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15 **Opportunities for improving the foraging potential of urban waterways for bats**

16 **Paul R. Lintott[AB], Nils Bunnefeld[A], Kirsty J. Park[A]**

17 [A] Biological and Environmental Sciences, School of Natural Sciences, University of Stirling, Scotland,

18 FK9 4LA

19 [B] Corresponding author: Paul Lintott, Address: Biological and Environmental Sciences, School of

20 Natural Sciences, University of Stirling, Scotland, FK9 4LA, Email: p.r.lintott@stir.ac.uk   Telephone:

21 +44 (0)1786 467787

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42 **Abstract**

43 The rapid rate of urbanisation over the past century has occurred over a relatively small proportion

44 of the earth's surface, yet it has had considerable ecological impact at a global scale. Urban

45 waterways have historically been regarded as a disposable resource for human benefit which has

46 had severe biological consequences. River rehabilitation schemes are attempting to address this;

47 however restoration is frequently undertaken with minimal scientific input and fails to improve

48 biodiversity. Many bat species are strongly associated with aquatic or adjacent riparian habitats but

49 respond negatively to the built environment; however, we know little about the utilisation of urban

50 waterways by bats. We recorded a total of 19,689 bat passes of seven species/genera from 30 urban

51 waterways throughout the U.K. We show that the built environment can negatively affect a variety

52 of species from the riparian zone up to 3km from a waterway. Additionally, *Myotis* sp. activity was

53 greater in waterways bounded by steep banksides and clear of invasive plant species. We also found

54 differences in the response of two cryptic pipistrelle species to the built environment at multiple

55 spatial scales indicating the difficulties of assessing how adaptable even morphologically similar

56 species are to urbanisation. Beneficial urban waterway rehabilitation schemes for bats require

57 management at multiple spatial scales. At a local scale, retaining a vegetated riparian zone, with a

58 reduction in invasive aquatic plant species, is likely to benefit a variety of taxa. At a landscape scale,

59 our results show that the influence of the built environment can stretch a considerable distance

60 highlighting the necessity for conservation funding to be spent on the implementation of landscape

61 scale environmental improvement schemes which encompass the entire urban matrix.

62 **Keywords**: Chiroptera; Cryptic species; Fragmentation; Invasive species; Landscape management;

63 River habitat; Urban ecology

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Introduction

The unprecedented rate of urbanisation over the past century has occurred on a small proportion of the earth's terrestrial surface (<3%), yet its ecological footprint is widespread and its impact global (Grimm et al. 2008). Urbanisation can fragment and dramatically modify large parcels of land, often permanently with little chance for recovery (McKinney 2006). As urban landscapes expand, they influence an increasing proportion of regional, national and global biodiversity (Dearborn & Kark 2010). Understanding how species respond to the built environment is therefore essential for mitigating and managing urban ecosystems.

Urban waterways have historically been regarded as a disposable resource for human benefit including their modification for flood mitigation, water supply, and use as sinks for pollution (Paul & Meyer 2001). These alterations have had severe biological consequences creating disturbed ecological systems with water quality problems, highly variable flow regimes and an extremely modified physical habitat (Beavan et al. 2001). However in recent decades, an increasing recognition of the importance of urban greenspace (including urban waterways) for its environmental and human wellbeing benefits has led to efforts to rehabilitate urban waterways (Matsuoka & Kaplan 2008). Supported by legislation and policy frameworks (e.g. the EU Water Framework Directive, the Australian Commonwealth Wetlands Policy 1997), pollution problems and habitat degradation are being addressed for urban waterways and associated surrounding riparian habitat. Despite the fact that urban waterways are frequently recorded as key habitats within the built environment for maintaining biodiversity (e.g. Gaisler et al. 1998), restoration efforts in these habitats have often failed to increase native biodiversity for taxa including fish and benthic macroinvertebrates (Stranko et al. 2012). Many river restoration projects are undertaken with minimal scientific input (Wohl et al. 2005), indicating the need for a greater understanding of species requirements to inform management strategies.

90   Within fragmented and disturbed landscapes, urban waterways may function as corridors linking

91   fragmented greenspace patches (i.e. woodland, parkland; Bryant 2006) alongside connecting urban

92   landscape with surrounding rural habitat. Waterways can therefore improve gene flow between

93   populations, act as migration routes out of urban areas, and facilitate movement throughout the

94   urban matrix whilst avoiding areas of high anthropogenic disturbance (Baschak & Brown 1995).

95   However, waterways can increase the dispersal of invasive species, for example Dallimer et al.

96   (2012) found that neophyte richness increased in the direction of water flow along urban rivers.

97   Understanding which local factors (e.g. riparian vegetation characteristics) influence the use of

98   waterways by species is essential in ensuring that native species are able to utilise these ecological

99   corridors to travel within the urban environment. Additionally, there is an increasing emphasis being

100   placed on understanding species distributions within urban areas at a landscape scale (Ignatieva et

101   al. 2011), for example determining how the surrounding built environment may influence which

102   species are able to access waterways. Examining how best to restore biodiversity in urban rivers and

103   canals therefore requires assessment at multiple spatial scales to examine how species respond to

104   modified waterways and the complexity of the surrounding urban matrix.

105   The prevalence of species within the urban matrix depends on their capacity to survive and adapt to

106   heavily modified landscapes and anthropogenic disturbances. In this regard, although many species

107   of bats (Chiroptera) have adapted to exploit human resources (e.g. insects at artificial light sources;

108   Mathews et al. 2015), the majority of bat species are negatively impacted by urbanisation (Russo &

109   Ancillotto 2014). The highest rates of bat foraging activity within the urban matrix are often found by

110   waterways due to drinking opportunities and high insect prey concentrations (Li & Wilkins 2014).

111   Although a substantial volume of work has been conducted in non-urban environments investigating

112   how vegetation characteristics and habitat composition at multiple spatial scales influence bat use of

113   waterways (e.g. Akasaka et al. 2009), relatively little is known about the factors that influence

114   foraging bats along urban waterways.

115 Although *M. daubentonii* is widespread throughout Europe and parts of Asia and is classified as a

116 species of 'Least Concern' by the IUCN Red List of Threatened Species (2008), its strong association

117 with riverine habitats makes this species particularly vulnerable to changes in river management

118 which may isolate populations or have a severe effect on available foraging habitat (Warren et al.

119 2000). Langton et al. (2010) found that *M. daubentonii* activity was negatively associated with the

120 percentage of built land in the surrounding 1 km indicating that this species may be negatively

121 impacted by urbanisation.

