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

15

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26

27 **1. Introduction**

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

41 Despite the radical land transformation incurred through urbanisation, many species can still
42 persist, and sometimes thrive, in urban environments (McKinney, 2006). However, the majority of
43 native species are negatively impacted due to habitat loss (McKinney, 2002; McDonnell and Hahs,
44 2008), urban noise (Slabbekoorn and Peet, 2003; Ditchkoff et al., 2006), increased artificial lighting
45 (Longcore and Rich, 2004; Hölker et al., 2010; Pauwels et al., 2019), road construction (Benítez-
46 López et al., 2010; Claireau et al., 2019) and presence of wind turbines (Barré et al., 2018). However,
47 our understanding of what constitutes a suitable habitat in urban areas and what determines a species'
48 adaptability to an urban environment is currently very limited (Jung and Threlfall, 2016), and there
49 are still gaps in our knowledge of the basic ecological patterns and processes in urban landscapes
50 (Hahs et al., 2009).

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

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

76 impacts on bats when new housing developments are planned, and hence improve the suitability of
77 existing human-modified habitats for bats.

78

79 2. **Materials and Methods**

80 2.1 *Bat data*

81 Data analysed in this study were derived from the Norfolk Bat Survey (www.batsurvey.org;
82 Newson et al., 2014, 2015), a citizen science project based in Norfolk, south-east England. The project
83 was launched in 2013 and relies on a system of 23 “Bat Monitoring Centres” located throughout the
84 county, from which members of the public can borrow a Song Meter SM2Bat + device (Wildlife
85 Acoustics Inc., Concord, MA, USA), recording in full-spectrum at 384 kHz (see Waters and Barlow,
86 2013), to monitor bat populations. Field monitoring followed a fixed protocol, described in detail in
87 Newson et al. (2015).

88 All recordings were firstly analysed by the automatic acoustic classifier built using TADARIDA
89 (a Toolbox for Animal Detection in Acoustic Recordings Integrating Discriminant Analysis; see Bas
90 et al., 2017). Manual inspection of spectrograms using software SonoBat (<http://sonobat.com>) was
91 used as an independent check of the original species identities assigned by the TADARIDA classifier.
92 For *Pipistrellus pipistrellus* and *Pipistrellus pygmaeus*, which accounted for > 95% of all bat
93 recordings, a random sample of 1000 recordings each of *P. pipistrellus* and *P. pygmaeus*, to verify
94 that classifier identification of these species was accurate. For the other species, we inspected all
95 recordings with SonoBat. Given the very similar call shape and frequencies of *Myotis mystacinus* and
96 *Myotis brandtii*, these two species were treated as a species pair. Data from four years of the survey
97 (2013–2016) were used in this study, comprising more than 1 million bat recordings of the 12 bat
98 species that occur in the study area.

100 2.2 Site selection

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

117

118 2.3 Environmental data

119 The CSZ radius was used to extract environmental variables at an ecologically meaningful scale
120 for each species. Around each site, separate buffers were drawn to represent the different CSZs of
121 each species. Subsequently, the habitat composition inside each buffer was quantified. In the analysis,
122 the occurrence or activity (see below) of each species was analysed with respect to the habitat
123 composition within the CSZ of that species. Habitat composition was based on 17 variables

124 describing: the cover of waterbodies, the cover of woodlands, the cover of impervious surface (any
125 surface constructed of artificial impenetrable materials such as asphalt, concrete, brick or stone),
126 average elevation and average brightness influenced by artificial lighting. The latter was considered
127 because artificial lighting can greatly alter bat distribution and activity (Jung and Kalko, 2010; Stone
128 et al., 2015).

129 The inland waterbody data were derived from OS Master Map Water Network Layer
130 (www.ordnancesurvey.co.uk) partially modified for use in ecological analyses (see Méndez et al.,
131 2015). In each CSZ, the surface occupied by rivers, drains and lakes was calculated.

132 Impervious surface metrics were extracted from the Imperviousness 2012 raster dataset from the
133 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
134 dataset: the total area of impervious surface, the number of impervious patches (a higher number of
135 patches means there are more small villages and isolated houses in that area), and the area of the
136 largest continuous impervious patch (the largest impervious patch which intersects the CSZ, but is
137 not necessarily wholly included in it). Tree cover was estimated using the Tree Cover Density 2012
138 raster dataset from the Copernicus Pan-European HRL at 20-m resolution. A distinction between
139 three tree cover density levels was made: scattered trees (tree cover from 1% to 30%); discontinuous
140 woodland (31% to 70%); continuous woodland (71% to 100%). For each of the three categories, the
141 same three metrics calculated for the impervious cover (total surface, number of patches and area of
142 the largest patch) were calculated in each CSZ.

