred during the hunting season; see hunting dates above), vegetation (five classes listed above), the time of the day (morning vs. afternoon) and elevation. We also included two interaction terms between distance from the path and hiking activity, and between the time of day and hiking activity. To account for the close spatial proximity between cameras, we included the transect and the camera trap location as a random nested effect

(camera locations nested within transects). After checking for collinearity between the variables, we removed vegetation ($VIF > 5$; Zuur *et al.*, 2017).

We used a model selection approach and fitted all the possible combinations of the fixed effects from the global model using the R package ‘`MuMIn`’ (Bartoń, 2020). We compared the different fitted models using the Akaike Information Criterion for small sample sizes (AICc; Akaike *et al.* 1973), retaining models for inference when $\Delta AICc < 6$ and if they were not a more complex form of a model with a lower AICc. Given that we were interested in testing the hypothesis of hiking activity, we also retained the model with the hiking activity variables included (hiking activity and distance from the hiking path), whether or not it was in the set of models retained.

Movement direction analysis

We selected only deer images which exhibited movement behaviour (walking and running) during the daytime and analysed the direction of movement by calculating the percentage of each movement direction relative to the distance from the hiking path (25, 75, and 150 m) and depending on the hiking activity (quiet vs. busy). The direction “Parallel” was divided by two to represent the two directions associated with this variable and avoid over quantifying this variable in comparison to the other directions ‘Toward’ or ‘Away from’.

Results

Hiking activity

We found that 90% of hikers we surveyed did not go off track and 83% performed the full delimited hiking loop (Fig 2). We found that the percentages of hikers walking on the hiking path close to our camera traps were 94% in the West area, 87% in the East area, and 86% in the North area. We also found that 98% of the hikers were arriving and leaving the area by crossing the automatic people counter. We showed that the hiking path was the most intensively used area by hikers (see Kernel density in Fig. 2). Hikers spent more time around the four main summits of the hiking trail. Most of the hikers performed the loop from West to East, with their ascension occurring in the West part of the hiking loop. Thus, overall this area was slightly more used due to the slower pace of the hikers.

Behavioural trade-off

Over the three periods of data collection, we captured 2906 independent sequences of red deer, of which 1063 occurred during the day. We observed the behaviour 'eating' 395 times, 'walking' 519 times, 'vigilant' 320 times, and 'running' 223 times. Red deer behavioural trade-off (i.e. time allocation) did not change with distance from the hiking path (Fig. 4a). The most frequently observed behaviour was eating, followed by walking. Overall, despite some fine variation between the distances, no change in red deer time allocation was observed depending on the distance from the hiking path. This does not support our trade-off hypothesis (i.e. change in time allocation depending on the distance from the hiking path).

We did not observe a change in time allocation amongst the different behaviours depending on the level of hiking activity (Fig 4b). Flight and vigilance behaviour were observed more often during the quiet hiking period (4.27 and 16.4%, respectively) than during the busy hiking period (2.62 and 10.17%). Overall, red deer displayed undisturbed behaviour more frequently during busy hiking periods than during quiet hiking periods (87.21 vs. 78.28%). We did not observe an increase in the time allocated to flight or vigilance behaviour during busy hiking periods. This also does not support our trade-off hypothesis (i.e. change in time allocation depending on the hiking activity).

Vigilance and flight behaviour

Vigilance

In Table 1a we summarise the model selection table and present GLMMs with $\Delta AIC < 6$ from the model with the lowest AIC and only models that are not a more complex version than a model with a lower AIC. For vigilance, all these models cannot be considered as distinguishable from each other as they are within $\Delta AIC < 6$ from each other (Richards, 2005). However, all these models included at least distance, elevation, or hunting season as an independent variable (Table 1a). Thus,

we used the model with all these variables for inference (Table 2a).

The detection of vigilance was greater at the distance 75 m, relative to that at 25 m (Table 2a). We also compared the detection of vigilance behaviour in the model which included only the variables of our hypothesis (hiking activity and distance from hiking path; Table 2b). We obtained similar results with more red deer vigilant at 75 m than at the closer distance, but we did not detect an impact of the hiking activity on the detection of vigilance behaviour.

Flight behaviour

In Table 1b, we summarise the results of the model selection and present GLMMs with $\Delta AIC < 6$ from the model with the lowest AIC and only models that are not a more complex version than a model with a lower AIC. These models cannot be considered as distinguishable from each other as they are within $\Delta AIC < 6$ from each other (Richards, 2005). These models included at least the group size, the time of the day, and the hiking activity as an independent variable (Table 1b). Thus, we used the model with the variable group size and time of the day for inference (Table 3a).

