



Drivers of roe deer use in fragmented forest landscapes; implications for current and future management in the context of policy driven forest expansion

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ABSTRACT

Forest expansion is a major current land use change across Europe. How this will affect the forest use of the most common European wild ungulate species, roe deer (*Capreolus capreolus*), and associated forest ecosystem services and disservices is poorly understood. Using a forest-agricultural mosaic landscape in northeast Scotland, we selected forests across a size and connectivity gradient as a proxy of expansion. We predicted that roe deer forest use estimated using camera traps would be driven by: i) higher structural and functional forest connectivity at a landscape scale, ii) within-forest structural characteristics including higher shrub density, deciduous cover and lower canopy cover, and iii) lower human usage. In line with predictions, roe deer preferred more connected forests and smaller forests in areas of the landscape with higher forest edge density. Within forests, roe deer preferred forest edge, and usage increased with higher tree density and variation in tree diameter, supportive of a preference for structurally complex forests. Human usage of forests was associated with lower roe deer use. This study has implications for current and future forest management. Firstly, targeted monitoring of forest patches predicted to have high roe deer usage for impacts could inform priorities and approaches to deer management. Secondly, as forest configuration changes with expansion policies, this study provides insights into how deer usage may change. We highlight how this knowledge can be used in forest planning to optimise deer management to minimise disservices to forestry, biodiversity and human and livestock health.

1. Introduction

Policy targets to expand forests across Europe to enhance biodiversity and mitigate climate change are driving large-scale changes to forest extent and connectivity. Between 1990 and 2023 forest cover in Europe expanded at a rate of 0.3% per year resulting in an increase of 19.3 million hectares of forest, and forecasts are for this trend to continue (Forest Europe, 2020). In the United Kingdom and other parts of Europe, there is a policy focus on expanding native woodlands and reconnecting ecological networks to support biodiversity (DEFRA, 2018, Scottish Government, 2019, Scottish Government, 2024). This major land use

shift will significantly change the spatial distribution of resources across landscapes for wildlife species. How this will impact behaviour, movement and habitat selection of key forest ungulate species such as roe deer (*Capreolus capreolus*) is not well understood and is important for forest management and restoration.

Roe deer are non-specialist herbivores which thrive in disturbed heterogeneous forest landscapes such as those created during forest expansion (Abbas et al., 2011; Gill et al., 1996; Hewison et al., 2001). In this paper, the term forest is used for a wooded area at least 0.5 ha with canopy cover > 20%, and includes both native woodland and commercial forestry (Forestry Commission, 2019). As the most abundant and

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widespread wild herbivore in Europe, roe deer can act as ecosystem engineers due to their ability to impact ecological processes and nutrient cycling through grazing and browsing (Côté et al., 2004; Fuller and Gill, 2001). However, at high densities, roe deer can be responsible for a range of disservices to forestry, biodiversity and human and livestock health. Roe deer can be detrimental for forest restoration and regeneration by browsing on woody vegetation and forest specialist ground flora, adversely affecting biodiversity and timber production (Gill and Fuller, 2007; Joys et al., 2004) and can also impact surrounding agricultural resources (Putman and Moore, 1998). With respect to biodiversity, sustained heavy browsing is the most widespread threat to designated forest features in Scotland (NatureScot, 2016). Further, overgrazing is the second largest negative pressure on protected sites after invasive species (although this includes impacts from domestic and feral species; NatureScot., 2025). Where high deer and human activity co-occur, there can be risks to humans, by increasing the risk of traffic collisions (Lush and Lush, 2026; Nelli et al., 2018), increasing the risk of transmitting shared parasites and pathogens to livestock (Böhm et al., 2007) and increasing the risk of some zoonotic pathogens, particularly those transmitted by the tick *Ixodes ricinus* (Gilbert et al., 2012; Linard et al., 2007; Myrsterud et al., 2016; Rizzoli et al., 2009). Thus, knowledge of how landscape and forest characteristics influence roe deer use of forests is important to understand for current and future forest management and a suite of deer-human interactions.

Roe deer habitat selection at the home range level is primarily driven by needs for shelter, feeding, and reproduction (Myrsterud et al., 1999; Saïd and Servanty, 2005). In mixed, multi-use landscapes, ungulates typically utilise forests for cover and browsing, and may move into areas of neighbouring agricultural land where they provide high quality feeding resources (Bjorneraas et al., 2011). Therefore, landscape structure may influence large herbivore behaviour through a 'risk-resource' trade off (Martin et al., 2018) as they balance foraging and feeding with factors like predation, hunting pressure and other human disturbance (Brown et al., 1999). In Europe, roe deer thrive in fragmented forest-agricultural landscapes and show strong preferences for forest habitat and forest-agricultural ecotones (Hewison et al., 2001; Lovari et al., 2017; Marshall et al., 2026a; Morellet et al., 2011) with predation, roads, urban areas and hunting acting as deterrents (Ciach and Fröhlich, 2019; Loro et al., 2016; Martin et al., 2018). Their use of open habitat is influenced by their perception of risk and affected by the time of day, season and distance from a forest, with strong preference to stay within or nearby forest (Martin et al., 2018; Torretta et al., 2025). Therefore, more structurally connected forest patches (i.e., those with more forest in close proximity) would be expected to have higher roe deer usage as compared to more isolated forests, which could pose higher risks from traversing open habitats. This effect could be modulated by this species' preferences for forest edges and could result in an intermediate level of structural connectivity having highest usage. However, measures of structural connectivity may under appreciate the role of the intervening land cover between forest patches as roe deer show differential responses to different land cover types and are somewhat reluctant to cross roads (Marshall et al., 2026a). By accounting for this differential response we can estimate the functional connectivity of a forest, where the characteristics of the non-forest habitat are accounted for (such as open grassland, moorland or the presence of roads). Functional connectivity of forests, estimated from analysis of deer movement patterns, is therefore expected to explain roe deer habitat use more comprehensively than structural connectivity if the differential responses in non-forest areas are a significant driver of roe deer distributions at a landscape-level.

Forest characteristics which describe the quality of forests for shelter and feeding have also been found to influence usage by roe deer (Schwegmann et al., 2023). The influence of these forest characteristics is likely to be affected by the landscape context and availability of resources nearby; for example, relatively poor-quality forest for foraging may be used for shelter when there are high quality feeding resources in

nearby agricultural fields (Hewison et al., 2009). Roe deer have been found to prefer younger broadleaf forests (Marshall et al., 2026a; Spake et al., 2020; Torres et al., 2011) with higher quality and more palatable ground vegetation (Bobrowski et al., 2020). Higher forage availability associated with a more open canopy and higher light transmittance has been associated with higher roe deer use (Ramirez et al., 2023). Within-forest heterogeneity can increase opportunities for sheltering, and forests with higher shrub cover, tree species richness and variation in tree diameter at breast height have been found to have higher deer habitat use (Schwegmann et al., 2023; Spake et al., 2020). Deadwood left in forests to improve biodiversity and nutrient cycling can reduce roe deer habitat use, possibly by impedance of roe deer movement (Hagge et al., 2019; Schwegmann et al., 2023). Forest usage by roe deer can also be driven by the intensity of human recreational use of forest patches, due to human disturbance and hunting pressure (Bonnot et al., 2013; Mols et al., 2022a, Mols et al., 2022b). Within forests, lower roe deer usage has been found near more frequently used trails compared to less frequently used trails in recreational forest parks (Mols et al., 2022a, Mols et al., 2022b).

