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Research article

Artificial supplementary food influences hedgehog occupancy and activity patterns more than predator presence or natural food availability

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Supplementary feeding for declining hedgehog *Erinaceus europaeus* populations is popular in Great Britain and has been suggested as an important factor in explaining higher densities in urban areas compared with rural ones. Occupancy modelling was used to test whether spatial variation in supplementary feeding, natural food, habitat, or predator presence best explained patterns of hedgehog occupancy and diel activity. Supplementary food and urban habitats had a strong effect on hedgehog occupancy and detection, with all supplementary feeding sites recording hedgehog presence. Natural prey availability and the presence of predators was relatively higher in rural areas, and although the top-ranked occupancy models ($AIC < 2$) contained natural food and predator covariates, the strength of these relationships was negative and non-significant. This suggests local hedgehog site use is influenced by access to artificial supplementary feeding in urban areas. There was no significant difference in diel activity overlap between rural, urban, and urban feeding sites, but peaks in activity early in the activity period suggest preferential access to feeding site by hedgehogs compared with later in the evening. This is the first study to show the importance of supplementary feeding as a covariate of hedgehog occupancy in relation to natural food availability, and we recommend that future studies quantify supplementary feeding in population and distribution studies of urban mammals.

Keywords: competition, diel activity, diet, intra-guild predation, life on land, top-down and bottom-up processes, urban ecology



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Introduction

Artificial and supplementary feeding is occurring on a global scale and can have a profound effect on wildlife population dynamics (Dubois and Fraser 2013). Contexts of supplementary feeding include recreation (Jones and Reynolds 2008), game management (Putman and Staines 2004), diversionary feeding, and conservation (Murray et al. 2016). Ad hoc feeding by the general public is a common occurrence and, in the case of feeding garden birds, can alter population and community dynamics (Robb et al. 2008), by being detrimental to non-provisioned competitors (Shutt and Lees 2021). Despite widespread local feeding of wildlife increasing density, it can also have negative consequences such as increased risk of disease transmission caused by unnaturally high contact rates at feeding stations, increase in intra-specific competition at feeding sites, and inter-specific interactions that may lead to injury or predation (Scott et al. 2023). Furthermore, concerns have been raised about the nutritional value provided by artificial food types and how this may affect the fitness of individuals compared to those that have a more natural diet (Gimmel et al. 2021).

One species that is increasingly being supplementary fed is the widespread but declining western European hedgehog *Erinaceus europaeus* (Gazzard and Baker 2020). Hedgehog densities vary across a rural urban gradient, with relatively lower densities in rural compared to urban areas (Schaus et al. 2020). Reasons for the variability in hedgehog density along this gradient are suspected to include the increasing levels of supplementary feeding by homeowners in urban areas and hedgehogs avoiding rural areas with low resource availability, which are also inhabited by their main predator, the European badger *Meles meles* (Hubert et al. 2011, Lee et al. 2025).

Hedgehog populations are of conservation concern due to a reported decline in numbers (Wembridge et al. 2022) and are listed as 'Vulnerable' on the IUCN's Great Britain Red List for Mammals (Mathews and Harrower 2020), and 'Near Threatened' on the Global IUCN Red List (Gazzard and Rasmussen 2024). Hedgehog decline in rural environments is thought to be primarily attributed to habitat loss through agricultural intensification (Williams et al. 2018a, Yarnell and Pettett 2020). An increase in badger abundance (Judge et al. 2017) has also been implicated in the decline in hedgehog populations, with several studies documenting both negative numerical and spatial responses of hedgehogs to the presence of badgers (Young et al. 2006, Hof et al. 2012, 2019, Trewby et al. 2014, Lee et al. 2025).

The decreasing availability of natural food in agricultural landscapes has been associated with increasing hedgehog presence within human-dominated areas (Hof and Bright 2009). Hedgehogs feed on a wide range of invertebrates, including earthworms, slugs, and arthropods (Rautio et al. 2016). Invertebrate declines in agricultural landscapes are well documented (Postma-Blaauw et al. 2010, Brooks et al. 2012), as are the cascading effects on higher trophic levels, for example in birds (Benton et al. 2002, Hallmann et al. 2017). Consequently, the low occupancy rates of hedgehogs

observed in rural landscapes may be due to limited prey availability (Williams et al. 2018a, Yarnell et al. 2014).

As the presence of hedgehog populations in human-dominated areas has increased, so too has the species' access to anthropogenic food sources (Gazzard and Baker 2020, Gimmel et al. 2021). Hedgehogs can often be observed in gardens, using food bowls intended for pets and feral cats (Hubert et al. 2011). Also, being a charismatic and well-loved species across Europe, deliberate food provisioning for hedgehogs is becoming increasingly popular in urban areas (Gimmel et al. 2021). Furthermore, some members of the public are supplementary feeding through winter, which is causing increased hedgehog activity at a time when they would ordinarily be hibernating (Gazzard and Baker 2020).

The effects of supplementary feeding on the survival (Schmidt and Hoi 2002) and reproduction (Ruffino et al. 2014) of species has been extensively researched in birds and mammalian game species. However, information on the impact of supplementary feeding on the behaviour and distribution of non-game mammals is limited (Gazzard and Baker 2020). There is no accurate consensus of how frequently and in what quantity supplementary feeding of hedgehogs takes place and what effect this has on the species' habitat use. Quantifying the occupancy of hedgehogs in relation to environmental and anthropogenic variables is fundamental to the species' conservation, as it will provide evidence-based recommendations to inform the management of this vulnerable species in the UK.