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

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

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

159

160 *2.4 Statistical analysis*

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

172 Bat data were analysed using two different measures: distribution (based on the presence or
173 absence/non-detection of a species at a given sampling site during one night of monitoring) and

174 activity (the number of recorded bat passes of a given species at a given sampling site during one
175 night of monitoring). Bat activity cannot be used to quantify bat abundance, as each bat pass recorded
176 may refer to a different individual bat or to one or more bats passing a bat detector repeatedly, but
177 can be considered as an index of the amount of use bats make of an area (Hundt, 2012).

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

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

198

199 $D \text{ (or) } A \sim s(E, N, k=30) + D + L + R + I + N + DW + CW + El + S + Y$

200

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

205

206 *2.5 Scenarios of future development*

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

224 distribution would change, and consequently quantify the importance of that habitat component for a
225 species.

226 Five different scenarios were considered (full details are given in Appendix 2):

227 • Scenario 1: Continuous impervious surface expansion - In each CSZ, a progressive increase of the
228 current total impervious surface by intervals of 5% was simulated, up to a maximum of 100%.

229 This simulates the progressive expansion of existing inhabited areas.

230 • Scenario 2: Discontinuous impervious surface expansion - An increase in the current total
231 impervious surface by 50% was assumed in each CSZ, and the distribution of the additional
232 impervious surface was altered by dividing it into different amounts of new impervious patches.

233 This simulates a range of development patterns, from many small villages to few large urban
234 centres.

235 • Scenario 3: Discontinuous woodland surface expansion - In each CSZ, a progressive increase of
236 the current total discontinuous woodland surface by intervals of 5% was simulated, up to a
237 maximum of 100%. This scenario simulated the possible outcomes of reforestation actions and the
238 creation of discontinuous wooded areas in urban contexts.

239 • Scenario 4: Continuous woodland surface expansion - A progressive increase in the amount of the
240 current total continuous woodland surface was considered, as per Scenario 3. This scenario
241 simulated the results of reforestation actions to increase the amount of continuous forest
242 plantations at the edge of urban centres and in the countryside.

243 • Scenario 5: Continuous urban surface expansion associated with discontinuous woodland
244 reforestation - In each CSZ, the progressive increase of the current total impervious surface
245 assumed in Scenario 1 was associated with an increase in current discontinuous woodland surface,
246 with the new wooded area being always as large as the new impervious surface. This simulated
247 the expansion of existing urban areas when mitigation policies are applied.

248 Scenario illustration examples for a hypothetical site are given in Figure 2.

249

250 **3. Results**

251 *3.1 Survey coverage*

252 From a total of 5,939 sites surveyed, we selected 5,690 sites within and adjacent to urban areas,
253 from which there were 1,169,058 bat recordings. Among the 12 species studied, *P. pipistrellus* and
254 *P. pygmaeus* were the most common and widespread, being recorded respectively in 97% and 87%
255 of sites. None of the other species occurred in more than 40% of sites. The two rarest species were
256 *Nyctalus leisleri* and the species pair *Myotis mystacinus/brandtii*, recorded respectively in 5% and
257 4% of sites. In terms of bat activity, 62% of all bat passes were of *P. pipistrellus* and 33% were of *P.*
258 *pygmaeus*.

259

260 *3.2 Model results*

261 A summary of effects of habitat, season and year on the probability of occurrence and activity of
262 each bat species is shown in Table 2 (full model results are given in Appendix 3). In general, a
263 relatively high percentage of deviance was explained by the models, especially for activity ratio
264 (Table 2), although there was a reasonable amount of variation between species, e.g. for activity ratio,
265 *Nyctalus leisleri* showed the highest deviance explained (c. 55%) and *Pipistrellus pipistrellus* the
266 lowest (c. 6%). In general, distribution and activity models showed similar trends. The probability of
267 occurrence and activity increased significantly with increasing cover of water surface, in particular
268 lake surface, although some species showed quadratic associations, suggesting a peak in occurrence,
269 activity or both at intermediate cover of lakes (*N. leisleri*, *P. pygmaeus*), rivers (*Eptesicus serotinus*,
270 *Myotis daubentonii*, *M. mystacinus/brandtii*) or drains (*Nyctalus noctula*). However, there were also
271 some negative associations: *Plecotus auritus* occurrence decreased significantly with increasing lake
272 and river surface and *N. noctula* with increasing river surface, and the activity of *E. serotinus*, *M.*
273 *daubentonii* and *P. pipistrellus* decreased significantly with increasing drain surface. In general, the

