Habitat and predator heterogeneity influence density of a declining mammal

Article

Published Version

Yu, H. ORCID: https://orcid.org/0009-0005-5715-9260, Barlow, A., Davis, R. S. ORCID: https://orcid.org/0000-0002-9953-1340, Gentle, L. K., Uzal, A., Baker, P. J. and Yarnell, R. W. ORCID: https://orcid.org/0000-0001-6584-7374 (2026) Habitat and predator heterogeneity influence density of a declining mammal. Oikos, 2026 (1). e11706. ISSN 1600-0706 doi: 10.1002/oik.11706 Available at https://centaur.reading.ac.uk/125554/

To link to this article DOI: http://dx.doi.org/10.1002/oik.11706

Publisher: Wiley

OIKOS

Research Article

Habitat and predator heterogeneity influence density of a declining mammal

Hongli Yu[1], Axel Barlow[2], Robert S. Davis[3], Louise K. Gentle[1], Antonio Uzal[1], Philip J. Baker[4] and Richard W. Yarnell[1]

[1]School of Animal, Rural and Environmental Sciences, Brackenhurst Campus, Nottingham Trent University, Southwell, UK
[2]School of Environmental and Natural Sciences, Bangor University, Gwynedd, UK
[3]Department of Conservation Management, Nelson Mandela University, George, South Africa
[4]School of Biological Science, University of Reading, Reading, Berkshire, UK

Correspondence: Hongli Yu (hongli.yu2020@my.ntu.ac.uk)

Oikos
2026: e11706
doi: 10.1002/oik.11706
Subject Editor: William Severud
Editor-in-Chief:
Paulo R. Guimaraes
Accepted 23 August 2025

Accurate density estimates are crucial for effective conservation management. However, in highly dynamic landscapes where variation in habitat composition and predator–prey interactions in both space and time is likely, integrating spatiotemporal covariate effects in density estimation is challenging and often large datasets are needed. Here, we used an 11-year spatial capture–recapture (SCR) dataset from a typical mixed agroecosystem in England to estimate landscape-scale densities of western European hedgehogs *Erinaceus europaeus*. We simultaneously integrated spatially varied habitat covariates, and the spatiotemporal variation in predator (Eurasian badger *Meles meles*) den site into one SCR framework. Density was spatially structured (range 0.39–13.54 on a 1 km^2 grid), and was lower in arable fields and highest in amenity grasslands next to buildings. Density was also positively associated with soil permeability, density of edge habitats, proximity to the nearest building, and distance from the nearest badger sett. A new badger sett appeared halfway through the study period, resulting in a hedgehog density-weighted population centre over the study area shift away from the badger sett and a decrease in annual hedgehog density estimates, supporting the landscape of fear for hedgehogs in response to their main predator the badger. Density estimates were also 43% lower after incorporating spatiotemporal covariate heterogeneity into the modelling process, highlighting the need to integrate dynamic habitat and predator influences into density modelling to provide more accurate estimations. Finally, our findings demonstrate the importance of long-term monitoring for understanding population responses to changes in predator presence and provide clear empirical evidence for a prey species altering space use in relation to the increased predator, supporting the landscape of fear hypothesis.

Keywords: *Erinaceus europaeus*, landscapes of fear, *Meles meles*, population ecology, spatial capture–recapture, spatiotemporal covariate heterogeneity

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

Accurate estimates of population density are necessary to understand population dynamics (Fryxell et al. 2014). However, quantifying animal density is particularly difficult when population processes exhibit both spatial and temporal variability (Royle et al. 2015), due to changes in habitat composition and predator–prey interactions. Spatial capture–recapture (SCR) is one technique that can incorporate within-population variation into overall estimates of density (Royle et al. 2015). SCR studies collect individual encounter history data, i.e. when and where individuals are and are not detected, and estimate the number and distribution of individuals that have never been detected, based on the detection probability of known individuals (Efford 2004). In this process, density modelling can be based on an assumption of either habitat uniformity or heterogeneity, with the former assuming all individuals are randomly distributed, and the latter assuming individual distribution is shaped by the effects of habitats (Efford and Fewster 2013). The majority of SCR density estimates to date have been based on an assumption of uniformity (Tourani 2022). However, the extent to which this could affect density estimates is yet to be fully understood.

Studies that have directly compared the density values between those based on habitat uniformity versus assumptions of heterogeneity have contrasting findings. Efford and Fewster (2013) and Gerber and Parmenter (2015) showed no considerable difference between density estimates from both assumptions. By contrast, the density of American mink *Neovison vison* was found to be 1.9 times higher when distance to nearest city was integrated into density modelling (Fuller et al. 2016). Furthermore, for highly dynamic habitats (e.g. agricultural landscapes) where variation in habitat composition and predator density in both space and time is likely, the performance of SCR models that integrate both spatial and temporal covariate changes is recommended to improve our understanding of how density varies in the landscape (Royle et al. 2017).

The western European hedgehog *Erinaceus europaeus* (hereafter hedgehog) is a nocturnal, solitary and small (< 2 kg) terrestrial insectivore (Reeve 1994) and has been used as a model organism for investigating the effects of changes in landscape connectivity (Yu et al. 2025a) and evaluating the impacts of agri-environment schemes (Hof et al. 2012, Pettett et al. 2017). Hedgehogs were traditionally considered a rural-dwelling species (Yarnell and Pettett 2020) that feeds primarily on macroinvertebrates (Yalden 1976). However, in Great Britain, hedgehogs are experiencing faster declines in rural areas than urban ones, based on indices of relative abundance (Wilson and Wembridge 2018), likely related to agricultural intensification and potentially an increase in the abundance of their main predator, the badger *Meles meles* (Judge et al. 2014). In addition, hedgehogs also appear absent from many rural areas (Williams et al. 2018) and, where they do occur, their densities are often low (Schaus et al. 2020). Estimating rural hedgehog densities is particularly challenging due to their typically low population density and considerable variation within and between habitats (Hubert et al. 2011, Pettett et al. 2017). Consequently, fine-scale sampling across different habitat types is likely to increase the accuracy of density estimates, and help inform future conservation management for the species.

In addition to agricultural intensification, badgers, an intra-guild predator, are implicated in hedgehog declines (Young et al. 2006, Trewby et al. 2014, Pettett et al. 2017). However, the reported negative correlation between hedgehogs and badgers in previous studies might be confounded by other factors, such as variation in the levels of anthropogenically provided food (Hubert et al. 2011, Pettett et al. 2017) or differences in hedgehog and badger activity in different habitats (Lee et al. 2025). Hedgehogs may also have developed strategies to co-exist with badgers, such as spatial (Young et al. 2006, Williams et al. 2018) and dietary niche-partitioning (Lee 2021), although to date no temporal niche-patterning has been found between the two species (Lee et al. 2025). In order to better understand the population responses of hedgehogs to their main intraguild predator, longitudinal studies tracking the variation in abundance of both species are needed to determine whether the correlations from past studies translate into causative processes.

