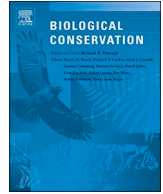




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Bats in urbanising landscapes: habitat selection and recommendations for a sustainable future

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ABSTRACT

Urbanisation is among the most ecologically damaging change in land use, posing significant threats to global biodiversity. Most bat species are threatened by urbanisation, although urban areas can also offer important roosting and foraging opportunities. Urban development should consider how bats are likely to respond to development, and take measures to minimise impacts. We used acoustic data from four years of citizen science monitoring (2013–2016) to quantify the importance of fine-scale habitat configuration and composition for bats in urban areas in eastern England. Bat distribution and activity were analysed in relation to remote sensing data representing impervious surface, waterbodies and tree-cover density. Furthermore, hypothetical future scenarios of urban development were considered, assuming an increase in impervious or woodland surface. Lakes and discontinuous woodland were the most selected habitats and urban areas were the least selected, with *Barbastellus*, *Myotis* and *Plecotus* species being the most vulnerable. *Nyctalus*, *Pipistrellus* and *Eptesicus* species were less influenced by the presence of urban areas. Our results suggest that urban growth should be sought through the expansion of existing urban blocks, rather than creating new urban patches, to minimise impacts on commuting or foraging sites. Creating bat-friendly habitat of an area at least equal to any new urban settlement could provide mitigation for negative effects of urbanisation. Opportunities to increase areas of discontinuous woodland should be encouraged, while preserving unmanaged areas within large plantations would likely support the exploitation of continuous woodland by bats.

1. Introduction

Urbanisation poses significant threats to global biodiversity (Grimm et al., 2008), primarily through the direct loss of natural areas (McDonald et al., 2010), but also indirectly through the processes aimed at producing energy flows, tangible goods and services supporting human wellbeing and quality of life (Kaye et al., 2006). Increased temperature and noise levels, habitat fragmentation and light pollution are some of the major anthropogenic stressors caused by the expansion of cities (Grimm et al., 2008). Around the world, the movement for sustainable and resilient urban areas has been accompanied by a growing call for locally relevant ecological information and principles to guide urban development and management (Nassauer and Opdam, 2008; Pickett et al., 2013) in order to minimise negative impacts of urbanisation and improve the urban habitat for both biodiversity and the human population. It is therefore vital to understand how human-ecological interactions function if we are to target questions that are relevant to policy decisions (Alberti, 2008). Urban

ecology can provide a broad understanding of these processes and thus help societies in their efforts to become more sustainable (Marzluff et al., 2008).

Despite the radical land transformation incurred through urbanisation, many species can still persist, and sometimes thrive, in urban environments (McKinney, 2006). However, the majority of native species are negatively impacted due to habitat loss (McKinney, 2002; McDonnell and Hahs, 2008), urban noise (Slabbekoorn and Peet, 2003; Ditchkoff et al., 2006), increased artificial lighting (Longcore and Rich, 2004; Hölker et al., 2010; Pauwels et al., 2019), road construction (Benítez-López et al., 2010; Claireau et al., 2019) and presence of wind turbines (Barré et al., 2018). However, our understanding of what constitutes a suitable habitat in urban areas and what determines a species' adaptability to an urban environment is currently very limited (Jung and Threlfall, 2016), and there are still gaps in our knowledge of the basic ecological patterns and processes in urban landscapes (Hahs et al., 2009).

Bat populations face a range of severe threats in many regions of the

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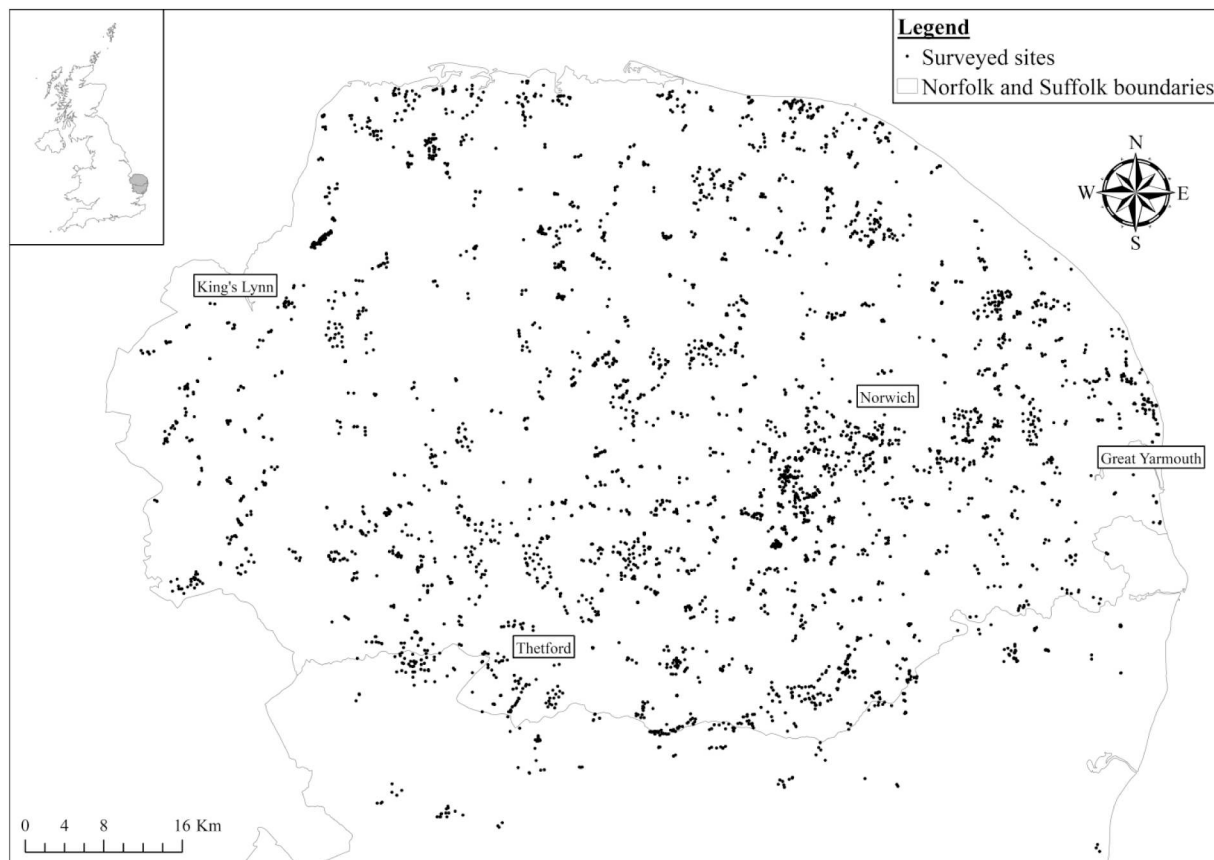