274 cover of artificial surface had negative effects, showing that for the most part, urban areas are less
275 likely to host bat species, although there was some suggestion that fragmented urban areas might
276 benefit the occurrence of *M. daubentonii*, *P. pygmaeus* and *P. auritus*. Seven species (*Myotis* bats, *N.*
277 *noctula*, *Pipistrellus nathusii*, *P. pygmaeus* and *P. auritus*) showed positive associations with
278 discontinuous woodland surface, and this was particularly evident in the models of activity, while *E.*
279 *serotinus* was the only species showing a negative association, for both occurrence and activity
280 models. Six species (*Barbastella barbastellus*, *E. serotinus*, *Myotis nattereri*, *M. mystacinus/brandtii*,
281 *N. noctula* and *P. pipistrellus*) showed quadratic or negative associations with continuous woodland,
282 whereas *P. pygmaeus* activity was the only positive relationship. Despite low variation in elevation
283 across the county, for seven species (*B. barbastellus*, *M. daubentonii*, *N. noctula*, *P. nathusii*, *P.*
284 *pipistrellus*, *P. pygmaeus* and *P. auritus*) there was a significant correlation between
285 distribution/activity and elevation. For each species, occurrence and activity were higher late in the
286 season, with the exception of *P. nathusii*, for which occurrence and activity were higher in the early
287 season.

288

289 3.3 Scenarios of future development

290 In Figure 3 we present the scenario results for four representative species, three of which (*B.*
291 *barbastellus*, *M. nattereri* and *P. auritus*) summarise the negative effects of urbanisation on bat
292 populations and the potential mitigating effect provided by reforestation, and one (*E. serotinus*) which
293 was the only species for which there was a negative effect of discontinuous woodland cover
294 expansion. The scenario results for all species are given in Appendix 4.

295 Predictions based on the scenario of continuous urban expansion (Scenario 1) showed a moderate
296 decrease in the occurrence and activity ratio of all the considered species. *B. barbastellus*, *M.*
297 *mystacinus/brandtii*, *M. nattereri* and *P. nathusii* responded most negatively, showing a 4–6%
298 decrease in their occurrence ratio for a 50% increment in the total impervious surface, and up to a 8–

299 12% decrease for a 100% increment (this assumes that the current amount of impervious surface is
300 doubled). Activity ratio of *B. barbastellus* decreased by 19% assuming a 100% increment in the total
301 impervious surface. *P. pygmaeus* and *P. auritus* showed some tolerance to the increase in the total
302 impervious surface, maintaining approximately unchanged occurrence and activity ratios.

303 Changes in the distribution of the new impervious surface (Scenario 2) caused minor variations
304 in bat occurrence ratio, but considerable effects on bat activity ratio. In general, for the same increase
305 in impervious surface assumed, the scenario that envisages the progressive expansion of existing
306 inhabited areas without the creation of new impervious patches caused an increase in bat activity ratio
307 ranging from 13% (*M. nattereri*) to 26% (*B. barbastellus*). Assuming, instead, that the estimated
308 number of new impervious patches is trebled, the activity ratio of the species considered showed a
309 32–50% decrease, with *B. barbastellus* being the worst hit species.

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

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

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

330

331 **4. Discussion**

332 *4.1 Model results*

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

344 Lakes were the most selected freshwater habitat, while rivers are extremely important for species
345 which extensively use them both as commuting corridors and foraging sites (e.g. *M. daubentonii* and
346 *P. pygmaeus*; Warren et al., 2000). Higher flying species, such as the two *Nyctalus* bats, were found
347 to prefer lakes to narrower water bodies. Drains were in general not associated with bat occurrence

348 or activity, as in Norfolk these are located in intensive agricultural landscapes, where the absence of
349 trees for roosting makes them unsuitable for many bat species. One exception was *P. nathusii*, known
350 to exploit large wetlands in Europe (Flaquer et al., 2009) and to have maternity roosts in the area of
351 the Norfolk Broads, where many recordings have been collected and the species is probably resident
352 (www.nathusius.org.uk; Newson et al., 2015).