Therefore, in this study, we analysed an 11-year hedgehog population monitoring dataset from a typical mixed agro-ecosystem in England using SCR to estimate spatiotemporal variation in animal density. Specifically, we modelled spatial variation in density across different land use (Hubert et al. 2011) and habitat features including buildings (Schaus et al. 2020), edges (Hof et al. 2012, Rodriguez Recio et al. 2013, Bearman-Brown et al. 2020), and soil texture (Jackson 2007) that have been indicated to affect hedgehogs, and the influence of spatiotemporal changes in predator (badger) den sites. Based on previous research, we predict that hedgehog density will be spatially structured with land use and habitat features, and negatively impacted by the addition of a badger sett (den) that appeared mid-way through the study period. We also expect that the population trend would reflect wider geographic population declines reported for this species and potentially identify drivers of population change.

Material and methods

Study site and hedgehog surveys

The study took place at Nottingham Trent University's Brackenhurst Campus, Nottinghamshire, UK (site coordinates 53°03′47.5′′N, 00°57′49.9′′W , Fig. 1), which consists of 2.07 km^2 of mixed agricultural land (55.8% arable, 37.3% pasture, 6.9% amenity), including university campus buildings (Supporting information). The total length of all edge types was 18.54 km, with buildings covering an area of 0.03 km^2. Between 2009–2014, there were three active badger setts, two within the survey area and one beyond (approx. 500 m to the edge of nearest survey area). An additional

Figure 1. Habitat composition of the study site at Brackenhurst Campus, Southwell, England, showing badger sett locations, land use and state space. Amenity, pasture and arable fields are indicated in progressively darker shades of grey respectively. The study site is bisected by one major road (A621) towards the west. The state space for the hedgehog density modelling is shown within the dashed polygon. Triangles show the location of badger setts, with black triangles representing the setts that were active for the entire study period (2009–2022) and the red triangle representing the additional badger sett that appeared in 2015 and remained active beyond 2022.

badger sett was found during annual surveys in 2015, resulting in a total of four active setts between 2015–2022.

Hedgehogs were located during nocturnal spotlight (1 million candlepower) surveys conducted annually between March and October, 2009–2022; data from 2016, 2019, and 2020 were not included in the analysis due to low survey effort (sensu Schaus et al. 2020). Searches were conducted by walking the perimeter of all fields (Supporting information), usually from dusk to two hours after midnight, and hedgehogs were captured by hand. All captured animals were marked by attaching coloured heat shrink tubes to dorsal spines for individual identification (Glasby and Yarnell 2013). For each capture, the animal's ID, sex, age (young or adult), weight (g), GPS coordinates, and time were recorded. Animals were released at the point of capture, typically within five minutes. Young hedgehogs were classified as those born in that year, and adults as those that had survived their first winter (Yarnell et al. 2019). As young hedgehogs and adults have different detection rates and habitat use, based on our preliminary analysis, this study utilises data from adults only.

For density modelling, the variables Building, Edge, Badger, Soil and Landuse were used as covariates (Table 1). Building describes the euclidean distance from the centre of each grid cell to the nearest building. Edge is the total length of all edge habitats (e.g. hedgerows, woodland edges, fences [limited in extent and are likely permeable to hedgehog movement], etc.) in each grid cell. Badger is the euclidean distance from the centre of each grid cell to the nearest badger sett). Soil describes soil types that are identified on site based on the permeability of topsoil and subsoil, including low permeability (type 0, slowly permeable reddish clay, mainly Worcester, passing to a blocky Mudstone), and high permeability (type 1, moderately permeable loams or silts overlaying slowly permeable reddish clay, mainly Whimple,

Table 1. Description of the spatial capture–recapture model parameters and covariates included in the modelling. Where p_0, is the baseline encounter probability; σ, sigma, is the movement parameter; and D, is hedgehog density.

Parameter	Notation	Description
p_0	Sex	Sex (categorical: female or male).
σ	Sex	Sex (categorical: female or male)
D	Landuse	Land use (categorical: 0, arable; 1, amenity; 2, pasture). The composition of land use types varied across the state space, but was constant across years
	Soil	Soil types (categorical: type 0, low permeability, slowly permeable reddish clay (mainly Worcester) overlaying a blocky Mudstone, and type 1, high permeability, moderately permeable loams or silts overlaying reddish clay (mainly Whimple, Hopsford, and Mathon), then passing to slightly permeable Dolomite. Soil composition was varied across the state space, but was constant across years
	Building	Euclidean distance from the centre of the 50 × 50 m grid cell to the nearest building (continuous and standardised by z-score). This covariate was constant across years
	Badger	Euclidean distance from centre of the grid cell to the nearest badger sett (continuous and standardised by z-score). This covariate was varied across the state space, and was varied temporally as a new badger sett was created in 2015
	Edge	Edge density, refers to the total length of all types of edges within each grid cell (continuous and standardised by z-score). This covariate was constant across years
	Session	Search year (categorical)

Hopsford and Mathon, passing to slightly permeable Dolomite) (Ambrose et al. 2006). Landuse is land use types, including amenity, arable and pasture. Data on buildings (all buildings with roofs) and edge habitats were extracted from OS MasterMap Topography Layers and high-resolution (25 m) Vertical Aerial Imagery (https://digimap.edina.ac.uk/). Land use data were extracted from the 2021 UKCEH Land Cover Maps (Marston et al. 2022) and validated based on field observations. All habitat covariates were extracted based on 50 × 50 m grid cells across the state space (Schaus et al. 2020, Fig. 2). Spatial analyses were conducted using ArcGIS (ESRI 2015) and R ver. 4.2.2 (www.r-project.org) packages 'sf' (Pebesma 2018, Pebesma and Bivand 2023), 'tmap' (Tennekes 2018) and 'terra' (Hijmans et al. 2023).

SCR modelling

Density was estimated using multi-session SCR models in the 'oSCR' package (Sutherlandet al. 2019) with each hedgehog survey year defined as a Session (Table 1) and each search night (usually dusk to midnight) defined as an occasion. If an individual was captured more than once on a given occasion, only the first capture location was utilised. 50 × 50 m grid cells were regarded as effective traps (Schaus et al. 2020), such that survey effort was taken as the number of times each grid cell was surveyed in each session. Differences in survey effort over years (Supporting information) were incorporated in the density modelling process. Surveys were not equally distributed within or between seasons (supporting information), so the estimated densities represent yearly densities, assuming little effects of seasons on the yearly density estimates. The total state space was also based on a 50 × 50 m pixel grid (Fig. 2) covering a total area of 3.70 km^2, which included the search area (2.07 km^2)(Supporting information; sensu Fuller et al. 2016, Morin et al. 2017). This is assumed to be large enough to contain probable animal locations (Efford 2004) based on the approximate home range size of male hedgehogs (e.g. 0.22 km^2 in Pettett et al. 2017, in rural sites in England).