122 The two most common species of pipistrelle bat found within the study area, *P. pygmaeus* and *P.*

123 *pipistrellus*, are cryptic species with very similar flight morphologies (Jones & Van Parijs 1993) but

124 different foraging behaviours. In a non-urban setting, Watts et al. (2006) found that *P. pygmaeus*

125 preferentially selected riparian habitats over all other habitat types in its core foraging areas,

126 whereas *P. pipistrellus* was more of a generalist, foraging in a wider range of habitats. Little is known

127 of the response of these species to the built environment although Hale et al. (2012) found that *P.*

128 *pipistrellus* activity at urban ponds peaked with moderate levels of adjacent urban grey space.

129 This paper addresses how waterway and bank vegetation characteristics and the composition of the

130 riparian zone influence activity levels for a range of bat species/genera. Given their relatively high

131 mobility, we also assess how the wider landscape influence bat activity. Additionally, we examine if

132 two morphologically similar species respond differently to the extent of urban grey space. We use

133 these results to recommend management strategies to protect and improve urban waterways for

134 the benefit of bats.

135 **2. Materials & methods**

136 *2.1 Site selection*

137 A total of 30 stretches of urban waterways within the U.K. were identified using digital maps (EDINA

138 2013). Stretches of waterway measuring at least 8km in length, where a minimum of a third of the

139   watercourse was contained within an urban area, were selected (Figure 1). Urban areas were

140   designated as those where urban cover was the dominant land use within a 1km grid square as

141   categorised by the UK Land Cover Map 2000. Waterways were selected by latitude, longitude, safety

142   issues (e.g. avoiding stretches of river containing weirs), and degree of urbanisation in the

143   surrounding 1km using a stratified random sampling method. Sites surveyed on consecutive nights

144   were a minimum of 50km apart to minimise any bias. Starting points were randomised between

145   sites to ensure there was no spatial bias towards urban or rural areas. Each waterway was surveyed

146   once by a single surveyor. We recognise that a single visit to each waterway provides only a coarse

147   description of local bat activity but here we are interested in the relative influence of waterway

148   characteristics on bat activity which requires that the number of replicates is maximised.

149   *2.2 Vegetation surveys*

150   Daytime vegetation surveys were conducted on the same day as the bat survey to ensure that

151   appropriate vegetative conditions were recorded. A total of 16 point count locations were

152   designated along each waterway, a minimum of 400m apart. Vegetation characteristics, based upon

153   the Environment Agency's River Habitat Survey (Raven et al. 1998), were recorded at each location

154   (listed in section 2.61).

155   *2.3 Bat surveys*

156   Determining how bats respond to waterway quality and characteristics is difficult given that the vast

157   majority of waterway surveys (e.g. Langton et al. 2010) are conducted bankside which limits

158   surveying to those locations where the bankside is accessible (i.e. missing heavily vegetated areas or

159   stretches of river bounded by private land). We therefore used the technique of surveying by kayak

160   to enable us to record bat activity along entire stretches of waterway through contrasting

161   landscapes.

162 Bat activity was quantified using a frequency division bat detector (Anabat SD2, Titley Electronics)

163 with the detector microphone mounted on a helmet. The helmet was worn by the surveyor who

164 paddled the waterway stopping for 8 minute point counts at each of the 16 locations surveyed for

165 vegetation. During surveying the microphone was approximately 1m above the river surface and

166 pointed in the direction of travel. Each transect section between point counts was paddled at

167 approximately 5km/h. Wherever possible, the transect sections and point counts were undertaken 4

168 metres from the right hand bank to minimise differences in non-aquatic habitat surveyed between

169 point counts. Artificial lighting was recorded at each point count using a light meter. Surveying was

170 conducted between May and August in 2012. Each survey commenced 30 minutes after sunset, and

171 was conducted in dry weather, when the temperature was ≥ 10°C, and wind speed ≤ 4 on the

172 Beaufort scale.

173 *2.4 Sound analysis*

174 All bat recordings were analysed using Analook W (Corben 2006). One bat pass was defined as a

175 continuous sequence of at least two echolocation calls from a passing bat (Walsh & Harris 1996). All

176 seven bat genera present within the study area can be identified from detector recordings based

177 upon the search-phase of their echolocation call. However, it can often be difficult to distinguish

178 between the echolocation calls of species within the same bat genus due to similarities in call

179 structure (Schnitzler & Kalko 2001). As a consequence, recordings of *Myotis*, *Nyctalus*, and *Plectous*

180 were identified to genus level and were grouped together within genera-wide categories. The three

181 *Pipistrellus* species in this area (*P. pipistrellus*, *P. pygmaeus* and *P. nathusii*) can be determined by

182 the characteristic frequency (F_c = the frequency at the right hand end of the flattest portion of a call;

183 Corben 2006) of their search-phase echolocation calls. Bat passes with a F_c of between 49 and 51

184 kHz were classed as *Pipistrellus* sp..

185 *2.5 Landscape analysis*

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186 Point count locations and transect route were recorded using the BatNav GPS unit (Wildwood

187 Ecology) and plotted using ArcGIS 10 (ESRI Inc 2013). Buffers of 200m were placed around each point

188 count location covering the waterway and the surrounding riparian landscape. Bats may perceive

189 the landscape at different scales (e.g. Fabianek et al. 2011; Dixon 2012), therefore buffers of 1 and

190 3km were placed around each transect to calculate the composition of the wider landscape. We

191 used data from the OS MasterMap Topography Layer (EDINA 2013) to reclassify the landscape

192 within each buffer into a set of discrete biotope types. These were (i) grey space (e.g. buildings,

193 roads); (ii) greenspace (gardens, parkland, managed grassland, farmland); (iii) inland freshwater and

194 (iv) woodland. The Shannon diversity index (SHDI, a measure of landscape heterogeneity) was

195 calculated as previous studies have found that this influences bat foraging activity in human-

196 disturbed landscapes (Fuentes-Montemayor et al. 2013). The proportion of land covered by each

197 biotope, and SHDI were calculated for each buffer using Fragstats v4.0 (McGarigal et al. 2012).

198 *2.6 Data analysis*

199 Statistical analysis was conducted at two spatial scales; the local scale (using point count data), and

200 the landscape scale (using all calls recorded on the waterway i.e. point count and transects

201 combined). Data analysis was undertaken using R version 2.14 (R Core Team 2012) using the lme4

202 (Bates et al. 2013), effects (Fox 2003), and ggplot2 packages (Wickham 2009).

203 *2.61 Local vegetation and habitat characteristics*

204 We performed a series of Generalised Linear Mixed-Effects models (GLMMs) with binomial error

205 distribution and a logit link to quantify the influence of vegetation and riparian habitat type on bats.

