Using citizen science to understand and map habitat suitability for a synurbic mammal in an urban landscape: the hedgehog *Erinaceus europaeus*

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ABSTRACT

1. Urban environments are important for west European hedgehogs *Erinaceus europaeus*. The species has been recorded in 73% of large urban areas throughout its geographic range. However, the environmental relationships determining hedgehog distribution within these landscapes are not well understood.
2. Taking a city-wide perspective, this study identifies hedgehogs' habitat relationships with urban environmental characteristics and predicts habitat suitability in a major urban centre, Greater London, UK.
3. We use a collated citizen science dataset of 3012 hedgehog occurrence records from Greater London, and pseudoabsences inferred from other mammal taxa, to construct a multiscale generalised linear model identifying the influence of 10 variables representing urban greenspace, built infrastructure, and the presence of the European badger *Meles meles* (as a predator or competitor) on hedgehog distribution.
4. We find a positive association of hedgehog presence with availability of gardens, parks, allotments, percentage of terraced housing, traffic, and intermediate impervious cover (roads and buildings, peaking at 31%). High impervious cover, woodland, water, human densities (above 2262 people km^{-2}), and badger presence were negatively related to hedgehog presence. Predicted habitat suitability was high across much of Greater London but declined towards the centre and in some locations around the outskirts of the study region.
5. Our results emphasise the importance of public and private greenspaces for urban hedgehogs, and suggest that loss of garden, park, and allotment habitats and disturbance associated with high human densities may restrict hedgehog distribution. Despite the inherent complexity of urban environments, this study shows that citizen science is useful for developing an understanding of large-scale species–habitat relationships in diverse urban landscapes.

INTRODUCTION

Rapid expansion of urban environments poses a major threat to biodiversity globally (McDonald et al. 2020). Urbanisation dramatically and permanently alters environmental conditions, with profound impacts on native biological communities; many native species become locally extinct, whilst those that persist exhibit wide-ranging responses allowing them to survive within novel urban environments (McDonnell & Hahs 2015).

Conservation strategies to promote urban biodiversity are increasingly important, both as numerous threatened species are found in urban landscapes (Soanes & Lentini 2019) and as we recognise the beneficial role of urban wildlife for human well-being (Carrus et al. 2015). Critical for successful conservation in urban areas is an understanding of where species occur and their relationships with the anthropogenic environment. Species' ability to exploit new resources and tolerate disturbance, combined with mortality risks and human–wildlife conflict, is an important driver of species' occurrence in urban areas (Baker & Harris 2007). Yet, understanding species' distributions is challenging in complex urban environments, where sharp boundaries occur between land uses at fine spatial scales (Norton et al. 2016), and there are intense physical gradients, including elevated temperatures, pollution, human population density, road density, and impervious cover, from outskirts to centres (McKinney 2002).

Habitat suitability models are widely used to quantify taxon–environment relationships and predict distributions, through relating observations of species to environmental variables (Guisan et al. 2017). In urban areas, where surveys may be complicated by inaccessible and private land (Scott et al. 2014), predictive mapping of habitat suitability may be particularly useful. Large human populations also present opportunities for citizen science, in which volunteers collect information for scientific research (Walter et al. 2018). Whilst opportunistic occurrence data contain biases that need to be accounted for in analysis (Scott et al. 2014), urban wildlife studies often use citizen science data, for example to examine hot spots of human–wildlife conflict (Wine et al. 2015), and wildlife colonisation into urban areas (Mayer & Sunde 2020). In this study, we apply generalised linear modelling of a citizen science dataset of west European hedgehog Erinaceus europaeus occurrence in Greater London to identify habitat relationships influencing hedgehog presence and to predict how habitat suitability for the hedgehog varies within this large, heterogeneous urban landscape.

The hedgehog is a small, spiny nocturnal mammal experiencing severe population declines in the UK (Roos et al. 2012). Urban areas are important habitats for the species, with higher occupancy (Williams et al. 2018a) and abundance associated with built-up areas (Hubert et al. 2011, Schaus et al. 2020) than with rural areas. However, the species may also face pressure within urban environments; in Zurich, Switzerland, for example, a 41% decline in abundance and 18% loss in geographic range have been reported over 25 years (Taucher et al. 2020). A greater understanding of the hedgehog's habitat

preferences and distribution in urban environments is therefore increasingly important.

Hedgehog presence is thought to depend on the availability of food and suitable vegetation for nesting, and on predation risk (Pettett et al. 2017). Urban hedgehogs are closely associated with greenspaces, where there are high invertebrate prey availability (Young et al. 2006, Hubert et al. 2011), supplemental feeding from householders (Gazzard & Baker 2020), and sheltered conditions, wildlife-friendly features, and structured vegetation in gardens (Hof & Bright 2009, Braaker et al. 2014). Connectivity between these habitats is important; juvenile hedgehogs in Denmark use a minimum of 10 gardens (Rasmussen et al. 2019). In the UK, gaps in fencing have been positively associated with hedgehog presence in gardens, whereas barriers from streams and rivers have been related to low hedgehog presence (Hof & Bright 2009).

Loss of greenspaces to development, and disruption of the networks they form for wildlife movement, may threaten urban hedgehog populations. Roads in particular obstruct movement between habitats, as hedgehogs avoid foraging in road verges (Rondinini & Doncaster 2002), and are a major cause of mortality, with an estimated 167000–335000 hedgehogs killed by traffic annually in the UK (Wembridge et al. 2016).