The baseline encounter probability (p_0) was the probability that an individual is detected at its activity centre (home-range centre). The movement parameter sigma (sig, σ) describes the distance over which the animal is likely to be detected. Both p_0 and σ were modelled as a function of sex (p_0 ~ sex, σ ~ sex) as male hedgehogs often move larger distances than females (Reeve 1994, Pettett et al. 2017). Before modelling the density, continuous covariates were standardized by converting to z-scores (Donovan and Hines 2007). Correlation among predictor variables was checked with the cor() function in R, with the Pearson correlation index > 0.7 indicating considerable correlation; no covariates were strongly correlated (≤ 0.4). Density was first modelled with the assumption of habitat uniformity (D ~ 1) and then by incorporating the heterogeneity of the following covariates: land use type (Landuse: 0 [arable], 1 [amenity], 2 [pasture]); soil type (Soil: type 0 [low permeability], type 1 [high permeability]); euclidean distance to the nearest building (Building) and badger sett (Badger); and density of edge habitats (Edge). Session was also included to infer population trends across years.

To avoid having to test too many models, we conducted a hierarchical selection, based on Akaike information criterion values (AIC, Burnham and Anderson 2002). We fitted the detection and movement models first and, using the most supported detection and movement model, fitted the density models (Kervellec et al. 2023). We tested habitat effects on constant density models based on all combinations of spatial covariates but limited the maximum number of spatial covariates to three, as models with ≥ 4 spatial covariates failed to converge. Temporal effects on density were modelled with Session as a covariate only and compared to the null density model. As the session-specific model outperformed the null density model, Session was added to the best-supported constant model that included other covariates for their additive effects (sensu Fondell et al. 2008). Session was initially run in chronological order (with 2009 as the intercept) for model fitting and for testing whether annual density estimates varied through time; density calculated based on the

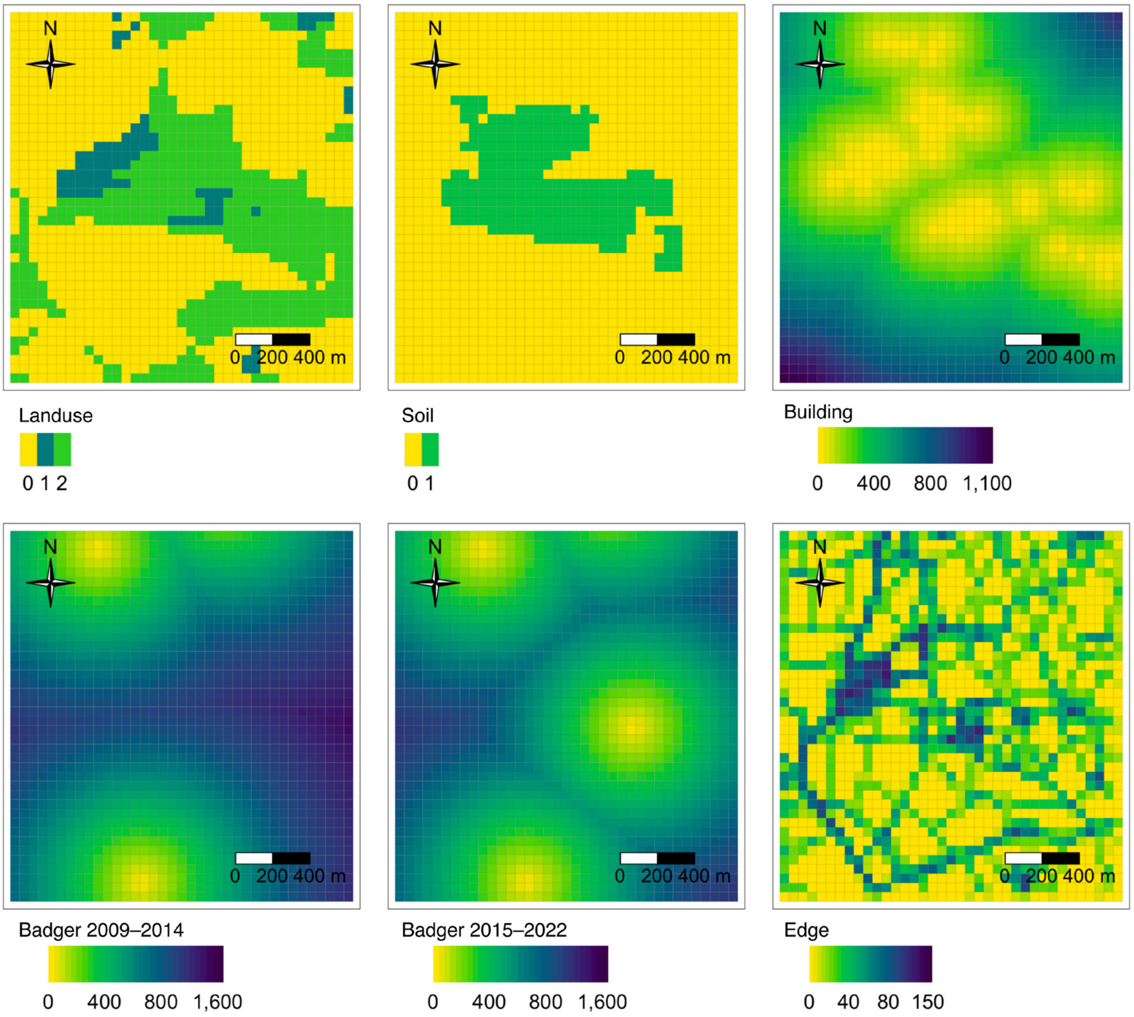

Figure 2. Map of habitat covariates used in hedgehog density modelling at Brackenhurst Campus, Southwell, England between 2009 and 2022. Resolution: 50 × 50 m. Notations are summarised in Table 1. Landuse: arable (0), amenity (1), and pasture (2); Soil: soil types, low permeability (type 0); high permeability (type 1). Building and Badger: straight line distance (m) from the centre of each grid cell to the nearest building, and badger sett (for 2009–2014, and 2015–2022), respectively. Edge: total length (m) of edge habitats within each grid cell.

top-ranking model was presented unless otherwise specified. We then identified that the last Session (year 2022) had one of the lowest densities, and we therefore reordered Session so that the reference Session (intercept) for annual significance testing was year 2022.

We modelled both the realised density (indicating a single realisation of the point process model describing the number of individual activity centres per state space pixel; the density refers to the local density unscaled by area) and estimated density (conditional on the observed capture history data but takes the random effects into account based on maximum-likelihoods; the density can be scaled to other areas) (Morin et al. 2017, Royle et al. 2017). As Badger composition varied in relation to the presence of different numbers of badger setts in 2009–2014 and 2015–2022 (Fig. 1–2), we simultaneously integrated two sets of Badger composition in the SCR framework (Sutherland et al. 2019). To compare with other studies, the total number of hedgehogs was divided by 3.70 km^2 state space to produce a mean estimated density per year. The density-weighted gravity centre was inferred using the wt.centroid() function in the 'spatialEco' package (Evans and Murphy 2021). To show the spatial variation in estimated density, we used a 50 m moving window to quantify the total number of hedgehogs on any of the 1 × 1 km grids, using the *focal()* function in the 'terra' package (Hijmans et al. 2023), which takes into account a central cell and its neighbours for continuous space, and applying an aggregation function to all cells within the specified neighbourhood (Hijmans et al. 2023). The density was scaled up for land use types and fields by using a *sum()* function in R to sum the value in each pixel included (Royle et al. 2017). The relationship between hedgehog density and covariates was plotted using the package 'ggplot2' with a linear model method (Wickham 2016).