The aim of this study was to determine the best predictors of hedgehog occupancy, whether this is supplementary feeding, habitat, natural prey availability, or the presence of predators. We predict hedgehog occupancy will be positively related to supplementary food availability and local abundance of ground-dwelling invertebrates (their prey), and negatively influenced by the presence of their potential predators, badgers and red foxes *Vulpes vulpes*, at the local scale across rural and urban areas. Further, we assess hedgehog activity patterns at sites with and without supplementary feeding and hypothesise that activity levels at sites with supplementary feeding will differ from areas where supplementary feeding is absent (Gazzard and Baker 2020).

Material and methods

Study area

The study was carried out during June and July 2021 over a 10 km² area of Nottinghamshire, England (53°4'58.8"N, 0°59'20.04"W). The area was selected as it reflected a range of rural and urban habitats that would likely show variation in natural and artificial supplementary food (hereafter termed 'feeding') availability and predator presence, from which relationships with hedgehog occupancy could be elucidated. Within this area, three core study areas were chosen within which surveys took place, which allowed ease of access based on permissions from landowners. These comprised a rural landscape with no feeding (principally Brackenhurst

Campus), and two urban residential areas comprising gardens with or without feeding (Southwell and Farnsfield) (Fig. 1). Several additional survey locations were identified in the wider landscape and surveyed to increase the sample size of rural locations without feeding. As the rural sites were located in the wider countryside and under management by farming businesses, no feeding was associated with those sites. Consequently, all feeding sites occurred in urban gardens. Fine-scale survey locations were randomly selected within each core study area, and adapted based on landowner permissions, resulting in a total of 77 survey locations (14 urban gardens without feeding, 18 urban gardens with feeding, and 45 rural locations without feeding). Survey locations comprised a camera trap to detect hedgehogs, badgers, and foxes, and a pitfall trap to measure invertebrate activity density, which was used as a proxy for hedgehog natural food availability in the landscape (Thomas et al. 1998). Each survey location was at least 100 m apart and therefore individual hedgehogs could be detected at multiple locations in any given survey occasion (24 h period), violating temporal and geographic closure assumptions of occupancy modelling

(MacKenzie et al. 2017). We therefore relaxed the closure assumption of occupancy modelling by interpreting occupancy as the probability of site use, rather than the proportion of area occupied (sensu Davis et al. 2022).

In urban areas, gardens were selected for surveys. Permission to carry out surveys was granted by landowners. Landowners were also asked to provide information on whether they provided supplementary food at all, either targeting hedgehogs or other species, and if so what type of food and how often. Approximately 28 sites were surveyed at any one time period with subsequent surveys taking place on rotation until all sites were surveyed.

Camera trapping

Camera trapping was conducted to provide information on mammal occupancy and temporal activity patterns. Cameras (Bushnell Trophy Cam HD) were placed facing either north or south, to avoid false triggers from sunlight, and were positioned 20 cm above ground level (Apps and McNutt 2018). Three images per trigger were recorded and each burst of images was recorded as a detection event. A separate and