Studies quantifying roe deer habitat use in the UK have largely used indirect measures such as dung and track counts (Gilbert et al., 2012; Putman et al., 2011). Relatively few studies have quantified roe deer habitat use in the UK directly using camera traps (but see Hsing et al., 2022; Mason et al., 2022) and none designed at a landscape scale. Whereas dung counts record previous deer space use over an indeterminate period (from minutes to several weeks before survey); they only record where the deer dropped dung, not their entire space use; and the species of deer is not always identified. Additionally, indirect methods can have lower detectability rates compared to direct camera trapping methods and are sensitive to vegetation structure, climate and weather conditions (Dickinson et al., 2020; Pfeffer et al., 2018; Wearn and Glover-Kapfer, 2019). Other studies have used alternate proxies for relative density or population change, such as gaming kill counts or herbivory damage (Noble et al., 2012; Spake et al., 2020). However, the latter indicator conflates the impacts resulting from deer presence with actual deer habitat use, relative abundance or density; thereby, making it difficult to disentangle the relationship between the two. In contrast, cameras record real-time space use for a known deer species over a known period and record their presence in that area.

In this study we measured roe deer habitat use in forests selected across a landscape gradient of forest patch size and connectivity, as a proxy of forest expansion using camera traps. The overarching aim of this study was to determine the wider landscape and between and within forest structural habitat drivers on current roe deer forest use and to use this knowledge to understand how patterns may change in future. The study landscape was a mosaic of fragmented forest and agricultural land in Aberdeenshire, Scotland, an area currently undergoing forest expansion (Scottish Government, 2019). Camera traps were used to measure roe deer encounter rates as an estimate of the intensity of forest use by roe deer, and to measure human encounter rates as a measure of human recreational use of forest patches. We firstly predicted that roe deer forest use will be higher in more connected forests, as this will offer increased opportunities for shelter and minimise risks which are likely to be higher in open habitats. Further we predict that this relationship may be non-linear due this species preference for forest edge habitat (P1). We predicted that the effects of functional connectivity on roe deer forest use, which accounts for behaviour and relative preference or avoidance of intervening habitats such as open arable and pasture, roads and urban environments (Marshall et al., 2026a) would be greater than effects of forest connectivity measured as a structural metric which does not account for composition of the intervening matrix (Hanski, 1998) (P2). Thirdly, we predicted that roe deer forest use will be affected by the structural characteristics of the forest patch and that forests with a higher percentage of deciduous trees, higher shrub cover and lower canopy cover will have higher roe deer forest use due to increased attractiveness for feeding and shelter (P3). Fourthly, we predicted that

roe deer forest use would be higher nearer the forest edge, reflecting this species preference for edge and ecotonal habitat (P4). And finally, we predicted that roe deer forest use would be modulated by human infrastructure and activities in the landscape measured as the proportion of urban landcover in the surrounding landscape (Martin et al., 2018) and encounter rates of humans on camera traps, as a proxy of disturbance within the forest patch (Brown et al., 1999) (P5).

2. Methods

2.1. Study landscape

The study was conducted in forests distributed across a 2780 km² fragmented forest and agricultural landscape in Aberdeenshire, Scotland in 2022–2023 (57°8.75'N, 2°42.24'W, Fig. 1). The landscape is predominately underlain with metamorphosed bedrock, with higher elevation areas consisting of igneous intrusions. Much of the lower elevation areas are covered in glaciogenic sedimentary deposits that ceased deposition ~11,000 years ago (BGS (British Geological Survey), 2026). The landscape is composed of a mosaic of different habitats: heather moorland and acid grasslands which cover 33.4% of the landscape, some of which are used for extensive livestock grazing; 14.5% arable land used for growing crops; 25% improved grassland, used for grazing or producing silage for livestock; and 25% of the land area is fragmented forest patches. With an average population density of 59 persons per km², built-up land covers only 1.7% of the area, mostly concentrated in farmhouses, small towns and villages. Land cover proportions are obtained from UKCEH Land Cover Maps 2023 (Morton et al., 2024). Ethical permission for the study was granted by the University of Liverpool Veterinary Research Ethics Committee, reference VREC1183.

2.2. Forest site selection and landscape metrics

We selected 30 forests along a gradient of forest patch size and connectivity. Forest polygons were identified from the UKCEH Land Cover Map 2021 (Marston et al., 2022) and 30 forests were sampled equally across five quantiles of forest area and two quantiles of forest structural connectivity (Fig. 1, Fig A1.1). Forests smaller than the minimum estimated home range of a roe deer (0.16 km²) were excluded as candidate forests to ensure the study forest patches were large enough for resident roe deer populations. The mean patch size and connectivity index of the 30 study forests were 12.45 km² (Range: 0.17 – 224 km²) and 17.09 (Range: 0.22 – 119), respectively (Fig A1.1). All forests selected had no deer fencing. Forest patches comprised spruce dominated forests (*Picea* spp.), Scots pine-dominated forests (*Pinus sylvestris*), and mixed coniferous- deciduous forests. Across patches, birch (*Betula* spp.) was frequently present alongside Scots pine (*Pinus sylvestris*), spruce (*Picea* spp.), larch (*Larix* spp.), and rowan (*Sorbus aucuparia*), with additional broadleaved species such as oak (*Quercus* spp.), ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), sycamore (*Acer pseudoplatanus*), and willow (*Salix* spp.) in some sites.

Forest structural connectivity was estimated using a distance weighted area metric, by taking a sum of the area of forests > 0.5 ha within a buffer of 750 m from the focal forest edge, weighting the areas by the distance between the surrounding forest patch and the focal forest patch (Further details in Appendix, sections A1.1 & A1.2; Bender et al., 2003; Hanski, 1998). For inclusion in the forest structural connectivity metric, a threshold of forest patch size of greater than 0.5 ha was used in accordance with UK National Forest Inventory definition of forests (Forestry Commission, 2019). The buffer size of 750 m was selected as being biologically relevant as it corresponded to an estimation of roe deer home range in Aberdeenshire (Marshall et al., 2026a).