206 A binomial model was run for each species/genera using presence/absence at each point count

207 (n=480) as the response variable to account for highly skewed count data whilst losing relatively

208 little information. Waterway was included as a random (grouping) factor (n=30) to account for

209 pseudoreplication of multiple point counts along each waterway. Based upon vegetation

210   characteristics commonly recorded during river habitat surveys and scientific literature on the

211   ecology of urban bats (e.g. Langton et al. 2010) the following predictor variables were included in

212   the model: (i) waterway and bankside vegetation characteristics: bank profile, bank vegetation type

213   (categorised as either manmade, uniform vegetation structure (1 vegetation type), simple

214   vegetation structure (2-3 vegetation types), or complex (≥ 4 vegetation types) where vegetation

215   types were classified into bryophytes, grasses, tall herbs/grasses, scrub or shrubs, and samplings and

216   trees following Raven et al. 1998), extent of waterway overhung by vegetation, and invasive aquatic

217   species coverage within the waterway; (ii) local habitat characteristics: the extent of freshwater,

218   grey space and landscape heterogeneity in the surrounding 200m of the point count. As

219   temperature and date were positively correlated, only date was included as a covariate as it

220   explained a higher amount of variation in the response variable. Artificial lighting was strongly

221   positively correlated with the extent of grey space in the surrounding 200m of the point count. We

222   therefore only included the extent of localised grey space in our models as this gave a better

223   indication of the extent of anthropogenic pressure facing bats particularly at low light levels (i.e.

224   rural locations) where the light meter was not sensitive enough to distinguish slight differences in

225   surrounding artificial lighting. We present the result of the full model including standardised

226   parameters and confidence intervals for all explanatory variables. Prediction plots were constructed

227   by undertaking simulated draws (n = 2000) from the estimated distribution of one explanatory

228   variable whilst maintaining all other parameters in the model at their median observed values.

229   Spatial auto-correlation was assessed using a spline correlogram of the model residuals (Zuur et al.

230   2009) and Moran's I test (Paradis et al. 2004). On the one occasion where spatial auto-correlation

231   was observed (*Nyctalus* sp. model), the easting and northing Cartesian coordinates and their

232   interaction were added to the model as explanatory variables.

233   2.62 *Landscape characteristics*

234 Generalised linear models (GLMs) with a negative binomial distribution were conducted for each

235 species/genera to assess differences in bat activity between waterways surrounded by contrasting

236 landscapes. Given the high collinearity found between landscape metrics (i.e. between the

237 proportions of different biotope types or the same biotope type at differing spatial scales)

238 preliminary analyses were conducted to determine which landscape metrics should be included in

239 the final model. The approach we followed is outlined by Zuur et al. (2009) and is frequently used to

240 determine the most important landscape predictors to include in the full model (e.g. Fuentes-

241 Montemayor et al. 2013). We used individual GLMs, one per biome per spatial scale, with the total

242 number of passes recorded per waterway, selecting those metrics with the lowest Akaike

243 Information Criterion (AIC). If several landscape parameters were of equal importance (i.e. <5%

244 difference between the lowest AIC value) they were all selected, providing they were not strongly

245 correlated (Pearson correlation coefficient ≤ 0.6 and $p > 0.05$). The full model was run with the

246 landscape metric(s) and date included as explanatory variables and offset by the time taken to

247 complete each full transect to account for differences in transect length between waterways. We

248 used the same approach to determine influential explanatory variables as used in the local

249 vegetation and habitat characteristics models (see section 2.61).

250 *2.63 Differences between species in their response to urbanisation*

251 We assessed the differences between cryptic species *P. pipistrellus* and *P. pygmaeus* in their

252 response to urbanisation at both a 1 and 3km scale. As the proportion of grey space is highly

253 correlated between these two scales, we present only the results for the spatial scale which had the

254 largest effect size. In order to assess the relative effects of grey space, the model was run with the

255 proportion of point counts containing *P. pygmaeus* to *P. pipistrellus* passes (n=480) as the response

256 variable, with waterway included as a random (grouping) factor (n=30). We used the same approach

257 as section 2.61 to determine if there was a significant difference between species in their response

258 to urbanisation at the landscape scale. Differential responses to urbanisation were only assessed for

259   pipistrelle species as there is ecological interest in understanding if cryptic species respond

260   differently in their habitat selection.

261   We only assessed the differential response to urbanisation by pipistrelle species

262   **3. Results**

263   We recorded a total of 19,689 bat passes from 30 urban waterways across the U.K (Table 1). Of

264   these, 8,825 passes (45%) were of *P. pipistrellus*, 5,649 passes (29%) of *P. pygmaeus*, 3,846 (20%)

265   *Myotis* sp. passes, 505 (3%) *Nyctalus* sp. passes, and 43 *Eptesicus serotinus* (< 1%) passes, 40

266   *Plecotus auritus* passes (< 1%), and 18 *P. nathusii* passes (< 1%).

267   *3.1 Myotis sp.*

268   The probability of recording *Myotis* sp. was strongly negatively related to the extent of grey space in

269   the riparian zone surrounding urban waterways, negatively related to the presence of invasive plant

270   species and positively associated with bank profile (Table 2). At locations where the surrounding

271   habitat contained a low proportion of grey space (10%) there was a 68% probability of recording

272   *Myotis* sp. whilst in locations surrounded by highly urban areas (80% grey space) this was reduced to

273   32% (Figure 2a). In locations with little or no invasive plant species there was a 59-65% probability of

274   recording *Myotis* sp., whereas this declined to to 2% in locations where 30% of the river was covered

275   (Figure 2b). Where there was a shallow bank profile (40°) there was a 31% probability of recording

276   *Myotis* sp. whilst in locations with vertical bank sides this increased to a 64% probability (Figure 2c).

277   *Myotis* sp. activity was negatively related to the proportion of grey space in the surrounding 3km

278   (Appendix 1). Based on estimated coefficients in Table 2, the predicted activity rate of Myotis sp.

279   was 188 (95% confidence interval (CI): 94-373) passes in landscapes containing a low proportion of

280   urban grey space (10%). In highly urban areas (40% grey space) the predicted activity rate was only a

281   third of this (predicted 59 passes CI: 26-133) (Figure 2d).

282   *3.2 Nyctalus sp.*

283   The probability of recording Nyctalus *sp.* was greatest at locations with approximately 25%

284   freshwater coverage in the nearby (200m) landscape (Figure 3), dropping to < 1% in locations

285   containing either no water or high levels of water (40%). Both the extent of urban grey space and

286   extent of overhanging vegetation were statistically significant but had a low effect size and so little

287   biological significance. There were no significant landscape predictors of *Nyctalus sp.* activity (Table

288   2).

289   *3.3 Pipistrellus pipistrellus*

290   The proportion of freshwater was the strongest predictor of *P. pipistrellus* presence; where the

291   surrounding habitat was comprised of a low proportion of water (10%), the probability of recording

292   *P. pipistrellus* was 60%, but reduced to 31% in locations where water was a prominent habitat within

293   the local landscape (40%) (Figure 4a). The extent of the built environment adjacent to the waterway

294   was also important; in locations where the surrounding habitat contained a low proportion of grey

295   space (10%) there was a 66% probability of recording *P. pipistrellus,* whereas in highly urban areas

296   (80% grey space) this was reduced to 44% (Figure 4b). The extent of overhanging vegetation was

297   positively related to *P. pipistrellus* activity; however this was of only marginal significance. There

298   were no significant landscape predictors of *P. pipistrellus* activity (Table 3).