We also compared the detection of flight behaviour in the model which included only the variables of our hypothesis (hiking activity and distance from hiking path) (Table 3b). We observed significantly less flight behaviour when the group size was large (≥ 7 , Table 3a). We also detected less flight behaviour during the afternoon than during the morning. Finally, we did not detect more flight behaviour closer to the hiking path or during busy hiking days (Table 3b).

Direction of the movement

We found that the direction of the movement relative to the hiking path did not vary with the distance from the hiking path or with the level of hiking activity (Fig. 5). Overall, red deer moved parallel to the hiking path 60% of the time (after dividing the number of movements 'parallel' by two). Avoidance of the hiking path (i.e. movement 'Away') did not increase closer to the hiking path (Fig 5a).

Similarly, we did not detect an increase in movement away from the hiking path during periods of busy hiking activity. On the contrary, we detected more movement moving away from the hiking path during quiet hiking activity than during busy hiking activity (17 vs. 7.3%; Fig 5b). This does not support our movement hypothesis (i.e. more movement away from the hiking path close to the hiking path or during a busy hiking period).

Discussion

Our study shows very little evidence for elevated vigilance or flight behaviour in response to hiking activity or proximity to the hiking path at our study location. We investigated the impact of hiking activity on red deer behavioural trade-off, vigilance, and flight behaviour, and movement direction in close proximity (<150 m) to a hiking path. We found that most

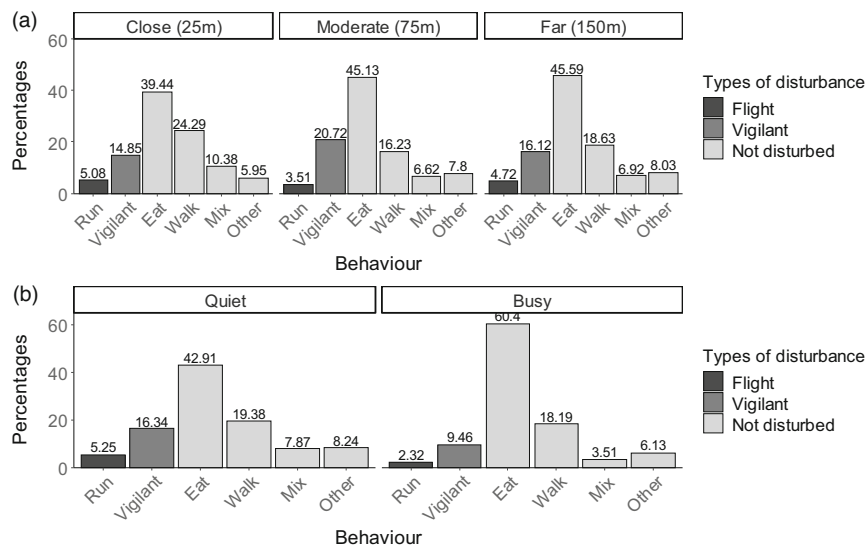


Figure 4 Percentages of each behaviour observed in red deer during the day and the corresponding level of disturbance (Flight, Vigilant, or not disturbed) for (a) at each distance from the path (25, 75, and 150 m) and (b) depending on the level of hiking activity (quiet vs. busy) during the day.

Table 1 Selected GLMMs ($\Delta AICc < 6$) and variables retained for the detection of (a) vigilance and (b) flight behaviour of red deer

	Variable retained	d.f.	LogLik	AICc	Delta	Weight
(a) Vigilance model						
M1	Distance + Elevation + Hunting	7	-420.956	856.072	0.000	0.050
M2	Distance + Elevation	6	-422.183	856.485	0.413	0.041
M3	Elevation + Hunting	5	-423.295	856.676	0.603	0.037
M4	Elevation	4	-424.462	856.981	0.909	0.032
M5	Distance + Hunting	6	-422.726	857.572	1.500	0.024
M6	Distance	5	-424.119	858.323	2.251	0.016
M7	Hunting	4	-425.238	858.533	2.461	0.015
M8	Null model	3	-426.595	859.225	3.152	0.010
(b) Flight model						
M1	Group size + Time of the day	7	-350.347	714.872	0.000	0.051
M2	Time of the day	4	-353.925	715.912	1.041	0.030
M3	Hiking + Group size	7	-351.214	716.605	1.733	0.021
M4	Group size	6	-352.312	716.758	1.885	0.020
M5	Hiking	4	-355.071	718.206	3.334	0.010
M6	Null model	3	-356.328	718.693	3.821	0.007