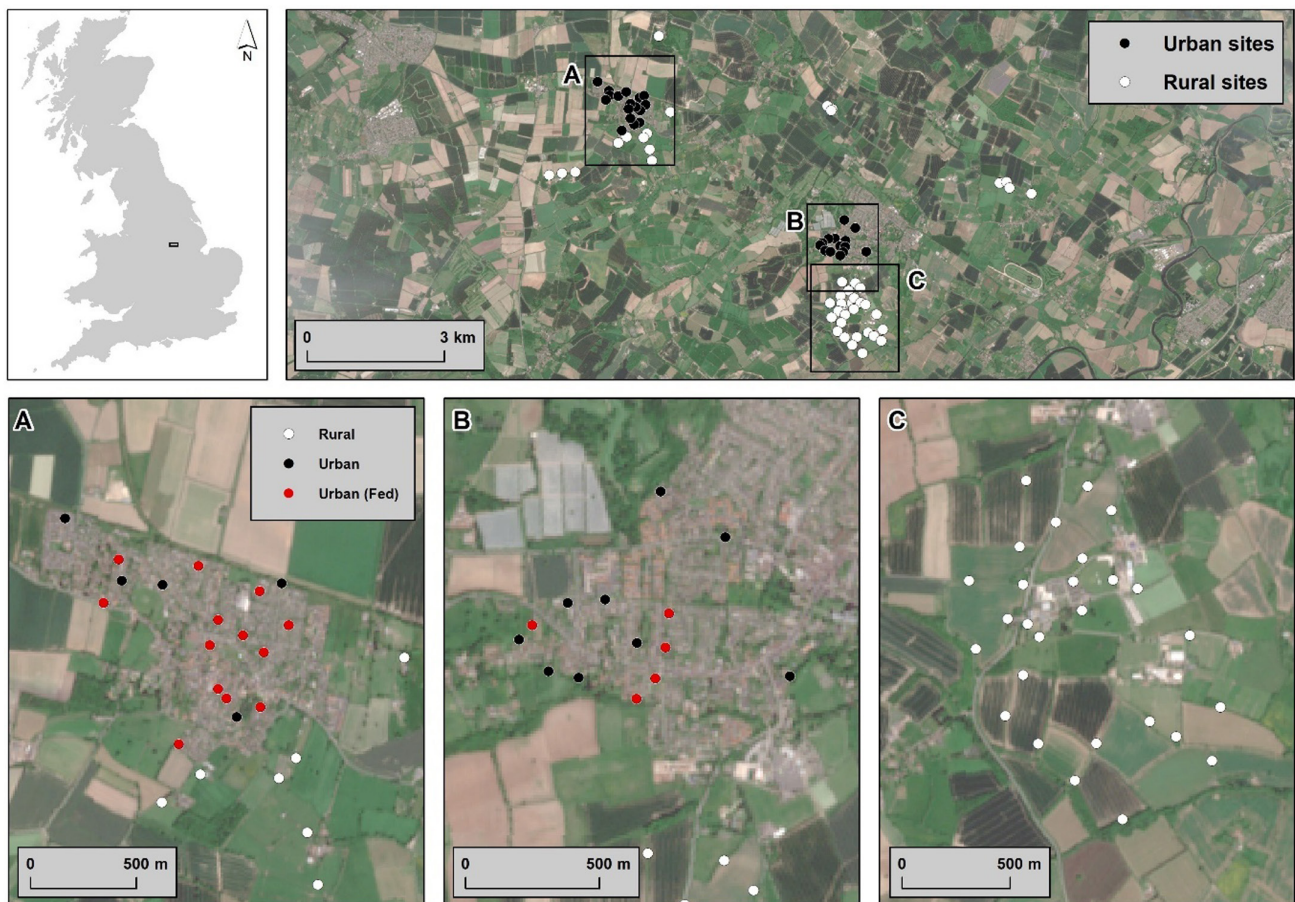


Figure 1. Study area (10 km²) in Nottinghamshire (53°4'58.8"N, 0°59'20.04"W, England, depicting survey locations and their urban and rural classifications: (A) Farnsfield, (B) Southwell, and (C) Brackenhurst. The locations of urban feeding sites are also shown in the close up insets in red. Background Imagery: Copernicus Sentinel-2 data (2021).

independent detection would be recorded if a hedgehog was subsequently observed over two minutes later (Peral et al. 2022).

Cameras were active 24 h per day and operated for nine days (from noon to noon) with each 24-h period being treated as a repeat survey session. Individual sites were considered occupied when a target species was logged on any of the sessions (Williams et al. 2018b). This included the two predator species (BADGER and FOX) included as covariates in the occupancy analysis, where the presence or absence of badgers and foxes at a camera location was logged.

Pitfall trapping

A proxy for prey availability at each camera trap location was derived from measuring surface active carabid (beetle) abundance, invertebrate abundance, richness, and diversity using pitfall traps (Thiele 1977), set approximately 2 m from each camera trap. Pitfall traps were not within view of the camera to ensure this did not influence mammal activity.

The pitfall traps consisted of a 0.2 l plastic cup, with an open diameter of 7 cm, which was buried with the rim of the cup level with the ground. The cups contained a 50% propylene glycol solution as a preservative (McCravy and Willand 2007). A mesh was secured over each trap to reduce bycatch of larger animals such as frogs and mice, and plastic covers protected the traps from rain to prevent dilution of the propylene glycol (Corti et al. 2013).

Pitfall traps were set for 9 days in parallel with the camera traps, and samples were collected into sealed plastic bags before being preserved in a refrigerator prior to identification. Invertebrates were identified to order level and recorded if over 3 mm in width or 5 mm in length, as anything below this was likely too small to be consumed by a hedgehog. As hedgehogs consume a wide range of invertebrate prey, we used pitfall captures to quantify total epigeic abundance, total number of carabids, species richness (number of different orders), and Shannon's diversity index, as proxy measures of natural food availability at each survey location (Mouhoub-Sayah et al. 2018). We focused on epigeic invertebrates as these include carabid beetles which have been shown to be the most frequent dietary item for hedgehogs (Lee 2021). We also only included carabids as the only invertebrate Order in the list of covariates to limit the number of parameters in the candidate list of models to maximise model convergence.

Data analysis

Hedgehog occupancy was modelled using single season, single-species occupancy models (Mackenzie et al. 2017) in the 'unmarked' package (Fiske and Chandler 2011) in R statistics software (www.r-project.org) with nine covariates relating to coarse scale habitat classifications (HABITAT (categorical covariate relating to three habitat treatments: rural, urban, and urban with feeding) and URBAN (rural or urban)), natural (CARABID (carabid abundance), P_ABUND (pitfall abundance), P_RICHNESS (pitfall richness), P_DIVERSITY (pitfall diversity), artificial supplementary food availability (FOOD (feeding or no feeding),

and predator occurrence (BADGER (badger presence or absence) and FOX (fox presence and absence)) (Table 1). The covariates were plotted against each other to assess collinearity, with a threshold correlation coefficient > 0.7 indicating collinearity. URBAN was collinear with FOOD ($r=0.7$), and URBAN was retained in the occupancy part of the model with FOOD being removed. URBAN was also collinear with HABITAT, and was therefore only used in the occupancy part of the model, whereas HABITAT was only used in the detection part of the model. Similarly, P_RICHNESS was collinear with P_DIVERSITY ($r=0.7$) and P_RICHNESS was removed from the list of candidate models. Remaining continuous variables (CARABID, P_ABUNDANCE, and P_DIVERSITY) were converted to standardized z-scores.

HABITAT was only added as a detection covariate to all models as it was considered likely that detection probability of hedgehogs would vary at cameras located in proximity to feeding sites, and in response to habitat-linked variability in hedgehog abundance. Previous studies have shown that hedgehog abundance is higher in urban areas than rural (Schaus et al. 2020) and that supplementary feeding stations often result in hedgehogs nesting in close proximity (Gazzard and Baker 2022), both of which are likely to influence detection probabilities. FOOD and HABITAT were also added as occupancy covariates originally, but as all sites with supplementary feeding detected hedgehogs, this was removed from the candidate set due to a lack of variability in sites being occupied (i.e. this was not modelled as occupancy equalled 1). Therefore, the final occupancy models had HABITAT as a detection covariate and combinations of predators and a proxies of natural food availability from pitfall trapping as occupancy covariates. The best fitting model was selected based on the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2000). We assumed survey locations were 'closed' to changes in occupancy over the study period, and species were never detected falsely when absent (Rota et al. 2009).