299   *3.4 Pipistrellus pygmaeus*

300   The probability of recording *P. pygmaeus* was negatively related to the extent of grey space and

301   positively related to the extent of overhanging vegetation on a waterway; however both these were

302   of only marginal significance (Table 3). *P. pygmaeus* activity was negatively related to the proportion

303   of water in the surrounding 3km. Based on estimated coefficients in Table 3, the predicted activity

304   rate of *P. pygmaeus* was 192 (95% CI: 75-494) passes in landscapes containing a relatively low level

305   of water (1%). In landscapes containing relatively high levels of water (5%) the predicted activity rate

306   was a tenth of this (21: 4-119) passes (Figure 5). *P. pygmaeus* activity was also positively related to

307   the proportion of woodland in the surrounding 1km however this was of only marginal significance.

308   *3.5 Differences between species in their response to urbanisation*

309   *P. pygmaeus* responded more negatively to urbanisation than *P. pipistrellus;* as the proportion of

310   grey space in the surrounding 3km increased, the probability of recording *P. pygmaeus* relative to *P.*

311   *pipistrellus* declined*.* Based on the estimated coefficients in Table 4 the probability of recording *P.*

312   *pygmaeus* or *P. pipistrellus* in waterways surrounded by low levels of grey space (20%; Figure 6) was

313   approximately equal. However, in waterways surrounded by high levels of grey space (50%), the

314   probability of recording *P. pygmaeus* relative to *P. pipistrellus* was 0.15 (95% CI: 0.09-0.25).

315   **4. Discussion**

316   Expanding urbanisation is increasing the extent to which wildlife comes into contact with the built

317   environment and anthropogenic disturbances. Understanding how species respond to the urban

318   landscape is essential for designing effective conservation strategies. In this study we show that a

319   range of bat species/genera utilise urban waterways but their use can be limited by vegetation cover

320   in riparian zones and both local and landscape habitat composition.

321   *4.1 Effects of local waterway characteristics*

322   The proportion of grey space in the immediate vicinity of a waterway negatively impacted the

323   foraging activity of all species/genera studied with the exception of *Nyctalus sp. P. pipistrellus* is

324   commonly regarded as a generalist species (Nicholls & Racey 2006) and therefore is often perceived

325   to be more adaptable to habitat change and degradation than specialist species (Berthinussen &

326   Altringham 2012). However, we show that even *P. pipistrellus* foraging activity is negatively affected

327   by highly urban surroundings. The continuous nature of urban waterways is thought to facilitate the

328   movement of species through the urban matrix (e.g. Rouqette et al. 2013). Our results show that

329   highly urbanised waterways may have similar barrier effects as roads or artificial lighting (e.g. Kerth

14

330   & Melber 2009), thus making the urban matrix increasingly fragmented and reducing connectivity

331   between green space patches.

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334   Although we only identified *Myotis* passes down to genus, it is likely that the majority of our calls

335   were of *M. daubentonii* given that this species is widespread throughout the U.K. and strongly

336   associated with riverine habitats (Warren et al. 2000). *Myotis* sp. activity was higher in locations with

337   vertical bank sides, which suggests that *Myotis* sp. are frequently using channelised river stretches

338   and canals. Channelised waterways are associated with steep banksides and reduced

339   macroinvertebrate diversity (Horsák et al. 2009), and would not be expected to support high

340   foraging opportunities. However, our results support Akasaka et al. (2009) who found that *M.*

341   *daubentonii* was most active in channelised reaches. Canals, by design, are locations where water

342   movement is either stationary or minimal. Sections of smooth water are favoured by *M. daubentonii*

343   as broken water may interfere with a bats' echolocation or make prey detection and capture more

344   difficult (Warren et al. 2000).Similarly, the presence of invasive aquatic plant species may interfere

345   with the echolocation calls of bats, particularly the trawling action of *M. daubentonii*, and also

346   reduce invertebrate abundance (Stiers et al. 2011), which may reduce foraging efficiency for *M.*

347   *daubentonii*.

348   The response of *Nyctalus* sp. to the extent of freshwater at the local scale supports Gaisler et al.

349   (1998) who found that riverine habitat was preferred by *N. noctula* in the urban landscape.

350   However, in contrast to the linear response Gaisler et al. (1998) found, in our study *Nyctalus* sp.

351   presence peaked at moderate levels of freshwater and declined at higher proportions. The reason

352   for this is unclear, but may correspond to *Nyctalus* sp. utilising a wide range of foraging habitats

353   including open woodland, parkland, and streetlights (Mackie & Racey 2007) which are reduced in

354 extent by a high proportion of freshwater. Moderate levels of freshwater may allow *Nyctalus* sp. to

355 commute through the urban matrix while providing a sufficient range of additional foraging

356 resources and habitats. In contrast to Boughey (2010) we found that *Nyctalus* sp. was affected by

357 the landscape at a relatively local scale (200m). In non-urban locations *Nyctalus* sp. are relatively fast

358 fliers with large home ranges and as such as are unlikely to be constrained by local habitat features.

359 However, in urban areas it appears that local habitat type is important, possibly as commuting and

360 foraging is restricted to fewer locations.

361 *4.2 Effects of the surrounding landscape*

362 The wider landscape was important in determining the use of waterways by both *P. pygmaeus* and

363 *Myotis* sp. Both taxa had the strongest response to the built environment at a 3km scale indicating

364 that the effect of urban grey space is wide reaching (Appendix 1). Although *P. pygmaeus* are strongly

365 associated with water and riparian woodland (Nicholls & Racey 2006), our results show that the

366 proportion of freshwater was negatively related to *P. pygmaeus* activity. This might reflect an

367 intensive use of freshwater in landscapes where this habitat is limited. Similar findings which

368 highlight the more intensive use of isolated key habitats within human-disturbed landscapes are

369 known for taxa including bats (Fuentes-Montemayor et al. 2013) and birds (Vanhinsbergh et al.

370 2002).

371 Our findings for *Myotis* sp. support those of Langton et al. (2010) who found a negative association

372 between *M. daubentonii* activity and built land in the surrounding 1km of a river. Biological water

373 quality declines with increasing urbanisation (Walsh et al. 2001) and is the primary limiting factor of

374 invertebrate diversity (Beavan et al. 2001). Lower prey abundance is therefore likely to reduce

375 *Myotis* sp. foraging efficiency and activity in urbanised waterways. Similarly, the extent of grey space

376 was inversely related to woodland coverage in the surrounding landscape. Many *Myotis* species

377 including *M. daubentonii* forage and roost within woodland (Parsons & Jones 2003) and

378 preferentially select woodland over the built environment to forage within (Sparks et al. 2005). The

379   absence of this habitat within the built landscape is therefore likely to contribute to reduced *Myotis*

380   sp. activity.