Results

Summary of search effort and captures

Two spatial outlier captures (380 and 208 m away from the state space, respectively) were excluded as they rendered a high coefficient of variation in sigma which can affect density estimation (Kendall et al. 2019). Consequently, search effort consisted of 440 search nights over 11 years yielding 860 independent captures of 134 adults (77 female: 57 male), with mean number of captures per individual being 6 (95% CI 5–8). Detailed search effort and captures are summarised in the Supporting information.

Population density

For both baseline detection (p_0) and spatial scale parameter sigma (σ), models with Sex as a covariate were consistently supported over the null model, and all subsequent analyses were presented with Sex effects (p_0 ~ Sex, σ ~ Sex). The sex-specific estimates of the movement scale parameter σ_{sex} were, $\sigma_{female} = 118$ m (95% CI 110–125), $\sigma_{male} = 205$ m (95% CI 183–227). Sex-specific estimates of the baseline encounter probability were, $p_{0female} = 0.014$ (95% CI 0.012–0.016), $p_{0male} = 0.005$ (95% CI 0.004–0.006).

Among all constant density models (density assumed to be constant over time) that converged, the model with the lowest AIC value included an additive effect of Soil type, distance to the nearest Badger sett, and Edge density (D ~ Soil + Badger + Edge, p_0 ~ Sex, σ ~ Sex). Based on this model, the addition of Session further improved model fit, supporting temporal variation in densities over the study area (Fig. 3). Thus, our top-ranking model was D ~ Session + Soil + Badger + Edge, p_0 ~ Sex, σ ~ Sex (Supporting information). Estimated hedgehog density per 50 × 50 m grid cell, based on the top-ranking model, was significantly higher on land with Soil type 1 (high permeability; $\beta_{Soil1} = 1.939$, SE 0.4; 0.063 per 50 m grid cell, 95% CI 0.035–0.116) than that on Soil type 0 (low permeability; 0.006 per 50 m grid cell, 95% CI 0.002–0.014), with the former being 11 times higher as the latter. Estimated hedgehog density per 50 × 50 m grid cell was also significantly higher with increasing distance from the nearest badger sett ($\beta_{Badger} = 0.412$, SE 0.123; $p \leq 0.001$), and with increasing edge density ($\beta_{Edge} = 0.321$, SE 0.102; $p \leq 0.05$) (Fig. 4). Across years, and in comparison to the intercept (Session 2022), all years between 2010 and 2015 had significantly higher hedgehog densities except 2009. There was no significant difference in hedgehog density in years 2017 to 2021 in comparison to 2022, which corresponds with years after which the additional badger sett appeared (Fig. 3, Supporting information). To illustrate the influence of an additional badger sett appearing in 2015, when the two Badger time periods were summarised, the average annual estimated density decreased after the new badger sett appeared from a mean of 8.52 km^{-2} (95% CI 4.58–16.27) between 2009 and 2014 to 3.03 km^{-2} (95% CI 1.35–6.96) between 2015 to 2022 (Supporting information).

To further illustrate the influence of spatiotemporal covariate heterogeneity on hedgehog density, the realised hedgehog density for each survey year was plotted (Fig. 5). The hedgehog population density-weighted gravity centre shifted approx. 300 m from where the new badger sett was located, to areas with more buildings to the northwest. For all the surrounding arable land, hedgehog densities were consistently low across all survey years (Supporting information).

Across all years, mean estimated density from the top-ranking model (6.36 km^{-2}, 95% CI 3.26–12.79) was 43% lower than the model (11.18 km^{-2}, 95% CI 6.87–18.40)

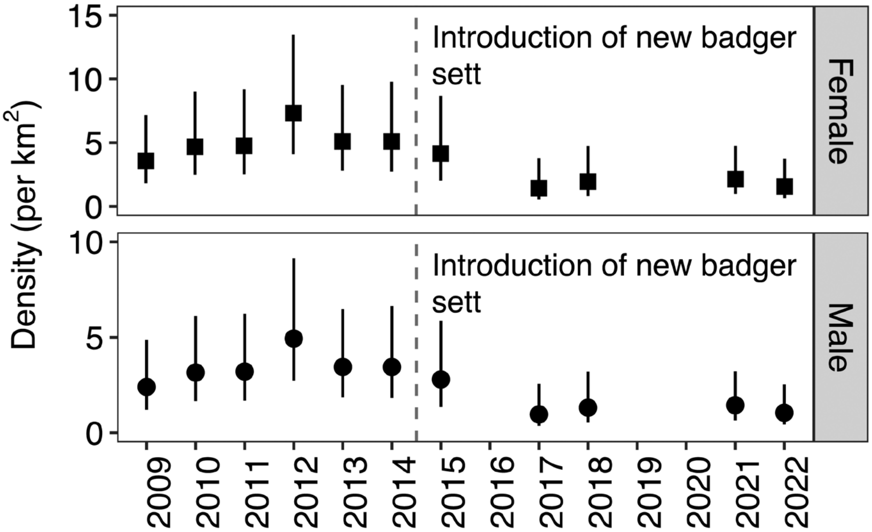

Figure 3. Estimated density (mean number of hedgehogs per km^2) of female (top) and male (bottom) adult hedgehogs at Brackenhurst Campus, England, between 2009 and 2022. Error bars correspond to 95% confidence intervals to the mean. Density estimates are derived from nocturnal spotlight surveys and spatial capture–recapture analysis. Estimates from 2016, 2019 and 2020 are missing due to low sampling effort in these years. Between 2009 and 2014, three Badger setts were present, and between 2015 and 2022, four Badger setts were present. The output is derived from model: D ~ Session + Soil + Badger + Edge, p_0 ~ Sex, sig ~ Sex.