Fig. 1. Locations of the 5690 sites included in the study.

world (Hutson et al., 2001; Jones et al., 2009; Frick et al., 2019). Globally, the major threats to bat species identified by IUCN assessments are logging, non-timber crops, urbanisation, hunting and persecution, quarrying and general human intrusions on bat habitats (Voigt and Kingston, 2016). Bats are particularly susceptible to human-induced habitat perturbations due to their low reproductive rate (Barclay et al., 2004) and high metabolic rate leading to a need for predictable and abundant prey (Zubaid et al., 2006). Of the few studies conducted to date, most have shown a general decrease in bat activity and species richness in urban areas compared with forested habitats (Lesiński et al., 2000; Avila-Flores and Fenton, 2005; Jung and Kalko, 2011) and sub-urban and rural areas (Legakis et al., 2000; Pacheco et al., 2010; Hale et al., 2012). However, some bat species can make use of urban areas, and in particular, cities with good tree cover and tree networks may improve the resilience of some bat populations to urbanisation (Dixon, 2012; Hale et al., 2012). Urban environments also offer abundant potential roosts (Jenkins et al., 1998; Duchamp et al., 2004). These ecological differences among species, the sensitivity to habitat changes and the reliability of monitoring make bats great bioindicators for assessing anthropogenically induced changes in environmental quality over time (Newson et al., 2009; Russo and Jones, 2015). Nevertheless, our general understanding of which features of urban environments are important to bats is still limited (Jung and Threlfall, 2016). Further studies are therefore needed to fill the gaps in our knowledge of the effects of urbanisation on bats, in order to apply the necessary preventive measures to improve conditions for coexistence between bats and humans.

The aim of this study is to use acoustic data from an ongoing large citizen science project based in eastern England to quantify the importance of key habitats for several bat species within and surrounding urban landscapes, and then to use this information to make predictions about how different scenarios of future urban development are likely to affect bat distribution and activity. In this way, we provide

recommended actions that urban planners could implement in order to minimise impacts on bats when new housing developments are planned, and hence improve the suitability of existing human-modified habitats for bats.

2. Materials and methods

2.1. Bat data

Data analysed in this study were derived from the Norfolk Bat Survey (www.batsurvey.org; Newson et al., 2014, 2015), a citizen science project based in Norfolk, south-east England. The project was launched in 2013 and relies on a system of 23 “Bat Monitoring Centres” located throughout the county, from which members of the public can borrow a Song Meter SM2Bat + device (Wildlife Acoustics Inc., Concord, MA, USA), recording in full-spectrum at 384 kHz (see Waters and Barlow, 2013), to monitor bat populations. Field monitoring followed a fixed protocol, described in detail in Newson et al. (2015).

All recordings were firstly analysed by the automatic acoustic classifier built using TADARIDA (a Toolbox for Animal Detection in Acoustic Recordings Integrating Discriminant Analysis; see Bas et al., 2017). Manual inspection of spectrograms using software SonoBat (<http://sonobat.com>) was used as an independent check of the original species identities assigned by the TADARIDA classifier. For *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, which accounted for > 95% of all bat recordings, a random sample of 1000 recordings each of *P. pipistrellus* and *P. pygmaeus* were checked, to verify that classifier identification of these species was accurate. For the other species, we inspected all recordings with SonoBat. Given the very similar call shape and frequencies of *Myotis mystacinus* and *Myotis brandtii*, these two species were treated as a species pair. Data from four years of the survey (2013–2016) were used in this study, comprising > 1 million bat

recordings of the 12 bat species that occur in the study area.

2.2. Site selection

In order to focus attention on urban areas, only the recording locations (hereafter “sites”) located close to high human population density areas were used. To select the sites, we used human population density data at 1-km square resolution from the GEOSTAT 2011 population-grid dataset provided by GISCO (the Geographic Information System of the Commission; ec.europa.eu/eurostat/web/gisco). After multiple trials in ArcGIS (ESRI, 2011) using different thresholds and comparing the various samples of squares with several basemaps, 1-km squares with a population density ≥ 200 were selected, producing a range of levels of urbanisation from small villages to larger towns and cities. Then, a 3-km buffer was drawn around these squares, and the sites located within the resulting area (the squares plus the buffer around them) were selected (Fig. 1). The sites used in this study were therefore located in the proximity of urban areas, but not exclusively within them, as the goal was to assess potential impacts of urban expansion from existing urban settlements to adjacent countryside. The choice of the 3-km buffer size was based on the average of the Core Sustainment Zone (CSZ) area of UK bat species (Table 1; Bat Conservation Trust, 2016). The CSZ is species-specific and is defined as the area surrounding a communal bat roost within which habitat availability and quality will have a significant influence on the resilience and conservation status of the colony using the roost (Bat Conservation Trust, 2016).

