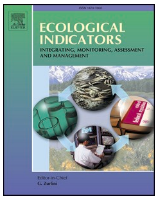
Ecological Indicators 189 (2026) 115113

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Contrasting wildlife detection trends without occupancy change: interpreting long-term camera-trap indicators in a protected woodland

Christopher Andrews [*], Jan Dick

UK Centre for Ecology and Hydrology, Bush Estate, Penicuik EH26 0QB, UK

ARTICLE INFO

Keywords:
Camera-trap monitoring
Detection indices
Dynamic occupancy models
Human recreation
Long-term ecological monitoring
Recreational disturbance
Temporal partitioning

ABSTRACT

Human recreation is increasingly widespread in protected landscapes, raising concern about its potential effects on wildlife. At the same time, long-term camera-trap networks are becoming central tools for biodiversity monitoring, yet detection-based indices integrate abundance, movement and behavioural activity, complicating interpretation. Long duration, standardised datasets therefore offer valuable opportunities to distinguish behavioural disturbance from broader ecological change.

We analysed 16 years of camera-trap data from five fixed woodland locations within a protected landscape to evaluate long-term wildlife trends and assess whether detection-based indicators reflect recreational disturbance or broader ecological dynamics. Species-specific temporal trends were estimated using generalised additive mixed models accounting for sampling effort and location. Dynamic occupancy models were used to distinguish changes in site use from changes in detection or behaviour, and short term disturbance models tested behavioural responses to daily variation in recreation.

Wildlife detection trajectories differed among species. Deer species showed overall declines, whereas mesopredators and small mammals were stable or increased. Despite these contrasting detection trends, occupancy probabilities remained stable. Recreational activity also varied among user types: cyclist and dog-related detections increased, while detections of people without dogs or bicycles showed little long-term change. Short-term disturbance effects were weak and inconsistent, and strong diel segregation between humans and wildlife persisted across recreation levels.

These findings suggest routine recreation alone is unlikely to explain long-term changes in wildlife detections. Long-term camera-trap monitoring can reveal shifts in wildlife activity patterns and community structure, but detection-based indicators require cautious interpretation alongside occupancy estimates and broader ecological context.

1. Introduction

Human recreation is a prominent feature of many protected landscapes (Bell et al., 2007; Monz et al., 2010), prompting concern about potential impacts on wildlife populations and behaviour (Larson et al., 2016). Recreational activities can influence wildlife directly through disturbance (Stankowich, 2008), indirectly through habitat modification (Pickering and Hill, 2007; Monz et al., 2010), or via behavioural displacement, including shifts in activity timing or space use (Larson et al., 2016). Global syntheses increasingly show that human presence often induces behavioural adjustments—especially increased nocturnality or temporal avoidance (Gaynor et al., 2018)—and can alter habitat use patterns in both ungulates and carnivores (Coppes et al., 2017; Baker and Leberg, 2018). Experimental work in low-visitation protected areas similarly shows that even modest levels of human activity can modify wildlife diel activity, with species exhibiting pronounced temporal shifts despite low on-site human presence (Sytsma et al., 2022). However, while behavioural responses are well documented, evidence for sustained demographic or occupancy level impacts of routine recreation is mixed (Larson et al., 2016; Marion et al., 2020). Distinguishing short term behavioural disturbance from longer term ecological change remains a central challenge. Recent multispecies work also shows that recreation effects vary strongly with landscape and management context, with no consistent main effect across species, further underscoring the difficulty of interpreting recreation impacts in general terms (Marion et al., 2024).

---

[*] Corresponding authors.
E-mail addresses: chan@ceh.ac.uk (C. Andrews), jand@ceh.ac.uk (J. Dick).

https://doi.org/10.1016/j.ecolind.2026.115113
Received 23 March 2026; Received in revised form 14 May 2026; Accepted 17 June 2026

Camera traps are widely used to assess wildlife communities and activity patterns in human used landscapes. Long term camera networks can reveal temporal trends (Blake et al., 2017), quantify behavioural partitioning (Ridout and Linkie, 2009; Frey et al., 2017), and evaluate responses to anthropogenic pressures (Baker and Leberg, 2018; Gaynor et al., 2018; Salvatori et al., 2023). However, interpreting detection data requires careful consideration: detection rates reflect a combination of relative abundance, movement, and behavioural activity within a camera's detection zone (Rowcliffe et al., 2008; Sollmann et al., 2013), whilst camera placement and sampling design can systematically bias detection rates and behavioural inferences (Tanwar et al., 2021). Camera-trap detectability can also be influenced by responses to camera noise, illumination, scent and model-specific sensitivity, which may bias which individuals or behaviours are recorded (Caravaggi et al., 2020). Assuming no changes in placement and design over a monitoring study, reduced detections may therefore reflect altered behaviour rather than reduced site use. Integrating detection based analyses with dynamic occupancy models (MacKenzie et al., 2003) can help distinguish changes in occupancy from changes in detectability or local activity.

The Cairngorms National Park in Scotland supports diverse woodland wildlife alongside sustained recreational use. Within the Allt a'Mharcaidh catchment of the Inshriach National Nature Reserve (NNR), a fixed camera trap network has operated since 2010, providing a unique 16 year record of wildlife and human activity. Prior work indicates that recreational impacts often manifest through behavioural change rather than site abandonment (Larson et al., 2016; Coppes et al., 2017; Baker and Leberg, 2018; Salvatori et al., 2023). This long term dataset therefore provides an opportunity to test whether observed detection trends reflect recreational disturbance, altered behavioural activity, or broader ecological processes within a consistently monitored woodland catchment.

Specifically, we asked: (1) Do camera trap locations represent distinct local wildlife assemblages? (2) How have wildlife detection rates changed over time? (3) Do changes in detections reflect altered site use or behavioural shifts (4) Are wildlife detections associated with levels of recreational activity? To address these questions, we integrated species specific trend models, dynamic occupancy analysis, diel overlap assessment, and disturbance modelling to evaluate whether long term detection trends reflect recreational effects or wider ecological dynamics.

2. Methods

2.1. Study area and camera-trap network

Research was conducted within the Allt a'Mharcaidh catchment (57°06′56″N, 003°50′47″W) of the Inshriach National Nature Reserve (Cairngorms National Park, Scotland). The catchment forms part of the Cairngorms Connect partnership, which aims to enhance woodland habitats, species and ecological processes over a 200 year period. Long term monitoring has been undertaken here since 1999 as part of the UK Environmental Change Network (Sier and Monteith, 2016; https://deims.org/5a04fee1-42aa-47e9-abfc-043a3eda12ac).

Throughout the manuscript, "camera" and "camera location" refers to the sampling site, while "camera model" refers to hardware type. Fixed camera locations and consistent placement reduce the design-related biases shown to occur when cameras are positioned to target specific species (Tanwar et al., 2021).