Pressure from predators has also been suggested as a key driver of hedgehog distribution and population declines (Pettett et al. 2018). In urban environments, domestic pets and synanthropic wild mammals such as the red fox Vulpes vulpes are potential hedgehog predators (Hof & Bright 2009). The European badger Meles meles is a hedgehog competitor and predator and has been shown to exclude hedgehogs from rural habitats (Young et al. 2006). Foxes and badgers are present in several cities in the UK (Huck et al. 2008), including London.

The aim of this study was to identify the hedgehog's habitat relationships with urban environmental characteristics, and to predict the configuration of suitable habitat for the species across Greater London. We construct a multiscale generalised linear model of habitat suitability using citizen science occurrence records collated from several datasets. Through taking a city-wide perspective, we aim to identify relationships across a broad range of urban characteristics and gradients. We hypothesise that hedgehogs will favour locations with more greenspace and those likely to have high connectivity between habitats. We expect hedgehog presence to be high where urban pressure is intermediate, reflecting the hedgehog's preference for built-up areas, but to decline at higher levels of urban pressure where disturbance, habitat loss, and habitat fragmentation are above levels which the species can tolerate (Hof & Bright 2009). We also predict that the presence of badgers

in several parts of the study area will negatively affect hedgehog presence within the urban environment. To place our findings into a broader context, we estimate the percentage of large urban areas in which hedgehogs are recorded throughout their geographic range in western Europe.

METHODS

Study area

The study area is Greater London (Fig. 1), comprising 32 London boroughs and a land area of 1572 km^2 (Office for National Statistics [ONS] 2020). London is the home of over 8.9 million people (ONS 2020) and has an average population density of 5701 people km^{-2} (ONS 2020). However, Greater London also possesses a large amount of greenspace, approximately 47% of the land area, with public open spaces accounting for 18% of the land area and private gardens 24% (Greenspace Information for Greater London [GiGL], https://www.gigl.org.uk/keyfigures/).

Occurrence records

Georeferenced occurrence records were sourced from databases held by the People's Trust for Endangered Species (PTES; https://ptes.org/), GiGL (https://www.gigl.org.uk), and the National Biodiversity Network Atlas (NBN; http://www.nbnatlas.org). Strict inclusion criteria were applied: systematic camera-trap and live-trap survey records were removed to leave ad hoc sightings, field records, and field signs, as were duplicated records with the same coordinates, year, and source dataset. Records were restricted to those collected between 2005 and 2020, as earlier data were comparatively sparse, and with a coordinate uncertainty of 100 m or less, to enable analysis of both local and landscape environmental relationships. From an initial 7654 records, 3012 hedgehog records were retained from six datasets, as shown in Table 1.

Spatial bias in opportunistically collected wildlife occurrence records – towards accessible or highly populated areas – may bias sampling of environmental conditions and resulting estimates of environmental relationships
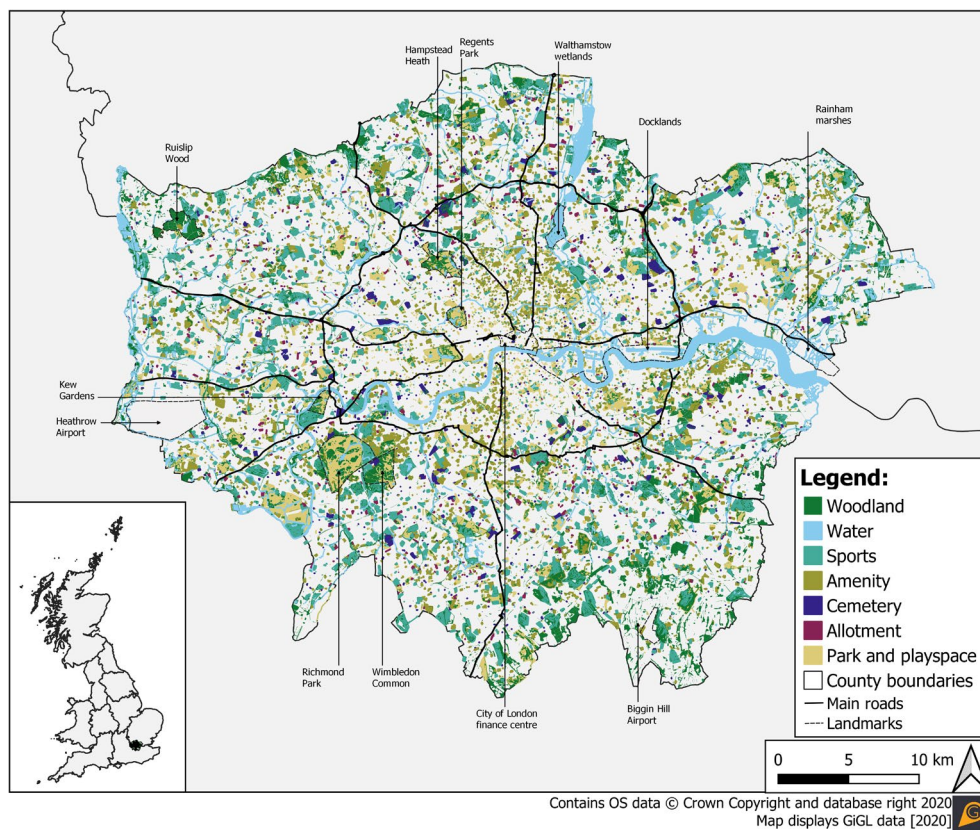

Fig. 1. Map showing the study area of Greater London, UK (inset map), used in mapping habitat suitability of west European hedgehog *Erinaceus europaeus*. Main roads and landmarks are labelled, and open greenspace classifications and water bodies used in the study are shown. Private gardens and impervious landcovers have been excluded for clarity.