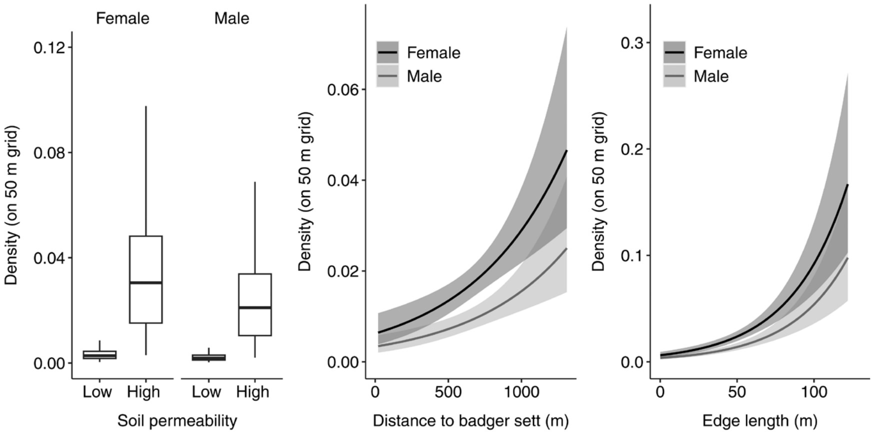

Figure 4. Estimated female and male adult hedgehog density at Brackenhurst Campus, England, in relation to Soil type, Badger sett proximity, and Edge length. Hedgehog density is presented as the number of hedgehogs per 50 × 50 m grid cell per year (females and males shown separately). Boxplots (median, 25% and 75% quartiles, 95% confidence intervals) of estimated hedgehog density values on soil permeability, and plots of mean estimated hedgehog density values on distance to the nearest badger sett (m), and edge length (m) within each 50 × 50 m grid cell. Grey shaded areas indicate 95% confidence intervals to the mean. The output is derived from model: D ~ Session + Soil + Badger + Edge, p_0 ~ Sex, σ ~ Sex..

that assumed landscape uniformity and no predator covariates (D ~ Session, p_0 ~ Sex, sig ~ Sex) (Supporting information). Therefore, incorporating spatiotemporal covariate heterogeneity into the SCR modelling process demonstrated that hedgehog density is substantially spatially structured. Indeed, hedgehog density ranged 0.39–13.54 per km^2 based on 50 m moving windows, showing the high variation in spatial density.

Discussion

Based on an 11-year SCR hedgehog dataset, our study represents the longest SCR density modelling of a mammal in an agroecosystem, and a rare example of long-term monitoring of a hedgehog population (Kristiansson 1990). The long-term monitoring allowed us to identify a decline in population density related to an increase in predator presence, while also being linked to habitat characteristics. By simultaneously integrating both spatially and temporally varied covariates into one SCR framework, our study illustrates how spatially structured population densities can be greatly overestimated (by 43%) if covariate heterogeneity is not integrated in the density modelling process.

Our findings provide evidence of spatial segregation between hedgehogs and badgers (Young et al. 2006, Pettett et al. 2017, Williams et al. 2018, Turner et al. 2022, Lee et al. 2025). Previous studies have shown the negative correlation between both species and typically explained the relationship as being a result of badgers exerting a negative influence via competition and/or predation. The alternative hypothesis of differential species-specific habitat selection has also been considered (Lee et al. 2025). Furthermore, none of the correlation studies were able to demonstrate a population response of hedgehogs to badgers over time as they provided a snapshot in time of the spatial distribution of each species. Trewby et al. (2014) were the first to survey hedgehog populations over a period of six years in relation to reductions in badger abundance due to culling for disease management. They showed that hedgehog indices of relative abundance increased in areas where badger abundance was expected to have decreased, and relative to control areas where badger abundance was assumed constant. However, there is some uncertainty in how the relative indices of abundance accurately reflect population density or varying activity patterns (Hayward et al. 2015).

This study is the first to show a hedgehog population response to increasing badger setts (a proxy for abundance, Judge et al. 2017). Hedgehogs shifted their density-weighted centre, away from the badger sett after it appeared in the middle of the study area. Prior to that, the density-weighted centre was similar across years. We were unable to determine the mechanism driving this observed pattern. Plausible non-exclusive explanations include: 1) direct predation of hedgehogs in the immediate vicinity of the new badger sett removing individuals, 2) reduced activity near the sett in response to a perception of increased predation risk (landscape of fear), and 3) increased competition for shared food resources causing hedgehogs to shift their foraging to areas away from the competing badgers (Lee et al. 2025). Some hedgehog predation was recorded during the study, but only one hedgehog carcass was found after 2015 with the characteristic signs of badger predation, namely a hollowed out skin. These rates of identified predation in the study were similar before the appearance of the new badger sett (unpublished data). Therefore, although a potentially contributory factor, it is more likely that the shift was caused by a landscape of fear and/or due to competition for shared food resources. Furthermore, the addition of a badger sett did not lead to overall extinction of the population, but rather a drop and subsequent stabilisation of density in response to the new predator spatial configuration in the landscape. This suggests