The proportions of arable, grassland, forest, urban land cover and forest edge density within a 750 m buffer from the edge of each forest

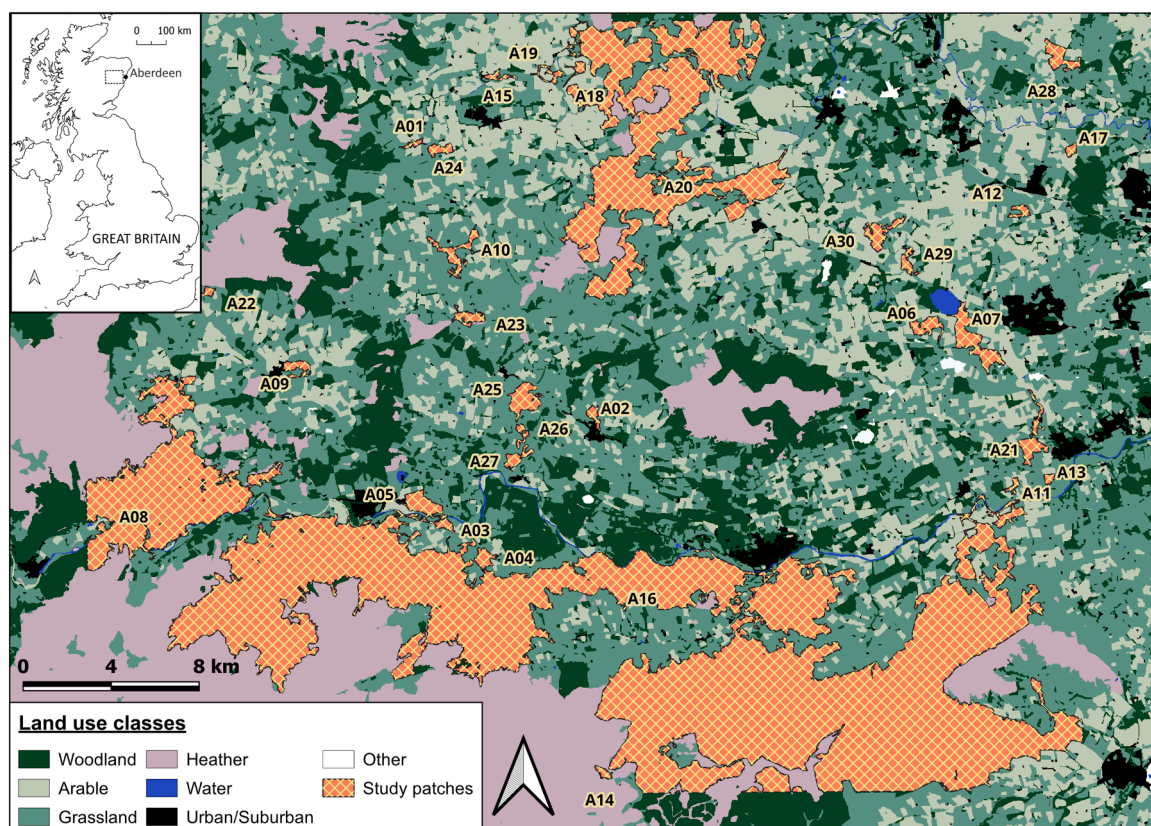


Fig. 1. Drivers of roe deer use in a fragmented forest mosaic landscape, Aberdeenshire, United Kingdom.

patch were obtained for each of the study forests by combining the finer land use classifications in the UKCEH Land Cover Map (Morton et al., 2024) into broader classes (Further details in Appendix, Section A1.2; Table A1.1). The grassland category in this study combines the finer land-use classifications of improved, neutral, calcareous and acid grassland, and heather and heather grassland. Heather and heather grassland were included in the grassland category, as this landcover type was absent in the surrounding buffer of most forest patches ($n = 25/30$). The largest nine of the thirty forests (> 80 ha) were surveyed with camera traps within a smaller focal area to provide comparable sampling effort per unit area to smaller forests and to ensure that distance between cameras within a patch did not increase with increasing patch size. For these forests, landscape metrics were extracted corresponding to a 750 m buffer around the edge of this focal sampled area. The focal area was defined by drawing a circle centred on the centroid of all camera trap deployments using a radius equal to the distance from the centroid to the camera farthest away.

2.3. Landscape functional connectivity

Landscape-wide estimates of functional connectivity for roe deer were estimated by building on a habitat use model from GPS collared roe deer captured in the study landscape (Marshall et al., 2026a). The habitat use model aimed to determine roe deer preference for various land use types, as well as how their movements are altered within them (Marshall et al., 2026a). Coefficients of a population level Poisson habitat preference model were used as a basis to estimate landscape level movement resistance/conductivity for roe deer. We projected these coefficients of preference and movement ease via the UKCEH Land Cover Map landscape raster (Morton et al., 2024), using Ordnance Survey, (2024) and Scholefield et al., (2016) to map the resistance impacts of roads and hedgerows respectively. This resulted in a landscape raster (at 25 m resolution) mapping out the relative resistance movement resistance/conductivity for roe deer (See Appendix A1.3; Fig. A1.2). We converted the resistance mapping to functional connectivity using a random shortest paths approach (Panzacchi et al., 2016). This approach consisted of generating repeated random walk between forest patches (6 per pair of patches; 3415 total patches), where the path routes were weighted by the estimated landscape resistance –areas of high resistance (as estimated from the Poisson habitat preference model) were less likely to house paths (see Appendix A1.3). We also ensured that the diffusion of the random paths matched the movement patterns of the roe deer (see Appendix A1.3; Fig. A1.3). Each random walk between patches produced a raster describing the likelihood of a roe deer crossing a cell (cell size was set to 25 m matching the land cover data and resistance map resolution). When compiled together the resulting rasters gave a landscape level mapping of the relative likelihood of a roe deer using that area to move between patches. We standardised this final landscape layer to be between 0 and 1 (where 0 is low functional connectivity and 1 is high functional connectivity). For inclusion in statistical models, we calculated a mean connectivity score for each forest patch. This mean included all raster cells that fell within a forest patch. Although we had no spatial covariates to differentiate within forest movement resistance (beyond the low resistance of forest compared to non-forest land uses), the inclusion of within-patch connectivity values was important as patches between other patch pairing could serve as stepping-stones. Further details can be found in the Appendix (section A1.3) concerning the estimation of path diffusion, required computation optimisations, and the validation measures using the roe deer movement data.

2.4. Within forest structural habitat characteristics

Forest habitat surveys were carried out in July-September 2023 at each of the forest sites, to collect data on forest structural habitat characteristics specifically, shrub, sapling and tree density, variation in

tree diameter at breast height (DBH), tree species richness, tree canopy closure and woody debris based on previously described methods (Fuentes-Montemayor et al., 2020). In each forest patch, surveys were carried out along five randomly generated 100 m transects located in the area where camera trapping was conducted. Every transect had 10 sampling points resulting in 50 sampling points per forest patch.