381   *4.3 Differences between species in their response to urbanisation*

382   Species with similar morphological traits are often inferred to respond similarly in their response to

383   highly modified landscapes (Safi & Kerth 2004). We show that two cryptic, and largely sympatric

384   European bat species, *P. pygmaeus* and *P. pipistrellus* respond differently in their response to the

385   urban matrix. Despite *P. pipistrellus* showing a stronger negative response to grey space in the

386   immediate vicinity of a waterway, the probability of recording *P. pipistrellus* relative to *P. pygmaeus*

387   was greater when the landscape contained a high proportion of grey space. This supports previous

388   studies identifying *P. pipistrellus* as a generalist species (Nicholls & Racey 2006) which can tolerate

389   moderate levels of urbanisation relative to *P. pygmaeus* (Hale et al. 2012). It may be that *P.*

390   *pygmaeus* can exploit local areas of anthropogenic disturbance for foraging purposes (i.e. foraging

391   around street lamps) but is less tolerant of wide-scale urbanisation than *P. pipistrellus*.

392   *P. auritus* was rarely detected which is not surprising given that it is a woodland species, although it

393   may also have been under-recorded due to its low intensity echolocation calls (Parsons & Jones

394   2000). *Nyctalus* sp. were recorded at almost two-thirds of the waterways surveyed which would be

395   expected given that they are open –adapted bats which are associated with a tolerance of urban

396   areas (Threlfall et al. 2011). However, they were only found at 11% of point count locations

397   indicating a patchy distribution within urban landscapes which may be explained by their consistent

398   use of specific foraging locations rather than foraging speculatively over larger areas (Mackie &

399   Racey 2007).

400   *4.4. Conservation Implications*

401   Species are frequently classed as either urban 'avoiders', 'adaptors' or 'exploiters' (McKinney 2006

402   but see Fischer et al. 2015) in order to determine the extent of conservation action required. Our

403 results show the difficulties associated with categorising species, for example *P. pipistrellus* has been

404 classified as an 'urban adaptor' (Hale et al. 2012) yet appears to show a strong negative response to

405 localised pockets of grey space. Caution should also be taken when inferring high population density

406 within urban areas as adaptation to the built environment, as urban biotopes can act as ecological

407 traps for bats (Russo & Ancillotto 2014). Similarly, there are strong sexual differences in habitat use

408 within the urban matrix which may distort our understanding of the adaptability of a species to

409 urbanisation (Lintott et al. 2014).

410 Historically, urban waterways have been regarded as biologically poor and as sinks for pollution,

411 however legislation and policy frameworks (e.g. the EU Water Framework Directive) are attempting

412 to readdress this. However, the present risk is that if the management actions used by practitioners

413 or decision-makers are not informed by evidence then biodiversity conservation may be negatively

414 impacted (Shwartz et al. 2014). The majority of research, and therefore conservation effort,

415 regarding urban conservation is focused on large, public, green spaces (e.g. parks) whilst relatively

416 little is known of the importance of the wider matrix (Shwartz et al. 2014). In this study we show that

417 a range of bat species (e.g. *M. daubentonii*), respond to both local attributes (e.g. bank profile) and

418 to the composition of the urban matrix and therefore require a more cohesive landscape approach

419 to their conservation. Whilst this study focussed on waterways throughout the UK, these findings are

420 of relevance to urban waterways elsewhere due to the strong connection between bats and riparian

421 habitats (e.g. Walsh & Harris 1996). Additionally, the consideration of bats as bioindicator species

422 (Jones et al. 2009), and the adoption of bats in the UK Government's *Biodiversity Indicators* (DEFRA

423 2014) highlights the potential utility of this taxa to inform on the responses of other taxa similarly

424 affected by urbanisation. Recent biodiversity strategies (e.g. Biodiversity 2020) implementing

425 international and EU legislation aim to establish coherent ecological networks for the benefit of

426 wildlife and people, and we show that at the local scale preventing urbanised riparian zones will

427 benefit many bat species by facilitating movement through the urban matrix. Additionally, the

428 retention of vegetated riparian zones will benefit biodiversity across a range of taxa (e.g. birds and

429   butterflies, Dallimer et al. 2012). Similarly the removal of invasive plant species may increase the

430   suitability of waterways for foraging *Myotis* sp. but also have wider biodiversity benefits (e.g.

431   recovery of native biodiversity; Zavaleta et al. 2001). The importance of local scale factors in

432   determining bat presence in our study indicates that small scale management strategies (e.g.

433   volunteer canal clean-ups or local urban greening schemes) which are generally more cost effective

434   and feasible than citywide conservation strategies (e.g. Barthel et al. 2005) are important in

435   retaining and restoring urban waterway biodiversity. At a landscape scale, we show that extensive

436   urbanisation has a similar negative effect on many bat species as is found across all major taxonomic

437   groups (Olden et al. 2006). The importance of maintaining waterways in good ecological conditions

438   within highly urbanised landscapes is highlighted by the increased use of waterways by *P. pygmaeus*

439   in locations where this resource is scarce. *P. pygmaeus* appear to be using nearby resources more

440   intensively rather than travelling further across the urban matrix to alternative foraging resources.

441   Although conservation strategies will not prevent urban expansion, they can help guide suitable

442   mitigation measures such as highlighting the value of maintaining isolated water bodies in good

443   ecological condition (e.g. removing invasive plant species) in contrast to focusing the majority of

444   effort on the establishment, restoration and maintenance of protected areas (Hoffman et al. 2010).

445   Our results therefore support Inger et al. (2015) in their call for an increasing proportion of

446   conservation funds to be spent on the implementation of landscape scale environmental

447   improvement schemes which will encompass the entire urban matrix and be beneficial for relatively

448   common species such as *P. pygmaeus*.

449   There has been increasing policy interest in promoting the use of semi-natural urban habitats to

450   benefit human health and well-being (Irvine et al. (2013), alongside using urban wildlife encounters

451   to reconnect the public with nature to increase ecological awareness (Prévot-Julliard et al. 2011).

452   Yet, waterways are rarely considered when assessing how greenspace contributes to public health or

453   their engagement with nature (Völker & Kistemann 2011). Well managed waterways therefore have

454   the potential to be important settings for recreational activities such as swimming or canoeing, for

455   human health and wellbeing, and for supporting a range of wildlife species. Town developers and

456   urban planners frequently prioritise the development of waterfronts as cities historically developed

457   on riversides and property/land prices are highest in these locations (Völker & Kistemann 2011); we

458   show that awareness of wildlife requirements and the implementation of relatively easy solutions

459   (e.g. reducing the abundance of invasive aquatic plant species) can have a considerable impact on

460   what species will be found along our urban rivers and canals.