Table 1. Table showing the number, timespan, and source of hedgehog *Erinaceus europaeus* occurrence records from Greater London used to construct a multiscale generalised linear model of habitat suitability

Dataset	Hedgehog records	Timespan	Source
Big Hedgehog Map (PTES/British Hedgehog Preservation Society)	1140	2013–2020	PTES
Available from GiGL	1117	2005–2020	GiGL
London Wildlife Trust	569	2005–2018	GiGL
National Mammal Atlas, online recording (Mammal Society)	71	2010–2019	NBN Atlas
Living with Mammals Survey (PTES)	70	2005–2019	NBN Atlas, PTES (2019–2020 records)
PTES (ad hoc hedgehog records)	45	2005–2010	GiGL

(Guillera-Arroita et al. 2015). If biases are unaccounted for, results can only indicate where human–wildlife encounters are likely to occur, and may not reflect the species' true distribution (Guillera-Arroita et al. 2015). To mitigate this potential bias, we selected background sites with the same sampling bias as presence records by inferring 'absences' from records of other species, to indicate where sampling is taking place (Phillips et al. 2009). Records of 'background species' were sourced from the same datasets as hedgehog records, for the red fox, European badger, brown rat *Rattus norvegicus*, European roe deer *Capreolus capreolus*, Reeves' muntjac *Muntiacus reevesi*, and European rabbit *Oryctolagus cuniculus*. These species are often found in urban environments in the UK, are easily recognisable, are often active at night, and are likely to be recorded by observers in a similar way to hedgehogs. Of an initial 7532 background mammal records, 4525 were retained for analysis after applying the same inclusion criteria as for hedgehogs.

To reduce spatial autocorrelation from clustered occurrences, records were converted into a 100 m presence/absence grid overlaid across Greater London containing a total of 161047 grid cells. A fine 100 m × 100 m cell size was chosen, as environmental conditions vary greatly at small spatial scales within urban environments. Cells containing hedgehog records were designated presences, whereas those containing only one or more background species were designated absences. Cells without any species records were considered non-sampled areas.

Environmental predictors

Environmental predictors were chosen to reflect elements of the urban environment expected to be influential for hedgehog presence (Table 2), with a total of 16 variables sourced to represent greenspace and water (eight variables), gradients of urbanisation (three variables), the structure of the built environment (three variables), and potential threats to hedgehog presence (two variables).

Greenspaces are considered vital for hedgehog populations (Hof & Bright 2009), yet greenspace characteristics and management can vary widely, potentially impacting their biodiversity value (Aronson et al. 2017). To explore whether function impacts greenspace importance for hedgehogs, Ordnance Survey (OS) open greenspace vector data (OS 2020a) were sourced for the Greater London area and separated into four primary use classifications in QGIS software (version 3.10.5; http://qgis.org): allotments, parks and play-spaces, cemeteries, and sports. Amenity and private garden landcover data were sourced from GiGL (https://www.gigl.org.uk/data-for-research/), and woodland and surface water data, from OS (2020b).

Gradients of urbanisation, or urban pressure, were measured using three variables. The impervious surface cover was calculated by combining the surface areas of roads (converted to polygons with a 5 m buffer) and buildings from OS (2020b), whilst the usual resident human population and number of dwellings were sourced at the Lower Super Output Area (LSOA) level from the 2011 Census (ONS 2011a, b). The percentage of each of detached, semi-detached, and terraced housing were also sourced as an indicator of the structure of the built environment, with detached housing anticipated to be more permeable for hedgehog movement than denser semi-detached or terraced housing (ONS 2011a, b). These were mapped onto LSOA boundaries (ONS 2011c), and the QGIS 'field calculator' tool was used to calculate human population and housing densities.

Two potential threats to hedgehog populations were also considered: traffic and predation. Urban areas have been predicted to be hot spots of hedgehog roadkill mortality (Wright et al. 2020). The effect of roads was investigated by sourcing local authority annual traffic volumes from the Department for Transport (2020), which were extracted and averaged for each London borough between 2005 and 2018 and mapped using OS boundary lines (OS 2020c). Predation by badgers was investigated using badger presence, determined by mapping badger records from

Table 2. Environmental predictor variables used in the model of hedgehog *Erinaceus europaeus* habitat associations, with abbreviations, descriptions, and sources. Variables are grouped into categories relating to greenspace or water, urbanisation, built environment, or potential threats. Note that landcover variables may overlap, such as water within woodlands; therefore, variables do not add to 100%. Housing type does not add to 100% as other housing types not relevant in this study (such as flats, caravans, and others) were excluded. Mean housing density was excluded from analysis due to high collinearity

