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

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**Bats in urbanising landscapes: habitat selection and recommendations**

**for a sustainable future**

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**Running title: Bats in urbanising landscapes**

## 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).

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

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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.

99

*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. 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 Sustenance 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, the 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 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) 90m 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).

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

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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 ($\Delta$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.

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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

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

*3.3 Scenarios of future development*

   In Figure 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 4.

   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–

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

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.

17

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

*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).

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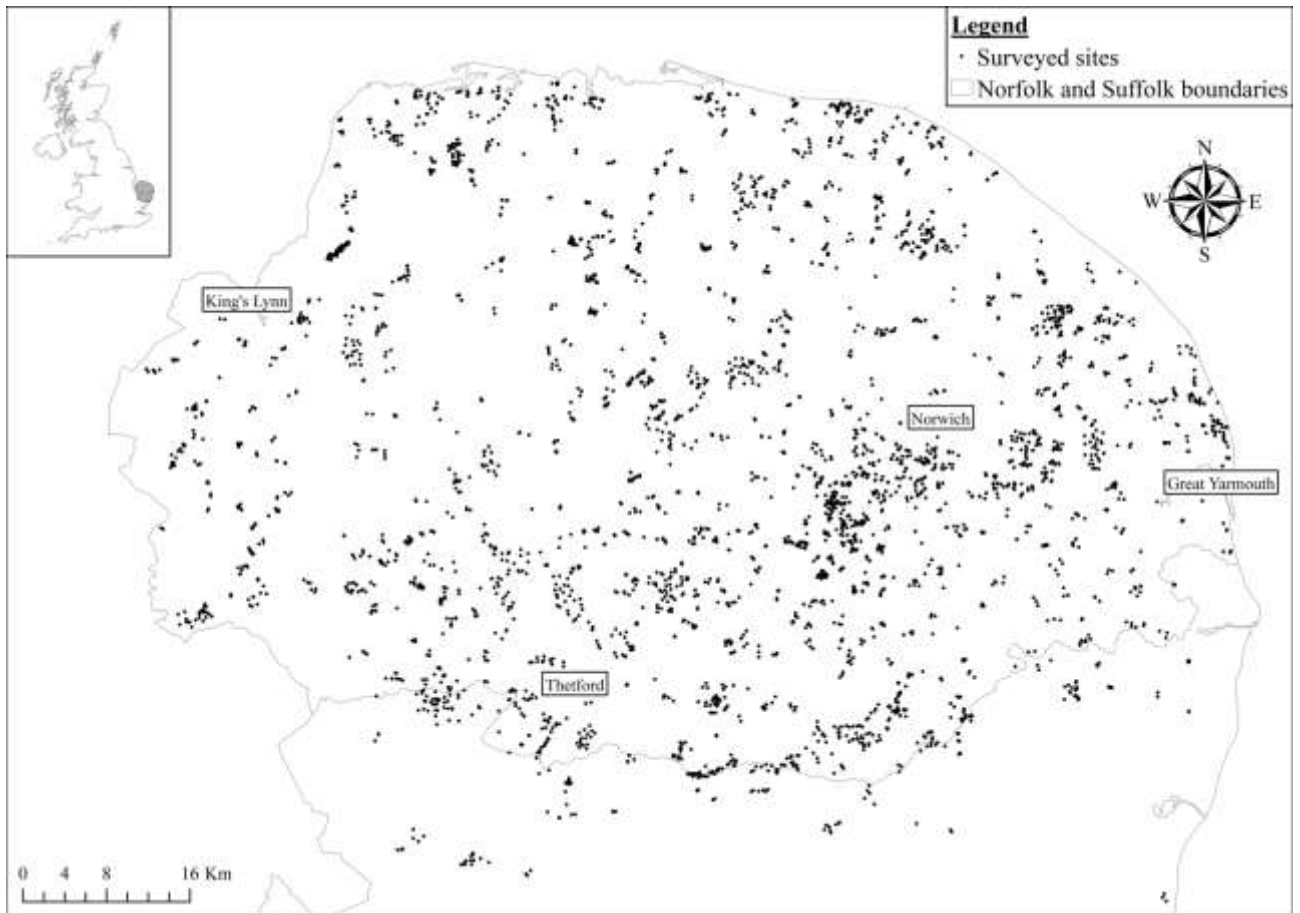665      University Press, New York. 342 pp.