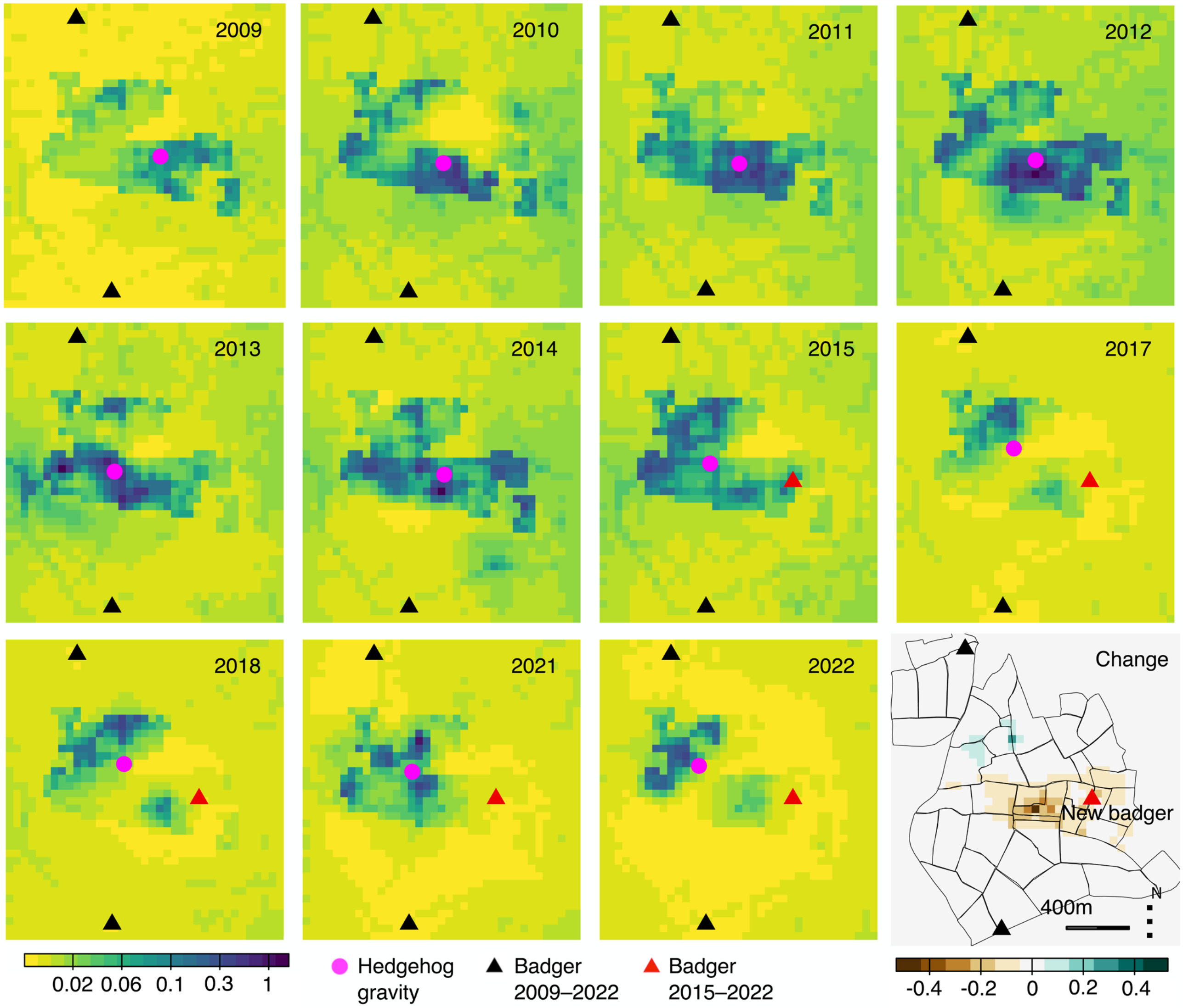

Figure 5. Realised density of adult hedgehogs at Brackenhurst Campus, England, between 2009 and 2022. Density estimates are derived from nocturnal spotlight surveys and spatial capture–recapture analysis. Hedgehog density is presented as the number of hedgehogs per 50 × 50 m grid cell per year (females and males combined). Pink point represents the hedgehog density-weighted gravity centre (hedgehog gravity) of the year. Triangles show the location of badger setts, with black triangles representing the setts that were active for the entire study period (2009–2022) and the red triangle representing the additional badger sett that appeared in 2015 and remained active beyond 2022. Spatial density estimates of hedgehogs are provided for each year separately, with yellow to dark purple indicating density from low to high (with 2016, 2019 and 2020 excluded due to low sampling effort in these years). The density-weighted gravity centre shifted approximately 300 m from southeast (i.e. from where the new badger sett was located) to northwest. Spatial changes in density estimates between two time periods relating to different Badger sett locations during the study are provided in the last panel (Change), with orange indicating where hedgehog density declined, to white indicating no changes in density, and then to blue indicating hedgehog density increasing, showing spatial changes in hedgehog density in response to the additional badger sett. The output is derived from model: D ~ Session + Soil + Badger + Edge, p_0 ~ Sex, σ ~ Sex..

that if badgers increase in an area, and there are refuges in the landscape that provide the resources for hedgehogs to access, hedgehogs can shift local habitat selection and remain in the wider area. However, the ability of hedgehog populations to respond to increasing badger abundance is likely to be affected not only by the habitat and resource availability in the area, but also by the magnitude of and spatial extent of the badger increase. Our results suggest that the appearance of badgers in previously occupied hedgehog habitat led to on average lower hedgehog densities overall, suggesting that badgers may have had a negative influence on hedgehog abundance at this site. Badger densities at the study site are relatively high for England (7 per km^2, Lee et al. 2025), but our results do suggest that the potential for badgers to influence hedgehog densities at various scales is possible (Williams et al. 2018).

Our findings further confirmed predictions that hedgehog density is substantially spatially structured at a local scale and linked to previously reported habitat and land use associations (Yarnell et al. 2014, Williams et al. 2018, Lee et al. 2025, Supporting information). Hedgehog density was lowest in arable fields (Pettett et al. 2017), and highest in amenity, with pasture fields being intermediate (Parrott et al. 2014). The higher density on amenity grassland is likely associated with the close proximity of buildings which was also demonstrated here (Supporting information) and supports previous studies showing hedgehog density is typically higher in urban environments (Hubert et al. 2011, Schaus et al. 2020). The low density estimates associated with arable fields add to a growing evidence base that suggests these are unsuitable for hedgehogs (Pettett et al. 2017, Lee et al. 2025). These habitat associations are likely driven by varying food and shelter resources in each habitat, with intensive arable farming leading to lower macroinvertebrate abundance caused by soil compaction, homogenisation of landscapes, and use of macroinvertebrate pesticides.

Indeed, our study demonstrates that hedgehog density is positively related to edge density. Edge habitats, such as hedgerows, have previously been identified as being important for hedgehogs (Rodriguez Recio et al. 2013) in facilitating movements (Hof et al. 2012), providing nest sites (Bearman-Brown et al. 2020), a refuge from predators, and food resources (Hof and Bright 2010, Hof et al. 2012, Pettett et al. 2017). The edge effect supports the view that homogenisation of habitat is detrimental for hedgehog populations, and that habitat complexity and resulting high edge densities may help improve connectivity in the landscape and be beneficial. We recommend that in general, edge habitats such as hedgerows should be maintained and improved to increase habitat suitability for hedgehogs.

A novel finding from this study is the positive association of hedgehog density and the area with high soil permeability. The suggestion that soil permeability may influence the distribution of hedgehogs was raised by Jackson (2007), where the density of island translocated hedgehogs was twice as high on more permeable sandy-soiled machair versus peaty-soiled blacklands. Unfortunately, in both our study and Jackson's (2007), the location of more permeable soil was confounded by overlapping amenity and pasture fields. By contrast, less permeable soils, where hedgehog densities were lower in the present study, were largely associated with arable fields, which are used infrequently by hedgehogs (Pettett et al. 2017). Disentangling and determining whether soil or land use influences hedgehog density is worthy of further research. However, the observed correlation between the hedgehog density and soil raises the possibility that the habitat effects on hedgehogs may be beyond the contemporary land cover or land use, and may also be related to historical land use or geology. Hedgehog density estimates are needed on more sites that quantify soil types, to better understand the mechanisms underlying the observed relationship between soil types and hedgehog density.

The estimated hedgehog density was negatively related to distance to the nearest buildings, as has been documented in previous studies (Yarnell et al. 2014, Williams et al. 2018, Yu et al. 2025a). The higher hedgehog densities found in built-up areas or urban areas are often suggested to be driven by hedgehog's attraction to anthropogenically provided food (Hubert et al. 2011, Pettett et al. 2017) and lower risk of predation by badgers (Hubert et al. 2011, Pettett et al. 2017), but the two effects are often difficult to disentangle (Lee et al 2025). Interestingly, our study area lacked intentional anthropogenically provided food, suggesting that the hedgehog's association with buildings could be due to the landscape of fear response of hedgehogs to badgers (Young et al. 2006). However, we were unable to quantify the variability of natural food availability across the state space, which may have helped explain some of the spatial patterns observed in this hedgehog population (Hof et al. 2012).