Category	Predictor	Abbreviation	Description	Source
Greenspaces and water	Percent garden cover	GDN	Private gardens	GiGL
	Percent allotment cover	ALT	Allotments or community growing spaces	OS (2020a)
	Percent amenity cover	AMN	Village greens, hospital grounds, educational grounds, landscaping	GiGL
	Percent cemetery cover	CEM	Cemetery or religious grounds	OS (2020a)
	Percent sport cover	SPRT	Bowling, tennis courts, golf courses, other sports and playing fields	OS (2020a)
	Percent park and play-space cover	PLPK	Public park or garden, play-spaces	OS (2020a)
	Percent woodland cover	WD	Woodland	OS (2020b)
	Percent water cover	WAT	Water area	OS (2020b)
Gradients of urbanisation	Percent impervious cover	IMP	Buildings and 5 m buffered roads	OS (2020b)
	Mean human population density (per km^2)	HD	Usual resident population divided by LSOA boundary area	ONS (2011a, c)
	Mean housing density (per km^2)	DWL	Total number of dwellings divided by LSOA boundary area	ONS (2011b, c)
Built environment	Percent detached housing	DTCH	Percent of LSOA dwellings that are detached	ONS (2011b, c)
	Percent semi-detached housing	SEMI	Percent of LSOA dwellings that are semi-detached	ONS (2011b, c)
	Percent terraced housing	TERR	Percent of LSOA dwellings that are terraced	ONS (2011b, c)
Potential threats	Average traffic volume (2005–2018)	TRAF	Average annual traffic volume for each London borough	ONS (2011c), Department for Transport (2020)
	Badger presence	BDG	Binary variable representing badger presence or absence	PTES, GiGL, NBN Atlas

the background mammal dataset to the 100 m × 100 m study area grid. All predictor variables, excluding badger presence, were mapped onto the study area and converted to raster format with 10 m resolution. Greenspaces, water, and impervious cover layers were reclassified so that cells containing the landcover type had the value 1 and other cells had zero, to enable the proportion of each landcover type in consecutive circular buffers from the centre of each grid cell to be calculated.

Consecutive circular buffers with radii of 100, 250, 500, 750 and 1000 m were constructed around the centroid of each 100 m × 100 m grid cell across the study area, and values for each environmental variable within each buffer were calculated using the 'mean' function in the QGIS 'zonal statistics' tool. For greenspace types, and impervious cover, results were calculated as a proportion cover of the areas and converted to percentages by multiplying by 100. As landcover types could overlap, such as water within woodland or sports facilities within parks, the percentage covers do not add to 100%. Buffers overlapping a badger presence cell were selected using the QGIS 'select by location' tool and given the value 1 to indicate badger presence. To exclude buffers that

overlapped the edge of the city and had missing data, a 1000 m buffer was constructed around Greater London's boundary, and cells within this boundary buffer were removed from the dataset. The resulting data table was exported for analysis in R (version 3.6.3; R Core Team 2020).

Scale optimisation of environmental variables

Species respond to both local and wider habitat characteristics; therefore, it is important to identify the scale at which environmental variables have the greatest influence through relating species' occurrence to habitat variables at a range of distances (Green et al. 2020). Univariate binomial regression models with a logit link function were constructed to relate hedgehog presence to each environmental predictor within 100, 250, 500, 750, and 1000 m circular buffers. Model performance was assessed using the area under the curve (AUC) after 20 repeat split-sample cross-validations, in which 70% of the data were used for training and 30% withheld for testing. The scale with the highest AUC was selected for inclusion in the full model.

Habitat suitability model fitting

Scale-optimised variables were visualised using Cleveland plots prior to analysis, and log transformations were applied to human population density, housing density, and traffic volume. Highly colinear variables were identified and removed using the 'vif' function in the 'usdm' package (Naimi et al. 2014), which identifies variables with the highest variable inflation factor (VIF). As recommended, the threshold for variable retention was set to 3 (Zuur et al. 2009), resulting in the removal of housing density from analysis. The impervious cover was retained despite a VIF of 3.08, as it was anticipated to be important, resulting in 15 variables retained for use in analysis.

A generalised linear model with binomial distribution and logit link function was fitted to the full set of remaining predictors. Stepwise model selection was performed in both the backward and forward direction using 'stepAIC' from the 'mass' package (Venables & Ripley 2002), to select only predictors that give the most parsimonious model as evaluated using Akaike's information criterion (AIC). As hedgehogs were hypothesised to show non-linear responses to human density and impervious cover, quadratic polynomial terms were added for these variables and change in AIC and model evaluation metrics explored. Response curves were generated to visualise the relationship between hedgehog presence and each predictor using 'ggeffects' (Ludecke 2018). Although a generalised linear modelling framework was chosen to produce interpretable relationships, alternative modelling approaches were also explored, including a generalised additive model, random forest, artificial neural network, and Maxent, using the BIOMOD2 package (Thuiller et al. 2020; see Appendix S1). To assess the use of selected absences on the results, Maxent was also applied to randomly generated background points.

To generate binary presence–absence predictions, a threshold to distinguish between presence and absence sites was selected by evaluating the true skill statistic (TSS) for each run across 101 possible thresholds between zero and one, at 0.01 increments. The threshold at which TSS was maximised was stored for each run and averaged to give a final value, above which the presence is predicted and below which the absence is predicted.