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

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ORIGINAL SITUATION



Scenario 1    Scenario 2    Scenario 3    Scenario 4    Scenario 5
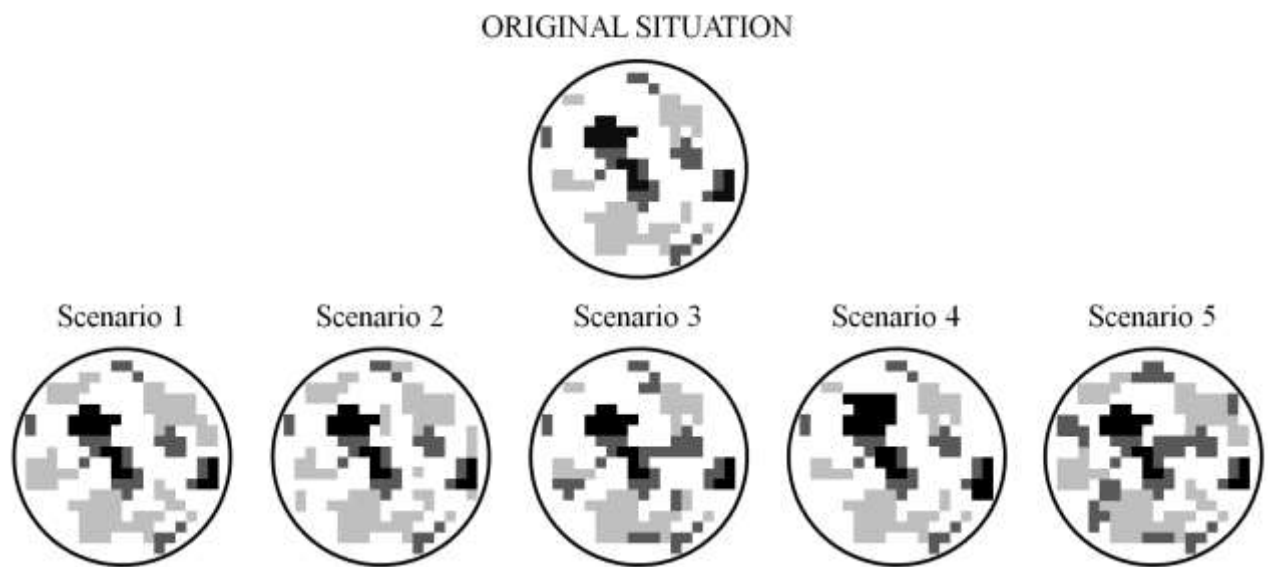
**Figure 2.** Scenario illustration examples for a hypothetical site. The black circle represents the buffer drawn around the site to characterize the CSZ of a certain species. Inside the CSZ, the three habitat components considered in scenarios are shown: impervious areas (light grey), discontinuous 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.