Each model was fitted using a binomial family and the transect ID and the camera trap location were used as a nested random effect.

of the hikers stayed on the hiking track. Contrary to our hypotheses, based on behavioural ecology literature, we found that flight behaviour and movement direction did not depend on distance from the hiking path (Flight and Movement hypothesis). Red deer were more vigilant at moderate (75 m) than at close (25 m) distances but were not less vigilant at 150 m than at 25 m. In our study, red deer flight behaviour was more frequently detected in the morning than in the afternoon, and overall was less frequent when the deer were in large groups.

Habituation to disturbance is a common result of outdoor recreation-wildlife interactions (Griffin *et al.*, 2007; Hansen & Aanes, 2015; Malo *et al.*, 2011). Habituation typically depends

on the animal's risk perception and time exposure to the disturbance: the more the animal is exposed to the activity the more it is habituated and the less it shows flight or vigilance behaviours (e.g. Villanueva *et al.*, 2012). Here, times allocated to flight and vigilance behaviours were less important during busy hiking periods, which corroborates red deer habituation to hikers. In response to the intensity of hiker activity or distance from the path (Trade-off hypothesis), red deer did not alter the amount of time they allocated to flight or vigilance, relative to non-vigilant activities like feeding and resting. This finding suggests that red deer in this area are not perturbed by hikers or are habituated to their presence due to repeat encounters with them (Hansen & Aanes, 2015). Red deer in Scotland have existed for the last

Table 2 Results of (a) the best generalized linear mixed-effects models (GLMMs) of red deer vigilance behaviour and (b) of the hiking pressure which corresponds to our hypothesis for the vigilance behaviour detection

	Estimate	SE	P-value
(a) Best model			
(Intercept)	1.626	1.354	0.223
Distance 25 m	Reference	Reference	Reference
Distance 75 m	0.759	0.345	0.028
Distance 150 m	0.209	0.327	0.522
Elevation	-0.004	0.002	0.053
Hunting season (No)	Reference	Reference	Reference
Hunting season (Yes)	0.398	0.250	0.112
(b) Hiking pressure			
(Intercept)	-0.818	0.372	0.028
Distance (25 m)	Reference	Reference	Reference
Distance (75 m)	0.806	0.369	0.029
Distance (150 m)	0.280	0.345	0.416
Hiking (quiet)	Reference	Reference	Reference
Hiking (busy)	0.015	0.557	0.976
Distance (25 m):Hiking (quiet)	Reference	Reference	Reference
Distance (75 m): Hiking (busy)	-0.217	0.686	0.752
Distance (150 m): Hiking (busy)	-0.622	0.692	0.369

Bolded rows show statistically significant variables (p-value < 0.05).

Table 3 Results of (a) the best generalized linear mixed-effects models (GLMMs) of red deer flight behaviour and (b) of the hiking pressure which correspond to our hypothesis for the flight behaviour detection

	Estimate	SE	P-value
(a) Best model			
(Intercept)	-1.080	0.233	<0.001
Group size (1)	Reference	Reference	Reference
Group size (2)	0.027	0.262	0.918
Group size (3-6)	0.115	0.232	0.620
Group size (≥7)	-0.935	0.415	0.025
Time of the day (morning)	Reference	Reference	Reference
Time of the day (afternoon)	-0.384	0.195	0.048
(b) Hiking pressure			
(Intercept)	-1.298	0.341	<0.001
Distance (25 m)	Ref	Reference	Reference
Distance (75 m)	0.448	0.458	0.327
Distance (150 m)	-0.284	0.448	0.526
Hiking (quiet)	Reference	Reference	Reference
Hiking (busy)	-0.038	0.588	0.948
Distance (25 m):Hiking (quiet)	Reference	Reference	Reference
Distance (75 m): Hiking (busy)	-0.384	0.782	0.624
Distance (150 m): Hiking (busy)	-0.663	0.740	0.370

Bolded rows show statistically significant variables (p-value < 0.05).

250 years without natural predators which might have impacted their risk perception. Specifically, the lack of predation might have impacted the behavioural response to predators, multiple generations of red deer not being hunted might have impacted patterns of animal movement and vigilance. The adaptive antipredator response is the ability of prey to distinguish between threatening stimuli such as predators and non-threatening stimuli (Brown & Chivers, 2005). Red deer in Scotland might perceive hikers as a non-risk due to the multiple

generations of red deer in the area being exposed to hikers without lethal interaction (Ferrari & Chivers, 2011).