At each sampling point along a transect, 4 quadrants were identified by laying two sticks crossing one another in the north-south and east-west directions respectively. The four nearest trees (defined as woody plants greater than 2 m in height, and diameter at breast height > 5 cm), one in each quadrant were located, and the diameter at breast height (DBH, cm), tree species and distance from the sampling point recorded. Tree density (tree per m^2) was then calculated at every sampling point using the point-quadrant method (Hill et al., 2005) using the equation $1/(\text{Mean sampling point-to-tree distance})^2$. At each sampling point, woody debris was scored from a scale of 1–3 with the indices corresponding to the following: 1 – leaf litter and twigs ≤ 1 cm in diameter, 2 – larger branches ≤ 10 cm, 3 – coarse debris > 10 cm in diameter. Tree canopy closure (%) was estimated using an Android app (CanopyViewer, <https://apkpure.com/canopy-surveyor/skipper.com.canopyviewer>). Shrub and sapling density was estimated at 3 sampling points (1st, 5th, 10th) per transect by counting the number of shrubs (woody bushes with height between 40 cm and 2 m) and saplings (plants with DBH ≤ 5 cm and height > 2 m) within a circle of radius 15 m centred at the sampling point.

For inclusion in statistical models, forest patch-scale tree, shrub and sapling densities and tree canopy closure were estimated by averaging across all sampling points within a site. Variation in tree DBH was obtained by taking the standard deviation of tree DBH across all sampling points. Tree species richness was estimated by counting the number of distinct tree species across all sampling points within a forest. For woody debris, the most frequent value (mode) was taken as a forest patch scale index of deadwood.

We obtained forest patch deciduous cover and distance of the camera location to the edge of the forest patch using the UKCEH Land Cover Map (Morton et al., 2024). The proportion of deciduous cover within each forest patch was obtained by the proportion of 25×25 m cells within a forest polygon categorised as 'Deciduous woodland' in the Land Cover Map. To test if roe deer preferred forest edges compared to forest interior, the Euclidean distance between the camera location coordinates and the closest edge of the forest was measured.

2.5. Use of forests by roe deer and humans

To estimate roe deer encounter rates as a measure of forest habitat use, we carried out camera trap surveys conducted from May to November 2022 and April to September 2023 in the selected forests in Aberdeenshire (Fig. 1). Surveys were carried out in the spring and summer months only as they were conducted as a part of a larger project quantifying the availability of forest vertebrates to the seasonally active tick vector *Ixodes ricinus* (results reported in Venkatesan et al., in prep). In each forest, three trail cameras (Spec Ops Elite HP5, Browning, Morgan, UT, USA) were deployed at randomly generated locations within the forest patch and moved every 3–5 weeks, giving a total of 27 sampling points per forest. Deployment locations were generated randomly ensuring that locations were at least 30 m apart and at least 20 m away from the forest edge. Methods were based on those previously described (Hofmeester et al., 2017). Briefly, cameras were mounted on a tree nearest to the random survey point, and positioned at a height of 40 cm with a field-of-view parallel to the ground, facing north or southwards to avoid direct sunlight during dawn and dusk (Hofmeester et al., 2017). Cameras were positioned to avoid trails or paths to minimise sampling bias in estimates of wildlife usage, and for privacy reasons. Additionally, as mentioned in Section 2.2, cameras were deployed within a smaller sub-region in the 9 largest patches (>80 ha) to ensure that the mean and median distance between cameras

was not associated with patch size (further details in [Appendix A1.4](#)). Cameras were programmed to capture still images using motion detection, with a 1-second delay between images, and vegetation was pruned within 3 m of the camera to reduce false triggers and obstruction to field of view.

We used the software Wildlife Insights (www.wildlifeinsights.org) ([Ahumada et al., 2020](#)) to identify roe deer and humans detected in camera trap images using a combination of AI automated and manual classification. Deployments shorter than 7 days due to camera malfunction were removed from the analysis (33/723 deployments). First, we evaluated the performance of the Wildlife Insights in-built algorithm in identifying false triggers (with no animal present in the frame) and deer species, within a sub-sample of manually identified images. The algorithm identified false triggers with a precision of 99% and deer with a precision and recall of 97.7% and 89.4% respectively (further details in [Appendix A1.5](#)). Therefore, we used the algorithm to remove blank images and to classify the deer images. All images classified as “non-deer” were reviewed manually to classify any overlooked deer images as well as human images. Once classified as roe deer or human, images were grouped into sequences, defined as consecutive images taken within a 15-minute period. For each sequence, the maximum number of animals (roe deer or humans) per image was calculated. The number of sequences and maximum animal count were multiplied and divided by the deployment duration (in days) of that camera to estimate the encounter rate defined as the number of observations per day at each deployment. A 15-min threshold was chosen to reduce overdispersion from overcounting the same individuals while still reflecting the intensity of use at each deployment location ([Hofmeester et al., 2017](#)). To assess the sensitivity of encounter rates to the 15-minute threshold, we recalculated rates using alternative thresholds of 16, 18, and 20 min between consecutive detections and found that they were almost perfectly correlated with those obtained using the 15-minute threshold ($r > 0.999$ in all cases). Roe deer and human encounter rates were thus obtained at each deployment location per focal forest. Since cameras were placed to avoid trails or paths to reduce bias in recording wildlife species, this may underestimate human encounter rates at the deployment-scale. We therefore obtained a relative measure of human recreational use at the forest-scale by averaging deployment-level human encounter rates across all deployments within each focal forest for use in the statistical analyses.

2.6. Statistical analysis

2.6.1. Variable selection

To avoid inclusion of colinear landscape variables and overfitting the statistical models, relationships between variables were first explored using pairwise correlation tests ([Fig. A1.6](#)). Where landscape and forest variable pairs with $r > 0.7$ were identified, the variables which were most closely related to the study questions were retained to be included in the full model. The proportion of forest in a 750 m buffer surrounding the focal forest was dropped as it was significantly correlated with both edge density ($r = 0.71$, $p = < 0.001$) and log-transformed forest patch area ($r = 0.84$, $p < 0.001$). Additionally, edge density and the proportion of grassland in a buffer surrounding the forest were also excluded from the full model as they had Variance Inflation Factor > 4 .