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

362 Five species showed a clear significant decrease in occurrence as the total impervious surface
363 increased, indicating strong avoidance of large urban areas (*B. barbastellus*, *M. daubentonii*, *M.*
364 *mystacinus/brandtii*, *M. nattereri* and *P. auritus*). These are generally woodland-foraging species
365 (Entwistle et al., 1996; Parsons and Jones, 2003; Buckley et al., 2013) and the high level of
366 disturbance and artificial lighting (Aughney et al., 2012; Zeale et al., 2012; Claireau et al., 2019), in
367 addition to the scarcity of old, traditional and wooden buildings (Howard and Richardson, 2009) are
368 likely the main factors reducing their chance of exploitation of urban habitats. *Pipistrellus* and
369 *Nyctalus* species, as well as *E. serotinus*, were in general less influenced by the presence of urban
370 areas, demonstrating an ability to exploit a wider range of habitats. Nevertheless, the occurrence of
371 *P. pygmaeus* was negatively associated with continuous impervious surface and positively associated
372 with the number of impervious patches, meaning a tendency to select small villages and groups of

373 isolated houses for roosting. Other studies confirmed that this species depends on buildings for
374 roosting (Oakeley and Jones, 1998), often forages near streetlamps (Bartonička et al., 2008) and forms
375 large and stable maternity colonies in buildings in Europe (Barlow and Jones, 1999). However,
376 buildings which are close to tree cover and linear vegetation elements, and within 0.5 km of a major
377 river or a woodland, are preferred (Jenkins et al., 1998). In the most urban centres in Norfolk, such
378 as Norwich and Thetford, where *P. pygmaeus* was recorded, activity was mainly restricted to water
379 courses.

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

387

388 4.2 Scenarios

389 Expansion of existing inhabited areas (Scenario 1) in general resulted in negative impacts on the
390 bat community, in particular for species such as *B. barbastellus*, *M. mystacinus/brandtii* and *M.*
391 *nattereri*, which are associated with woodland and riparian habitats (Parsons and Jones, 2003; Kaňuch
392 et al., 2008; Zeale et al., 2012). Nevertheless, impacts were not universal, with other species either
393 showing no effect or limited negative impacts (*P. pygmaeus* and *P. auritus*). Increasing the
394 fragmentation of impervious surface (Scenario 2) had little effect on bat occurrence but clear negative
395 effects on bat activity, suggesting that overall, urban growth should be sought through the expansion
396 of existing urban blocks, rather than creating new urban patches, in order to avoid disturbance in
397 potential commuting or foraging sites.

398 Clear positive effects on bat occurrence and activity were associated with increasing the
399 discontinuous woodland surface (Scenario 3). The preservation of this habitat, tree planting and
400 woodland creation, should therefore be of primary importance. The only exception was *E. serotinus*,
401 which instead appears adapted to take advantage of built-up areas (Catto et al., 1996), and would
402 benefit from continuous woodland expansion (Scenario 4). Foraging habitat of *E. serotinus* shifts
403 from woodland from May to July, to pastures from August to October (Robinson and Stebbings,
404 1997), and the selection of continuous woodland may be due to an increase in prey abundance in
405 dense vegetation (Müller et al., 2012). On the contrary, continuous woodland expansion, which in
406 Norfolk relates to coniferous plantations, may have negative effects on the activity of *B. barbastellus*,
407 *M. nattereri* and *N. noctula*, suggesting that this habitat is not selected for foraging by these species,
408 and in general its expansion may not be the ideal solution to safeguard bat populations.

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

419 In addition to planning development in a way that will minimise impacts on bat communities, it
420 may also be possible to compensate for any potential negative effects by creating or enhancing semi-
421 natural habitats. According to our scenarios, creation or expansion of existing large woodland blocks
422 would not likely be a suitable strategy to offset any potential losses caused by increased urbanisation,

423 as effects of expanding continuous woodland varied among species and were negative for the species
424 which would be most impacted by the expansion of impervious areas (*B. barbastellus* and *M.*
425 *nattereri*). With the exception of *E. serotinus*, effects of increasing open woodland habitats tended to
426 positive. Expansion of discontinuous woodland, which according to our definition includes areas with
427 an intermediate level of tree cover in addition to hedgerows, tree lines and even gardens, would be a
428 better strategy to compensate for potential negative effects of urban expansion. There is, however, a
429 caveat here in that most of dense woodland blocks in the study area were commercial coniferous
430 plantations. Not enough native woodland exists to assess whether in fact large blocks of this habitat
431 would benefit the bat community, although there would seem little likelihood of introducing such a
432 habitat in the study area. Nevertheless, these analyses suggest that encouragement of unmanaged
433 areas within the existing continuous woodland plantations may be a beneficial management strategy
434 to explore.