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470   **References**

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631   **Table 1** Summary table of the species recorded from 30 urban waterways across the U.K.

Species	Total passes recorded	% of bat calls	Waterways recorded (%)	Point counts recorded (%)
Pipistrellus pipistrellus	8825	45	100	58
Pipistrellus pygmaeus	5649	29	90	45
Myotis sp.	3846	20	97	54
Nyctalus sp.	505	3	63	11
Eptesicus serotinus	43	< 1%	17	1
Plecotus auritus	40	< 1%	30	1
Pipistrellus nathusii	18	< 1%	27	1

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646 **Table 2** Parameter estimates and likelihood ratio tests of the GLMM for the probability of recording

647 either *Myotis* sp. or *Nyctalus* sp. along an urban waterway. Additionally, the parameter estimate and

648 likelihood ratio test of the GLM for the most important landscape parameter at the most important

649 spatial scale is included.

Species	Scale	Fixed effects	Estimate (± SE)	Log Likelihood	χ2	p
Myotis sp.		Intercept	0.38 ± 0.39			
Myotis sp.	Local	**Bank profile**	**0.23 ± 0.12**	**-288.55**	**3.93**	**0.04**
Myotis sp.	Local	Bank vegetation	0.14 ± 0.37	-287.06	0.94	0.82
Myotis sp.	Local	Date	0.02 ± 0.22	-286.59	0.01	0.92
Myotis sp.	Local	Invasive species	0.35 ± 0.32	-287.19	1.2	0.27
Myotis sp.	Local	**Invasive species (quadratic)**	**-0.26 ± 0.13**	**-289.73**	**6.28**	**0.01**
Myotis sp.	Local	Overhanging vegetation	0.16 ± 0.12	-287.44	1.7	0.19
Myotis sp.	Local	Freshwater (200m)	-0.01 ± 0.12	-286.59	0.01	0.96
Myotis sp.	Local	**Greyspace (200m)**	**-0.46 ± 0.15**	**-291.57**	**10**	**0.002**
Myotis sp.	Local	Landscape heterogeneity (200m)	-0.04 ± 0.13	-286.66	0.15	0.69
Myotis sp.	Landscape	Intercept	-0.50 ± 0.17			
Myotis sp.	Landscape	Date	-0.06 ± 0.17	-343.26	0.11	0.74
Myotis sp.	Landscape	**Proportion of greyspace (3km)**	**-0.44 ± 0.17**	**-347.14**	**3.99**	**0.04**
Nyctalus sp.		Intercept	-3.52 ± 0.80			
Nyctalus sp.	Local	Bank profile	0.33 ± 0.19	-141.25	2.17	0.14
Nyctalus sp.	Local	Bank vegetation	1.45 ± 0.83	-142.92	5.51	0.14
Nyctalus sp.	Local	Date	-0.02 ± 0.19	-140.19	0.05	0.82
Nyctalus sp.	Local	Invasive species	0.04 ± 0.20	-140.26	0.19	0.66
Nyctalus sp.	Local	**Overhanging vegetation**	**-0.42 ± 0.29**	**-142.19**	**4.05**	**0.04**
Nyctalus sp.	Local	**Freshwater (200m)**	**1.23 ± 0.30**	**-144.54**	**8.76**	**0.003**
Nyctalus sp.	Local	**Freshwater (200m) quadratic**	**-0.41 ± 0.14**	**-140.16**	**11.52**	**<0.001**
Nyctalus sp.	Local	**Greyspace (200m)**	**-0.37 ± 0.25**	**-142.29**	**4.25**	**0.04**
Nyctalus sp.	Local	Landscape heterogeneity (200m)	-0.06 ± 0.18	-140.17	0.01	0.94
Nyctalus sp.	Landscape	Intercept	-2.86 ± 0.30			
Nyctalus sp.	Landscape	Date	0.58 ± 0.31	-196.61	4.03	0.44
Nyctalus sp.	Landscape	Proportion of woodland (1km)	-0.81 ± 0.33	-195.13	2.56	0.11

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Table 3 Parameter estimates and likelihood ratio tests of the GLMM for the probability of recording

656   either *P. pipistrellus* or *P. pygmaeus* along an urban waterway. Additionally, the parameter estimate

657   and likelihood ratio test of the GLM for the most important landscape parameter at the most

658   important spatial scale is included.

| Species	Scale	Fixed effects	Estimate (± SE)	Log Likelihood	χ2	p
P. pipistrellus		Intercept	0.27 ± 0.39			
P. pipistrellus	Local	Bank profile	0.02 ± 0.12	-288.11	0.03	0.87
P. pipistrellus	Local	Bank vegetation	0.39 ± 0.37	-289.14	2.1	0.55
P. pipistrellus	Local	Date	-0.22 ± 0.24	-288.5	0.81	0.37
P. pipistrellus	Local	Invasive species	0.05 ± 0.11	-288.21	0.24	0.63
P. pipistrellus	Local	Overhanging vegetation	0.22 ± 0.13	-289.62	3.05	0.08
P. pipistrellus	Local	**Freshwater (200m)**	**0.29 ± 0.12**	**-290.92**	**5.66**	**0.02**
P. pipistrellus	Local	**Greyspace (200m)**	**0.28 ± 0.14**	**-289.98**	**3.79**	**0.05**
P. pipistrellus	Local	Landscape heterogeneity (200m)	0.10 ± 0.13	-288.39	0.61	0.44
P. pipistrellus	Landscape	Intercept	-0.25 ± 0.21			
P. pipistrellus	Landscape	**Date**	**-0.46 ± 0.18**	**-395.53**	**4.87**	**0.03**
P. pipistrellus	Landscape	Proportion of freshwater (3km)	-0.03 ± 0.21	-390.7	0.04	0.84
P. pygmaeus		Intercept	-0.75 ± 0.49			
P. pygmaeus	Local	Bank profile	0.10 ± 0.12	-259.18	0.71	0.40
P. pygmaeus	Local	Bank vegetation	0.25 ± 0.43	-259.45	1.23	0.75
P. pygmaeus	Local	Date	-0.18 ± 0.34	-258.96	0.26	0.61
P. pygmaeus	Local	Invasive species	0.04 ± 0.12	-258.88	0.09	0.77
P. pygmaeus	Local	Overhanging vegetation	0.24 ± 0.13	-260.56	3.46	0.06
P. pygmaeus	Local	Freshwater (200m)	0.01 ± 0.14	-258.83	0.01	0.99
P. pygmaeus	Local	Greyspace (200m)	-0.31 ± 0.16	-260.61	3.53	0.06
P. pygmaeus	Local	Landscape heterogeneity (200m)	0.12 ± 0.13	-259.19	0.71	0.40
P. pygmaeus	Landscape	Intercept	-0.22 ± 0.27			
P. pygmaeus	Landscape	Date	-0.25 ± 0.28	-346.58	0.88	0.35
P. pygmaeus	Landscape	**Proportion of freshwater (3km)**	**-0.77 ± 0.28**	**-350.22**	**4.53**	**0.03***

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664 **Table 4** Parameter estimates and likelihood ratio tests of the GLMM for the probability of recording

665 *P. pygmaeus* relative to *P. pipistrellus* along urban waterways. The model was run to calculate the

666 probability of recording *P. pygmaeus* relative to *P. pipistrellus*; hence positive estimates indicate an

667 increased probability of detecting *P. pygmaeus* and negative estimates indicate a decreased

668 probability of detecting *P. pygmaeus* for a given explanatory variable.