2.6.2. Model fitting

To assess how landscape metrics and within-forest characteristics influence habitat use by roe deer and test predictions P1 and P3–5, a Generalised Linear Mixed Model (GLMM) was fitted with the total number of roe deer observations at each deployment as the response variable with a negative binomial error distribution and log-transformed deployment survey duration (days) as an offset (Model 1). Fixed explanatory variables in the full model included log-transformed forest area (patch size), log-transformed forest structural connectivity, the proportion of arable, and proportion of urban land cover within a 750 m

buffer surrounding each forest, the proportion of deciduous cover within the forest, mean human encounter rate and forest habitat variables (listed in [Table 1](#)). We also included a second-order effect of structural connectivity to test if forest patches of intermediate connectivity had the highest deer usage. Forest ID, year, and month were included as nested random effects to account for temporal variation in roe deer observations and repeated sampling within forest patches.

Since patch area was colinear with edge density and forest cover in a 750 m buffer, and we expected that these variables would be important drivers of roe deer forest use, we conducted additional analyses replacing forest patch area with edge density and forest cover in a 750 m buffer, keeping the other variables same as in Model 1.

Next, to test our prediction (P2) that roe deer functional forest connectivity would provide greater explanatory power of habitat use by roe deer, we fitted a second GLMM with the same response and random and fixed explanatory variables as above, substituting functional connectivity for structural connectivity (Model 2). Stepwise backward model selection was carried out on Model 1 and 2, to obtain final models with the lowest AIC ([Bolker et al., 2009](#)).

Finally, to explore which landscape metrics predicted roe deer functional connectivity, we fitted a linear model with mean forest functional connectivity as a response variable. Explanatory variables included structural connectivity, urban and arable landcover and the % deciduous cover in the patch.

All statistical analyses were carried out using R (v.4.4.1) ([R Core Team, 2024](#)) and RStudio (v.2024.09.1 +394) ([Posit team, 2024](#)). Generalised Linear Mixed Models (GLMMs) were fitted using the package *glmmTMB* (v.1.1.10) ([Brooks et al., 2017](#)). Models were assessed for collinearity between explanatory variables by calculating Variance Inflation Factors ([Zuur et al., 2010](#)) using the package *performance* (v.0.13.0) ([Lüdtke et al., 2021](#)). Other model diagnostics e.g., testing for normality, overdispersion, zero-inflation and outliers were carried out using the package *DHARMA* (v.0.4.7) ([Hartig, Lohse, 2022](#)). Stepwise backward model selection was carried out using the `drop1` function in R. All numeric explanatory variables were mean-centred and scaled.

3. Results

Roe deer encounter rates were obtained from a total of 690 trail camera deployments placed between May and September/October in 2022 and 2023 from 29 forest patches, with an average of ~24 (range: 20–27) deployment locations and 681 (range: 544–786) survey days per forest patch. Data from one forest was excluded due to large scale felling of trees in the second year of the study. The mean survey time for a camera deployment was roughly 29 days (SD: 8.6; range: 8–59). The mean roe deer encounter rate at the forest patch scale was 0.68 (SD: 0.29, range 0.15–1.24) encounters per day. At the deployment scale, roe deer encounter rates varied within forest patches ([Fig. A2](#)), with a mean of 0.55 (SD: 0.65, Range: 0–5.05) roe deer encounters per day. Among a sub-sample of 13,699 images which were manually screened ([Appendix A1.5](#)), we found only 3 occurrences of red deer (*Cervus elaphus*) limited to 2 out of the 30 forest patches in Aberdeenshire. All AI-classified images of deer from these two forest patches were manually screened and did not contain any red deer. Domestic cattle were detected at a single camera location each in two out of the 30 forests.

3.1. Landscape scale drivers of roe deer forest usage

We obtained reduced models with structural connectivity (Model 1) and functional connectivity (Model 2) each having a positive effect on roe deer forest use ([Fig. 2, Table A2.1](#)). Both models accounted for roughly 27% of variation in roe deer forest use (conditional R^2 : 0.272 & 0.273) with the fixed effect components of the model accounting for roughly 10% variation in roe deer forest use (marginal R^2 : 0.097 & 0.095). Structural and functional connectivity were supported in the best fit model as linear effects on deer forest usage as models with

Table 1

Descriptions of fixed and random explanatory variables included in the full statistical models, with the number of roe deer observations per camera deployment as the response variable with a negative binomial error distribution and deployment duration (in days) as an offset. All explanatory variables were estimated at the forest scale, apart from deployment distance to forest edge. Two different models were fitted: one with structural connectivity (Model 1) and the other with functional connectivity (Model 2); they otherwise had the same explanatory variables. Random effects were nested. All fixed variables were mean centred and scaled. The mean and range are provided for the raw variables prior to any transformations.

Variable	Description	Spatial scale for analysis	Mean (Range)
<i>a) Landscape variables</i>			
Structural Connectivity (log)	Hanski connectivity metric quantifying proximity and size of surrounding forests within 750 m buffer	750 m forest buffer	17.09 (0.22–118.79)
Functional connectivity	Mean forest patch connectivity derived from standardised likelihood of weighted random shortest paths.	Forest	0.06 (0.02–0.12)
Urban land cover	Proportion of urban land cover surrounding patch within a buffer of 750 m	750 m forest buffer	0.02 (0–0.14)
Arable land cover	Proportion of arable land cover surrounding patch within a buffer of 750 m	750 m forest buffer	0.25 (0–0.88)
Distance to forest edge	Distance (m) of deployed camera from forest patch edge	Camera deployment	77.3 (0.3–345.7)
<i>b) Forest variables</i>			
Area (log)	Forest patch area (sq. km); log-transformed	Forest	12.45 (0.17 – 228.14)
Shrub density (log)	Number of shrubs within 15 m of sampling point, averaged across all sampling points within forest patch and log-transformed	Forest	6.9 (0 – 55.4)
Sapling density (log)	Number of saplings within 15 m of sampling point, averaged across all sampling points within forest patch and log-transformed	Forest	55.524 (0–249.6)
Tree density	No. of trees / sq. m	Forest	0.09 (0.03–0.27)
Tree species richness	Number of unique tree species across all transects in a forest patch	Forest	4.931 (2–14)
Woody debris	Index scoring woody debris on forest floor (1–3); the mode across all sampling points was used per forest; categorical (2 levels)	Forest	2, 3 (categorical index)
DBH (SD)	Standard deviation of tree trunk diameter at breast height (cm) across all sampling points within a forest patch	Forest	12.90 (10.2 – 46)
Canopy closure (%)	Percentage closure of tree canopy, averaged across all sampling points within the forest patch	Forest	58.75 (39.66 – 76.06)
Deciduous cover	Proportion deciduous cover within the forest patch	Forest	0.35 (0–1)
Human encounter rate	Number of human observations per day, averaged across all camera deployments within the forest patch	Forest	0.06 (0 – 0.29)
<i>c) Random effects</i>			
Patch ID	Focal Forest identification (29 levels)		
Year	Year of sampling (2021, 2022)		
Month	Month of sampling (April–Oct)		

Further details on the extraction of a) landscape variables and b) forest variables can be found in [sections A1.1 & A1.2](#) and Methods, [Section 2.4](#) respectively.

second-order coefficients of connectivity had higher AIC and were removed during model selection ([Table A2.5](#)). Forests with higher structural connectivity to other forests had higher roe deer encounter rates (Model 1, RR: 1.18, 95% CI: 1.03 – 1.36) as did forests with greater functional connectivity (Model 2, RR: 1.24, 95% CI: 1.08 – 1.42), consistent with prediction P2. Forest patch area was a significant predictor in Model 1, with smaller forests having higher roe deer encounter rates (Model 1: RR: 0.82, 95% CI: 0.71 – 0.94); however, patch size was not retained post model-reduction in Model 2 (with functional connectivity) ([Table A2.5](#)).