Five camera trap monitoring locations were variably established in *Pinus sylvestris* L. (Scots Pine) woodland habitats between 2010 and 2025 (Fig. 1); two locations were monitored in 2010, four in 2011–2012, and all five from 2013 onwards (supplementary plot S4). Cameras were placed along woodland paths and tracks used by wildlife and recreational users. Locations included plantation woodland (TR), mature semi natural Scots pine woodland (PA, TL), regenerating woodland (SN), and a movement bottleneck at a footbridge (BR). Cameras operated continuously, recording a single image per trigger and additional images if the subject remained within the detection zone. Detections were aggregated into independent events using a 5 min threshold, retaining the maximum number of individuals per event. Sampling effort was

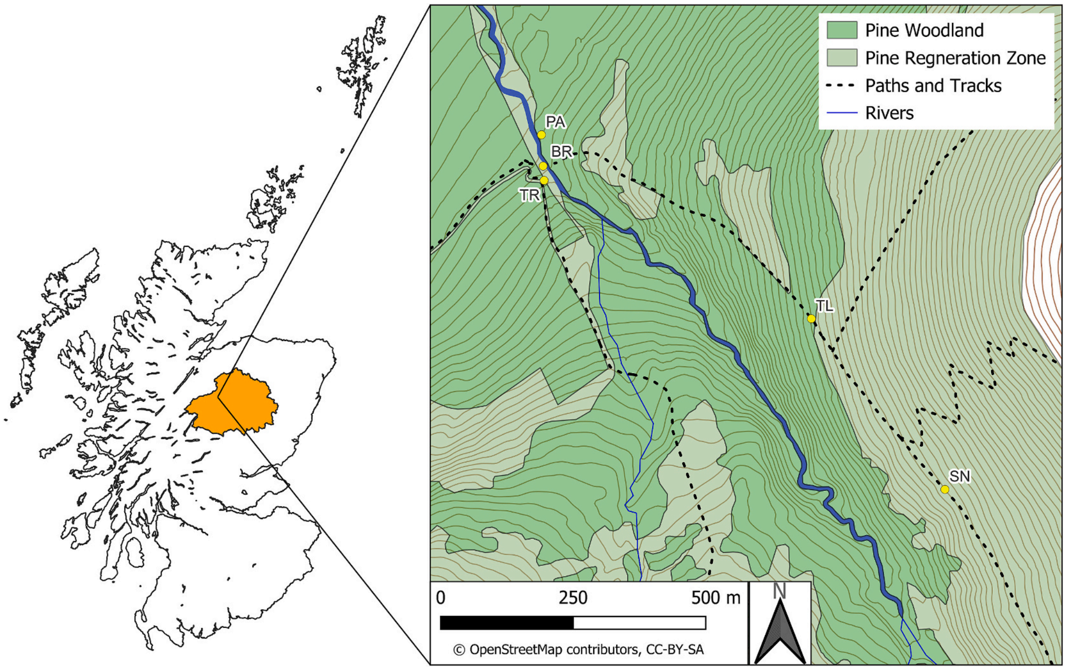


Fig. 1. Location of five camera trapping locations within the Allt a'Mharcaidh catchment, Cairngorms National Park (in orange), Scotland, between 2010 and 2025. All cameras were located along paths or tracks (dotted lines) within various *Pinus sylvestris* L. (Scots Pine) woodland habitats, including: plantation (TR), mature semi-natural (PA, TL), natural tree regeneration (SN), and riparian woodland overlooking a footbridge (BR). Green areas on the map represent mature woodland areas, whilst white areas are generally covered by naturally regenerating trees (< 30 years old) on moorland. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

quantified as camera days per location per year.

Despite close spatial proximity, camera locations TR and PA are located on different footpaths on opposite sides of a river spanned by a footbridge (monitored by BR). All three camera locations showed high pairwise Bray–Curtis dissimilarity (0.62–0.99), indicating that they sampled markedly different detection assemblages within the monitoring network. However, given the spatial clustering of camera locations, analyses were designed to assess temporal dynamics and behavioural responses within a fixed monitoring network rather than to support independent spatial comparisons among sites.

2.2. *Effort standardisation and recreational group identification*

Although the number of active cameras increased during the early years, sampling effort was quantified as camera-days for each camera-year. All statistical models included camera identity (sampling location) as a random effect, ensuring that annual detection estimates were comparable despite changes in camera-trap network size. Detection rates were standardised by including camera deployment duration as an effort offset in the models, while descriptive detection rates were annualised to 365 camera-days. Recreational detections were first collapsed within each camera to a single record per event, recording start and end time, maximum detected group size, and the presence of dogs or bicycles, to avoid double-counting within locations.

To identify recreational groups moving between camera locations, we used the Louvain community detection algorithm (Blondel et al., 2008). Each camera event was treated as a node in a network. Events at different camera locations were considered potential matches if the arrival time at one camera occurred within 30 min of the departure time from another, represented plausible camera-to-camera movement transitions, and were of similar group size (difference ≤ 1 person). Candidate links were weighted using exponential decay functions based on time and group-size difference, such that closer matches in time and group size were assigned higher weights, whilst links with low weights (≤ 0.3) were discarded. The remaining network was clustered using Louvain (R package igraph v2.2.1) to assign group identities across cameras, thereby reducing double counting of the same group at multiple locations and generating annualised counts of people, dogs, and bicycles.

2.3. *Community composition analysis*

To characterise variation in assemblage among camera locations within the monitoring network, species-specific detection rates (annualised to 365 camera-days) were used to construct camera–year community matrices representing relative activity levels of each species at each camera in each year. To represent the persistent assemblage and reduce noise from sporadic taxa, analyses were restricted to species detected in at least half the study years (≥ 8 years), and ambiguous taxa not identifiable to species level were excluded, leaving nine species (see Fig. 3 for list of species). Relative activity abundance per camera location was calculated as the proportion of total detections attributable to each species. To quantify the dissimilarity in species composition between different locations, Bray–Curtis dissimilarities were computed using the R vegan package (v2.7–1). Differences among locations were tested using PERMANOVA (adonis2, 999 permutations) with camera location as the main factor and year as a stratification variable. Homogeneity of dispersion was assessed using betadisper and permutest. Non-metric multidimensional scaling (NMDS) was used to visualise community differences, and species vectors were fitted using vegan envfit function to identify taxa driving ordination axes. Indicator species analysis was conducted on both activity abundance and presence–absence data using multipatt (R package: indicspecies v1.8.0).

2.4. *Temporal trend modelling*

Long-term temporal trends in wildlife and recreational detections were analysed using generalised additive mixed models (GAMMs) implemented in R using the mgcv package (v1.9–3). These analyses describe broad changes in detection rates through time but are not intended to test mechanistic links between long-term trends in recreational activity and wildlife responses. To ensure robust analyses, only species which occurred in at least half the years, and had a minimum of 200 detections, were included, reducing the number of species analysed to a focal group of five (see Fig. 5). Annual detection counts per species and camera location were modelled with a negative binomial error distribution and log link to account for overdispersion in count data. Sampling effort was standardised by including the log of camera deployment duration as an offset.

The candidate model included species-specific smooth functions of year and a fixed effect for camera model:

$$\log\left(\mu_{i,s,t}\right) = \beta_s + s_s(year_t) + \beta_m(model) + u_i + \log\left(camera - days_{i,t}\right)$$

where $\mu_{i,s,t}$ is the expected number of detections for species s at camera location i in year t, $s_s(year_t)$ represents a species-specific smooth temporal trend, and u_i is a random intercept for camera location implemented as a penalised spline ($s\left(camera\_id, bs = \text{"}re\text{"}\right)$). Smooth terms were fitted using thin-plate regression splines with a maximum basis dimension $k = 6$, allowing flexible but constrained temporal responses.