2.3. Environmental data

The CSZ radius was used to extract environmental variables at an ecologically meaningful scale for each species. Around each site, separate buffers were drawn to represent the different CSZs of each species. Subsequently, habitat composition inside each buffer was quantified. In the analysis, the occurrence or activity (see below) of each species was analysed with respect to the habitat composition within the CSZ of that species. Habitat composition was based on 17 variables describing: the cover of waterbodies, the cover of woodlands, the cover of impervious surface (any surface constructed of artificial impenetrable materials such as asphalt, concrete, brick or stone), average elevation and average brightness influenced by artificial lighting. The latter was considered because artificial lighting can greatly alter bat distribution and activity (Jung and Kalko, 2010; Stone et al., 2015).

The inland waterbody data were derived from OS Master Map Water Network Layer (www.ordnancesurvey.co.uk) partially modified for use in ecological analyses (see Méndez et al., 2015). In each CSZ, the

Table 1
Core Sustainment Zone (CSZ) radius for each species considered in the study.
Data from: Bat Conservation Trust (2016).

Species (scientific name), author and year	Species (common name)	CSZ radius (km)
<i>Barbastella barbastellus</i> Schreber, 1774	Barbastelle	6
<i>Eptesicus serotinus</i> Schreber, 1774	Serotine	4
<i>Myotis daubentonii</i> Kuhl, 1817	Daubenton's bat	2
<i>Myotis mystacinus</i> Kuhl, 1817	Whiskered/Brandt's bat	1
<i>Myotis brandtii</i> Eversmann, 1845		
<i>Myotis nattereri</i> Kuhl, 1817	Natterer's bat	4
<i>Nyctalus leisleri</i> Kuhl, 1817	Leisler's bat	3
<i>Nyctalus noctula</i> Schreber, 1774	Common noctule	4
<i>Pipistrellus nathusii</i> Keyserling & Blasius, 1839	Nathusius' pipistrelle	3
<i>Pipistrellus pipistrellus</i> Schreber, 1774	Common pipistrelle	2
<i>Pipistrellus pygmaeus</i> Leach, 1825	Soprano pipistrelle	3
<i>Plecotus auritus</i> Linnaeus, 1758	Brown long-eared bat	3

surface occupied by rivers, drains and lakes was calculated.

Impervious surface metrics were extracted from the Imperviousness 2012 raster dataset from the Copernicus Pan-European High Resolution Layers (HRL; land.copernicus.eu/pan-european/high-resolution-layers), at 20-m resolution. For each CSZ, three metrics were calculated based on this dataset: the total area of impervious surface, the number of impervious patches (a higher number of patches means there are more small villages and isolated houses in that area), and the area of the largest continuous impervious patch (the largest impervious patch which intersects the CSZ, but is not necessarily wholly included in it). Tree cover was estimated using the Tree Cover Density 2012 raster dataset from the Copernicus Pan-European HRL at 20-m resolution. A distinction between three tree cover density levels was made: scattered trees (tree cover from 1% to 30%); discontinuous woodland (31% to 70%); continuous woodland (71% to 100%). For each of the three categories, the same three metrics calculated for the impervious cover (total surface, number of patches and area of the largest patch) were calculated in each CSZ.

Average elevation in each buffer of each dimension was extracted using version 4.1 of the Shuttle Radar Topographic Mission (SRTM) 90 m Digital Elevation Data (from CGIAR-CSI; srtm.csi.cgiar.org; Jarvis et al., 2008). Areas with regions of no data in the original SRTM database (where water or heavy shadow prevented the quantification of elevation) were filled using interpolation methods described by Reuter et al. (2007).

The average brightness in each CSZ was derived from the Version 4 DMSP-OLS Nighttime Lights Time Series (ngdc.noaa.gov/eog/dmsp/downloadV4composites.html), which consists of cloud-free composites made using all the available archived DMSP-OLS smooth resolution data. In particular, we used the nighttime lights product known as Avg Lights X Pct, derived from the average visible band digital number (DN) of cloud-free light detections multiplied by the percent frequency of light detection.

All the metrics were calculated in ArcGIS and R (R Core Team, 2018), making use of the following packages: dplyr (Wickham et al., 2018), plyr (Wickham, 2011), raster (Hijmans, 2017), rgdal (Bivand et al., 2018), rgeos (Bivand and Rundel, 2018) and sp (Pebesma and Bivand, 2005; Bivand et al., 2013).

2.4. Statistical analysis

We tested for collinearity between predictor variables using the Pearson Product-Moment Correlation Coefficient. For highly correlated pairs ($r > 0.7$), the variable which was considered either more representative of landscape configuration and composition, or more ecologically meaningful was taken forward to the main analysis. In summary, we used the following environmental variables in the models: river surface; drain surface; lake surface; total impervious surface; number of impervious patches; total discontinuous woodland surface; total continuous woodland surface; average elevation. The cover of scattered trees and the average brightness were excluded from the analysis due to high correlations with other variables. Two categorical variables were included in the models, year and season of monitoring (two levels: early season, from April to June, and late season, from July to November), to account for potential temporal variations in bat activity (e.g. Parsons et al., 2003).

Bat data were analysed using two different measures: distribution (based on the presence or absence/non-detection of a species at a given sampling site during one night of monitoring) and activity (the number of recorded bat passes of a given species at a given sampling site during one night of monitoring). Bat activity cannot be used to quantify bat abundance, as each bat pass recorded may refer to a different individual bat or to one or more bats passing a bat detector repeatedly, but can be considered as an index of the amount of use bats make of an area (Hundt, 2012).