435 We have considered bats in generally urbanised landscapes within a matrix of intensive
436 agriculture. It should be noted that, in common with most citizen science surveys, the survey locations
437 were not random and were more likely representative of locations that were more accessible to
438 observers. Nevertheless, given that the focus of the paper was on urban settlements, and adjacent
439 areas that potentially could be developed in the future, we do not believe this is likely to have caused
440 any significant bias in our results. We should stress, however, the importance of natural habitats for
441 bats, which were largely absent from our study area. Habitats such as lakes, water courses, wetlands,
442 and generally every area characterised by the presence of trees and shrubs, with special reference to
443 unmanaged wooded patches, need to be preserved as unaltered as possible. Where these areas have
444 already been altered, minimising disturbance should be of primary importance.

445

446 *4.3 Conclusions*

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

459

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464

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466

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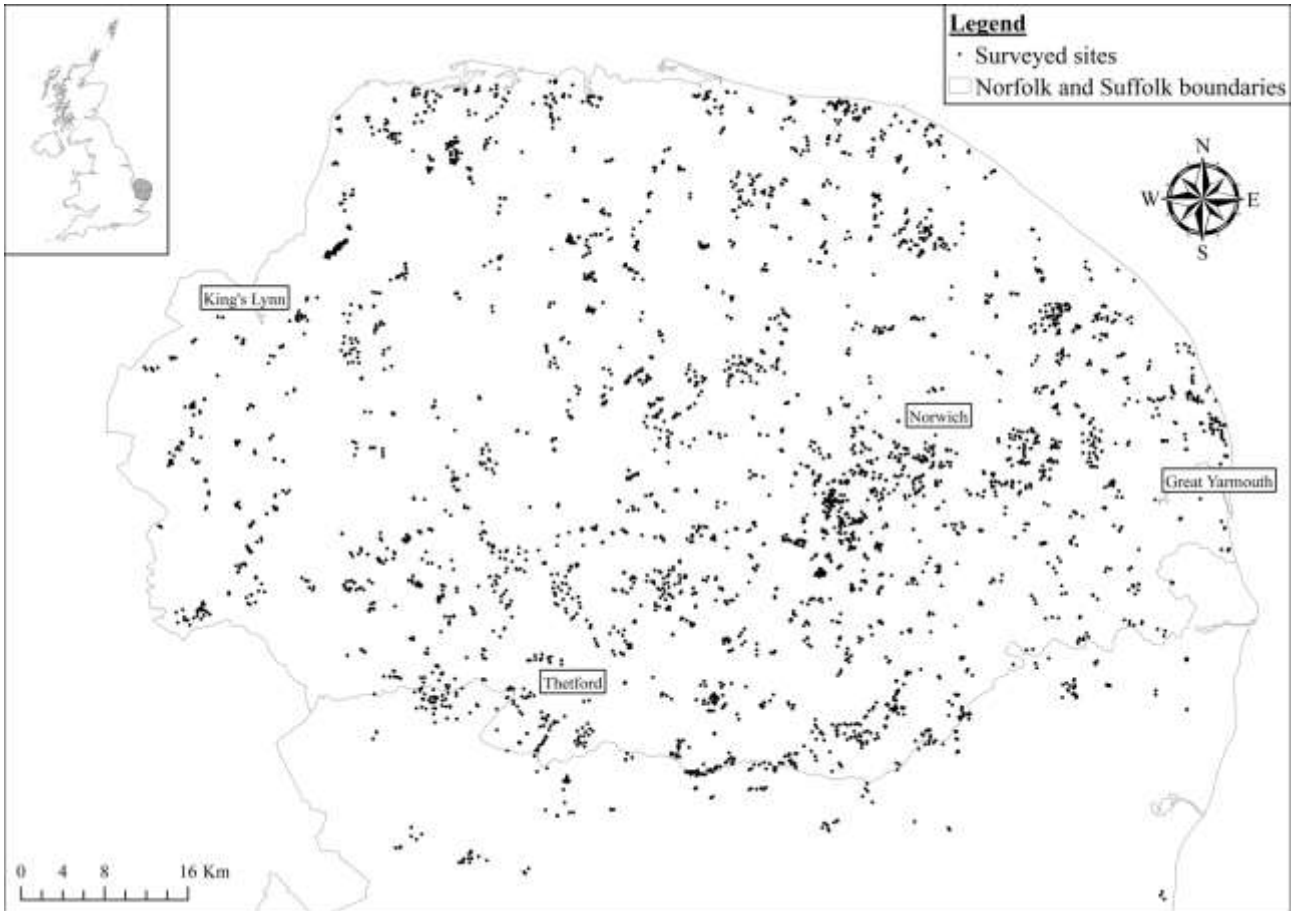
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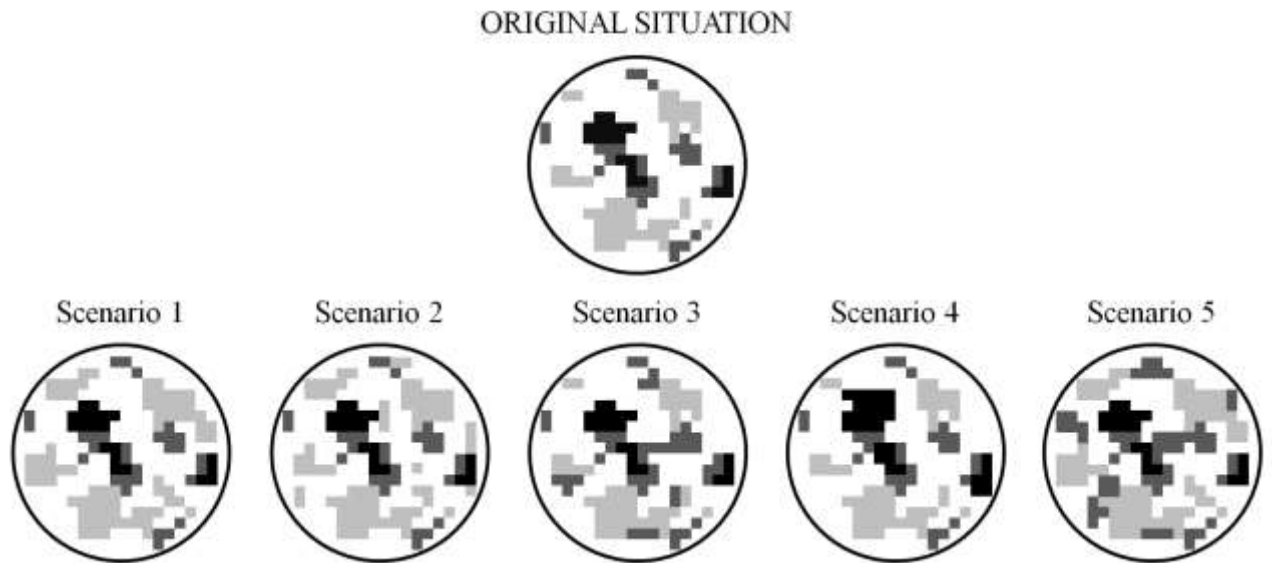