To understand whether HABITAT had any influence on diel activity patterns of hedgehogs, we used the time stamps from camera traps following Ridout and Linkie (2009). Time of day was converted to solar time, adjusting times for mean average sunrise and sunset times, using average anchoring (Vazquez et al. 2019). We used the package 'overlap' (Meredith et al. 2024) to calculate kernel density estimators and quantified the degree of overlap (Δ) in hedgehog activity patterns between cameras located in the three HABITAT categories: 1) rural, 2) urban without feeding, and 3) urban with feeding sites. We used the Δ_1 estimator, as the rural and urban without feeding sample sizes were < 75 observations (Meredith et al. 2024) and calculated 95% confidence intervals using 10 000 smoothed bootstrap repetitions. We used the package 'activity' ver. 1.3. (Rowcliffe 2019) to estimate activity levels for both sets of observations and the *compare-Act* function to test for statistical differences in activity level estimates between the populations with and without supplementary feeding.

Table 1. Candidate list of covariate names, variable type, description, and rationale for their inclusion in the occupancy modelling. Variables that were collinear and excluded from the occupancy modelling are denoted with *.

Covariate name	Variable type	Description	Rationale
Urban	Categorical	Areas with over 20 settlements ha ⁻¹ were regarded as being urban, while all areas with fewer than 20 settlements ha ⁻¹ were classed as rural	Hedgehog density is higher in urban areas compared to rural in England (Schaus et al. 2020)
Habitat	Categorical	Comprised three treatment areas classified on their urbanisation classification and whether anthropogenic artificial supplementary feeding occurred. These were 1) rural, 2) urban, and 3) urban with supplementary feeding	Hedgehog density is higher in urban areas compared to rural in England (Schaus et al. 2020) Hedgehogs were more often seen in gardens by people who provide food for wildlife (Hof and Bright 2009); and supplementary food is suggested as having a positive effect on hedgehog density in France (Hubert et al. 2011)
Food*	Categorical	Presence or absence of supplementary food at each survey location	Hedgehogs were more often seen in gardens by people who provide food for wildlife (Hof and Bright 2009); and supplementary food is suggested as having a positive effect on hedgehog density in France (Hubert et al. 2011)
Badger	Categorical	The presence or absence of badgers at each survey location	Hedgehogs have negative relationship with badger presence (Yarnell et al. 2014, Williams et al. 2018a)
Fox	Categorical	The presence or absence of foxes at each survey location	Fox density may relate to hedgehog distribution as foxes likely compete for food and potentially act as predators (Pettett et al. 2018)
Carabid	Z-score	The total abundance of most frequently consumed invertebrate by hedgehogs	DNA metabarcoding showed that carabid beetles were the most frequently consumed items in hedgehog diet (Lee et al. 2021)
P_ABUND	Z-score	The total abundance of likely invertebrate prey in each pitfall trap per location	Prey availability was the main factor influencing hedgehog distribution in Haigh et al. (2012), and a more diverse fauna is likely to lead to more consistent temporal availability of prey
P_RICHNESS *	Z-score	The count of orders present in each pitfall trap per location	Prey availability was the main factor influencing hedgehog distribution in Haigh et al. (2012), and a more diverse fauna is likely to lead to more consistent temporal availability of prey
P_DIVERSITY	Z-score	Shannon's diversity in each pitfall trap per location	Prey availability was the main factor influencing hedgehog distribution in Haigh et al. (2012), and a more diverse fauna is likely to lead to more consistent temporal availability of prey

Results

Site characteristics

A total of 77 sites were surveyed comprising 14 urban gardens without feeding, 18 urban gardens with feeding, and 45 rural locations without feeding. Hedgehogs were present at 41 (53%) sites, foxes at 32 (42%), and badgers at 12 (15%) (Table 2). No badgers were detected at any urban site. Rural areas had a higher average carabid abundance, invertebrate

richness, and diversity than urban sites with and without feeding. Average invertebrate abundance was highest in the urban sites without feeding due to four sites capturing a large number of woodlice. Rural invertebrate abundance was also higher than at urban sites with feeding. Together, these results suggest natural prey availability for hedgehogs is higher in rural than urban locations (Table 2). Of the 32 urban sites surveyed, more than half (56.2%) participated in feeding, with the remainder not feeding hedgehogs. Out of

Table 2. Comparison of variables used in hedgehog occupancy models across three habitat and supplementary feeding treatments. The mean and standard error (in parenthesis) values are given for the number of carabid beetles, total invertebrate abundance, richness and diversity (Shannon's diversity index) from pitfall traps. The proportion of camera trap sites in each treatment that detected hedgehogs and their main predators, foxes and badgers, is also shown.

Covariate	Rural (n=45)	Urban (n=14)	Urban with feeding (n=18)
Carabid count	13.71 (2.45)	2.93 (0.86)	1.17 (0.44)
Invertebrate abundance	46.33 (5.71)	53.60 (13.8)	23.50 (4.27)
Invertebrate richness	5.58 (0.30)	5.50 (0.66)	3.67 (0.30)
Invertebrate diversity	1.18 (0.06)	0.95 (0.11)	0.91 (0.08)
Proportion of sites with hedgehogs	0.31	0.64	1.00
Proportion of sites with foxes	0.55	0.35	0.11
Proportion of sites with badgers	0.27	0	0

the feeding sites, 13 were located in Farnsfield and five in Southwell, which corresponds to 72.2 and 35.7% of households feeding hedgehogs in Farnsfield and Southwell, respectively. Each household participating in feeding ($n=18$) was targeting hedgehogs and provided food every night. The most common food provided was commercial dry hedgehog specific food (55.6%), followed by cat food (33.3%). One site fed dog food, and one site fed chicken bones every night.