For bat distribution, presence-absence was modelled using binomial

Generalized Additive Models (GAMs) with a complementary log-log link function. Bat activity data was modelled by fitting negative binomial GAMs, since attempts at fitting GAMs with Poisson and quasi-Poisson distributions resulted in high overdispersion. GAMs were used to allow large-scale spatial effects to be assessed by fitting smoothing functions to easting and northing coordinates for both analyses of distribution and activity, hence accounting for potential spatial autocorrelation. We used the thin plate regression spline method with $k = 30$. This level of k was chosen through visual assessment of the residuals, to ensure sufficient smoothing while avoiding overfitting. In order to maintain relatively simple models for running the scenarios, and to minimise overfitting, smoothed terms were not used for the other continuous explanatory environmental variables. For these variables, linear and quadratic terms were initially fitted to each model, and the models were then compared using the Bayesian Information Criterion (BIC) which is appropriate when there is high heterogeneity in the data (Schwarz, 1978; Brewer et al., 2016). The model with the lowest BIC was selected to carry forward to the main analysis. In cases of model equivalence ($\Delta BIC \leq 2$; see Raftery, 1995), the model with the least number of non-linear relationships was chosen, in order to minimise overfitting. We also carried out a further check for collinearity by calculating Variance Inflation Factors (VIFs) for each full model using the mctest package (Imdadullah et al., 2016; Imdadullah and Aslam, 2018).

For each species, two models were built (distribution and activity), for a total of 22 models. Models were fitted using the mgcv package in R (Wood, 2003, 2011). The general model formula was as follows:

D (or) $A \sim s(E, N, k = 30) + D + L + R + I + N + DW + CW + El + S + Y$

where D = bat presence or absence, A = bat activity, E = easting, N = northing, D = drain surface area, L = lake surface area, R = river surface area, I = total impervious surface, N = number of impervious patches, DW = total discontinuous woodland surface, CW = total continuous woodland surface, El = average elevation, S = season, Y = year.

2.5. Scenarios of future development

The models derived from the above analyses were used in conjunction with future scenarios of potential urban development to

predict possible consequences of increasing urbanisation for bat populations in Norfolk. It has previously been estimated for Norfolk that planned housing for the period 2016–2026 includes provision for around 66,442 new homes (Border et al., 2017). Furthermore, the potential to benefit bat populations through increasing woodland areas (i.e. as a management strategy) was also considered. All scenarios involved increasing the current impervious surface or the woodland surface within each CSZ by different amounts, at the expense of largely agricultural land. The resulting distribution or activity (as appropriate) was then predicted site by site from the relevant model based on this new dataset. To avoid misleading predictions, the species considered in each type of scenario were only those for which the habitat component altered in the given scenario was significantly correlated with their distribution or activity in the models. The outcomes of each scenario were considered by calculating the occurrence ratio or the activity ratio in relation to different levels of urban or forest cover as appropriate for each scenario. The occurrence ratio is the ratio between the new predicted occurrence, based on the scenario considered, and the predicted occurrence based on the original dataset. Similarly, the activity ratio is the ratio between new and original predicted activity. By progressively increasing the current impervious or woodland surface and calculating the different ratios, it is possible to estimate the rate at which bat activity and distribution would change, and consequently quantify the importance of that habitat component for a species.

Five different scenarios were considered (full details are given in Appendix 1):

- Scenario 1: Continuous impervious surface expansion - in each CSZ, a progressive increase of the current total impervious surface by intervals of 5% was simulated, up to a maximum of 100%. This simulates the progressive expansion of existing inhabited areas.
- Scenario 2: Discontinuous impervious surface expansion - an increase in the current total impervious surface by 50% was assumed in each CSZ, and the distribution of the additional impervious surface was altered by dividing it into different amounts of new impervious patches. This simulates a range of development patterns, from many small villages to few large urban centres.
- Scenario 3: Discontinuous woodland surface expansion - in each

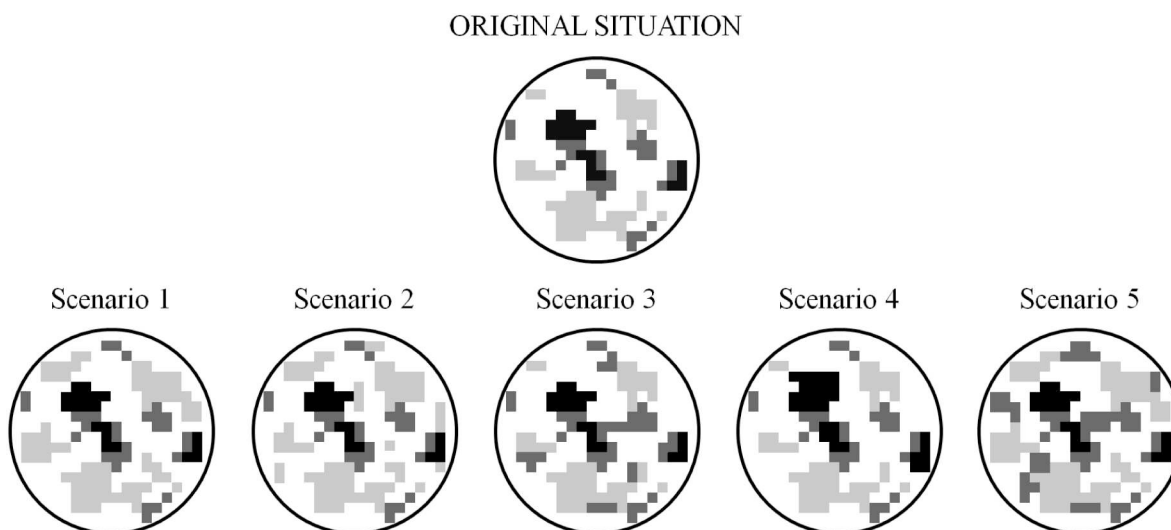


Fig. 2. Scenario illustration examples for a hypothetical site. The black circle represents the buffer drawn around the site to characterise the CSZ of a certain species. Inside the CSZ, the three habitat components considered in scenarios are shown: impervious areas (light grey), discontinuous woodland areas (dark grey) and continuous woodland areas (black). Above, a hypothetical original situation was illustrated. Below, an example of situation for each type of scenario was given. In Scenario 1, a 50% increase in total impervious surface was assumed, without the creation of new impervious patches. In Scenario 2, for the same amount of new impervious surface assumed in Scenario 1, a 100% increase in the number of impervious patches was assumed. In Scenario 3, a 50% increase in total discontinuous woodland surface was assumed. In Scenario 4, a 50% increase in total continuous woodland surface was assumed. In Scenario 5, a 50% increase in total impervious surface was associated with an increase in current discontinuous woodland surface, with the new wooded area being as large as the new impervious surface.