## Barbastella barbastellus
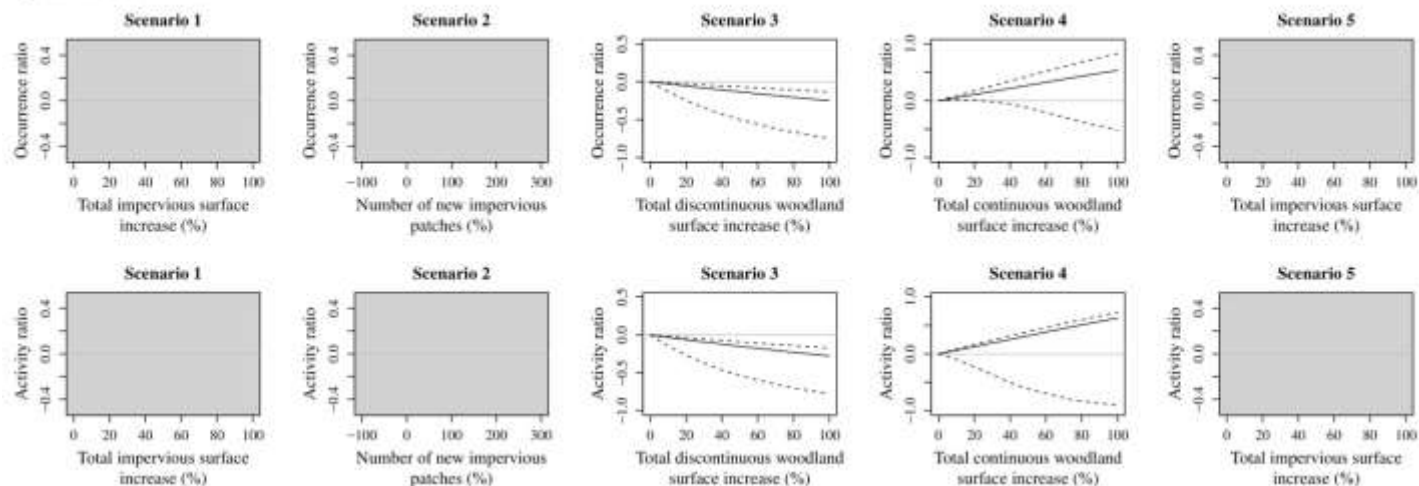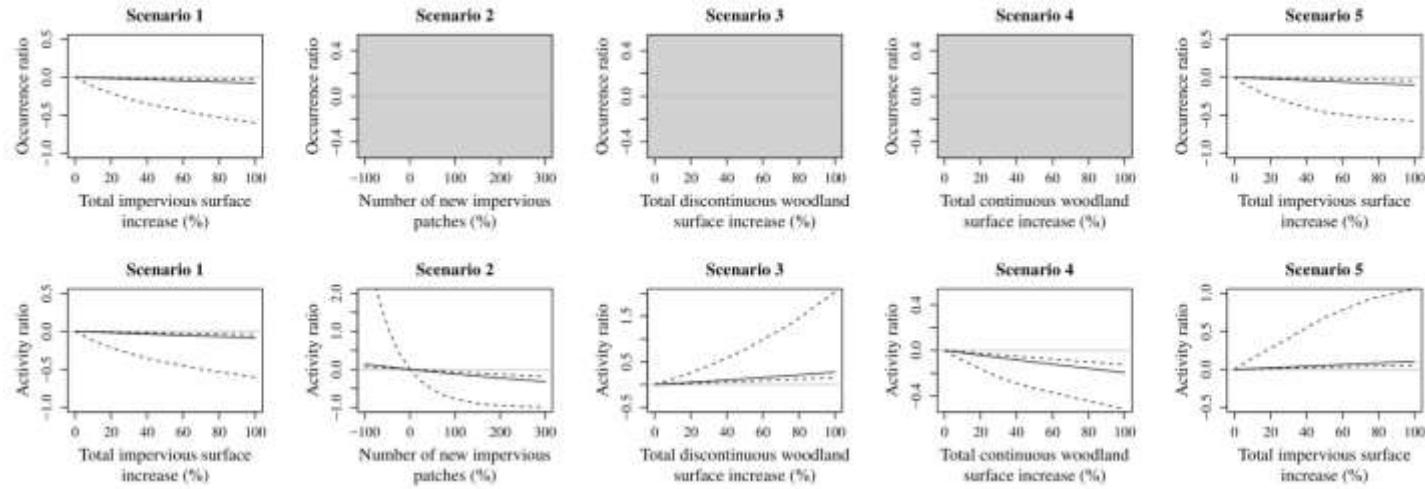


## Eptesicus serotinus



31
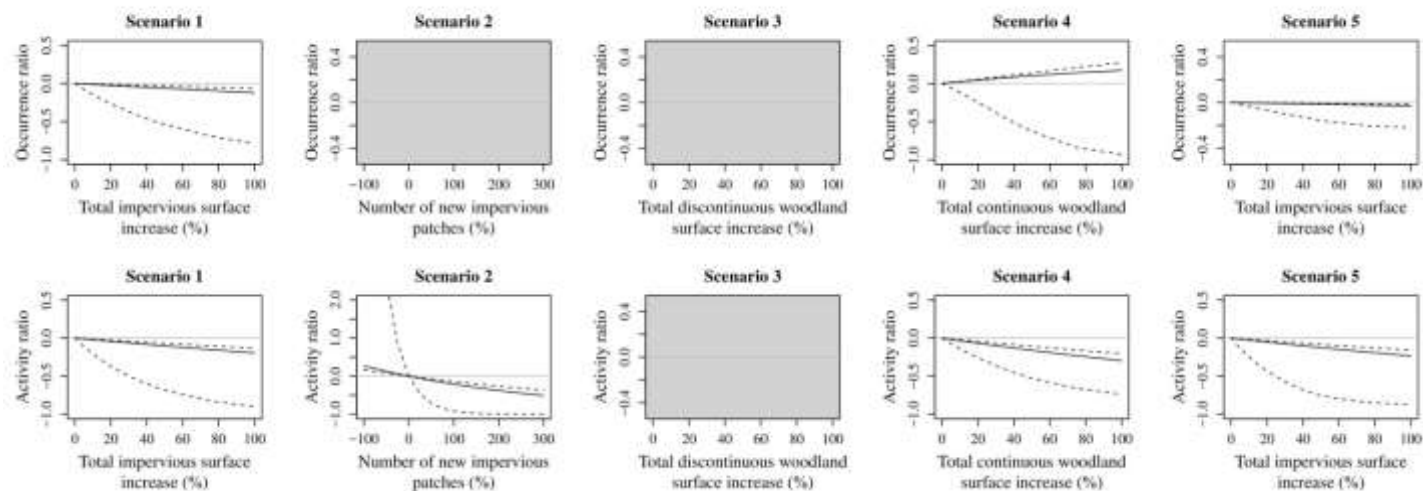
**Figure 3.** Scenario results for four representative species in the study. Scenarios are presented in order from left (Scenario 1) to right (Scenario 5). Grey panels indicate no significant effect of the habitat variable addressed in the given scenario.