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Figure 1. Locations of the 5690 sites included in the study.

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Figure 2. Scenario illustration examples for a hypothetical site. The black circle represents the buffer drawn around the site to characterize 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.

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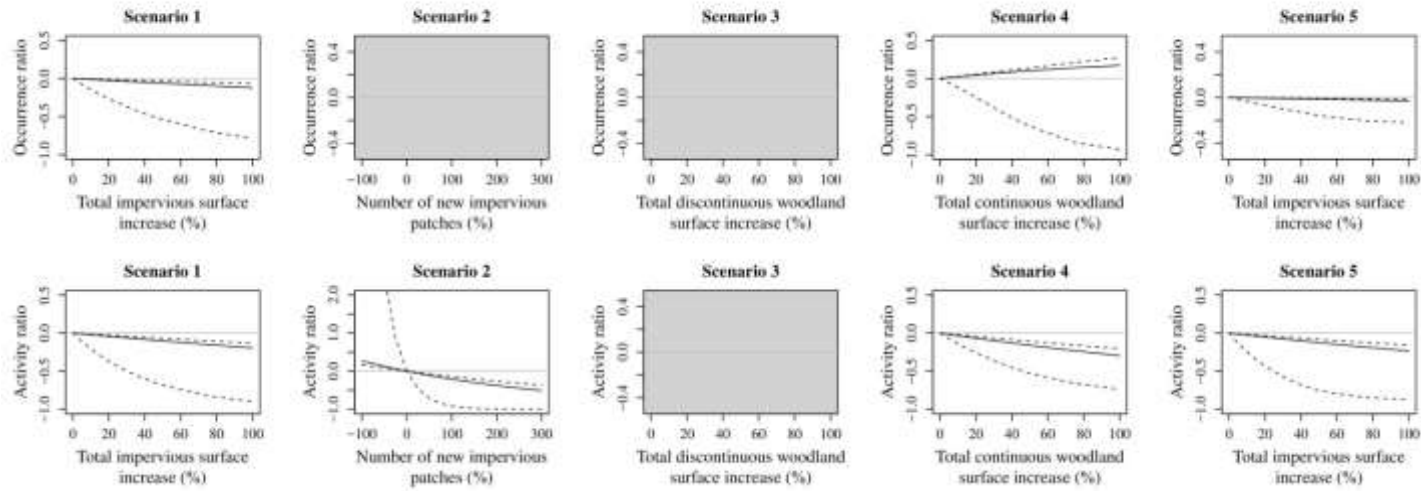
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Barbastella barbastellus



Eptesicus serotinus

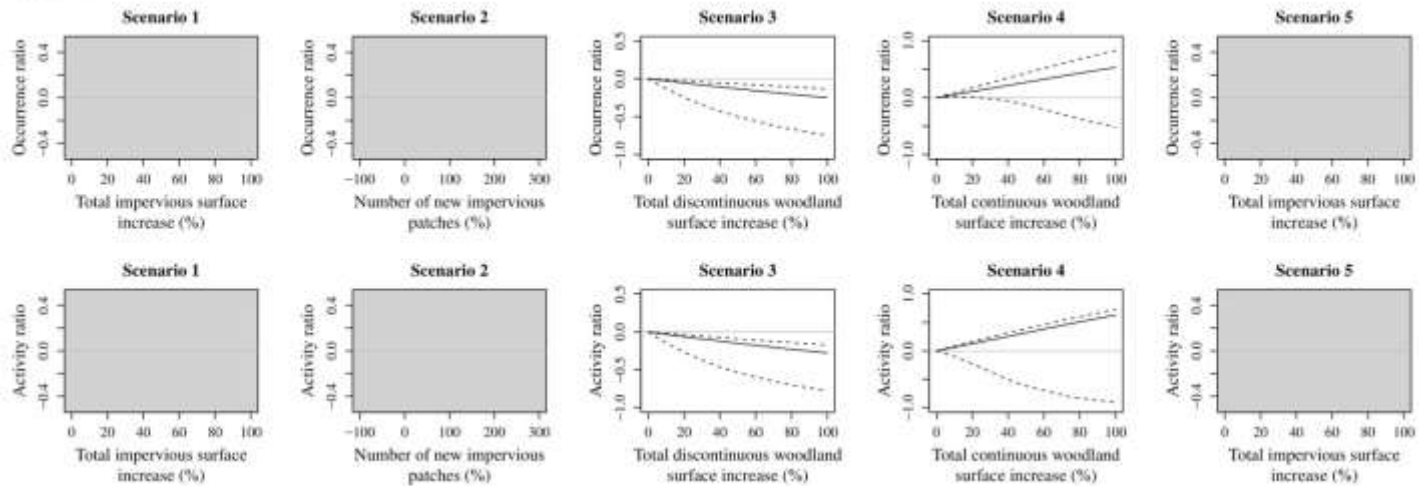
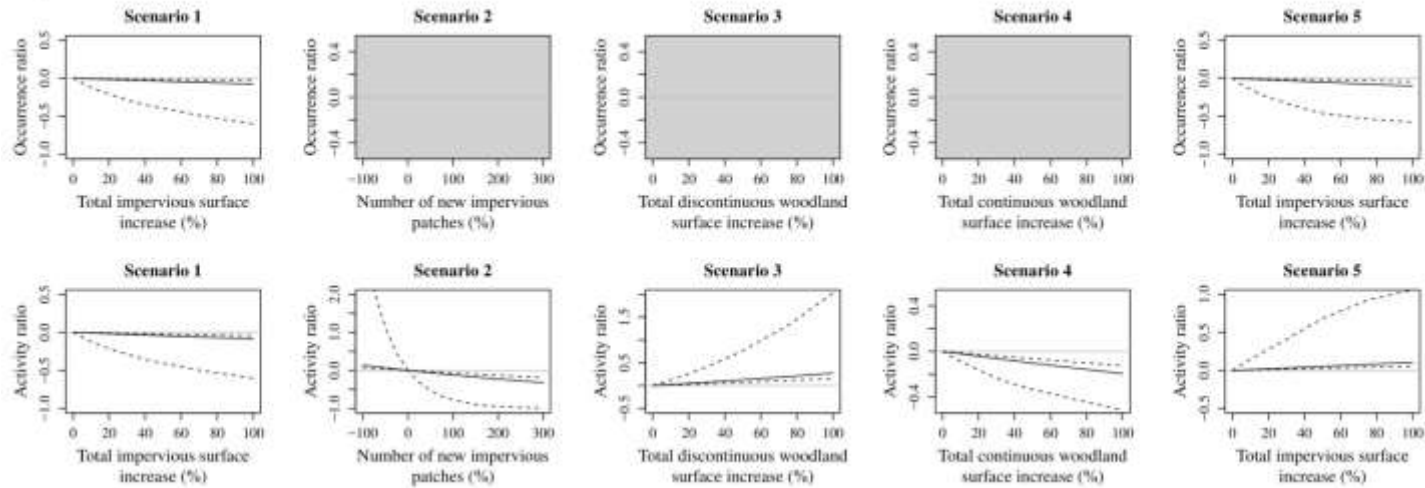