CSZ, a progressive increase of the current total discontinuous woodland surface by intervals of 5% was simulated, up to a maximum of 100%. This scenario simulated the possible outcomes of reforestation actions and the creation of discontinuous wooded areas in urban contexts.

- Scenario 4: Continuous woodland surface expansion - a progressive increase in the amount of the current total continuous woodland surface was considered, as per Scenario 3. This scenario simulated the results of reforestation actions to increase the amount of continuous forest plantations at the edge of urban centres and in the countryside.
- Scenario 5: Continuous urban surface expansion associated with discontinuous woodland reforestation - in each CSZ, the progressive increase of the current total impervious surface assumed in Scenario 1 was associated with an increase in current discontinuous woodland surface, with the new wooded area being always as large as the new impervious surface. This simulated the expansion of existing urban areas when mitigation policies are applied.

Scenario illustration examples for a hypothetical site are given in Fig. 2. As predictions were calculated site by site, occurrence ratios and activity ratios were also calculated site by site for each increment in the habitat component altered in the scenario considered. For each scenario of each species, the median and interquartile range of each increment were then organised in a graph showing the predicted trends of bat occurrence and activity (Fig. 3).

3. Results

3.1. Survey coverage

From a total of 5939 sites surveyed, we selected 5690 sites within and adjacent to urban areas, from which there were 1,169,058 bat recordings. Among the 12 species studied, *P. pipistrellus* and *P. pygmaeus* were the most common and widespread, being recorded respectively in 97% and 87% of sites. None of the other species occurred in > 40% of sites. The two rarest species were *Nyctalus leisleri* and the species pair *Myotis mystacinus/brandtii*, recorded respectively in 5% and 4% of sites. In terms of bat activity, 62% of all bat passes were of *P. pipistrellus* and 33% were of *P. pygmaeus*.

Table 2

Summary results of distribution models and activity models. Positive relationships are expressed by a “+” sign, negative relationships are expressed by a “-” sign, and for quadratic relationships the shape of the prediction curve is given. Non-significant relationships are expressed by “NS”, while codes for significant relationships are the following: “*” for 0.01 < p < 0.05; “**” for 0.001 < p < 0.01; “***” for p < 0.001. For quadratic relationships, the significance code refers to the squared term. Deviance explained of both distribution and activity models is shown in the last two columns.

Bat species	Waterbodies																		Year						Deviance explained (%)			
	Drain surface area		Lake surface area		River surface area		Total impervious surface		Number of impervious patches		Total discontinuous woodland surface		Total continuous woodland surface		Average elevation		Late season		2014		2015		2016					
	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.		
<i>Barbastella barbastellus</i>	NS	NS	NS	NS	NS	NS	-**	-***	NS	-	NS	NS	∩**	-*	∩***	∩***	+	+	NS	NS	NS	NS	+	+	+	+	9.91	22.90
<i>Eptesicus serotinus</i>	NS	-***	NS	NS	NS	∩***	NS	NS	NS	NS	-***	-**	∩***	∩***	NS	NS	+	+	+	+	+	+	+	+	+	+	10.70	22.70
<i>Myotis daubentonii</i>	NS	-***	+	NS	+	∩***	-*	NS	+	NS	NS	NS	+	NS	-*	∩***	+	NS	+	NS	NS	NS	+	+	+	+	6.39	28.70
<i>Myotis mystacinus/brandtii</i>	NS	NS	+	+	∩**	NS	-***	-*	NS	NS	+	NS	NS	∩**	NS	NS	+	+	+	+	+	NS	NS	NS	-*	NS	15.60	31.80
<i>Myotis nattereri</i>	NS	NS	+	+	NS	NS	-**	-**	NS	-**	NS	+	NS	-*	NS	NS	+	+	+	+	+	+	+	+	+	+	12.30	22.70
<i>Nyctalus leisleri</i>	NS	NS	∩**	∩***	NS	NS	NS	NS	NS	-*	NS	NS	NS	NS	NS	NS	+	+	+	+	+	+	+	+	+	+	27.70	55.20
<i>Nyctalus noctula</i>	∩***	∩***	+	+	-*	NS	NS	NS	NS	NS	NS	NS	+	∩***	-*	∩***	NS	+	+	+	+	+	+	+	+	+	9.38	17.30
<i>Pipistrellus nathusii</i>	NS	+	+	+	NS	NS	∩**	NS	NS	NS	NS	+	NS	NS	∩***	NS	-**	-**	NS	NS	NS	NS	NS	NS	-**	NS	12.60	34.70
<i>Pipistrellus pipistrellus</i>	NS	-***	NS	∩***	∩**	+	NS	NS	NS	NS	NS	NS	-*	NS	NS	∩***	+	+	NS	NS	NS	NS	NS	NS	+	+	6.59	5.76
<i>Pipistrellus pygmaeus</i>	NS	+	+	∩***	∩**	NS	∩***	∩***	+	NS	+	NS	NS	+	-	-	+	+	NS	-*	NS	NS	NS	NS	NS	NS	12.70	11.30
<i>Plecotus auritus</i>	NS	NS	-*	NS	-*	NS	-***	-***	+	NS	+	+	NS	NS	∩**	∩**	+	+	NS	NS	NS	NS	+	+	+	+	8.85	14.00

3.3. Scenarios of future development

In Fig. 3 we present the scenario results for four representative species, three of which (*B. barbastellus*, *M. nattereri* and *P. auritus*) summarise the negative effects of urbanisation on bat populations and the potential mitigating effect provided by reforestation, and one (*E. serotinus*) which was the only species for which there was a negative effect of discontinuous woodland cover expansion. The scenario results for all species are given in Appendix 3. As the predicted occurrence ratio and activity ratio were calculated site by site, for each increment in the habitat component altered in the scenario considered, the median

and interquartile range out of all predictions are presented in the graphs, and a trend line was added across the median points to show the predicted effects on bat populations with increasing habitat changes.