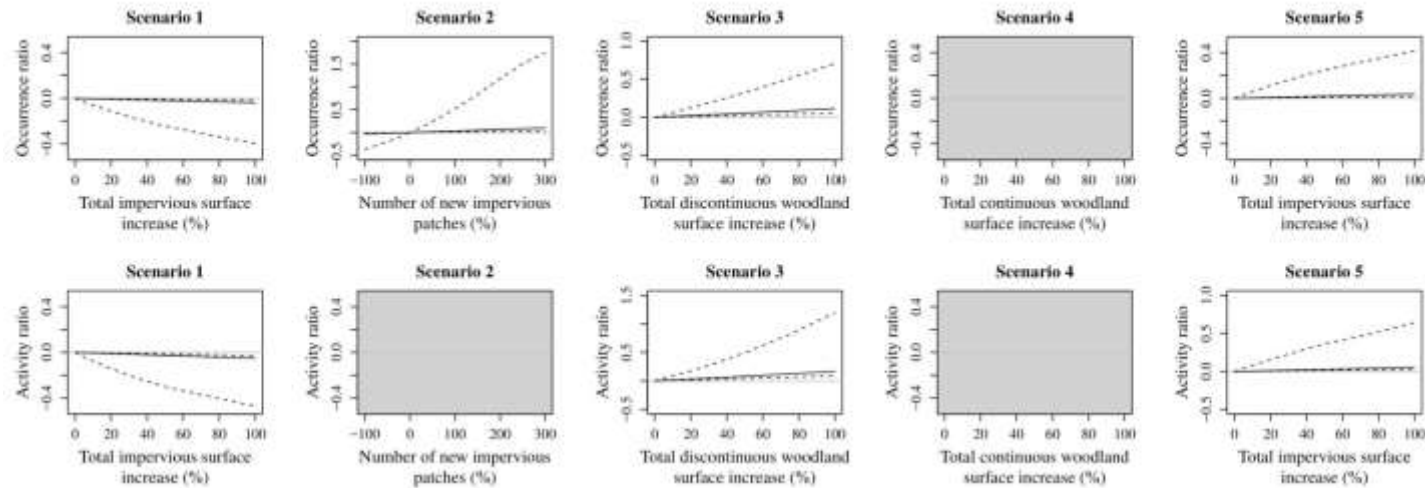*Myotis nattereri*



*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) |
|---|---|---|
| *Barbastella barbastellus* Schreber, 1774 | Barbastelle | 6 |
| *Eptesicus serotinus* Schreber, 1774 | Serotine | 4 |
| *Myotis daubentonii* Kuhl, 1817 | Daubenton's bat | 2 |
| *Myotis mystacinus* Kuhl, 1817 *Myotis brandtii* Eversmann, 1845 | Whiskered/Brandt's bat | 1 |
| *Myotis nattereri* Kuhl, 1817 | Natterer's bat | 4 |
| *Nyctalus leisleri* Kuhl, 1817 | Leisler's bat | 3 |
| *Nyctalus noctula* Schreber, 1774 | Common noctule | 4 |
| *Pipistrellus nathusii* Keyserling & Blasius, 1839 | Nathusius' pipistrelle | 3 |
| *Pipistrellus pipistrellus* Schreber, 1774 | Common pipistrelle | 2 |
| *Pipistrellus pygmaeus* Leach, 1825 | Soprano pipistrelle | 3 |
| *Plecotus auritus* 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 | Drain surface area Distr. | Drain surface area Activ. | Lake surface area Distr. | Lake surface area Activ. | River surface area Distr. | River surface area Activ. | Total impervious surface Distr. | Total impervious surface Activ. | Number of impervious patches Distr. | Number of impervious patches Activ. | Total discontinuous woodland surface Distr. | Total discontinuous woodland surface Activ. | Total continuous woodland surface Distr. | Total continuous woodland surface Activ. | Average elevation Distr. | Average elevation Activ. | Late season Distr. | Late season Activ. | 2014 Distr. | 2014 Activ. | 2015 Distr. | 2015 Activ. | 2016 Distr. | 2016 Activ. | Deviance explained (%) Distr. | Deviance explained (%) Activ. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Barbastella barbastellus* | NS | NS | NS | NS | NS | NS | -** | -*** | NS | -* | NS | NS | ∩** | -* | ↗*** | ∩*** | +*** | +*** | NS | NS | NS | NS | +*** | +** | 9.91 | 22.90 |