In this study, density estimates were 43% lower after incorporating spatiotemporal covariate heterogeneity into the modelling process, suggesting that where habitats affect the within-population individuals' distribution, population density estimates can be dramatically biased if such effects are not accounted for. Further, as one of the few studies to tackle both spatially and temporally varying covariates in the density modelling process, our study highlights the utilisation of SCR as a framework for population monitoring studies in complex landscapes (Sutherland et al. 2019). This is particularly important for the assessment of population size trends in space and time. In our example, without taking into account spatiotemporal covariate heterogeneity, we would have almost doubled our estimated number of animals occurring across the state space, and would have been unable to link certain habitats with hedgehog density, which would lead to misleading assumptions about the population state of this declining species. We therefore recommend that future SCR studies incorporate dynamic influences of habitats and/or predators into the modelling process to provide greater inference into variation of density across landscapes, and provide more accurate densities from which management decisions can be based and evidenced.

Conclusion

This study demonstrates the value of long-term population datasets combined with habitat and predator covariates. Using this approach, we have shown that population density varies over small spatial scales and that prey population centres can shift in response to the presence of predators, supporting the landscape of fear hypothesis. Understanding how declining populations use habitat differentially at varying spatial scales can inform wildlife management, providing greater insight into how species preferentially use and move through landscapes. Furthermore, incorporating spatiotemporal covariate heterogeneity into the SCR modelling framework produced lower density estimates than models that assumed habitat uniformity. This is important because there is a risk of overestimating abundance of species of conservation concern by taking a landscape uniformity approach, which could lead to the incorrect conservation assessment of endangered species.

Acknowledgements – We thank students from Nottingham Trent University who kindly helped with fieldwork : Alice Gibson, Carlie Wood, Courtenay Holden, Debra Holliday, Emma Franks, Hannah Tabor, Jake Robinson, Jo Dent, Jo Surgey, Katie Peat, Lee Glasby, Rachael Ford, Shangnan Xu and Zoe Mitsis. We thank Simon Taylor and the Security Team at Nottingham Trent University for helping with fieldwork. Thanks to Marcello Di Bonito for providing the soil map. Thanks to Daniel Linden and Maëlis Kervellec for providing R scripts for plotting the density as a function of covariates. We are grateful to Samantha Ward and Andrew Overall for providing helpful comments.

Funding – Funding was provided by Nottingham Trent University.

Permits – All work in this study was conducted under Natural England Licences (20121788 and 2018-36011-SCI-SCI) and was approved by Nottingham Trent University's ethical review committee (Ethics approval code: ARE10).

Author contributions

Hongli Yu: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Axel Barlow**: Conceptualization (equal); Formal analysis (supporting); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Robert S. Davis**: Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Louise K. Gentle**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Antonio Uzal**: Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Philip J. Baker**: Conceptualization (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Richard W. Yarnell**: Conceptualization (lead); Data curation (lead); Formal analysis (supporting); Methodology (equal); Project administration (lead); Resources (lead); Supervision (lead); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from Github: https://github.com/Hongliyu2021/Brackenhurst_hedgehog_density (Yu et al. 2025b).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Ambrose, K., Buckley, D., Entwisle, D., Jones, D., Jordan, C. J., Kessler, H., Kuras, O., Lelliott, M., McManus, K., Nice, S. E., Palmer, R., Pearson, S., Price, S., Scheib, A., Scheib, C. and Smith, B. 2006. The 3D soils modelling project: results, feedback and recommendations of the Brackenhurst site survey 2005. – British Geological Survey (IR/06/074).

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L. and Yarnell, R. W. 2020. Over-winter survival and nest site selection of the west-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. – Animals 10: 1449.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Donovan, M. and Hines, J. E. 2007. Exercises in occupancy estimation and modeling, pp. 1–17. – http://www.uvm.edu/envnr/vtcfwru/spreadsheets/occupancy.htm/.

Efford, M. 2004. Density estimation in live-trapping studies. – Oikos 106: 598–610.

Efford, M. G. and Fewster, R. M. 2013. Estimating population size by spatially explicit capture−recapture. – Oikos 122: 918–928.

Environmental Systems Resource Institute (ESRI) 2015. ArcGIS 10. – ESRI ArcGIS desktop: release 10. – Environmental Systems Research Institute.

Evans, J. S. and Murphy, M. A. 2021. spatialEco. – R package ver.1.3-6, https://github.com/jeffreyevans/spatialEco.

Fondell, T. F., Miller, D. A., Grand, J. B. and Anthony, R. M. 2008. Survival of dusky Canada goose goslings in relation to weather and annual nest success. – J. Wildl. Manage. 72: 1614–1621.

Fryxell, J. M., Sinclair, A. R. E. and Caughley, G. 2014. Wildlife ecology, conservation, and management, 3rd edn. – Wiley-Blackwell.

Fuller, A. K., Sutherland, C. S., Royle, J. A. and Hare, M. P. 2016. Estimating population density and connectivity of American mink using spatial capture–recapture. – Ecol. Appl. 26: 1125–1135.

Gerber, B. D. and Parmenter, R. R. 2015. Spatial capture–recapture model performance with known small-mammal densities. – Ecol. Appl. 25: 695–705.

Glasby, L. and Yarnell, R. W. 2013. Evaluation of the performance and accuracy of global positioning system bug transmitters deployed on a small mammal. – J. Wildl. Res. 59: 915–919.

Hayward, M. W., Boitani, L., Burrows, N. D., Funston, P. J., Karanth, K. U., MacKenzie, D. I., Pollock, K. H. and Yarnell, R. W. 2015. Ecologists need robust survey designs, sampling and analytical methods. – J. Appl. Ecol. 52: 286–290.

Hijmans, R. J., Bivand, R., Pebesma, E. and Sumner, M. D. 2023. terra: spatial data analysis. – R package ver. 1.7-29, https://cran.r-project.org/web/packages/terra/index.html.

Hof, A. R. and Bright, P. W. 2010. The value of agri-environment schemes for macro-invertebrate feeders: hedgehogs on arable farms in Britain. – Anim. Behav. 13: 467–473.

Hof, A. R., Snellenberg, J. and Bright, P. W. 2012. Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. – Anim. Behav. 83: 1099–1106.

Hubert, P., Julliard, R., Biagianti, S. and Poulle, M. L. 2011. Ecological factors driving the higher hedgehog (*Erinaceus europeaus*) density in an urban area compared to the adjacent rural area. – Landsc. Urban Plan. 103: 34–43.

Jackson, D. B. 2007. Factors affecting the abundance of introduced hedgehogs (*Erinaceus europaeus*) to the Hebridean island of south Uist in the absence of natural predators and implications for nesting birds. – J. Zool. 271: 210–217.

Judge, J., Wilson, G. J., Macarthur, R., Delahay, R. J. and McDonald, R. A. 2014. Density and abundance of badger social groups in England and Wales in 2011–2013. – Sci. Rep. 4: 3809.

Judge, J., Wilson, G. J., Macarthur, R., McDonald, R. A. and Delahay, R. J. 2017. Abundance of badgers (*Meles meles*) in England and Wales. – Sci. Rep. 7: 276.