Hedgehogs were detected at all ($n=18$) feeding sites compared to 57.1% of urban sites without feeding. Additionally, 50% of feeding sites detected hedgehogs every night, with an average of 46.9 hedgehog sightings per camera, compared to 1.47 sightings per camera over the 9-day survey period at non-feeding sites. Only supplementary fed sites had multiple hedgehog detections in a single image, the maximum being three, where cat food was provided. This particular site also had the highest total number of sightings over the study period, with 265 detections. Of the 14 urban sites without feeding that detected hedgehogs, none of them detected hedgehogs every night.

Occupancy

Hedgehogs were detected at 41 sites out of 77 surveyed, resulting in a naïve occupancy across the study area of 0.53. The naïve occupancy for hedgehogs across 45 rural sites was 0.31, which was lower than at the 14 urban sites without feeding, which was 0.64, and at urban sites with feeding, which was 1.00 (Table 2).

Hedgehog detection was significantly higher at urban sites with feeding than rural sites ($\beta=2.611$, 95% CI=1.84, 3.37). Urban sites without feeding were also higher than rural sites, but non-significant ($\beta=0.733$, 95% CI=-0.086, 1.55). Therefore rural, urban, and urban feeding sites were

all retained as a detection covariate (HABITAT) in all further occupancy models (Fig. 2).

Three of the top-ranked occupancy models had a delta AIC < 2, and all of these models contained HABITAT as a detection covariate, and occupancy covariates including CARABID and URBAN (Table 3). The inclusion of FOX, BADGER, and P_ABUND were considered uninformative as they did not worsen fit, suggesting the only informative occupancy covariates were CARABID and URBAN. Therefore, the best fitting model was considered as being occupancy (CARABID + URBAN), detection (HABITAT).

The best fitting hedgehog occupancy model included URBAN as a significant positive covariate ($\beta=2.129$, CI=0.52, 3.73; Fig. 3) and CARABID ($\beta=-0.85$, CI=-2.10, 0.40) which had non-significant relationships with hedgehog occupancy (Table 2). Goodness of fit of the top model gave a variance of inflation factor (c-hat) estimate for dispersion of 0.73 (1000 simulations), indicating that the data are slightly under-dispersed.

Diel activity patterns

There was a strong degree of temporal overlap between hedgehogs at urban sites with and without supplementary feeding and rural sites ($\Delta > 0.70$; Fig. 4). The overall activity levels (proportion of time spent active) were 0.27 ($\pm$ SE 0.03, 95% CI=0.19, 0.32) for hedgehogs in rural locations; 0.21 ($\pm$ SE 0.03, 95% CI=0.13, 0.35) for hedgehogs in urban locations without supplementary feeding; and 0.24 ($\pm$ SE 0.01, 95% CI=0.25, 0.30) for hedgehogs in urban locations with supplementary feeding. A Wald test indicated that activity patterns were not significantly different between any of the rural and urban locations (Wald df=1, $p > 0.05$). The earliest hedgehog image recorded was at 19:28 at a feeding site and the earliest image recorded at a non-feeding site was at 21:31.

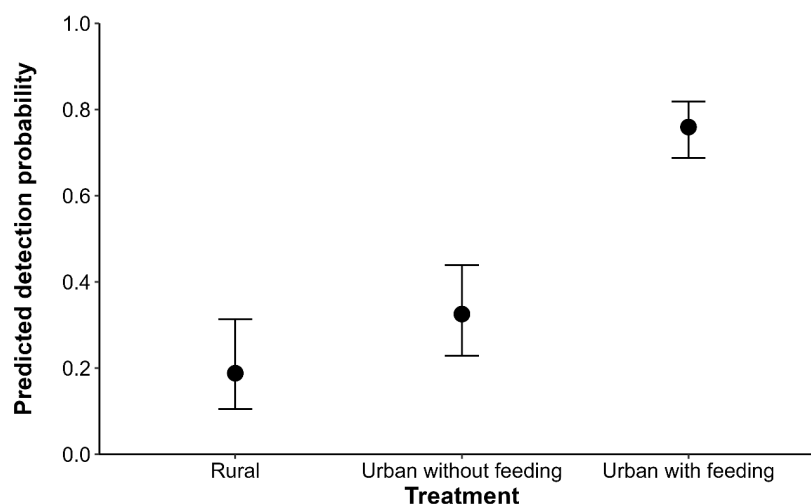


Figure 2. Comparison of predicted hedgehog detection probability at rural sites ($n=45$), urban gardens that provided supplementary feeding ($n=18$), and urban gardens that did not ($n=14$), in Nottinghamshire, England.

Table 3. Summary of hedgehog occupancy models run on 77 survey sites across Nottinghamshire, England. Covariates included in each model are listed with P denoting detection and Ψ for occupancy. The top ranked models (AIC < 2) are in bold. * denotes the model considered to be the most informative and is presented in the 'Results'.