Fixed effects	Estimate (± SE)	Log Likelihood	χ2	p
Intercept	-0.66 ± 0.29			
Date	0.04 ± 0.19	-217.07	0.05	0.82
Proportion of grey space (3km)	**-0.76 ± 0.23**	**-222.41**	**10.73**	**0.001**

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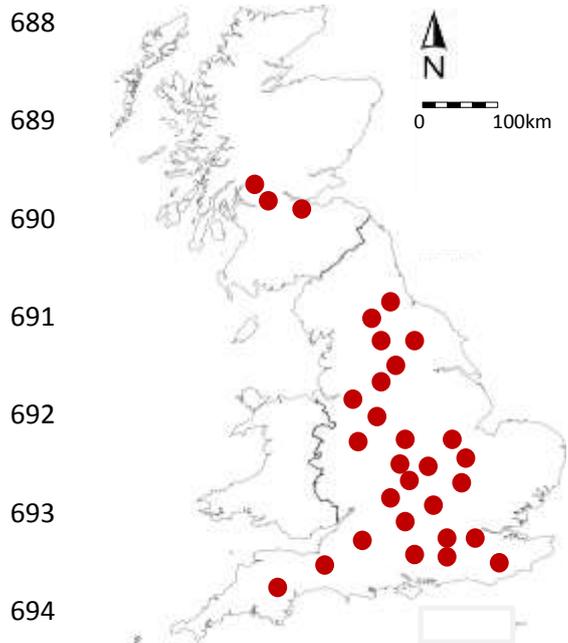
695   **Figure 1 S**urveyed urban waterways across the U.K. Reproduced from Ordnance Survey map data by

696   permission of the Ordnance Survey © Crown copyright 2001.
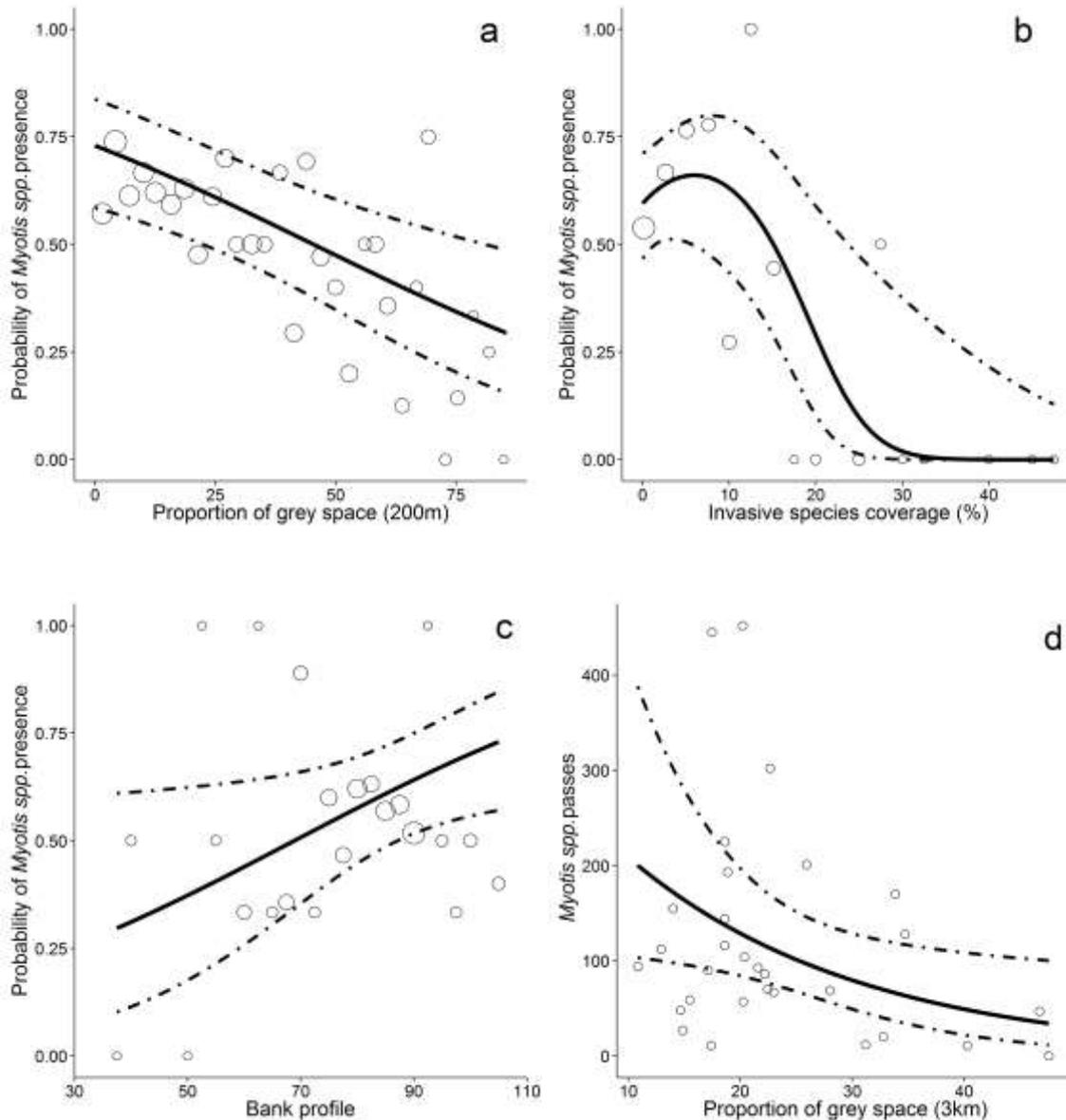
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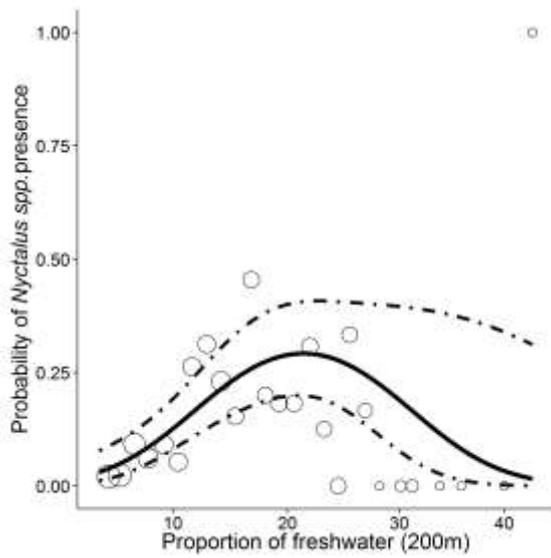
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Figure 2 Estimated probability of recording *Myotis* sp. against (a) the proportion of grey space in the

surrounding 200m of a waterway, (b) the percentage of invasive plant species found within the

waterway, and (c) average profile of both banksides. Figure 2d, the number of *Myotis* sp. passes in

relation to (d) the proportion of grey space in the surrounding 3km. Original data on the presence of