Predictions based on the scenario of continuous urban expansion (Scenario 1) showed a moderate decrease in the occurrence and activity ratio of all the considered species. *B. barbastellus*, *M. mystacinus/brandtii*, *M. nattereri* and *P. nathusii* responded most negatively, showing a 4–6% decrease in their occurrence ratio for a 50% increment in the total impervious surface, and up to a 8–12% decrease for a 100% increment (this assumes that the current amount of impervious surface is doubled). Activity ratio of *B. barbastellus* decreased by 19% assuming a

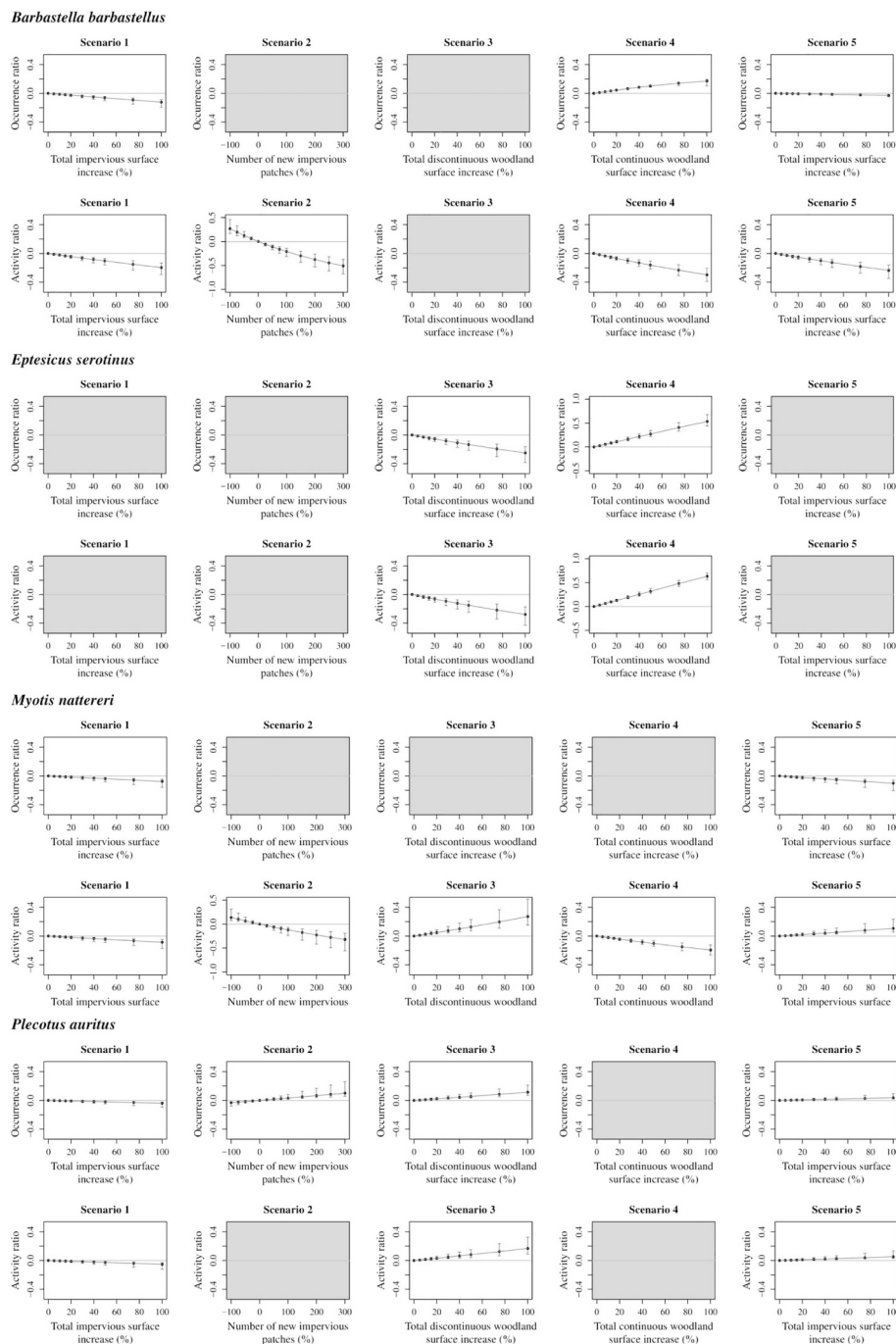


Fig. 3. Scenario results for four representative species in the study. Scenarios are presented in order from left (Scenario 1) to right (Scenario 5). Grey panels indicate no significant effect of the habitat variable addressed in the given scenario. As predicted occurrence and activity ratios were calculated site by site, for each increment in the habitat component altered in each scenario, the median and interquartile range out of the ratios of all sites are presented. The trend line across the median points shows the predicted effects on bat populations with increasing habitat changes.

100% increment in the total impervious surface. *P. pygmaeus* and *P. auritus* showed some tolerance to the increase in the total impervious surface, maintaining approximately unchanged occurrence and activity ratios.