Model	No. parameters	AIC	delta	AICwt	Rsqr	cumltvWt
Ψ (P_ABUND + CARABID + URBAN), P (HABITAT)	7	513.76	0.00	0.43	0.78	0.43
Ψ (CARABID + URBAN), P (HABITAT)*	6	515.03	1.27	0.23	0.77	0.66
Ψ (P_ABUND + CARABID + BADGER + FOX + URBAN), P (HABITAT)	9	515.27	1.51	0.20	0.79	0.86
Ψ (CARABID + P_ABUND + FOX + BADGER), P (HABITAT)	8	517.96	4.20	0.05	0.78	0.91
Ψ (URBAN), P (HABITAT)	5	518.68	4.91	0.04	0.76	0.95
Ψ (CARABID + P_ABUND), P (HABITAT)	6	519.36	5.60	0.03	0.76	0.97
Ψ (BADGER + FOX + URBAN), P (HABITAT)	7	519.39	5.63	0.03	0.77	1.00
Ψ (FOX + BADGER), P (HABITAT)	6	528.37	14.61	0.00	0.73	1.00
Ψ (P_ABUND), P (HABITAT)	5	529.90	16.14	0.00	0.72	1.00
Ψ (BADGER), P (HABITAT)	5	530.89	17.13	0.00	0.72	1.00
Ψ (P_DIVERSITY), P (HABITAT)	5	536.34	22.58	0.00	0.70	1.00
Ψ (.), P (URBAN)	3	600.91	87.15	0.00	0.26	1.00
Ψ (.), P (CARABID)	3	603.50	89.74	0.00	0.23	1.00
Ψ (.), P (P_ABUND)	3	615.33	101.57	0.00	0.10	1.00
Ψ (.), P (BADGER)	3	615.68	101.92	0.00	0.10	1.00
Ψ (.), P (FOX)	3	615.84	102.08	0.00	0.10	1.00
Ψ (.), P (.)	2	621.79	108.03	0.00	0.00	1.00

Discussion

As hypothesised, hedgehog occupancy was highest at sites where supplementary feeding took place, with every feeding site detecting hedgehogs. Sites with feeding were almost twice as likely to be occupied by hedgehogs in urban areas than those without supplementary food, a finding similar to Gazzard and Baker (2020). The high visitation rates of hedgehogs to supplementary feeding sites in both these studies highlights the importance of artificial supplementary feeding to urban-dwelling hedgehogs, and is likely a strong driver of the observed higher densities and occupancy in urban areas when compared with other rural habitats (Hubert et al. 2011, Yarnell et al. 2014, Schaus et al. 2020).

Sites with supplementary feeding also had substantially higher number of hedgehog detections, with hedgehogs being detected every night compared to occasional nights at non-feeding and rural sites. Despite this, there were no significant differences in temporal behaviour of hedgehogs between rural, urban, and urban feeding sites. This is not surprising given hedgehogs are nocturnal and high levels of temporal overlap are expected in different habitat. Both the urban feeding and rural sites had peaks in activity early in the evening, compared to activity in the same locations later in the night, while at the urban sites without feeding, activity peaked after midnight (Fig. 4). One possible explanation for the early peak at feeding sites is that hedgehogs know where feeding stations are and access them preferentially over natural foraging early

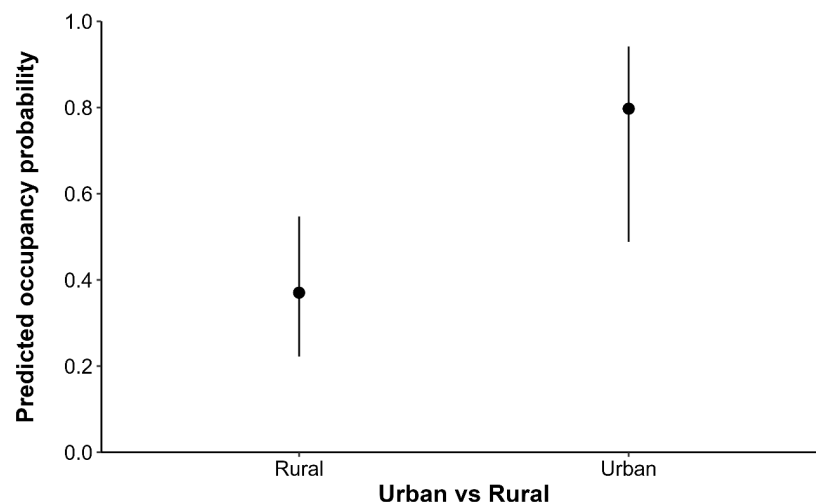


Figure 3. Comparison of predicted hedgehog occupancy probability at rural sites (n = 45), and urban gardens (n = 32), in Nottinghamshire, England.