Although camera model was initially included as a fixed effect to control for potential variation in detection probability among devices, exploratory diagnostics showed strong confounding between camera model and sampling year due to the sequential deployment of different camera types throughout the monitoring programme. Model comparison using Akaike's Information Criterion indicated that removing camera model improved parsimony and fit ($\Delta\text{AIC} = 12.5$), and therefore the final model excluded this term.

Model parameters were estimated by restricted maximum likelihood (REML). Model adequacy was assessed using diagnostic tools (R package: DHARMa v0.4.7), including tests for overdispersion and temporal autocorrelation. Temporal autocorrelation was evaluated using aggregated residuals by year. Basis dimension sufficiency for smooth terms was verified using gam.check.

Predicted annual detection rates were generated under standardised conditions (365 camera-days and average camera effects excluded) and visualised with 95% confidence intervals. Observed annual detection rates per camera location were also calculated to illustrate variability among sampling locations.

2.5. *Dynamic occupancy modelling*

To distinguish long-term changes in camera location use from changes in detection or activity, we fitted dynamic occupancy models to monthly detection histories for each species. For each camera location, year was treated as the primary periods (2010–2025), and months as secondary sampling occasions. For each species, monthly detections were reduced to binary observations ($1 = \geq 1$ detection; $0 =$ none). Months in which a camera was not operational were coded as missing (NA). Location–year combinations with fewer than six sampled months were excluded.

Models were fitted using the colext function (r package: ‘unmarked’), estimating initial occupancy (ψ), colonisation probability (γ), extinction probability (ε), and detection probability (p). To test for directional changes in site use at each camera location, extinction probability was modelled as a function of a standardised year covariate ($\varepsilon \sim t$), while colonisation was held constant ($\gamma \sim 1$). Detection probability was modelled as a function of sampling effort and seasonality, using log (uptime-days $+1$) and cyclic month terms (sine and cosine). Annual occupancy trajectories were derived from

$$\psi\_\{t+1\} = \psi\_t(1 - \varepsilon\_t) + (1 - \psi\_t)\gamma\_t.$$

Uncertainty was estimated via parametric simulation from the coefficient variance–covariance matrix (500 simulations).

2.6. Diel activity overlap

Diel activity overlap between pooled human detections and each focal wildlife species was quantified using kernel density estimation of detection times, treating time of day as a circular variable over the 24-h cycle, and calculating the coefficient of overlap (Δ; R package: overlap v0.3.9). Overlap was estimated for the full dataset and repeated after stratifying detections by (i) high vs low recreation years (median split of annual human detections) and (ii) high vs lower recreation camera-days (upper quartile of daily human detections within camera). Uncertainty was estimated using nonparametric bootstrap resampling within each stratum (2000 replicates). The Δ4 estimator was used when both samples were ≥ 75 detections, with Δ1 used otherwise.

2.7. Recreational disturbance models

To test for short-term behavioural responses to recreation, detections were aggregated to a biological camera-day scale. A “biological day” was defined as 06:00–06:00 so that nocturnal wildlife detections were associated with the preceding daylight recreation period. (Fig. 2). Daily effort was reconstructed from camera uptime logs; a biological day was treated as sampled only when the camera was operational on both calendar dates spanning that 06:00–06:00 window, and only sampled days were retained. Daily wildlife and human detections were then summed for each sampled camera-day, with days without detections included as zeros. Month and weekday were included to account for seasonal and weekly variation in recreation. Camera model was included as a fixed effect to control for differences in detection sensitivity among camera models deployed during the study.

Daily wildlife detections were modelled with negative binomial generalised linear mixed models (log link; glmmTMB):

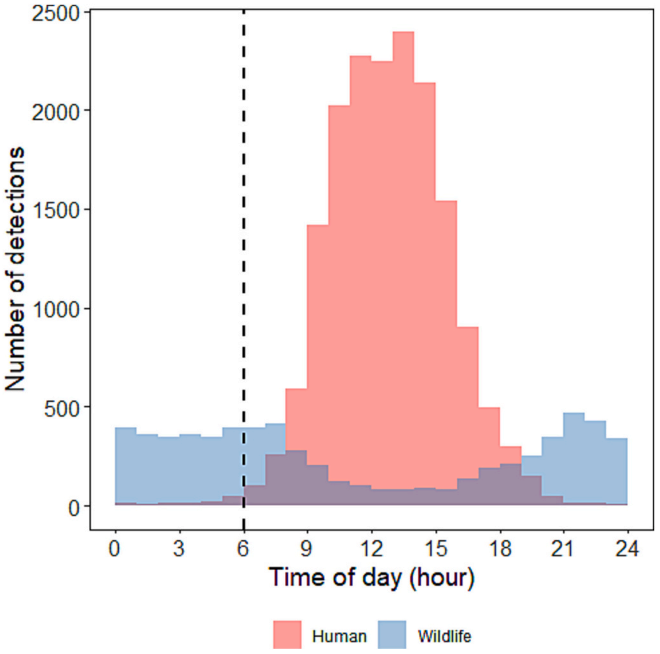


Fig. 2. Frequency of camera-trap detections across the 24-h day for recreational and wildlife events pooled across all cameras and years. The dashed vertical line indicates the 06:00 boundary used to define the biological day (06:00–06:00) in daily disturbance models. The shaded purple area highlights the area of overlap between wildlife detections and recreational activity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

$$y_{i,t} \sim \mathrm{NegBin}(\mu_{i,t}, \theta), \log(\mu_{i,t}) = \alpha + \beta_w H^{dev}_{i,t} + \beta_b \overline{H}_i + \mathrm{X}_{i,t}\gamma + u_i + v_{year(t)} + \log(effort_{i,t}).$$

where $y_{i,t}$ is the number of wildlife detections at camera location i on biological day t, $H^{dev}_{i,t}$ is within-camera daily deviation in human activity (human events minus the camera-specific mean), $\overline{H}_i$ is the between-camera mean human activity, $\mathrm{X}_{i,t}$ includes month, weekday and camera model, and u_i and $v_{year(t)}$ are random intercepts for camera location and year. Recreational activity was decomposed into within-camera and between-camera components following a contextual-effects approach. The within-camera term captures short-term fluctuations in daily recreation pressure, whereas the between-camera term represents differences in long-term average recreational use among cameras. This decomposition allows short-term behavioural responses to variation in daily recreation to be estimated independently of persistent differences in recreational intensity among sampling locations. A lagged model additionally included within-camera deviations in recreational activity one and two biological days earlier ($H^{dev}_{i,t-1}$, $H^{dev}_{i,t-2}$) to test for delayed disturbance responses. Lagged predictors were calculated by shifting daily human detection counts within each camera time series and centring them on the camera-specific mean. Model fit was assessed using DHARMa simulated residual diagnostics.

Activity-type disturbance models: To test whether specific recreation types had distinct effects, daily recreational detections were partitioned into (i) people, (ii) people with dogs and (iii) people with bicycles. For each type, predictors were expressed as within-camera daily deviations from the camera-specific mean. Between-camera mean terms were excluded because activity types were strongly collinear across cameras and the small number of camera locations ($n = 5$) limited reliable estimation of additional site-level parameters. A sensitivity analysis evaluated the potentially positive effect of dogs (where increased dog activity resulted in increased wildlife detections) to ensure that no single camera was driving the response. We implemented a leave-one-out approach, iteratively refitting the activity-type disturbance model while excluding each camera in turn and evaluating the stability of the estimated dog effect (expressed as incidence rate ratios) across all model refits.