Changes in the distribution of the new impervious surface (Scenario 2) caused minor variations in bat occurrence ratio, but considerable effects on bat activity ratio. In general, for the same increase in impervious surface assumed, the scenario that envisages the progressive expansion of existing inhabited areas without the creation of new impervious patches caused an increase in bat activity ratio ranging from 13% (*M. nattereri*) to 26% (*B. barbastellus*). Assuming, instead, that the estimated number of new impervious patches is trebled, the activity ratio of the species considered showed a 32–50% decrease, with *B. barbastellus* being the worst hit species.

Bats showed a general increase in their occurrence and especially in their activity ratio in response to discontinuous woodland expansion (Scenario 3). For a 100% increment in the total discontinuous woodland surface, *M. mystacinus/brandtii* occurrence ratio increased by > 20%, while *M. daubentonii*, *M. nattereri*, *N. noctula* and *P. nathusii* showed a 27–55% increase in their activity ratio, with *M. daubentonii* being the most influenced. *P. auritus* occurrence and activity ratio also showed a minor increase, respectively up to 11% and 16%. The only species which showed an opposite trend was *E. serotinus*, whose occurrence and activity ratio decreased respectively by 25% and 27% for a 100% increment in the total discontinuous woodland surface.

Continuous woodland expansion (Scenario 4) showed different effects depending on the species considered. While *E. serotinus* occurrence and activity ratio showed a > 50% increase for a 100% increment in the total continuous woodland surface, *B. barbastellus* and *N. noctula* showed an increase in their occurrence ratio but a decrease in their activity ratio. Activity ratio of *M. nattereri* also showed a negative trend, whereas minor effects were shown for *Pipistrellus* species.

A comparison between Scenario 1 and Scenario 5 shows a general mitigation effect given by the presence of new discontinuous woodland areas alongside the new urban areas. The occurrence ratio of *M. daubentonii*, *M. mystacinus/brandtii* and *P. auritus* inverted its trend from negative to positive, while for the other species the mitigation effect, although present, did not cause the inversion of the trend, which remained negative. The activity of *M. mystacinus/brandtii*, *M. nattereri* and *P. auritus* also showed an inversion of the trend. A negative effect, albeit very small (< 4%), was shown for the occurrence of *M. nattereri* and for the activity of *B. barbastellus* and *P. pygmaeus*.

4. Discussion

4.1. Model results

The species considered represent a range of species with different ecological and behavioural adaptations for which there was variation in response to environmental variables in the models. Nevertheless, some general patterns emerged. First, several species showed positive associations with waterbodies, in particular lakes and rivers. Second, many species were significantly associated with the cover of either continuous or discontinuous woodland surface. In most cases, these results implied a greater occurrence or activity in landscapes with areas of open woodland, demonstrated respectively through positive linear associations with discontinuous woodland, and non-linear associations with continuous woodland. Third, a number of species showed negative associations with impervious surface. Except for *P. nathusii*, an increase in occurrence and activity of all species from early to late season was evident, probably due to the dispersal of newly weaned juveniles, swarming activity and pre-hibernal fat accumulation (Parsons et al., 2003; Ciechanowski et al., 2010).

Lakes were the most selected freshwater habitat, while rivers are extremely important for species which extensively use them both as commuting corridors and foraging sites (e.g. *M. daubentonii* and *P.*

pygmaeus; Warren et al., 2000). Higher flying species, such as the two *Nyctalus* bats, were found to prefer lakes to narrower water bodies. Drains were in general not associated with bat occurrence or activity, as in Norfolk these are located in intensive agricultural landscapes, where the absence of trees for roosting makes them unsuitable for many bat species. One exception was *P. nathusii*, known to exploit large wetlands in Europe (Flaquer et al., 2009) and to have maternity roosts in the area of the Norfolk Broads, where many recordings have been collected and the species is probably resident (www.nathusius.org.uk; Newson et al., 2015).

We found woodland was used by the majority of species. The preference for fragmented woodland blocks suggests a tendency for most bats to prefer a greater habitat complexity and heterogeneity, being able to exploit a wide range of landscape features including woodland-meadow ecotones and woodland margins. Nevertheless, the apparent avoidance of large continuous woodland blocks for some species has been influenced by the fact that most continuous woodland in Norfolk is composed of coniferous plantations, where mature trees are almost absent and roosting opportunities are strongly limited. For example, the loss of old mature woodland and ancient trees with loose bark or wood crevices is one of the main threats for *B. barbastellus* (Piraccini, 2016), which shows a clear preference for unmanaged woodland to managed plantations (Russo et al., 2010).

Five species showed a clear significant decrease in occurrence as the total impervious surface increased, indicating strong avoidance of large urban areas (*B. barbastellus*, *M. daubentonii*, *M. mystacinus/brandtii*, *M. nattereri* and *P. auritus*). These are generally woodland-foraging species (Entwistle et al., 1996; Parsons and Jones, 2003; Buckley et al., 2013) and the high level of disturbance and artificial lighting (Aughney et al., 2012; Zeale et al., 2012; Claireau et al., 2019), in addition to the scarcity of old, traditional and wooden buildings (Howard and Richardson, 2009) are likely the main factors reducing their chance of exploitation of urban habitats. *Pipistrellus* and *Nyctalus* species, as well as *E. serotinus*, were in general less influenced by the presence of urban areas, demonstrating an ability to exploit a wider range of habitats. Nevertheless, the occurrence of *P. pygmaeus* was negatively associated with continuous impervious surface and positively associated with the number of impervious patches, meaning a tendency to select small villages and groups of isolated houses for roosting. Other studies confirmed that this species depends on buildings for roosting (Oakeley and Jones, 1998), often forages near streetlamps (Bartonička et al., 2008) and forms large and stable maternity colonies in buildings in Europe (Barlow and Jones, 1999). However, buildings which are close to tree cover and linear vegetation elements, and within 0.5 km of a major river or a woodland, are preferred (Jenkins et al., 1998). In the most urban centres in Norfolk, such as Norwich and Thetford, where *P. pygmaeus* was recorded, activity was mainly restricted to water courses.