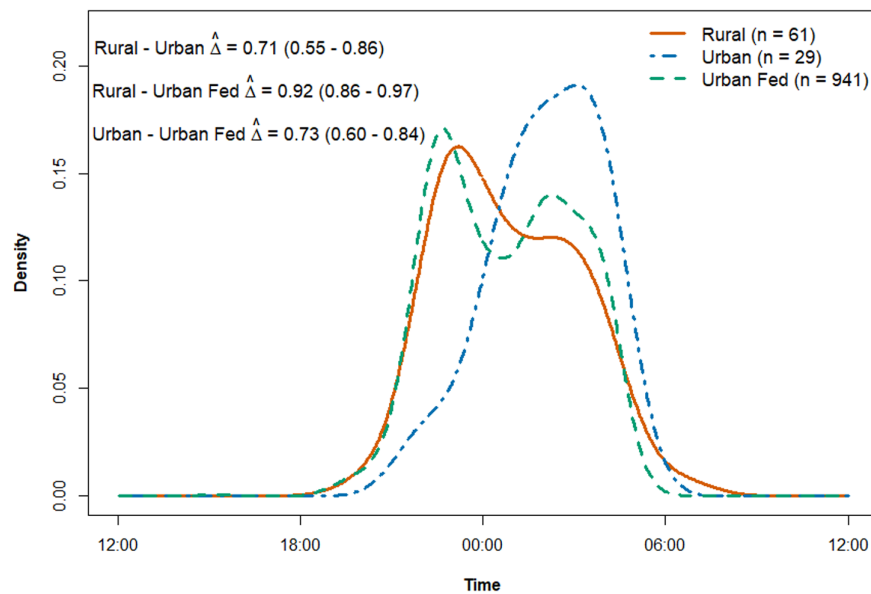


Figure 4. Estimates of the daily activity patterns of hedgehogs from camera traps located in rural (Rural) areas, urban gardens without supplementary feeding (Urban) and urban gardens with supplementary feeding (Urban Fed). The x- and y-axes represent the time of the day and kernel density, respectively. The estimate of overlap (Δ) and 95% CI are also displayed.

in the daily activity period. Furthermore, hedgehogs have been shown to use nest boxes that are in the same gardens as feeding stations more frequently than at locations without feeding stations (Gazzard and Baker 2022), suggesting that feeding site may influence nest site selection, and partly explain the early peak in activity recorded here. The similar peak in activity in rural habitats may also be due to the proximity of nest location to camera traps. Most rural camera traps in this study were located on edge habitat such as hedgerows, a potential nesting and refuge habitat for hedgehogs. The observed peak may be due to hedgehogs more readily being detected as they emerge from nests and initially staying close to edge refugia early in the activity cycle before moving and foraging more widely and away from edge habitat, and cameras, as the evening progresses.

The regular presence of supplementary food likely reduces the need for increased foraging time and contributes to reduced activity levels in areas of provisioned resources. Further, the energetic costs associated with reduced levels of activity around supplementary food sites may have benefits for reproductive success and overall fitness, thus contributing to observed higher densities in urban areas (Schaus et al. 2020). Other studies have reported the influence of supplementary feeding on hedgehog behaviour, with hedgehogs being more active during hibernation at sites with supplementary feeding (Gazzard and Baker 2020) and having smaller home ranges from the increased food availability (Pettet et al. 2017). Hedgehogs have also been shown to spend significantly more time in gardens where artificial food was provided (Gazzard et al. 2022), and significantly increased the likelihood that a nest box had been used (Gazzard and Baker 2022). Our study adds to the growing evidence that hedgehogs are changing their behaviour in response to

supplementary food provision. However, the extent and frequency of supplementary food provision varies in space and time and how different levels of feeding will influence individual fitness and population dynamics remains unknown.

In this study, a high proportion (56%) of homeowners in the urban sites fed hedgehogs on a daily basis. Gazzard and Baker (2020) also reported high proportions of garden owners feeding hedgehogs (39–60%). It is likely that these high proportions are overestimates of the true level of artificial supplementary feeding taking place across residential areas of urban UK, and not representative of the amount of artificial feeding taking place across the hedgehog's range. This is because site selection was based on seeking people with a prior interest in hedgehogs to take part in the study, and therefore not representative of the propensity of all homeowners to feed hedgehogs. Future studies investigating supplementary feeding and its effects on individual behaviour and population dynamics need to randomly sample the urban environment, before the influence of feeding on population size can be more widely inferred. Therefore, the extent to which people are feeding hedgehogs across western Europe remains unknown, and linking the true extent and quantity of supplementary feeding of hedgehogs to their current population status would provide a better understanding of how hedgehog populations are responding to this artificial resource and how this then impacts current and future conservation management.

Further research is also required into the potential positive and negative consequences of artificial supplementary feeding of mammals, given the high potential for it to be occurring in gardens throughout Europe (Davies et al. 2009). Currently, the evidence suggests supplementary feeding can have a positive influence on hedgehog density and local occupancy in the urban environment. However, the potential negative

consequences of supplementary feeding on hedgehogs and the wider sustainability of the practice are unknown. In this study, a large proportion of the supplementary food provided was commercial hedgehog food, with the remainder typically comprising pet (cat and dog) food. There have been concerns raised that commercial hedgehog food and other forms of pet food may not meet the nutritional requirements for wild hedgehogs and that the nutritional content does not match that of a hedgehog's natural diet (Gimmel et al. 2021), which may have knock-on effects on individual growth, health, and fitness.

Congregations of hedgehogs at feeding sites can also increase intra- and inter-specific contact rates that are atypical and lead to negative consequences. For example, multiple individuals accessing unhygienic feeding stations can lead to increased mortality from salmonella infections (Rasmussen et al. 2019). Feeding stations can also be vectors for disease transmission, owing to species interacting where they may not typically co-occur (Taucher et al. 2020, Shutt and Lees 2021).

Atypical congregations of hedgehogs at supplementary feeding stations can also increase intra- and interspecific competition and potentially predation. In many urban areas across Europe, the urban mammal guild of hedgehogs, badgers, and foxes frequent supplementary feeding sites. Scott et al. (2023) demonstrated that many interactions between hedgehogs were agonistic in nature at feeding stations, although injuries from such interactions are unknown. With regards to interactions with their predators (badgers and foxes) at feeding stations, foxes and badgers appear dominant to hedgehogs, but typically feed alongside hedgehogs in the majority of occasions. Potential predatory behaviours were observed in 10% of the interactions between the species, suggesting that at sites where feeding is provided there is a potential for predation to take place, but that this is rare, on the whole. There were twice as many hedgehogs present at sites where foxes were absent, which may be due to competition between these species for food as they both prey on earthworms, invertebrates, and human waste foods (Pettett et al. 2017). Alternatively, Williams et al. (2018b) hypothesised that supplementary feeding may act to reduce competition between species by increasing food availability and minimising risk of predation, as anthropogenic food requires minimum effort compared to predating on hedgehogs. Hedgehogs have been shown to avoid rural areas frequented by their predators (Young et al. 2006, Lee et al. 2025), but the benefit of accessing resource-rich supplementary feeding sites as demonstrated here may outweigh the risks of predation in urban areas at feeding stations.