Figure 3. Scenario results for four representative species in the study. Scenarios are presented in order from left (Scenario 1) to right (Scenario 5). Grey panels indicate no significant effect of the habitat variable addressed in the given scenario.

Myotis nattereri



Plecotus auritus

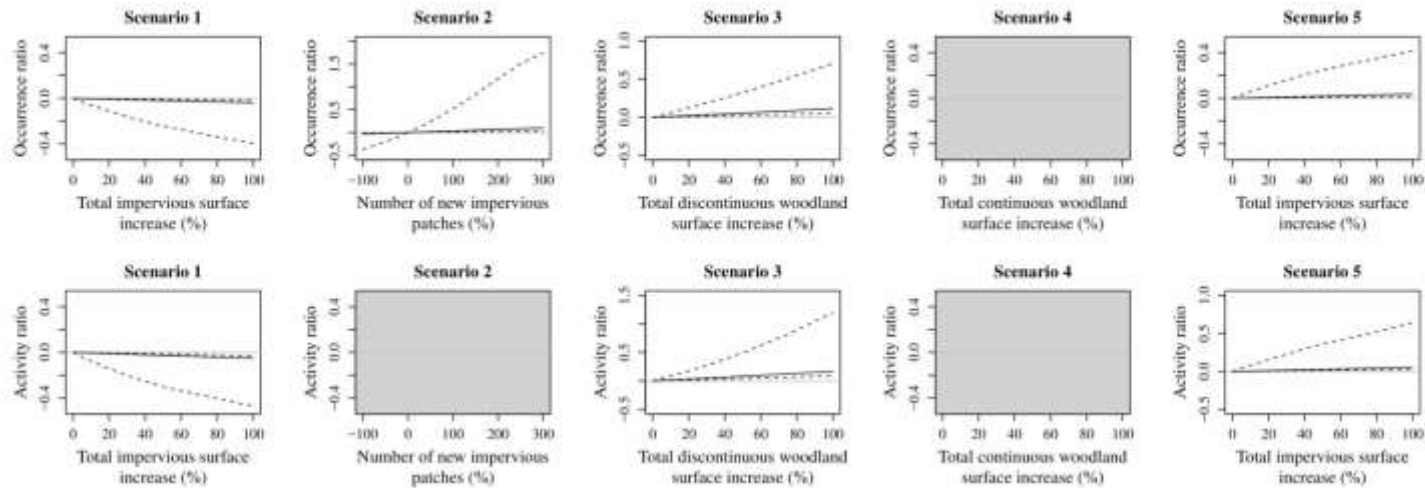


Figure 3 (continued). Scenario results for four representative species in the study.

Table 1. Core Sustenance 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

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						Total impervious surface		Number of impervious patches		Total discontinuous woodland surface		Total continuous woodland surface		Average elevation		Late season		Year						Deviance explained (%)			
	Dmin surface area		Lake surface area		River surface area		Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	Distr.	Activ.	2014		2015		2016		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	+	+	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	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	+	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	+	+	NS	NS	8.85	14.00