Two additional species, *M. daubentonii* and *P. auritus*, showed positive associations with the number of impervious patches, suggesting that small inhabited areas in the countryside can offer important roost sites for these species which avoid large urban centres (for building roost selection by *P. auritus*, see Entwistle et al., 1997). However, negative associations with the activity of three species (*B. barbastellus*, *M. nattereri* and *N. leisleri*), suggests that these may not offer enough foraging opportunities, as highlighted by some previous studies (e.g. Sierro and Arlettaz, 1997; Waters et al., 1999).

4.2. Scenarios

Expansion of existing inhabited areas (Scenario 1) in general resulted in negative impacts on the bat community, in particular for species such as *B. barbastellus*, *M. mystacinus/brandtii* and *M. nattereri*, which are associated with woodland and riparian habitats (Parsons and Jones, 2003; Kaňuch et al., 2008; Zeale et al., 2012). Nevertheless, impacts were not universal, with other species either showing no effect or limited negative impacts (*P. pygmaeus* and *P. auritus*). Increasing the

fragmentation of impervious surface (Scenario 2) had little effect on bat occurrence but clear negative effects on bat activity, suggesting that overall, urban growth should be sought through the expansion of existing urban blocks, rather than creating new urban patches, in order to avoid disturbance in potential commuting or foraging sites.

Clear positive effects on bat occurrence and activity were associated with increasing the discontinuous woodland surface (Scenario 3). The preservation of this habitat, tree planting and woodland creation, should therefore be of primary importance. The only exception was *E. serotinus*, which instead appears adapted to take advantage of built-up areas (Catto et al., 1996), and would benefit from continuous woodland expansion (Scenario 4). Foraging habitat of *E. serotinus* shifts from woodland from May to July, to pastures from August to October (Robinson and Stebbings, 1997), and the selection of continuous woodland may be due to an increase in prey abundance in dense vegetation (Müller et al., 2012). On the contrary, continuous woodland expansion, which in Norfolk relates to coniferous plantations, may have negative effects on the activity of *B. barbastellus*, *M. nattereri* and *N. noctula*, suggesting that this habitat is not selected for foraging by these species, and in general its expansion may not be the ideal solution to safeguard bat populations.

All the UK bat species have been known to roost in buildings (www.bats.org.uk; Howard and Richardson, 2009) and some of them can be found foraging in urban habitats (Jung and Kalko, 2010; Polak et al., 2011). However, this study highlighted the potential negative effects on bat populations associated with an increase in impermeable surface. Scenario 5 showed how these negative effects may be mitigated through the expansion of discontinuous woodland cover, and that this would particularly benefit *Myotis* species and *P. auritus*. Although it was not tested in the present study, it is known that habitat connectivity plays a key role in bat conservation (Hale et al., 2012). The creation of links between woodland patches and in general the improvement of the connections between built up areas and the surrounding natural habitats should therefore be promoted (Pinaud et al., 2018; Laforge et al., 2019).

In addition to planning development in a way that will minimise impacts on bat communities, it may also be possible to compensate for any potential negative effects by creating or enhancing semi-natural habitats. According to our scenarios, creation or expansion of existing large woodland blocks would not likely be a suitable strategy to offset any potential losses caused by increased urbanisation, as effects of expanding continuous woodland varied among species and were negative for the species which would be most impacted by the expansion of impervious areas (*B. barbastellus* and *M. nattereri*). With the exception of *E. serotinus*, effects of increasing open woodland habitats tended to positive. Expansion of discontinuous woodland, which according to our definition includes areas with an intermediate level of tree cover in addition to hedgerows, tree lines and even gardens, would be a better strategy to compensate for potential negative effects of urban expansion. There is, however, a caveat here in that most of dense woodland blocks in the study area were commercial coniferous plantations. Not enough native woodland exists to assess whether in fact large blocks of this habitat would benefit the bat community, although there would seem little likelihood of introducing such a habitat in the study area. Nevertheless, these analyses suggest that encouragement of unmanaged areas within the existing continuous woodland plantations may be a beneficial management strategy to explore.

We have considered bats in generally urbanised landscapes within a matrix of intensive agriculture. It should be noted that, in common with most citizen science surveys, the survey locations were not random and were more likely representative of locations that were more accessible to observers. Nevertheless, given that the focus of the paper was on urban settlements, and adjacent areas that potentially could be developed in the future, we do not believe this is likely to have caused any significant bias in our results. We should stress, however, the importance of natural habitats for bats, which were largely absent from

our study area. Habitats such as lakes, water courses, wetlands, and generally every area characterised by the presence of trees and shrubs, with special reference to unmanaged wooded patches, need to be preserved as unaltered as possible. Where these areas have already been altered, minimising disturbance should be of primary importance.

4.3. Conclusions

In order to develop urban areas sustainably to accommodate a growing human population, strategies are needed that allow urban expansion while minimising impacts on biodiversity. Indeed, sustainable development of cities is one of the United Nations' key development goals for 2030 (United Nations, 2018). In the UK, a shortage of affordable homes has led to a strategy to create new housing, and the region within which this current study was carried out is one of the target areas (Border et al., 2017). Our results suggest that, for bats at least, urban expansion accompanied by strategies such as creating bat-friendly habitat of an area at least equal to any new urban settlement could provide mitigation for negative effects of urbanisation. Opportunities to increase discontinuous woodland surface should be encouraged, for example through planting small woods in adjacent farmland, or creating recreation areas that include open woodland and lakes. This would contribute to development of sustainable urban expansion, and provide wider benefits of green space for people (Fuller et al., 2007; Niemelä et al., 2010).

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Declaration of Competing Interest

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

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