A way to minimise disease spread and decrease intra- and inter-specific interactions caused by supplementary feeding could be to scatter hedgehog food around the garden, to avoid congregations of individuals in one area. This would also imitate natural foraging behaviour more closely, while continuing to provide beneficial aspects of feeding hedgehogs in gardens. Alternatively, anthropogenic food could be given

in covered feeding stations, thus avoiding the feeding of non-target species (Williams et al. 2018b).

There has been much support in the literature for hedgehog use of urban habitats being driven by a 'landscape of fear' from their main predator the badger, and that hedgehogs are unable to exist in the rural landscape where badgers are at high density or locally present (Young et al. 2006, Hof et al. 2012, Pettett et al. 2017, 2018). In this study hedgehog occupancy in relation to the presence of badgers and foxes had non-significant coefficients and was a poor predictor of hedgehog occupancy compared to habitat type and natural food availability. As with other studies that have investigated badger and hedgehog spatial patterns, this study did not find badgers occupying any of the urban areas surveyed, and therefore we are unable to ascertain whether hedgehogs are avoiding areas with badgers and foxes or whether they are occupying urban areas due to an abundance of supplementary food (Yarnell et al. 2014, Williams et al. 2018a).

To understand the importance of food availability to hedgehog occupancy, we also measured a proxy of natural food availability (ground-dwelling invertebrate abundance activity) at each site using pitfall traps. Epigeic invertebrate abundance activity was generally lower in urban sites compared with rural sites, suggesting that invertebrate activity-density at the time of our study was higher in areas where hedgehog occupancy was lower. Previous studies have shown contrasting relationships between hedgehog presence and proxies of food availability in agricultural settings. For example, several studies have shown hedgehog rural habitat use being positively related to proxies of food availability (Hof and Bright 2010, Haigh et al. 2012, Hof et al. 2012). This contrasts to a more recent study comprising 22 rural study sites across England and Wales which found no relationship between earthworm biomass as measured by earthworm cores, and a negative relationship with pitfall biomass and hedgehog occupancy, similar to the findings here (Lee et al. 2025). Most studies suggest that low food availability is a contributory factor in hedgehog absence and low density in rural landscapes (Williams et al. 2018a, Schaus et al. 2020). This study also found low hedgehog occurrence in rural locations and had hypothesised that possibly natural food availability may be higher in urban areas and that this was contributing to the observation of hedgehogs in urban areas. However, we found the opposite: that natural food availability was higher in the rural compared to urban settings. It therefore seems plausible that the high levels of artificial food provided in urban habitats more than compensates for lower natural food availability in urban areas, and that combined with a lack of badgers and foxes in this study explains the propensity for hedgehogs to exist in urban rather than rural settings more broadly (Hubert et al. 2011). However, other explanations for this unexpected negative relationship between hedgehog and natural food availability require investigation, especially considering it is unknown whether the difference in the overall abundance of epigeal invertebrates between rural and urban areas is large enough to be relevant for hedgehogs. Our proxy for food availability had a number of limitations and

our findings in relation to natural food should be treated with caution. For example, we were only able to measure epigeic invertebrates, which comprise only part of a hedgehog's diet (Lee 2021). Other key dietary components for hedgehogs were not surveyed here, including Gastropods, Lumbricidae, and Lepidoptera. It is plausible that hedgehog abundance may be higher in urban areas due to variation in these other dietary groups. Furthermore, invertebrate abundance and its availability to hedgehogs is highly variable in space and time, and more robust data collected over longer time frames are needed to link fine-scale food availability to population processes. It is also plausible that other non-food related variables such as increased habitat heterogeneity (Li and Wilkins 2014) and/or urban heat island effects (Jiménez et al. 2024) attract hedgehogs to areas or urbanisation, and both of these merit further consideration.

In conclusion, this study further demonstrates the influence that artificial supplementary feeding has on the distribution and activity of hedgehogs within urban settings. Indeed, artificial supplementary feeding in urban areas had a greater effect on hedgehog occupancy of a site than our natural food availability proxies and the presence of their main predators. Accordingly, we recommend that future hedgehog and other urban mammal population and distribution studies quantify levels of artificial supplementary food provision to better understand its influence on mammal populations over greater spatial scales. Furthermore, we encourage research into the wider effects of artificial supplementary feeding on hedgehog ecology, specifically quantifying how much artificial food is provisioned across its range, and whether the effects on hedgehog fitness are positive or negative.

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Eleanor S. Benjamin: Conceptualization (equal); Data curation (equal); Writing – original draft (lead); Writing – review and editing (equal). **Adam Bates:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Robert Davis:** Formal analysis (equal); Writing – review and editing (equal). **Anthony Sévêque:** Formal analysis (equal); Writing – review and editing (equal). **Jonathan Wild:** Conceptualization (supporting); Data curation (supporting); Writing – review and editing (supporting). **Ben Clutterbuck:** Data curation (equal); Formal analysis (equal);

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad698cz9dt> (Benjamin et al. 2025).

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