Similarly, the vigilance behaviour results also suggest that red deer are habituated to hikers in the area. Vigilance behaviour was not impacted by the level of the hiking activity (Vigilance hypothesis). Schuttler *et al.* (2017) showed that deer were less vigilant in areas with more human recreation, showing habituation to recreation activity. However, in a similar landscape to ours, Jayakody *et al.* (2008) found an increase in

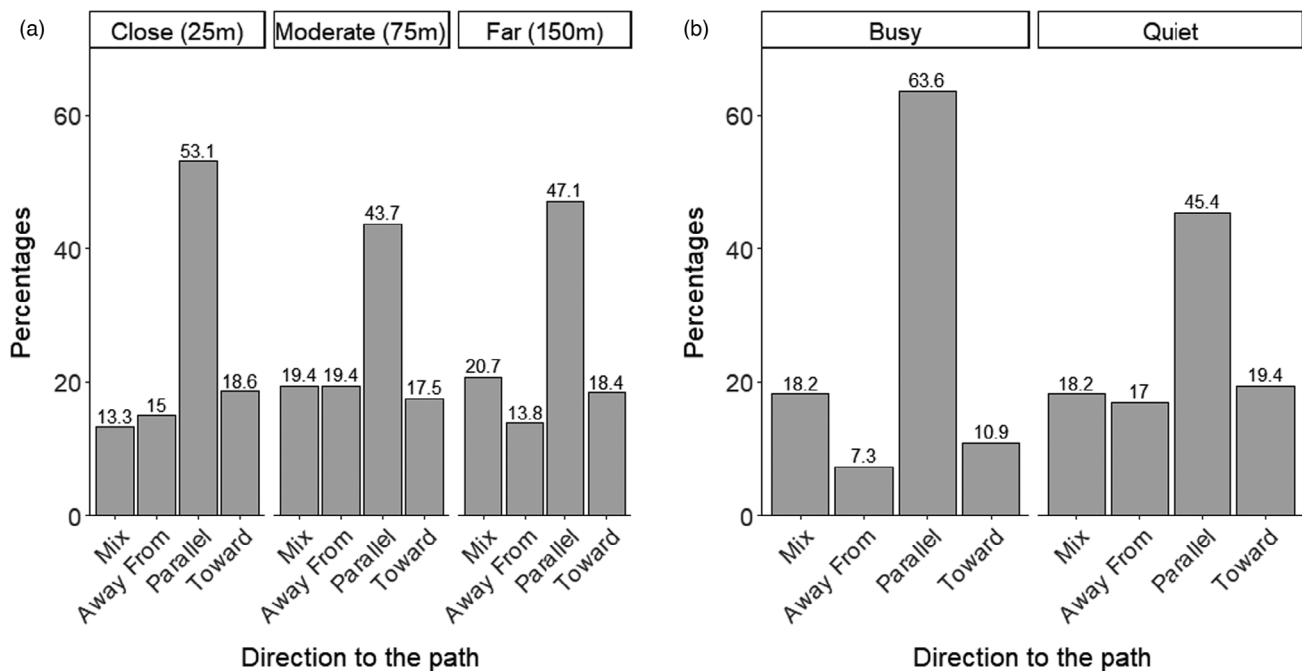


Figure 5 Percentage of each movement direction of red deer recorded during the day (a) at each distance from the path (25, 75, and 150 m) and (b) depending on the hiking activity (quiet vs. busy).

vigilance by red deer located in areas with more recreationists. In remote areas where animals are not used to encounters with humans, the interaction between wildlife and recreationists might lead to an increase in vigilance or flight behaviour (Jayakody *et al.*, 2008). As our study area is easily accessible for a day walk, red deer are frequently exposed to hikers and appear not to perceive them as a risk; this might explain why we did not observe an increase in vigilance associated with busy hiking days. Finally, we did not detect more flight behaviour related to more hiking activity or closer to the hiking path (Flight hypothesis). The habituation to hikers might also explain this result with animals more frequently exposed to recreationists able to spatially avoid the area close to the path when hiking activity is greater (Marion *et al.*, 2021). We also find that red deer displayed more flight behaviour in the morning than in the afternoon, also consistent with the hypothesis of habituation: in the morning when most of the hiking activity starts, red deer display more flight behaviour.