Species-specific disturbance models: Species-specific responses were assessed using separate daily negative binomial mixed models for wildlife species, using the same disturbance predictors, seasonal covariates, camera model term, offset and random-effects structure as the pooled model.

Long-term temporal trends in wildlife and recreational activity are presented as contextual background rather than mechanistic tests of causality. Inference regarding human disturbance is therefore restricted to short-term behavioural responses captured within the mixed-effects modelling framework.

3. Results

3.1. Sampling effort and data structure

Across the 16-year study period, cameras were operational for a total of 23,387 days out of a potential 26,292 days available, with a total reliability of 88.9% (min/max of 81.4–93.5% by camera), and a total of 23,445 camera-trap events were recorded. Of these, 17,037 were classified as recreational events (14,216 people detection events, 2028 events of people with dogs, and 793 events of people with bicycles), and 6408 were wildlife belonging to 29 species (Supplementary Table S1). After accounting for groups moving between cameras using Louvain community detection, the number of unique recreational events was lower, with 14,320 events at the catchment scale (11,855 people detection events, 1793 events of people with dogs, and 672 events of people with bicycles), representing an overall reduction of 16% in recreational event counts due to multi-camera detections.

Recreational and wildlife detections showed contrasting diel patterns (Fig. 2). Recreational detections were concentrated during daylight hours, whereas wildlife detections occurred throughout the 24-h cycle, with substantial nocturnal activity and minimal overlap between 06:00 and 21:00 h.

Sampling effort increased early in the time series as the network expanded from two cameras (2010) to four (2011–2012) and five from 2013 onwards (with SN used intermittently between 2013 and 2015). Total camera-days rose from 578 (2010) to consistently >1500 camera-days per year after 2016, with remaining interannual variation largely reflecting equipment failures rather than systematic deployment changes (supplementary plot S4).

3.2. Wildlife community composition

Full community-level metrics showed little evidence of temporal change over the 16-year monitoring period. Species richness remained stable across camera locations ($\beta = 0.04 \pm 0.07$ SE; $F(1,69) = 0.27$, $p = 0.603$), while Shannon diversity showed a weak but non-significant positive trend ($\beta = 0.02 \pm 0.01$ SE; $F(1,69) = 3.41$, $p = 0.069$). Total wildlife detections standardised to 365 camera-days also showed no consistent long-term trend ($\beta = -0.45$ detections $\mathrm{yr}^{-1} \pm 1.90$ SE; $F(1,69) = 0.06$, $p = 0.812$). Variation among cameras locations was substantial, indicating strong site-level differences in community composition and detection rates (supplimentary plot S2 and S3).

Relative activity abundance patterns differed strongly among camera locations (Fig. 3), with detections at the BR camera dominated by small mammals and mesopredators including Pine Marten (*Martes martes* L), Red Squirrel (*Sciurus vulgaris* L.), and European Badger (*Meles meles* L.), whilst the remaining camera locations (PA, SN, TL, TR) were ungulate-dominated, particularly by Roe Deer (*Capreolus capreolus* L.), Red Deer (*Cervus elaphus* L.)..

Community composition differed strongly among camera locations (PERMANOVA: $F(4,70) = 18.25$, $R^2 = 0.51$, $p = 0.001$), indicating strong differences in assemblage composition among camera locations. NMDS ordination (Bray–Curtis, stress ≈ 0.14) confirmed that the BR site supported a distinct assemblage dominated by mesopredators and small mammals, while ungulates structured assemblages at other cameras (Fig. 4).

Indicator species analysis highlighted clear spatial patterns in species associations (Table 1). BR was strongly characterized by Pine Marten, Badger, and Red Squirrel, while TL was associated with Red Fox (*Vulpes vulpes* L.). Ungulates primarily structured the SN–TL and SN–TL–TR groups, with Red Deer, Reindeer, and Roe Deer driving these associations. Woodpigeon was weakly associated with the BR–PA–TL group.

3.3. Long-term changes in wildlife detection rates

The GAMM explained a substantial proportion of variation in wildlife detections across species and cameras (59.7% deviance explained). Camera location contributed strongly to variation in detections ($\chi^2 = 237.8$, $p < 0.001$), indicating pronounced spatial heterogeneity among monitoring locations.

Species-specific trend models revealed significant temporal change for four of five focal species (Fig. 5; Table 2). Ungulate detections declined overall, while smaller mammals showed stable or increasing activity followed by recent declines in some cases. Patterns were predominantly nonlinear, indicating dynamic changes in detection rates through time. Declines were most pronounced for Red Deer, which showed a steady decrease across the monitoring period, falling from approximately 41 detections per 365 camera-days at the beginning of the study to around 9 by 2025 (a 79% decline).

3.4. Occupancy trends

Dynamic occupancy models showed no consistent temporal trends in

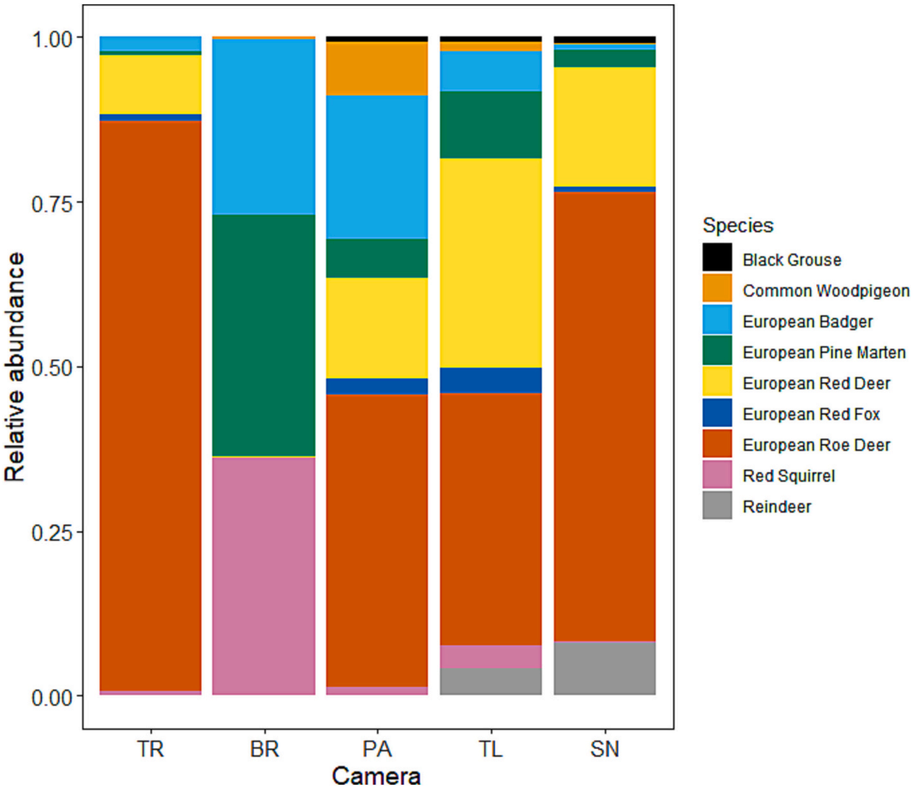


Fig. 3. Relative activity-abundances of wildlife species recorded across five different camera trap locations between 2010 and 2025, ordered from camera situated in plantation forest on the western side of the Allt a'Mharcaidh stream (TR), BR at the bottle neck across the stream, to cameras situated in old-growth forest (PA, TL) and regenerating forest (SN) on eastern side of the stream. Only species that had at least 8 years of data from any single camera are included.