Relative habitat suitability was predicted for the entire study area, excluding the 1000 m boundary buffer. Confidence intervals were calculated to identify high and low certainty in model predictions, and the maximum TSS value threshold was used to classify predictions into presence or absence. The contribution of variables to the model was examined by removing individual variables and assessing the change in mean AUC after 100 repeat split-sample cross-validation runs.

Model evaluation and broad context

Model performance was evaluated using repeat split-sample cross-validation, with data split randomly into 70% for model fitting and 30% for model testing, repeated 100 times. The AUC and TSS were used to measure model discrimination of occupied and unoccupied sites and predictive performance, respectively (Guisan et al. 2017). AUC was calculated using the 'presenceabsence' package (Freeman & Moisen 2008) and TSS using 'ecospat' (Broennimann et al. 2020). In addition, spatially blocked cross-validations were performed by training the model on 75% of data and predicting to a withheld 25% of the data, arranged in either three latitudinal or longitudinal stripes or one of four spatial quarters of the dataset (Appendix S1).

To place the findings of this study into a broader context, we investigated the presence of hedgehogs in major urban areas throughout the species' range. Hedgehog records for the years 2000–2020 were sourced from the Global Biodiversity Information Facility (https://www.gbif.org/) from throughout the species' range as identified by the International Union for Conservation of Nature (IUCN; iucnredlist.org). The records were overlaid onto core urban boundaries from the European Environment Agency Copernicus Urban Atlas 2018 (https://land.copernicus.eu/local/urban-atlas/urban-atlas-2018) to identify the percentage of major urban areas in which the species is recorded. Full method details and references are in Appendix S2.

RESULTS

After inclusion criteria were applied, 3012 hedgehog records and 4525 other mammal records were retained for analysis, giving 1942 presence and 1637 absence grid cells. Univariate models at each scale found that hedgehogs responded mostly to local scale environmental variables, with eight of the 16 variables selected at the 100 m buffer scale (Appendix S3).

The final model had an AUC of 0.779 (±0.011) and a TSS of 0.444 (±0.022), showing good overall fit and predictive capacity. Full model details are shown in Table 3. Of the greenspace types investigated, only percentage cover of gardens, allotments, and parks and play-spaces were significantly positively related to hedgehog presence, whereas woodland was significantly negatively related. The percentage of terraced housing was significantly positively associated with hedgehog presence, but other housing types were not significant. Impervious cover had a significant quadratic relationship with hedgehog presence: presence increased up 31% impervious cover but declined at higher levels. The model supported the inclusion of a quadratic relationship between hedgehog presence and human density,

Table 3. Hedgehog habitat associations in Greater London: generalised linear model parameter estimates, standard errors, *z*-values, and *P* values, and significance (Sig.; *P* < 0.05, **P* < 0.01, ***P* < 0.001, NS – non-significant). Only variables retained in the final model after forward and backwards stepwise selection are shown. Table also shows the mean model AUC (area under the curve) when single predictors are removed, and mean AUC change (Δ) compared with the complete model

Coefficient	Estimate	Std. error	*z* value	*P*-value	Sig.	AUC predictor removed	ΔAUC
Intercept	−11.078	2.275	−4.871	1.11e−06	***		
Garden, 100 m	0.024	0.003	8.547	<2e−16	***	0.766	−0.013
Allotment, 1000 m	0.305	0.050	6.109	1.00e−09	***	0.774	−0.005
Park/play-space, 100 m	0.012	0.002	6.964	3.31e−12	***	0.773	−0.006
Water, 100 m	−0.016	0.007	−2.164	0.030	*	0.779	−2.92e−4
Woodland, 100 m	−0.007	0.003	−2.235	0.025	*	0.779	−4.31e−04
Impervious cover, 100 m poly()1	17.161	4.418	3.884	1.03e−04	***	0.776	−0.003
Impervious cover, 100 m poly()2	−16.973	2.924	−5.806	6.42e−09	***		
Detached housing, 1000 m	−0.010	0.005	−1.952	0.051	NS	0.779	−5e−05
Semi-detached housing, 1000 m	−0.006	0.004	−1.697	0.090	NS	0.779	−3.77e−04
Terraced housing, 500 m	0.007	0.003	2.130	0.033	*	0.779	2.44e−04
Log human density, 100 m poly()1	5.045	4.436	1.137	0.255	NS	0.764	−0.015
Log human density, 100 m poly()2	−38.154	3.954	−9.649	<2e−16	***		
Log traffic volume, 100 m	0.516	0.114	4.507	6.56e−06	***	0.777	−0.002
Badger presence, 250 m	−1.618	0.151	−10.733	<2e−16	***	0.757	−0.022

although only a decline at human densities above 2262 people km^{-2} was significant. Hedgehog presence was negatively related to badger presence in the surrounding 250 m, but contrary to expectations, traffic volume showed a significant positive relationship with hedgehog presence.

Assessment of variable importance found badger presence to have the greatest contribution to the model, with a mean AUC reduction of 0.022 when removed, followed by human density and garden availability (shown in Table 3).

Prediction of habitat suitability for hedgehogs in Greater London (Fig. 2) indicates generally high suitability in the study area, but suitability declines towards the urban centre and in some locations at the study area edge. Habitat suitability varies widely at small spatial scales, and regions of high and low suitability are interspersed, as can be viewed in the interactive map (https://robfreeman.shiny apps.io/hedgehog_map/).