As forest patch size was correlated with edge density and the proportion of forest landcover in a 750 m buffer, separate analyses were carried out replacing forest patch size with each of these two variables. Forest edge density within a 750 m buffer was positively associated with roe deer forest use ([Table A2.2](#), RR: 1.21, 95% CI: 1.04 – 1.42) and the proportion of forest landcover was negatively associated with roe deer forest use ([Table A2.3](#), RR: 0.78, 95% CI: 0.67 – 0.92). Urban and arable land cover in a 750 m buffer around each forest were not retained in the final model for Model 1 or 2. ([Table A2.5](#)).

3.2. Within forest structural habitat drivers of roe deer forest use

Consistent with prediction P4, distance of the camera location from forest edge had a small but significant effect, with deployments closer to the forest edge having higher deer encounters compared to those farther

from the forest edge (Model 1, RR: 0.91, 95% CI: 0.83 – 0.99; Model 2, RR: 0.90, 95% CI: 0.83 – 0.98). In both Models 1 & 2, variation in tree DBH (Model 1, RR: 1.25, 95% CI: 1.08 – 1.44; Model 2, RR: 1.28, 95% CI: 1.11 – 1.48) and tree density (Model 1, RR: 1.22; 95% CI: 1.06 – 1.39; Model 2, RR: 1.22, 95% CI: 1.07 – 1.40) had a positive effect on roe deer forest use ([Fig. 2](#), [Table A2.1](#)), consistent with prediction P3, while the mean human encounter rate in a forest patch had a negative effect on roe deer habitat use consistent with prediction P5 (Model 1, RR: 0.86, 95% CI: 0.74 – 0.99; Model 2, RR: 0.85, 95% CI: 0.74 – 0.99). In contrast to prediction P3, woody debris, percentage canopy cover, proportion deciduous cover, tree species richness, shrub and sapling density were not retained in the final models ([Table A2.5](#)).

3.3. Predictors of roe deer functional connectivity

The model explained ~35% variation in roe deer functional connectivity ([Table A2.4](#)) with forest patch size and proportion of deciduous cover predicting functional connectivity but only with marginal significance. Contrary to expectations, structural connectivity was not a significant predictor of roe deer functional connectivity (Slope: –0.004, 95% CI: –0.011 – 0.002). Smaller forests had higher functional connectivity (Slope: –0.009, 95% CI: –0.015 – –0.002) as did more deciduous forests (Slope: 0.009, 95% CI: 0.000 – 0.018).

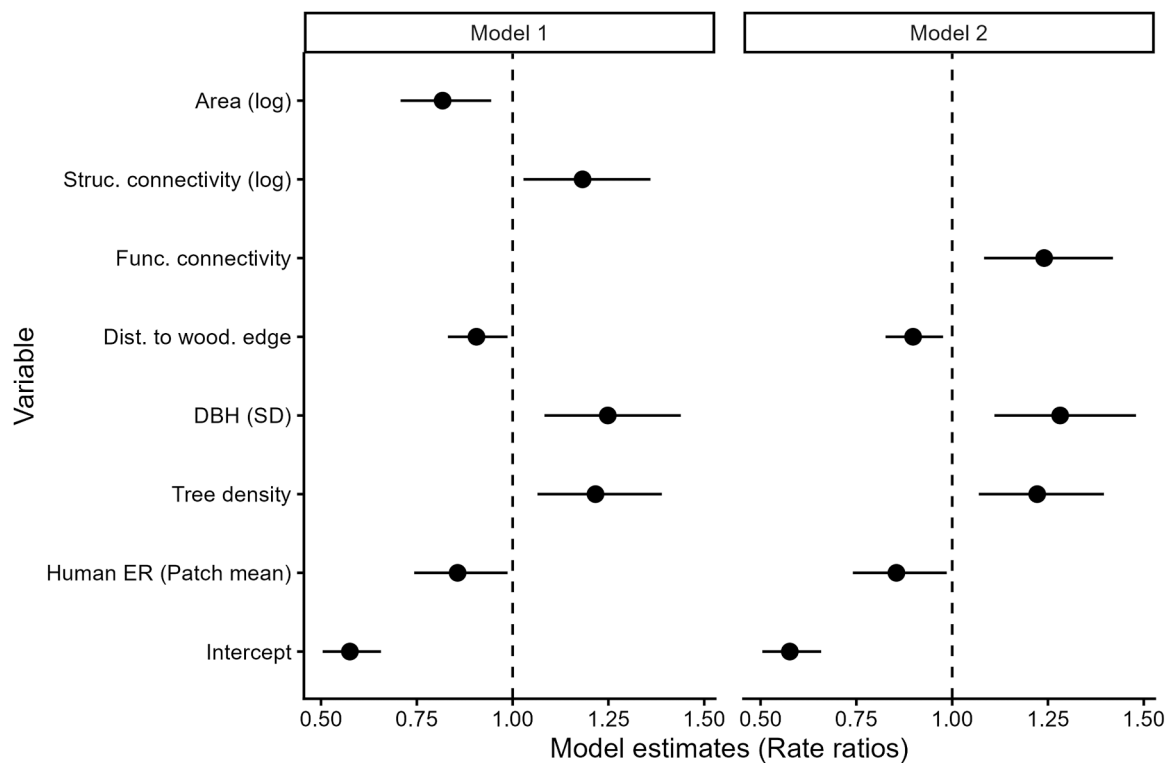


Fig. 2. Output estimates of model coefficients affecting roe deer deployment level encounter rates from the final models obtained after step-wise model reduction. Model 1 included structural connectivity as an explanatory variable while Model 2 included functional connectivity, while all other explanatory variables were the same in the two full models (Table 1). Urban and arable land cover, shrub and sapling density, tree species richness, woody debris and deciduous cover were not retained post model reduction in either model, while forest patch size was additionally not retained in Model 2. Points and error bars correspond to exponentiated model coefficients (rate ratios) of the final reduced negative binomial GLMMs and 95% confidence intervals respectively. Variables with coefficients greater than one (to the right of the dashed line) were positively associated with roe deer encounter rates while those with value less than one were negatively associated with roe deer encounter rates. Human ER is the mean forest encounter rate of humans on camera traps; DBH (SD) is the standard deviation of the diameter of tree trunk at breast height. Final model summaries can be found in Table A2.1.