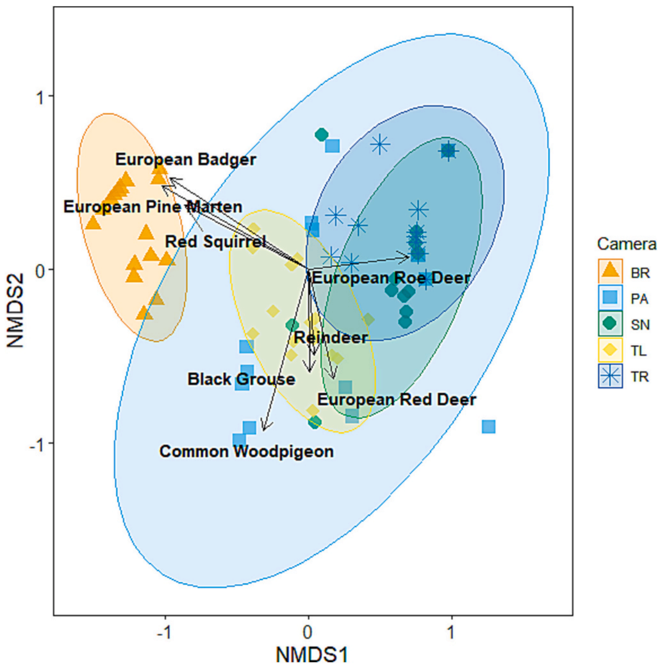


Fig. 4. Bray–Curtis ordination of wildlife community composition across cameras. Points represent camera–year combinations; colours indicate site identity. Species vectors indicate only significant contributors to community separation.

Table 1
Indicator species significantly associated with camera traps (α = 0.05). Values are the indicator statistic (stat) and permutation *P*-value. Camera/group labels indicate where the species was significantly associated.

Species	Camera / Camera Group	Indicator Stat (r.g)	P-value
Pine Marten	BR	0.801	0.001
European Badger	BR	0.794	0.001
Red Squirrel	BR	0.714	0.001
Red Fox	TL	0.450	0.002
Red Deer	SN + TL	0.659	0.001
Reindeer	SN + TL	0.420	0.001
Roe Deer	SN + TL + TR	0.657	0.001
Woodpigeon	BR + PA + TL	0.419	0.007

site occupancy for any focal species, (Badger $\beta = -0.106 \pm 0.548$, $p = 0.846$; Pine marten $\beta = -0.313 \pm 0.631$, $p = 0.620$; Red deer $\beta = 0.147 \pm 0.534$, $p = 0.783$; Red squirrel $\beta = -0.238 \pm 0.525$, $p = 0.650$; Roe deer $\beta = 0.686 \pm 0.760$, $p = 0.367$), despite pronounced changes in detection rates. In contrast, detection probability within the occupancy framework was strongly structured by seasonality (Roe Deer: sin_month = −0.731 ± 0.118, $p < 0.001$; cos_month = −0.341 ± 0.115, $p = 0.003$) and camera uptime (Badger: 1.15 ± 0.46, $p = 0.012$; Red Deer: 1.42 ± 0.44, $p = 0.001$; Roe Deer: 0.88 ± 0.27, p = 0.001).

3.5. *Recreational activity and short-term disturbance*

Recreational activity varied through time and among activity types (Fig. 6). Dog-related (edf = 3.44, $\chi^2 = 43.12$, $p < 0.001$) and cycling (edf = 3.12, $\chi^2 = 51.95$, $p < 0.001$) detections increased overall across the study period, while detections of people alone (edf = 2.29, $\chi^2 = 7.50$, $p = 0.061$) showed a weaker trend but declined slightly overall.

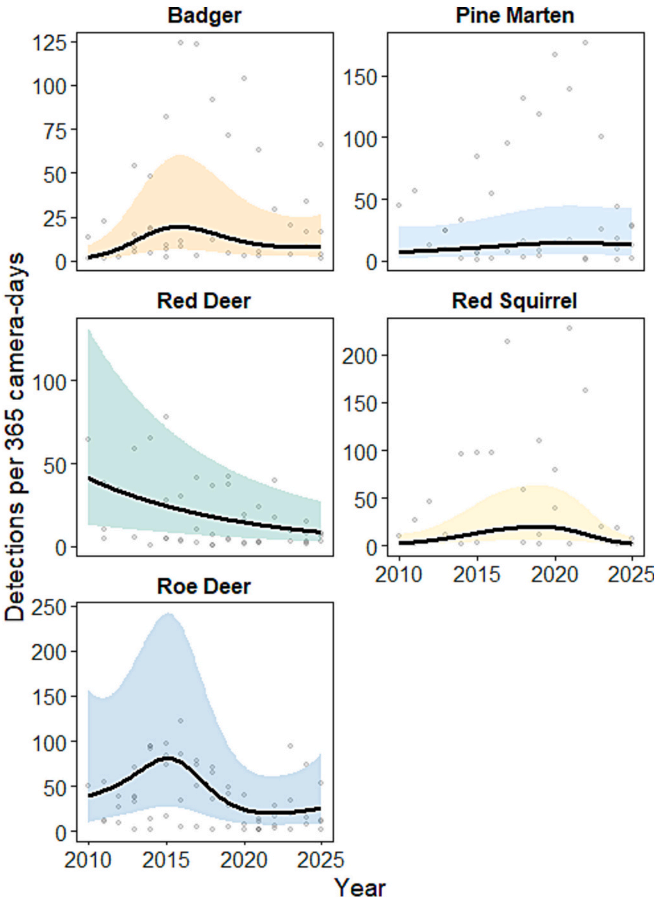


Fig. 5. Temporal trends in wildlife detections derived from a species-specific generalised additive mixed model. Points represent observed detection rates per camera location standardised to 365 camera-days. Solid black lines show predicted detection rates from the GAMM under standardised sampling effort, with shaded ribbons representing 95% confidence intervals. Predictions represent population-level trends averaged across camera locations (camera random effects excluded). Panels show species-specific smooth temporal trends estimated from the model, allowing nonlinear trajectories in detection rates over time.

Table 2
Summary statistics from species-specific temporal trend models (GAMMs) describing changes in wildlife detection rates over time. For each species, the table reports the effective degrees of freedom (edf) for the temporal smooth term, the associated test statistic (χ^2), and the significance of the smooth term. Values of edf ≈ 1 indicate linear trends, whereas edf > 1 indicate nonlinear temporal variation. Significant *p*-values ($p = 0.05$) indicate evidence for temporal change in detection rates over the study period.