Spatially blocked AUC values were lower (0.69 ± 0.05), but comparable to other modelling approaches explored. Whilst random forest models had a slightly higher AUC (0.73 ± 0.03) and may therefore produce more robust spatial predictions (Appendix S1), predictions were very similar to the linear model presented here, which provides more easily interpretable relationships. Maxent run with random background points gave lower AUC (0.763 ± 0.008) and TSS (0.388 ± 0.013) than selected absences in the generalised linear model.

Exploration of the presence of urban hedgehogs across their range in western Europe found that 73% of major urban areas had hedgehogs recorded.

DISCUSSION

Understanding the urban hedgehog's habitat relationships and distribution is important for identifying potential threats to populations and conservation opportunities. We present a generalised linear model of citizen science occurrence records to examine environmental relationships and predict the distribution of suitable habitat for hedgehogs across Greater London.

Environmental relationships

The availability of gardens, allotments, and parks and play-space were significantly positively related to hedgehog presence, supporting previous findings that urban greenspace is important for hedgehogs (Hof & Bright 2009, Capon et al. 2021). Private gardens particularly had the greatest contribution of greenspace types to the model (Table 2), emphasising their value as core habitat. Gardens offer high structural complexity, with diverse vegetation, trees, and multiple surfaces creating a range of habitats favourable for both hedgehog foraging and nesting, and thus may be critical for the large hedgehog populations seen in urban areas (Hubert et al. 2011).

Parks and allotments were the only publicly accessible greenspace types significantly positively associated with hedgehog presence. Allotments consist of parcels of land rented to individuals for growing food (Dobson et al. 2020), providing a highly varied habitat with mixtures of vegetation, overgrown areas, and high plant species richness (Speak et al. 2015). Parks also provide varied habitat for hedgehogs,
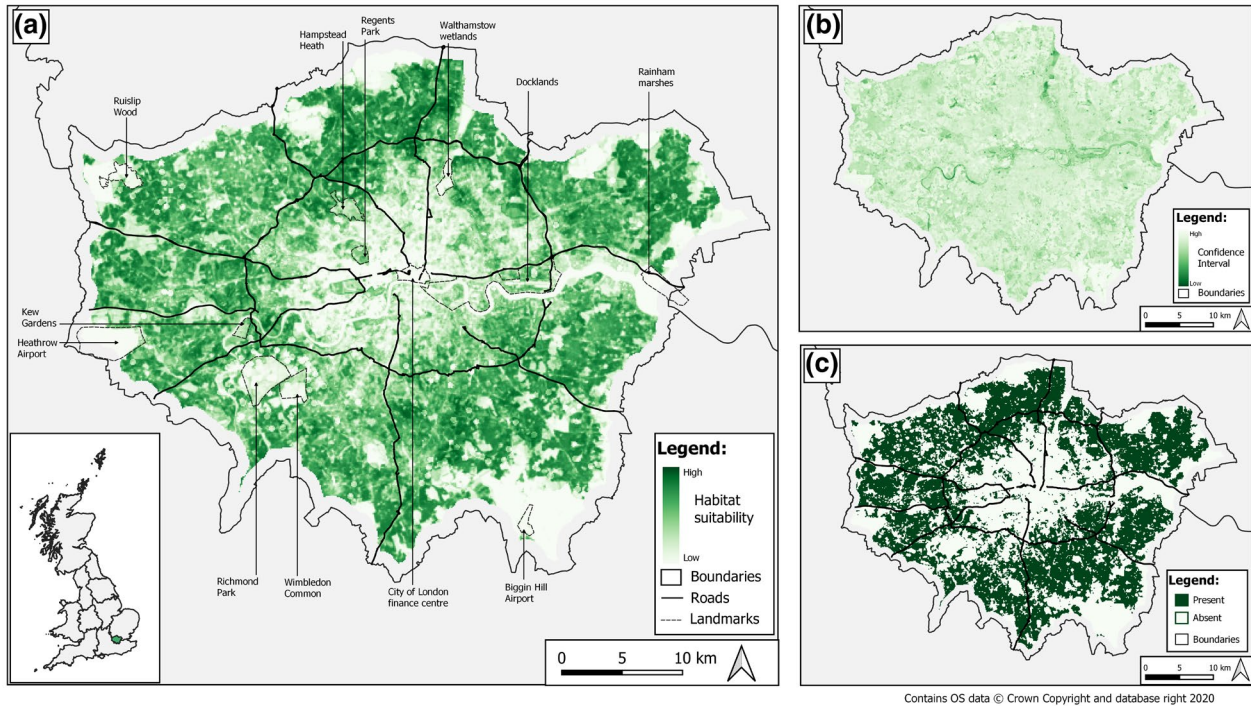
Fig. 2. (a) Map of predicted habitat suitability for the west European hedgehog *Erinaceus europaeus* in Greater London, with main roads and landmarks labelled. (b) Map showing model certainty (confidence intervals). (c) Binary conversion of habitat suitability to regions of predicted hedgehog presence and absence.

although they are often managed for shorter grass and higher tree densities than allotments, as well as including recreational features such as playgrounds and sports facilities such as tennis courts (Speak et al. 2015), which may contribute to their smaller influence on hedgehog presence.