Kendall, K. C., Graves, T. A., Royle, J. A., Macleod, A. C., McKelvey, K. S., Boulanger, J. and Waller, J. S. 2019. Using bear rub data and spatial capture–recapture models to estimate trend in a brown bear population. – Sci. Rep. 9: 16804.

Kervellec, M., Milleret, C., Vanpé, C., Quenette, P. Y., Sentilles, J., Palazón, S., Jordana, I. A., Jato, R., Elósegui Irurtia, M. M. and Gimenez, O. 2023. Integrating opportunistic and structured non-invasive surveys with spatial capture–recapture models to map connectivity of the Pyrenean brown bear population. – Biol. Conserv. 278: 109875.

Kristiansson, H. 1990. Population variables and causes of mortality in a hedgehog (*Erinaceus europaeus*) population in southern Sweden. – J. Zool. 220: 391–404.

Lee, K. A. 2021. Untangling the roles of prey availability, habitat quality and predation as predictors of hedgehog abundance. – PhD thesis, Nottingham Trent Univ.

Lee, K. A., Uzal, A., Gentle, L. K., Baker, P. J., Delahay, R. J., Sévêque, A., Davis, R. S. and Yarnell, R. W. 2025. Does differential habitat selection facilitate coexistence between badgers and hedgehogs? – Ecol. Evol. 15: e70744.

Marston, C., Rowland, C. S., O'Neil, A. W. and Morton, R. D. 2022. Land cover map 2021 (land parcels, GB). – NERC EDS Environmental Information Data Centre.

Morin, D. J., Fuller, A. K., Royle, J. A. and Sutherland, C. 2017. Model-based estimators of density and connectivity to inform conservation of spatially structured populations. – Ecosphere 8: 1–16.

Parrott, D., Etherington, T. R. and Dendy, J. 2014. A geographically extensive survey of hedgehogs (*Erinaceus europaeus*) in England. – J. Wildl. Res. 60: 399–403.

Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. – R J. 10: 439–446.

Pebesma, E. and Bivand, R. 2023. Spatial data science: with applications in R. – Chapman and Hall/CRC.

Pettett, C. E., Moorhouse, T. P., Johnson, P. J. and Macdonald, D. W. 2017. Factors affecting hedgehog (*Erinaceus europaeus*) attraction to rural villages in arable landscapes. – J. Wildl. Res. 63: 1–12.

Reeve, N. 1994. Hedgehogs. – T and AD Poyser.

Rodriguez Recio, M., Mathieu, R., Latham, M. C., Latham, A. D. M. and Seddon, P. J. 2013. Quantifying fine-scale resource selection by introduced European hedgehogs (*Erinaceus europaeus*) in ecologically sensitive areas. – Biol. Invas. 15: 1807–1818.

Royle, J. A., Sutherland, C., Fuller, A. K. and Sun, C. C. 2015. Likelihood analysis of spatial capture recapture models for stratified or class structured populations. – Ecosphere 6: 1–11.

Royle, J. A., Fuller, A. K. and Sutherland, C. 2017. Unifying population and landscape ecology with spatial capture–recapture. – Ecography 41: 444–456

Schaus, J., Uzal, A., Gentle, L. K., Baker, P. J., Bearman-Brown, L., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D. M., Sutherland, C. S. and Yarnell, R. W. 2020. Application of the random encounter model in citizen science projects to monitor animal densities. – Remote Sens. Ecol. Conserv. 6: 514–528.

Sutherland, C., Royle, J. A. and Linden, D. W. 2019. oSCR: a spatial capture–recapture R package for inference about spatial ecological processes. – Ecography 42: 1459–1469.

Tennekes, M. 2018. tmap: thematic maps in R. – J. Stat. Softw. 84: 1–39.

Tourani, M. 2022. A review of spatial capture–recapture: ecological insights, limitations, and prospects. – Ecol. Evol. 12: e8468.

Trewby, I. D., Young, R., McDonald, R. A., Wilson, G. J., Davison, J., Walker, N., Robertson, A., Doncaster, C. P. and Delahay, R. J. 2014. Impacts of removing badgers on localised counts of hedgehogs. – PLoS One 9: e95477.

Turner, J., Freeman, R. and Carbone, C. 2022. Using citizen science to understand and map habitat suitability for a synurbic mammal in an urban landscape: the hedgehog *Erinaceus europaeus*. – Mamm. Rev. 52: 291–303.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – Springer.

Williams, B. M., Baker, P. J., Thomas, E., Wilson, G., Judge, J. and Yarnell, R. W. 2018. Reduced occupancy of hedgehogs (*Erinaceus europaeus*) in rural England and Wales: the influence of habitat and an asymmetric intra-guild predator. – Sci. Rep. 8: 12156.

Wilson, E. and Wembridge, D. 2018. The state of Britain's hedgehogs 2018. – BHPS website 1–4, www.edgehogstreet.org/wp-content/uploads/2018/02/SoBH-2018_final-1.pdf.

Yalden, D. W. 1976. The food of the hedgehog in England. – Acta Theriol. 21: 401–424.

Yarnell, R. W. and Pettett, C. E. 2020. Beneficial land management for hedgehogs (*Erinaceus europaeus*) in the United Kingdom. – Animals 10: 1566.

Yarnell, R. W., Surgey, J., Grogan, A., Thompson, R., Davies, K., Kimbrough, C. and Scott, D. M. 2019. Should rehabilitated hedgehogs be released in winter? A comparison of survival, nest use and weight change in wild and rescued animals. – Eur. J. Wildl. Res. 65: 6.

Yarnell, R. W., Pacheco, M., Williams, B., Neumann, J. L., Rymer, D. J. and Baker, P. J. 2014. Using occupancy analysis to validate the use of footprint tunnels as a method for monitoring the hedgehog *Erinaceus europaeus*. – Mamm. Rev. 44: 234–238.

Young, R. P., Davison, J., Trewby, I. D., Wilson, G. J., Delahay, R. J. and Doncaster, C. P. 2006. Abundance of hedgehogs (*Erinaceus europaeus*) in relation to the density and distribution of badgers (*Meles meles*). – J. Zool. 269: 349–356.

Yu, H., Moore, L. J., Barlow, A., Gentle, L. K., Dawson, D. A., Horsburgh, G. J., Knowles, L., Baker, P. J., Bates, A., Hicks, H., Petrovan, S., Perkins, S. and Yarnell, R. W. 2025a. Unexpected landscape-scale contemporary gene flow and fine-scale genetic diversity in rural hedgehogs. – Conserv. Genet. 26: 391–401.

Yu, H., Barlow, A., Davis, R. S., Gentle, L. K., Uzal, A., Baker, P. J. and Yarnell, R. W. 2025b. Data from: Habitat and predator heterogeneity influence density of a declining mammal. – Github, https://github.com/Hongliyu2021/Brackenhurst_hedgehog_density.