Species	edf	χ^2	p-value	Trend direction
Badger	3.25	17.66	0.002	Increase → decline
Red Squirrel	3.08	21.14	<0.001	Increase → decline
Roe Deer	3.50	24.65	<0.001	Increase → decline
Red Deer	1.00	12.54	<0.001	Decline
Pine Marten	1.66	2.61	0.31	Stable

Diel overlap between pooled recreational activity ($n = 17{,}044$ detections) and wildlife was low to moderate (Δ = 0.026–0.378). Nocturnal species such as Badger (Δ = 0.026, 0.022–0.030) and Pine Marten (Δ = 0.108, 0.097–0.117) exhibited strong temporal segregation from recreational activity, whereas diurnal species such as Red Squirrel (Δ = 0.378, 95% CI: 0.351–0.400), Roe Deer (Δ = 0.311, 0.292–0.329) and Red Deer (Δ = 0.310, 0.283–0.332) exhibited higher overlap.. Stratifying by recreation intensity (supplementary table S5) produced broadly similar overlap estimates, with modest reductions for Red Squirrel and Pine Marten in high recreation periods, while Roe Deer overlap was nearly unchanged. Red Deer showed higher overlap on high recreation days (Δ = 0.385, 0.244–0.486), but this estimate was based

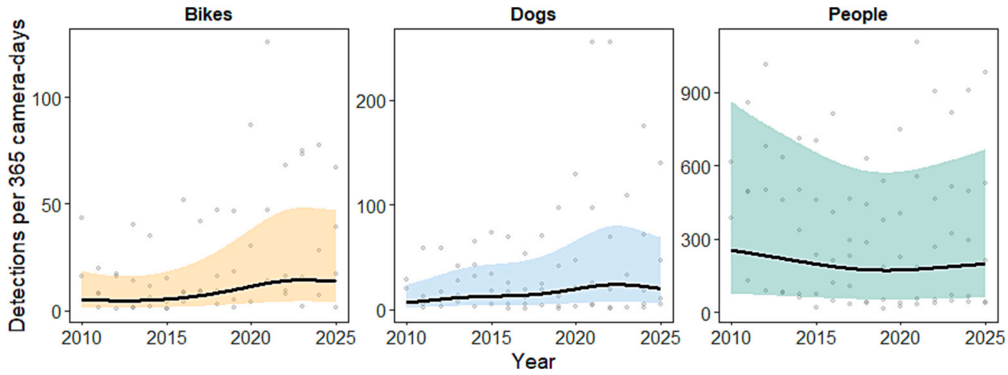


Fig. 6. Temporal trends in recreational activity recorded by camera traps between 2010 and 2025. Points show annual detection rates for individual camera locations standardised to 365 camera-days. Solid lines represent model-predicted detection rates from generalised additive mixed models, and shaded ribbons show 95% confidence intervals. Activity classes include people, people with bicycles, and people with dogs. Panels use independent y-axis scales to reflect differences in detection rates among activity types.

on few detections ($n = 23$) and had wide confidence intervals.

Short-term increases in recreational activity relative to a camera's typical level were not associated with changes in same-day ($\beta = 0.002 \pm 0.009$ SE, z = 0.18, $p = 0.857$) or lagged (lag 1: $\beta = -0.0036 \pm 0.0092$, z = −0.39, $p = 0.694$; lag 2: $\beta = -0.0098 \pm 0.0092$, z = −1.06, $p = 0.287$; Fig. 7a) wildlife detections at the community level (Fig. 7a). When partitioned by activity type, only dog activity showed a positive same-day association with wildlife detections ($\beta = 0.070 \pm 0.034$, z = 2.06, $p = 0.039$; IRR = 1.07, 95% CI: 1.00–1.15; Fig. 7b), while effects of people and bicycles were not supported.

As dog and wildlife detections were unevenly distributed among cameras (BR: dogs present on 838 days at BR vs ≤351 at other cameras), a leave-one-out sensitivity analysis was conducted which showed that the positive association was consistent across all camera subsets, with only minor variation in effect sizes (IRR range: 1.046–1.073; Fig. 7c).

Species-level disturbance models provided little evidence of short-term effects of recreational activity. Same-day effects were not supported for any species (Table 3), and lagged effects were generally weak, with the exception of a negative two-day lag for Roe Deer ($\beta = -0.096 \pm 0.031$, $p = 0.0016$).

Table 3
Species-level effects of same-day human activity on wildlife detections. Values show incidence rate ratios (IRR) for within-camera deviations in human activity, with 95% confidence intervals and FDR-adjusted *p*-values.

Species	IRR	lcl	ucl	p-value
Badger	1.007	0.975	1.041	0.654
Pine Marten	1.005	0.976	1.035	0.731
Red Squirrel	0.988	0.957	1.02	0.466
Red Deer	0.959	0.877	1.05	0.37
Roe Deer	0.974	0.921	1.03	0.349

4. Discussion

4.1. Temporal behaviour and disturbance dynamics

Across the camera network, wildlife and recreational users exhibited strong temporal segregation. Recreational detections were concentrated during daylight hours, whereas wildlife activity occurred throughout the 24 h cycle but was substantially higher at night. Such patterns are consistent with widespread shifts towards nocturnality or temporal avoidance in response to human disturbance (Gaynor et al., 2018), and mirror behavioural adjustments reported for ungulates and carnivores

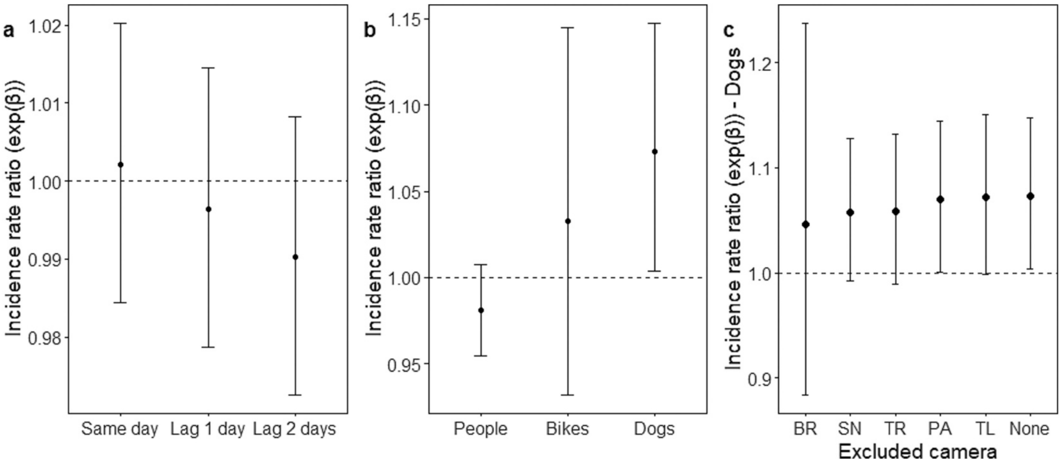


Fig. 7. Incidence rate ratios (IRRs) for within-camera deviations in pooled recreational activity from the negative binomial generalised linear mixed model on (a) the same day and at 1- and 2-day lags; (b) differing recreational activity types; and (c) Leave-one-out sensitivity analysis of the dog effect, showing IRRs for within-camera increases in dog detections from models refitted while excluding each camera location in turn. . Points show IRRs and vertical bars show 95% confidence intervals. All models included month, weekday and camera model number as fixed effects and camera identity and year as random intercepts. The dashed horizontal line at IRR = 1 indicates no change in wildlife detection rate with increasing recreational activity. Confidence intervals overlapping unity indicate no statistically supported effect.

near recreational trails (Coppes et al., 2017; Baker and Leberg, 2018). The persistence of diel segregation across recreation levels suggests that temporal partitioning is a stable feature of the system and naturally reduces direct encounters between wildlife and visitors.