While we did not find a link between the level of vigilance and the group size or the time of the day, they were key factors explaining the detection of flight behaviour. Prey are often found in large groups as an adaptive response for protection against predators (Roberts, 1996). Thus, flight responses are detected less in large groups than in small groups (Berger, 1978). Our results align with this, as we observed less flight behaviour in red deer in group sizes of 7+ individuals. Previous research focusing on interactions between wildlife and outdoor recreation activity have found that larger groups of ungulates are less likely to display flight behaviour than smaller groups (Recarte *et al.*, 1998; Taylor & Knight, 2003).

However, the link between the outdoor activity and the group size behaviour was not found in our study as we did not detect more flight behaviour related to more hiking activity or closer to the hiking path.

The hunting season was not a significant factor to explain red deer's level of vigilance or flight behaviour. Previous studies have found an increase in vigilance during hunting season but could not separate this from the time of the year (i.e. fall) when the appetite of the deer decrease (Jayakody *et al.*, 2008; Schuttler *et al.*, 2017). In our area, hunting rarely occurred in the areas close to the hiking path (i.e. where our camera traps were located) which might explain our result. Moreover, the hunting activity is the only predation risk for this red deer population which might create a landscape of fear (Cromsigt *et al.*, 2013). As a consequence, red deer might have found shelter from the hunting pressure in areas close to the hiking path. This human shield hypothesis has been suggested to explain prey response to outdoor recreation (Berger, 2007). Prey species positively select areas intensively used by human-use areas to protect themselves from predators (Berger, 2007; Kays *et al.*, 2017). In our case, the lack of vigilance or flight behaviour response in a zone where no hunting occurred could support the human shield hypothesis, but this needs further investigation.

Our study area is typical of the Scottish landscape with relatively shallow slopes and open vegetation, meaning that visibility is better at higher elevations. Elevation was a factor explaining vigilance behaviour in our study, and may be related to general visibility. Because of this, the negative relationship between vigilance and elevation suggests that animals may not

need to spend as much time being vigilant at higher elevations as they can more easily assess risk (Hopewell *et al.*, 2005). Due to higher visibility, flight behaviour might not be necessary as red deer have the opportunity to avoid hikers using lower energetic costs by simply walking (Stankowich & Blumstein, 2005). The animal flight behaviour is the strongest response to a disturbance and its physical costs make it a response of last resort to human avoidance (Jiang *et al.*, 2013). Similarly, the physical costs of movement might also explain that we did not observe any substantial differences in movement direction relative to the hiking path. The 'energy landscape' might explain this result as animals adapt their movement to the landscape (e.g. vegetation, slopes) to limit the metabolic costs of animal movement (Shepard *et al.*, 2013). Red deer in our study area seemed to move mostly parallel to the hiking path, which aligns along the summit of a ridge throughout most of the area. Thus, a direct movement toward or away from the path would involve moving up or down steeper parts of the slope. Red deer, by moving parallel to the hiking path, maintain a constant elevation which limits the energetic cost of movement (Shepard *et al.*, 2013).

Conclusions

Our study contributes to a growing body of research studying the impact of outdoor recreation activity on wildlife behaviour. Specifically, here we study how hiking activity along a popular hiking trail influenced red deer behavioural trade-off, vigilance, flight, and movement behaviour relative to a hiking path. We found little evidence for hiker impact on red deer behaviour, which suggests that red deer are habituated to hikers. This is evident in terms of the amount of time red deer spend in non-vigilant (feeding, resting) activities versus vigilance and flight behaviours, both of which were limited. Moreover, we found the general high visibility and the landscape influence the detection of flight behaviour and the movement direction in relation to the hiking path. This result should be compared with sites where avoidance responses are more prevalent, to understand animal responses at behavioural and physiological levels. Moreover, an additional measurement of stress levels (e.g. hormone levels, Rehnus *et al.*, 2014; Romero & Wikelski, 2002), long-term population monitoring (Garber & Burger, 1995) or studies of dietary changes (Jayakody *et al.*, 2011) could be further used to understand fully the impact of hikers on red deer. Despite the range of alternative approaches available, our study brings new perspectives on how camera traps may be used simultaneously to study both animal behaviour and movement direction relative to linear features.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Camera traps (CT) and transects distribution. Camera traps brand: Bushnell (Trophy Cam Trail 119456C), RE: Reconyx (UltraFire), BR: Browning (Strike Force HD Pro. See Fig. 1 for the transect ID and location (i.e. TW, TN, TE and TI); the signs + or – indicate if the transects were on the North or the South part of the hiking path, respectively.