4. Discussion

Using camera traps deployed across a gradient of forest patch size and connectivity, we found that roe deer living in a rural fragmented landscape preferred smaller, more connected forests. Within forests, roe deer showed a preference for utilising areas closer to the forest edge, and for forests with higher tree density and greater variability in tree size. Roe deer also exhibited lower use of forests that had higher human use.

4.1. Landscape drivers of roe deer forest patch use

Supporting our first prediction, we found that landscape features were strong determinants of roe deer habitat use. Forests which were more connected with other forests had higher roe deer usage. Results from previous studies on effects of connectivity on roe deer forest use are mixed, with some studies demonstrating a positive effect (Martin et al., 2018) while other studies do not find an effect (e.g., Schwegmann et al., 2023). In cases where studies do not detect an effect, this was suggested to be due to high levels of anthropogenic disturbance. Supporting this theory are studies demonstrating that functional connectivity can shift temporally depending on hunting pressure and other types of disturbance (Bonnot et al., 2013; Martin et al., 2018). Contrary to our expectations, functional connectivity (which we derived from GPS collar data from roe deer in the same study landscape; Marshall et al., 2026a) did not have more explanatory power than structural connectivity: both types of connectivity explained equal amounts of variation in roe deer forest use (Section 3.3, Table A2.1). However, of particular interest, functional connectivity was not closely correlated with structural connectivity ($r = -0.125$, $df = 27$, $p = 0.52$), suggesting that the two

connectivity metrics might be capturing different characteristics of the landscape (e.g., functional connectivity may be capturing the stepping-stone effect of sub-0.5 ha forest patches). Forests with higher functional connectivity were characterised by smaller patch size and a higher proportion of deciduous cover partially reflecting our finding of a preference of roe deer towards smaller forests and consistent with previous studies that have found a preference for more deciduous forests (Ramirez et al., 2023; Schwegmann et al., 2023; Spake et al., 2020; Zorzi et al., 2022). The finding that structural connectivity performed as well as functional connectivity in predicting roe deer forest use suggests that the simpler structural connectivity metric could be used by forest managers to understand which forests are likely to be used more by roe deer and which may therefore have higher disservices. However, results also support that these connectivity metrics are giving different information about the landscape effects on roe deer forest patch usage, with functional connectivity providing added mechanistic insight.

We also found an effect of forest patch size on roe deer use, with preference for smaller forests. Forest patch size in many fragmented landscapes is often correlated with the proportion of forest and arable land in the surrounding matrix. This is the case in our landscape where forest patch size is highly positively correlated with forest cover in the surrounding landscape and negatively correlated with arable landcover (Fig. A1.6). In this type of landscape, deer could be utilising smaller forests for cover and protection and feeding in surrounding arable and ecotonal habitats. For example, in a mixed agricultural-forest landscape roe deer females showed higher use of crop fields that were near forests and hedgerows (Mysterud, 1996; Rigoudy et al., 2024). The higher use of smaller forests in our study could also be driven by a higher density of forest-edge ecotones. In our landscape, forest patch size was

significantly negatively correlated with edge density, and replacing patch size with edge density in the model resulted in a significant positive effect of edge density on roe deer habitat use (see Appendix, Table A2.2). Roe deer have been shown to have a strong preference for forest edge habitats, due to field-forest ecotones providing a wide range of food resources from both forest and agricultural habitat, as well as providing cover from climatic factors and predation (Feng et al., 2021; Hewison et al., 2001; Torres et al., 2011). This is further supported by our finding that camera deployment locations closer to the forest edge had higher roe deer encounters compared to those located further inside the forest.

4.2. Within forest structural habitat drivers of roe deer forest use

Supporting our second prediction P2, we identified several structural forest habitat characteristics that were drivers of roe deer forest use. Forests with higher tree density, and higher variability in tree diameter had higher roe deer use. Variability in tree diameter can be interpreted as a measure of structural complexity of forests with older and more established natural and semi-natural forests containing trees of multiple species and ages which have more variation in tree diameter (Fuentes-Montemayor et al., 2020). Our results are consistent with a previous UK-wide study which found that the probability of damage by roe deer in forests increases with increasing tree density and age of the forest (Spake et al., 2020). Tree density is also positively correlated with canopy cover within our study landscapes, implying that roe deer may be preferentially selecting forests with more canopy cover. This contrasts with previous studies that have largely focused on extensive forest areas (Schwegmann et al., 2023) which found roe deer habitat use to be negatively associated with canopy cover and preferential selection for young stands in preference to pole-stage or mature stands (Welch et al., 1990). We predicted that with increasing canopy cover, lower light penetration would have a negative effect on understory vegetation, thus reducing available food and therefore habitat use by roe deer. However, our finding that roe deer prefer small forests surrounded by agricultural land, coupled with our finding that there is higher roe deer use in forests with greater tree density and therefore higher canopy closure could suggest that roe deer are using forests more for shelter and feeding in forest edges and nearby forest-agricultural ecotones (Mysterud, 1996; Rigoudy et al., 2024). This could be further investigated by analysing the temporal activity patterns of roe deer within forests, either by classification of behavioural states (e.g., feeding, moving, resting) from trail camera images and/or from deer tracking studies (Marshall et al., 2026a).

Despite several studies finding an effect of deciduous cover on roe deer habitat use (Ramirez et al., 2023; Schwegmann et al., 2023; Zorzi et al., 2022), our study did not detect this. As our study focused on variation in deer use at finer spatial scales (i.e., at the deployment level), local deployment habitat characteristics may have stronger explanatory power than the forest-scale habitat variables we used in the analysis. Also, as mentioned above, roe deer may rely on forests more for shelter in this landscape and as long as there are sufficient foraging opportunities nearby, particularly during critical periods of nutritional stress (late winter), forests with relatively high coniferous cover and less foraging opportunities could be as suitable as deciduous forests. Understanding both deer diet, and the relative availability of diet items in the landscape, would be a valuable extension of this study and could help assess herbivory impacts on forestry and agriculture. For example, within forests, collection of habitat features related to feeding behaviour, including the ground flora and woody species composition (and thus forage quality) could be assessed by carrying out a woodland herbivore impact assessment in early spring (Armstrong et al., 2025) which would indicate the net impact of deer over the whole year. Information on the cropping regimes surrounding forest patches is also highly relevant, since evidence from diet studies across Europe (Hirst et al., 2026) and a previous examination of food items in roe deer rumens from Aberdeenshire (Calder, 1994) suggests that when agricultural crops are

available, crops form a critical food item for roe deer during late winter when food in the forest becomes relatively scarce (Calder, 1994; Hirst et al., 2026).