Myotis sp. are superimposed as grey circles with diameter proportional to the number of point

counts where *Myotis* sp. was recorded. Dashed lines represent 95% confidence intervals around the

predictions.

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719 **Figure 3** The estimated probability of recording *Nyctalus* sp. in relation to the proportion of

720 freshwater in the surrounding 200m of a waterway. Original data on the presence of *Nyctalus* sp. are

721 superimposed as grey circles with diameter proportional to the number of point counts where

722 *Nyctalus* sp. was recorded. Dashed lines represent 95% confidence intervals around the predictions.
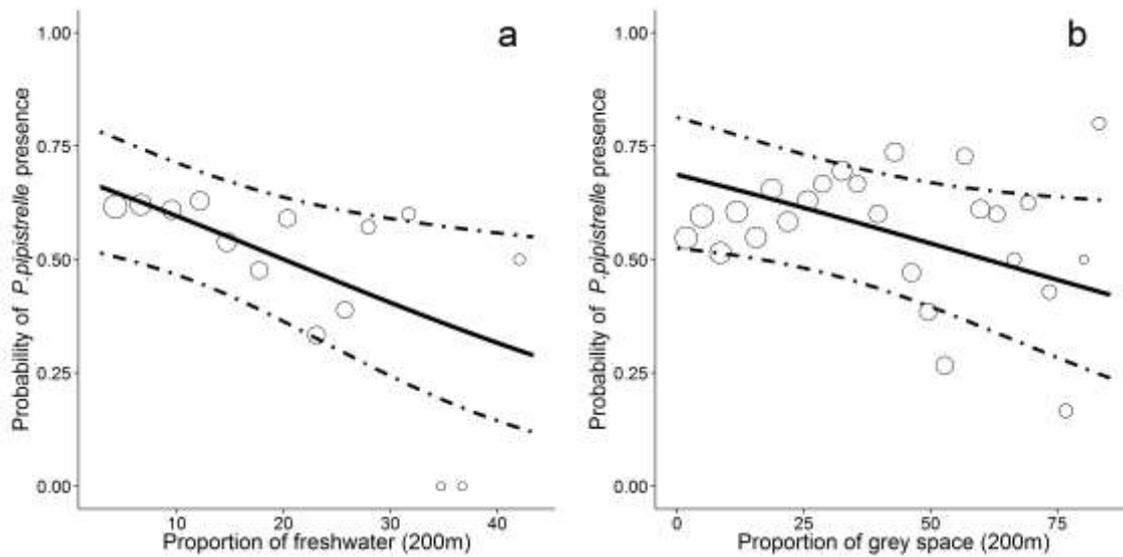
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732 **Figure 4** Estimated probability of recording *P. pipistrellus* in relation to (a) the proportion of

733 freshwater and (b) the proportion of grey space in the surrounding 200m of a waterway. Original

734 data on the presence of *P. pipistrellus* are superimposed as grey circles with diameter proportional

735 to the number of point counts where *P. pipistrellus* was recorded. Dashed lines represent 95%

736 confidence intervals around the predictions.

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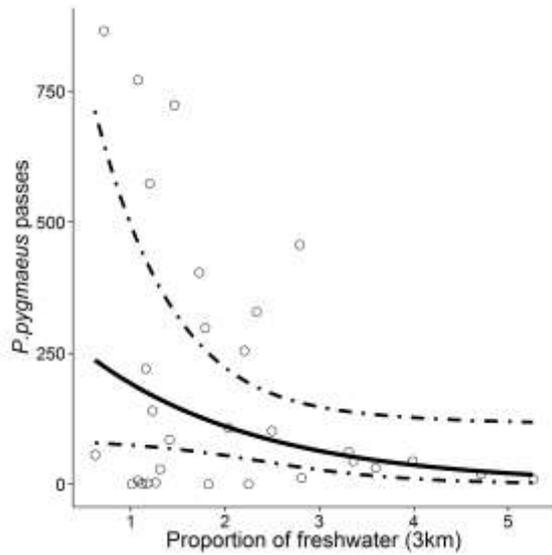
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747 **Figure 5** Estimated activity rate of *P. pygmaeus* in relation to the proportion of freshwater in the

748 surrounding 3km of a waterway. Original data on the presence of *P. pygmaeus* are superimposed as

749 grey circles with diameter proportional to the number of point counts where *P. pygmaeus* was

750 recorded. Dashed lines represent 95% confidence intervals around the predictions.
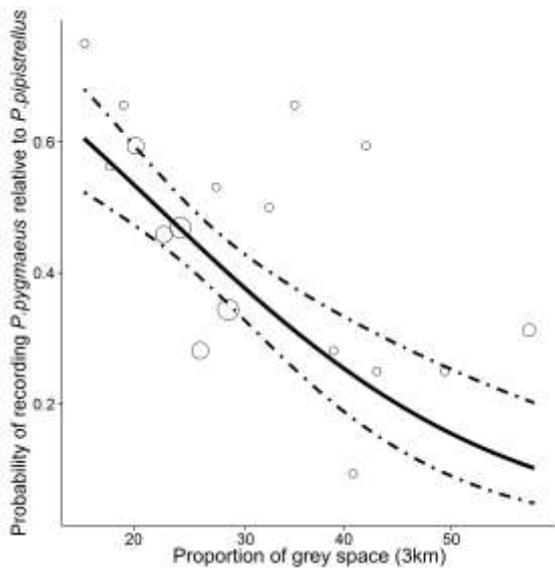
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761   **Figure 6** Estimated probability of recording *P. pygmaeus* relative to *P. pipistrellus* along urban

762   waterways. Dashed lines indicate 95% confidence intervals. Original data on the proportion of *P.*

763   *pygmaeus* passes are superimposed as grey circles with diameter proportion to the total number of

764   *P. pygmaeus* passes recorded.

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