| *Eptesicus serotinus* | NS | -*** | NS | NS | NS | ∩*** | NS | NS | NS | NS | -*** | -** | ∩*** | ∩*** | NS | NS | +*** | +*** | +*** | +*** | +*** | +*** | +*** | +*** | 10.70 | 22.70 |
| *Myotis daubentonii* | NS | -*** | +* | NS | +*** | ∩*** | -* | NS | +* | NS | NS | +*** | NS | NS | -* | ∪*** | +*** | NS | +*** | NS | NS | +*** | +*** | +*** | 6.39 | 28.70 |
| *Myotis mystacinus/brandtii* | NS | NS | +* | +* | ∩** | NS | -*** | -* | NS | NS | +*** | NS | NS | ∩** | NS | NS | +*** | +*** | +*** | +*** | NS | NS | -** | NS | 15.60 | 31.80 |
| *Myotis nattereri* | NS | NS | +* | +* | NS | NS | -** | -** | NS | -** | NS | +* | NS | -* | NS | NS | +*** | +*** | +*** | +*** | +*** | +*** | +*** | +*** | 12.30 | 22.70 |
| *Nyctalus leisleri* | NS | NS | ∩** | ∩*** | NS | NS | NS | NS | NS | -* | NS | NS | NS | NS | NS | NS | +* | +* | +* | +** | +*** | +* | +*** | +** | 27.70 | 55.20 |
| *Nyctalus noctula* | ∩*** | ∩*** | +** | +*** | -* | NS | NS | NS | NS | NS | NS | +*** | ∩*** | -* | ∩** | NS | +*** | +*** | +* | NS | +*** | +*** | +*** | +*** | 9.38 | 17.30 |
| *Pipistrellus nathusii* | NS | +*** | +* | +*** | NS | NS | ∪** | NS | NS | NS | NS | +** | NS | NS | ∪*** | NS | -** | -** | NS | NS | NS | NS | NS | -** | 12.60 | 34.70 |
| *Pipistrellus pipistrellus* | NS | -*** | NS | ∪*** | ∪* | +* | NS | NS | NS | NS | NS | NS | -* | NS | NS | ∪*** | +** | +** | NS | NS | NS | NS | NS | +** | 6.59 | 5.76 |
| *Pipistrellus pygmaeus* | NS | +** | +*** | ∩*** | +** | NS | ∩*** | ∪*** | +** | NS | +** | NS | NS | +*** | +*** | -*** | +*** | +*** | NS | -* | NS | NS | NS | NS | 12.70 | 11.30 |
| *Plecotus auritus* | NS | NS | -* | NS | -* | NS | -*** | -*** | +* | NS | +** | +* | NS | NS | ∩** | ∩*** | +*** | +*** | NS | NS | NS | NS | +*** | +*** | 8.85 | 14.00 |