4.3. Effects of human recreational use on roe deer habitat use

Forests were used more by roe deer if they were used less frequently by humans. However, in contrast to previous studies of deer in more urbanised environments (Gandy et al., 2026), we did not find an effect of the amount of urban area in the landscape surrounding forest patches on roe deer forest use. This was likely due to the low overall proportion of this land cover type in the landscape, and limited variation between sites. A negative effect of human activity within forest patches on roe deer habitat use is likely to be a direct effect of human disturbance, consistent with previous studies showing that deer reduce space use near areas of human activity such as trails (Mols et al., 2022a, Mols et al., 2022b). Our measure of human usage of the forests would have underestimated recreational use of forests due to placement of cameras to avoid trails; however, this method was consistent across all forest patches so is unlikely to cause bias. It could be argued that our measure of human forest use, which was of humans walking away from trails, may be more likely to be relevant to disturbance of deer. Our results are consistent with previous studies which have shown that recreational use of trails within forests impacts space use by deer at a fine scale of between 20 and 200 m within forests. This is extremely relevant to the disservices rendered by roe deer since this published work also shows that roe deer habitat use can also have cascading effects on the distribution of *Ixodes ricinus* ticks which are hosted by deer (Mols et al., 2022b).

4.4. Limitations

In terms of generalisability, the results from our study are likely to be specific to habitat use in a lowland agricultural-forest mosaic. Habitat use in different environments – e.g., in areas dominated by forestry, or open upland landscapes with fragmented forest – are likely to be different and highlight the need to examine deer habitat use within specific landscapes to better inform land use and forest management. Inclusion of effects of time from forest establishment on roe deer forest use as well as spatial landscape and forest structure drivers could be considered in future studies.

Our statistical models only explained 27% of the total variation in roe deer encounter rates likely due to explanatory factors we could not measure, including habitat characteristics at finer spatial scales (e.g., vegetation type at the camera location) as well as the effects of deer and forest management. For example, we had no access to hunting pressure data; cull intensity can influence roe deer population density, patterns of forest use, and the landscape's functional connectivity (Bonnot et al., 2013; Martin et al., 2018). Moreover, random effects had more explanatory power compared to fixed effects which explained only 10% of the total variation in roe deer encounter rates that may suggest the importance of unmeasured within-forest, landscape, or temporal effects (e.g., seasonal changes in roe deer forest use).

4.5. Management implications

Scotland and other European countries are undergoing significant forest expansion, (Forest Europe, 2020). Our research suggests that patterns of forest and surrounding agricultural land use by roe deer and associated impacts will change with forest expansion if these result in changes in forest configuration.

Our results could be useful for land and forest managers to develop targeted monitoring for disservices to underpin deer management. For example, managers may consider monitoring for disservices, and assessing the hazard of tick-borne diseases transmitted by *Ixodes ricinus*. This tick vector transmits a number of bacterial, viral and protozoal

pathogens which can cause high mortality and morbidity in cattle and sheep (Böhm et al., 2007; Johnson et al., 2022; Mitchell, 2019). Further *I. ricinus* transmits the bacteria causing Lyme disease in humans. Areas predicted to have higher roe deer usage; e.g., in smaller, more connected forest patches and within forest edge and ecotonal areas of forest patches, as well as surrounding agricultural land near forests may be at higher risk from ticks and other parasites hosted by roe deer. For example, a previous study has already highlighted the risks to livestock from the tick *I. ricinus* on pastures adjacent to woodland (Gilbert et al., 2017). Risks may be increased in areas of higher deer populations where deer can transport ticks from forest to pasture (Ruiz-Fons and Gilbert, 2010). Differential patterns of forest habitat use could also have important consequences for humans, from risks of tick transmitted Lyme disease, and road collisions, particularly where heightened human and deer activity coincide (Böhm et al., 2007; Gilbert et al., 2012; Gill and Fuller, 2007; Joys et al., 2004; Nelli et al., 2018).

Within forest creation schemes, this research could be used strategically to develop land manager guidelines to alter deer populations and distribution. For example, land managers may wish to incorporate habitat features that may be attractive to deer, such as edges, gaps or rides, so that hunters and wildlife managers might more effectively focus their activities. Apparent preference of roe deer for edge habitats, suggest that browsing impacts on forests and agriculture may be greatest near edges. Such patterns may highlight areas of heightened impacts on agriculture and present forest managers with opportunities to limit browsing by maximising the interior areas of forest patches.

Finally, this study demonstrates the use of camera traps and publicly available AI models in quantifying the utilisation of forest habitats by deer of relevance to management practitioners. Camera-traps provide non-invasive and more direct means of estimating habitat use and abundance of species of interest compared to indirect dung counts, with relatively low cost and effort compared to other methods such as GPS tracking or thermal imaging using Unmanned Aerial Vehicles (UAV). Because cameras can be deployed for long periods of time with minimal supervision, they can also be used to monitor population changes over time or in response to management efforts. Moreover, the availability of free and open-source image management software combined with shared image repositories e.g., Wildlife Insights (Ahumada et al., 2020) and MammalWeb (Hsing et al., 2022) allow for efficient processing of images and faster extraction of estimates – such as population density or relative abundance, in an accessible manner to non-expert practitioners.

Data statement

The data and R script used for analysis in this manuscript have been made available at DOI: <https://doi.org/10.5281/zenodo.18951596> (Venkatesan et al., 2026).

Data used by Marshall et al. (2026a) and here to generate functional connectivity estimates is available at: <https://doi.org/10.5281/zenodo.18699745> (Marshall et al., 2026b).

Code used to generate functional connectivity estimates is available at: https://github.com/BenMMarshall/TICKSOLVE_DeerMovement; and archived at: <https://doi.org/10.5281/zenodo.18701055> (Marshall, 2026).

A complete list of software used can be found in Appendix A1.7.

CRediT authorship contribution statement

Mark S. Greener: Project administration, Methodology, Investigation, Data curation. **Caroline Millins:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Benjamin M. Marshall:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Isla Sligo-Young:** Writing – original draft, Validation, Formal analysis. **Anna Kinghorn:** Writing – original draft, Validation, Methodology.

Thomas A. Morrison: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Lucy Gilbert:** Writing – review & editing, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Roman Biek:** Resources, Project administration, Funding acquisition. **Saudamini Venkatesan:** Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Robin Gill:** Writing – review & editing. **Richard Hassall:** Methodology, Investigation. **Jeanette Hall:** Writing – review & editing. **Ben McKeown:** Writing – review & editing.

Declaration of Generative AI and AI-assisted technologies in the writing process

Generative AI was not used in this paper.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123852](https://doi.org/10.1016/j.foreco.2026.123852).

Data availability

Please see Data statement in article.

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