This limited temporal overlap provides a clear explanation for the weak short term disturbance effects detected in the day to day models. Because wildlife and people are already active at different times, opportunities for direct disturbance are intrinsically low. The small and inconsistent disturbance responses observed here align with broader recreation studies showing that wildlife behavioural adjustments frequently occur without leading to sustained site abandonment or demographic change (Larson et al., 2016; Marion et al., 2020; Salvatori et al., 2023). Carnivores often avoid peak human activity while maintaining space use (Baker and Leberg, 2018; Naidoo and Burton, 2020), and ungulates similarly shift activity around trails without vacating sites (Coppes et al., 2017; Westekemper et al., 2018). In this study, temporal avoidance appears sufficient to buffer wildlife from most immediate disturbance effects. Recent multispecies and trail-based studies further show that recreation impacts are typically weak, species-specific and strongly context-dependent, with some species even increasing their use of heavily recreated areas (Marion et al., 2024; Uetrecht et al., 2023). Experimental work in low-visitation systems similarly demonstrates that even modest levels of human activity can alter wildlife behaviour—mainly via temporal adjustments rather than spatial displacement—while occupancy remains largely unchanged (Sytsma et al., 2022).

Most studies report negative interactions between wildlife and dogs, whether stray (Gutiérrez-Zapata et al., 2024) or domestic (Beasley et al., 2023). In contrast, we found a positive association between dog activity and wildlife detections at the daily scale. This pattern is unlikely to reflect a direct casual species interaction rather it most likely arises from co-occurrence driven by shared use of accessible sites or favourable climatic conditions, rather than any increase in wildlife activity in response to dogs.

4.2. *Community composition and long-term activity trends*

Community composition varied strongly across the camera network, with one monitoring location dominated by mesopredators and small mammals and others by ungulates. Such spatial structuring reinforces the need to account for camera level variation when interpreting trends (Burton et al., 2015; Kays et al., 2020). Against this backdrop, species exhibited divergent long term trajectories: Red Deer declined steadily, Roe Deer showed a mid-study peak followed by decline, Badger detections increased overall, and pine marten remained broadly stable. These contrasting patterns indicate shifts in activity or local abundance within the assemblage rather than a uniform system-wide trend. These trajectories may also reflect differences in habitat structure and regeneration across the catchment. Ongoing woodland expansion and structural change could alter detectability or habitat suitability unevenly among taxa, potentially amplifying contrasting detection patterns.

4.3. *Detection, occupancy, and ecological drivers*

Dynamic occupancy models showed no evidence of directional change in site-use probabilities for any focal species. This contrast with detection-based trends highlights the challenge of interpreting camera detections as abundance metrics. Detection indices integrate movement, behaviour and local abundance (Rowcliffe et al., 2008; Sollmann et al., 2013), meaning that changes in detections can occur even when site occupancy remains stable. Similar decoupling between occupancy and detection has been reported in other recreation-influenced systems (Larson et al., 2016; Sytsma et al., 2022). This aligns with evidence that camera placement can systematically bias relative abundance indices and activity estimates (Tanwar et al., 2021), and with broader methodological reviews showing that camera-trap detectability is influenced by sensor performance, model-specific sensitivity, light and noise emission, and behavioural variation among individuals (Delisle et al., 2021; Caravaggi et al., 2020). Furthermore, recent experimental research by Zeller et al. (2024) demonstrated that recreation-related noise can trigger rapid flight responses and altered space use, leading to behavioural avoidance without population displacement. Such responses may reduce camera-trap detections during periods of heightened human activity without affecting occupancy, providing a plausible mechanism for the observed decoupling between detection trends and site use.

For ungulates, ongoing deer management across the NNR and wider Cairngorms Connect landscape provides a possible explanation for declining detections. Reduced browsing pressure may facilitate woodland regeneration and alter understorey structure, influencing habitat conditions for smaller mammals and mesopredators. These landscape-scale drivers likely contribute to the contrasting detection trajectories observed between ungulates and smaller mammals.

4.4. *Spatial scale, location effects, and monitoring implications*

Interpretation of long-term detection change is shaped by the spatial scale of the monitoring network. With only five camera locations concentrated within a single catchment—and one monitoring location (BR) functioning as a movement bottleneck—some detection trends may be influenced by localised activity patterns. The spatial arrangement of cameras also means that individual sites may sample overlapping local populations, particularly for wide-ranging species. Consequently, site-level differences are not interpreted as independent spatial contrasts, and inference is focused on consistent temporal patterns and cross-species responses within the monitoring network. These differences therefore reflect spatial structuring of detections within the monitoring network rather than independent ecological populations. Sensitivity analyses showed that individual locations can disproportionately influence disturbance models, underscoring the importance of site-level effects in small networks.

Despite this limitation, the long operational duration and consistency of sampling at each site enhance confidence in the broad patterns identified. Multi-year consistency in species-specific trends further supports the robustness of the key findings. More broadly, long-term camera networks such as this can complement national biodiversity indicators by providing fine-resolution behavioural and activity-based metrics that occupancy-focused programmes may overlook.

4.5. *Synthesis*

Together, these results indicate that routine recreational activity is unlikely to be the primary driver of the long-term changes observed in wildlife detections across the camera network within this woodland catchment. It is important to note that this site has experienced sustained, low-level human presence for centuries and since the mid-1950s, the area has been owned and managed by a government environmental agency (now NatureScot), whose core remit is to protect, improve and promote Scotland's natural heritage, while supporting responsible public access and enjoyment. The long-term changes observed in wildlife in this study are more likely to be attributed to broader ecological processes—such as woodland regeneration, changing habitat structure, management and wider-scale population dynamics—are more likely to explain the contrasting detection trajectories among species, particularly the decline in ungulates alongside stable or increasing detections of mesopredators and small mammals. The persistence of strong diel segregation and the consistently weak short-term disturbance effects further suggest that behavioural avoidance and shifts in activity, rather than demographic change or site abandonment, already limit direct interactions with recreational users, helping maintain stable occupancy despite shifts in detection patterns.

While inference beyond similar systems should be made cautiously, these findings demonstrate how long-term camera-trap datasets can reveal changes in wildlife activity and community structure that may not be captured by occupancy metrics alone. By integrating detection trends with occupancy and behavioural analyses, long-term camera networks can provide a robust, complementary indicator of ecological change in restoration landscapes, offering valuable support for adaptive protected-area management and wider environmental monitoring programmes.

CRediT authorship contribution statement

Christopher Andrews: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jan Dick:** Writing – review & editing, Investigation.

Funding statement

This work was supported by Natural Environment Research Council NC-UK funding [grant number NE/Y006208/1]; and NatureScot [grant number NS85373-1].

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank NatureScot for providing access to the Inverseshie & Inshriach NNR, and for their continued funding of UK Environmental Change Network long-term ecological and environmental monitoring site without which this research would not have been undertaken.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.115113.

Data availability

An updated dataset (2010-2025) was used for this study, camera-trap data for the years 2010-2022 is available from EIDC - https://doi.org/10.5285/b0c13df5-f606-4bf2-9397-a9c51a7e8d93.

References

Baker, A.D., Leberg, P.L., 2018. Impacts of human recreation on carnivores in protected areas. PLoS One 13, e0195436. https://doi.org/10.1371/journal.pone.0195436.

Beasley, R., Carbone, C., Brooker, A., Rowcliffe, M., Waage, J., 2023. Investigating the impacts of humans and dogs on the spatial and temporal activity of wildlife in urban woodlands. Urban Ecosyst. 26, 1843–1852. https://doi.org/10.1007/s11252-023-01414-z.