Surprisingly, no significant relationships were found for sport, amenity, or cemetery cover, even though hedgehogs are known to use greenspaces such as golf courses (Reeve 1982), playing fields (Rondinini & Doncaster 2002), and amenity grassland (Young et al. 2006). Inclusion of facilities such as bowling greens and tennis courts, which are often fenced and lack vegetative structure, may impact this relationship, as lawns and greenspace without structure are less preferred by hedgehogs (Braaker et al. 2014). Woodland was the only greenspace negatively related to hedgehog presence, contrasting with previous findings where woodland was positively associated with hedgehog presence in nearby gardens (Hof & Bright 2009, Gazzard & Baker 2020). Woodland is an important habitat for human encounters with hedgehogs in Paris (Capon et al. 2021). The reasons behind this are not clear, although it has been suggested that resources available in woodlands, important for constructing winter hibernacula, are less preferred than anthropogenic alternatives in gardens (Gazzard & Baker 2020).

Housing type had little impact on hedgehog presence, with only a significant positive relationship with the percentage of terraced housing. Gardens of terraced houses are favoured at the individual level by foraging hedgehogs (Dowding et al. 2010). This contrasts with the expectation that low-density housing types would be more permeable for movement and thus more favourable for hedgehogs.

Notably, this study finds that urban pressure – investigated as human density and impervious cover – is an important correlate of hedgehog presence. Human density was the second most important contributing predictor variable in the model, with hedgehog occurrence significantly reduced at densities of 2262 people km^{-2}. High human densities are associated with increasing habitat disturbance, which may impact hedgehog populations negatively. Acute human disturbance from park music festivals has been found to impact hedgehog movement and behaviours in Berlin (Rast et al. 2019, Berger et al. 2020), whilst hedgehogs in Bristol become more active after midnight, potentially to avoid exposure to pedestrian and vehicular traffic (Dowding et al. 2010). Therefore, despite being found near to humans, these results suggest a threshold in hedgehog populations' capacity to tolerate high levels of human activity.

Hedgehog presence was positively related to impervious cover at low levels, peaking at approximately 31% (see Appendix S4 for response curves), but declined significantly at higher levels. Intermediate impervious cover may reflect the patchwork environment found in residential areas, with

mixtures of housing and greenspace providing rich and varied habitat. Hedgehogs not only avoid impervious cover (Rondinini & Doncaster 2002, Dowding et al. 2010, Braaker et al. 2014) but also display behavioural capacity to tolerate habitat fragmentation and to traverse impervious surfaces within fragmented habitats (Berger et al. 2020). It has been suggested that, excepting large roads, impervious cover does not pose a strong barrier for hedgehog movement (Rondinini & Doncaster 2002, Braaker et al. 2014). However, this study suggests that high impervious cover does impact the capacity of hedgehog populations to persist within urban areas, both by replacing high-quality habitat and, especially when combined with dense human populations, by reducing connectedness between habitats.

Badger presence also had a negative influence on hedgehog presence. As intraguild predators and competitors of hedgehogs, badgers are known to exclude hedgehogs from rural habitats (Doncaster 1992). Urban environments are considered to provide a refuge from the species (van de Poel et al. 2015), yet this study suggests that, where they are present, badgers can also influence urban hedgehog distribution. Further understanding of the dynamics of this relationship will be important to promote species coexistence, for example through increasing habitat structure and edge habitats as has been suggested in agricultural habitats (Hof et al. 2012).

Roads present a major threat to hedgehogs. Large roads pose a barrier to movement (Rondinini & Doncaster 2002), whilst traffic mortality can reduce local hedgehog populations by 30% (Huijser & Bergers 2000). Unexpectedly, this study found that hedgehog presence increased with traffic volume. It may be that high traffic leads to increased hedgehog records due to roadkill; however, there was insufficient information to investigate this. The highest traffic volumes were located towards the edge of the study area, coinciding with sites of high suitability due to other characteristics, such as high garden cover and lower urban pressure. As traffic volume data were only available at the local authority level, they may be too broad to detect hedgehogs' habitat relationships, a problem that has previously been highlighted (Bauder et al. 2021). More detailed research on fine-scale spatial relationships between hedgehogs and traffic within otherwise suitable suburban habitat is therefore important.

Habitat suitability map

Habitat suitability was predicted across Greater London to visualise how hedgehogs' environmental relationships relate to broad-scale distribution patterns. The map (Fig. 2a) reveals that habitat suitability is greatest in large areas of London's suburbs, where there are high availability of gardens, parks, and allotments, and intermediate urban pressure. Habitat suitability declines towards the city centre, where there is less greenspace, as it is largely replaced by impervious cover. Some areas around the edges of the study area were also predicted to be less suitable, particularly around Heathrow Airport in the west, and in agricultural areas in the southwest and north. However, it must be noted that the model, built to characterise the urban environment, may be less able to make inferences about the more rural edges of the study area; these areas had few gardens, a driving feature in the model (Table 2), and low recording effort for both hedgehogs and background species.

Positively, conversion to binary presence and absence predictions suggests that much of Greater London is suitable for hedgehogs (Fig. 2c). However, suitability within the 'presence' areas is variable, and both low and high suitability environments are interspersed. This has important implications, as hedgehog populations in intermediate areas may be at greater risk of decline if habitat suitability reduces, increasing the isolation of remaining populations. Furthermore, hedgehogs are unlikely to occupy all potentially suitable habitat. Previous findings from Reading, UK, for example, indicated that whilst hedgehogs were widely distributed, they only used 32–40% of available gardens (Williams et al. 2018b).

Limitations

A key limitation to the study design is that, whilst combining occurrence records from several projects increased the data quantity, the projects had different collection methods and biases. To account for this as much as possible, background records of other mammals were used to indicate where data contributors were recording, yet bias may remain towards environments where people spend more time, and our model may underestimate the importance of less-sampled environments. Gardens, for example, represent 43% of the greenspace area and contributed 35% of occurrence records, whereas sports areas comprise 13% of greenspace area yet contributed only 2.7% of occurrences (Appendix S5).

The model does not account for changes in hedgehog populations and environmental variables during the study. A relatively long time period, 15 years, was chosen to maximise the occurrence data available, and environmental variables range from 2011 to 2020. This creates an 'average' relationship, which is less affected by high sampling variability between years, but does not consider where populations have become extinct and environments have become unsuitable. Human density estimates were sourced from the 2011 census, whereas current human population densities are likely to have risen, meaning that habitat predictions of suitability may be optimistic.

As the relationships recovered are from citizen science presence and pseudoabsence data, it will be important to test the robustness of the findings using standardised systematic surveys, as has been recommended for validating citizen science results (Capon et al. 2021). In addition, as the structure of urban environments can be highly heterogeneous, with factors such as city size, age, and proportion of greenspace influencing biodiversity patterns (Norton et al. 2016), further investigation is needed into the applicability of the findings of this study to other cities. An important assumption is that the selected pseudoabsences represent true absences, which is challenging to quantify for combined datasets using different sampling approaches. We explored the effect of using random background points in Maxent, and found similar predictions but with slightly lower AUC and TSS scores, supporting our use of selected absences.

Our approach using generalised linear modelling allows us to consider more intuitive model results showing how different factors influence the suitability of habitat for hedgehogs. Exploration of other modelling approaches, including generalised additive model, random forest, artificial neural networks, and Maxent using the BIOMOD2 package (Appendix S1), found that more complex models may be slightly better at predicting withheld data, but that the overall conclusions from the model discussed in the paper were not changed.

Conservation implications

Hedgehogs are present in ~73% of large urban environments throughout their range, which highlights the importance of considering hedgehogs in urban planning and conservation projects.

Our findings have important implications for the conservation of hedgehogs in urban environments, suggesting several causes for concern. Allotment cover, for example, has declined in the UK from the mid-20th Century by 65%, with almost half of allotment lost converted to built infrastructure (Dobson et al. 2020). Private gardens are also undergoing significant changes in composition: London's gardens experienced a 12% loss in vegetative cover between 1998–1999 and 2006–2008, whereas hard surfaces from decking, patios, and paving increased by 26% (Smith et al. 2011). Individual decisions therefore have a large impact on habitat quality and connectivity for species such as hedgehogs, impeding cohesive conservation (Aronson et al. 2017). Furthermore, previous studies have suggested that householders are often not aware of hedgehogs' usage of their gardens (Williams et al. 2015, 2018b), so decisions may be made without realisation of the potential impact on hedgehog populations. Schemes to promote awareness of hedgehogs in gardens therefore are an important component of urban hedgehog conservation, particularly as the species is generally well-liked by householders (Baker & Harris 2007).

CONCLUSION

Overall, this study highlights the value of citizen science observation data to develop a habitat suitability model for the west European hedgehog and to allow a better understanding of the species' environmental relationships and distribution within a highly complex urban landscape.

This study finds high variability in habitat suitability for hedgehogs within Greater London and suggests that loss of habitats such as gardens, parks, and allotments, and disturbance associated with high human populations may be limiting their presence. As Greater London is predicted to expand and become increasingly densely populated by humans in future, this research highlights the importance of maintaining habitat features such as gardens, allotments, and public parks to allow the hedgehog to persist in this urban landscape.

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DATA AVAILABILITY STATEMENT

All occurrence data used in this study are available online from the National Biodiversity Network Atlas (http://www.nbnatlas.org), People's Trust for Endangered Species (https://ptes.org/), and Greenspace Information for Greater London CIC (https://www.gigl.org.uk/). Environmental data are available from Ordnance Survey open data (https://www.ordnancesurvey.co.uk/business-government/tools-support/open-data-support) (landcover, boundaries), Department for Transport (https://roadtraffic.dft.gov.uk/) (traffic

volumes), UK data service (https://borders.ukdataservice.ac.uk/ (LSOA boundaries), and NOMIS (https://www.nomisweb.co.uk) (ONS, 2011a, b Census). The dataset used will not be made publicly available online as it contains species records used under licence from GiGL and location information on sensitive species (European badger *Meles meles*). An interactive map showing our results is available here: https://robfreeman.shinyapps.io/hedgehog_map/.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Model cross-validation methodology, BIOMOD2 and Maxent results.
Appendix S2. Hedgehog *Erinaceus europaeus* presence records in major European urban areas methodology.
Appendix S3. Individual environmental variable scale optimisation boxplots.
Appendix S4. Response curves showing predicted hedgehog *Erinaceus europaeus* presence with change in individual variables in the habitat suitability model.
Appendix S5. Table of occurrence records by greenspace type and percent contribution of greenspace types.