Bell, S., Tyrväinen, L., Sievänen, T., Pröbstl, U., Simpson, M., 2007. Outdoor recreation and nature tourism: a European perspective. Living Rev. Landscape Res. 1. https://doi.org/10.12942/lrlr-2007-2.

Blake, J.G., Mosquera, D., Loiselle, B.A., Swing, K., Romo, D., 2017. Long-term variation in abundance of terrestrial mammals and birds in eastern Ecuador as measured by photographic rates and occupancy estimates. J. Mammal. 98, 1168–1178. https://doi.org/10.1093/jmammal/gyx046.

Blondel, V.D., Guillaume, J.-L., Lambiotte, R., Lefebvre, E., 2008. Fast unfolding of communities in large networks. J. Stat. Mech., P10008 https://doi.org/10.1088/1742-5468/2008/10/P10008.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. REVIEW: wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. 52, 675–685. https://doi.org/10.1111/1365-2664.12432.

Caravaggi, A., Burton, AC., Clark, D.A., et al., 2020. A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice*. 2020;2:e239. https://doi.org/10.1111/csp2.239.

Coppes, J., Burghardt, F., Hagen, R., Suchant, R., Braunisch, V., 2017. Human recreation affects spatio-temporal habitat use patterns in red deer (Cervus elaphus). PLoS One 12, e0175134. https://doi.org/10.1371/journal.pone.0175134.

Delisle, Z.J., Flaherty, E.A., Nobbe, M.R., Wzientek, C.M., Swihart, R.K., 2021. Next-generation camera trapping: systematic review of historic trends suggests keys to expanded research applications in ecology and conservation. Front. Ecol. Evol. 9, 617996. https://doi.org/10.3389/fevo.2021.617996.

Frey, S., Fisher, J.T., Burton, A.C., Volpe, J.P., 2017. Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. Remote Sens. Ecol. Conserv. 3, 123–132. https://doi.org/10.1002/rse2.60.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 360, 1232–1235. https://doi.org/10.1126/science.aar7121.

Gutiérrez-Zapata, S., Santoro, S., Gegundez-Arias, M.E., Selva, N., Calzada, J., 2024. Dog invasions in protected areas: a case study using camera trapping, citizen science and artificial intelligence. Global Ecol. Conservation 54, e03109. https://doi.org/10.1016/j.gecco.2024.e03109.

Kays, R., Arbogast, B.S., Baker-Whatton, M., Beirne, C., Boone, H.M., Bowler, M., Burneo, S.F., Cove, M.V., Ding, P., Espinosa, S., Gonçalves, A.L.S., Hansen, C.P., Jansen, P.A., Kolowski, J.M., Knowles, T.W., Lima, M.G.M., Millspaugh, J., McShea, W.J., Pacifici, K., Parsons, A.W., Pease, B.S., Rovero, F., Santos, F., Schuttler, S.G., Sheil, D., Si, X., Snider, M., Spironello, W.R., 2020. An empirical evaluation of camera trap study design: how many, how long and when? Methods Ecol. Evol. 11, 700–713. https://doi.org/10.1111/2041-210X.13370.

Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS One 11, e0167259. https://doi.org/10.1371/journal.pone.0167259.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84, 2200–2207. https://doi.org/10.1890/02-3090.

Marion, S., Davies, A., Demšar, U., Irvine, R.J., Stephens, P.A., Long, J., 2020. A systematic review of methods for studying the impacts of outdoor recreation on terrestrial wildlife. Global Ecol. Conservation 22, e00917. https://doi.org/10.1016/j.gecco.2020.e00917.

Marion, S., Curveira Santos, G., Herdman, E., Hubbs, A., Kearney, S.P., Burton, A.C., 2024. Mammal responses to human recreation depend on landscape context. PLoS One 19, e0300870. https://doi.org/10.1371/journal.pone.0300870.

Monz, C.A., Cole, D.N., Leung, Y.-F., Marion, J.L., 2010. Sustaining visitor use in protected areas: future opportunities in recreation ecology research based on the USA experience. Environ. Manag. 45, 551–562. https://doi.org/10.1007/s00267-009-9406-5.

Naidoo, R., Burton, A.C., 2020. Relative effects of recreational activities on a temperate terrestrial wildlife assemblage. Conservat Sci. Prac. 2, e271. https://doi.org/10.1111/csp2.271.

Pickering, C.M., Hill, W., 2007. Impacts of recreation and tourism on plant biodiversity and vegetation in protected areas in Australia. J. Environ. Manag. 85, 791–800. https://doi.org/10.1016/j.jenvman.2006.11.021.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. JABES 14, 322–337. https://doi.org/10.1198/jabes.2009.08038.

Rowcliffe, J.M., Field, J., Turvey, S.T., Carbone, C., 2008. Estimating animal density using camera traps without the need for individual recognition. J. Appl. Ecol. 45, 1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x.

Salvatori, M., Oberosler, V., Rinaldi, M., Franceschini, A., Truschi, S., Pedrini, P., Rovero, F., 2023. Crowded mountains: Long-term effects of human outdoor recreation on a community of wild mammals monitored with systematic camera trapping. Ambio 52, 1085–1097. https://doi.org/10.1007/s13280-022-01825-w.

Sier, A., Monteith, D., 2016. The UK environmental change network after twenty years of integrated ecosystem assessment: key findings and future perspectives. Ecol. Indic. 68, 1–12. https://doi.org/10.1016/j.ecolind.2016.02.008.

Sollmann, R., Mohamed, A., Samejima, H., Wilting, A., 2013. Risky business or simple solution – relative abundance indices from camera-trapping. Biol. Conserv. 159, 405–412. https://doi.org/10.1016/j.biocon.2012.12.025.

Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biol. Conserv. 141, 2159–2173. https://doi.org/10.1016/j.biocon.2008.06.026.

Sytsma, M.L.T., Lewis, T., Gardner, B., Prugh, L.R., 2022. Low levels of outdoor recreation alter wildlife behaviour. People Nat. 4, 1547–1559. https://doi.org/10.1002/pan3.10402.

Tanwar, K.S., Sadhu, A., Jhala, Y.V., 2021. Camera trap placement for evaluating species richness, abundance, and activity. Sci. Rep. 11, 23050. https://doi.org/10.1038/s41598-021-02459-w.

Uetrecht, M.R., Bermudez, A., Novoa, D., Reithel, J., Rodriguez, V., Smith, R., Sprott, S., Tingley, M.W., Blumstein, D.T., 2023. Differential response of three large mammal species to human recreation in the Rocky Mountains of Colorado, USA. Front. Conserv. Sci. 4, 1234157. https://doi.org/10.3389/fcosc.2023.1234157.

Westekemper, K., Reinecke, H., Signer, J., Meißner, M., Herzog, S., Balkenhol, N., 2018. Stay on trails – effects of human recreation on the spatiotemporal behavior of red deer *Cervus elaphus* in a German national park. Wildl. Biol. 2018, 1–9. https://doi.org/10.2981/wlb.00403.

Zeller, K.A., Ditmer, M.A., Squires, J.R., Rice, W.L., Wilder, J., DeLong, D., Egan, A., Pennington, N., Wang, C.A., Plucinski, J., Barber, J.R., 2024. Experimental recreationist noise alters behavior and space use of wildlife. Curr. Biol. 34, 2997–3004.e3. https://doi.org/10.1016/j.cub.2024.05.030.