Predicting hedgehog mortality risks on British roads using habitat suitability modelling

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Road vehicle collisions are likely to be an important contributory factor in the decline of the European hedgehog (*Erinaceus europaeus)* in Britain. Here, a collaborative roadkill dataset collected from multiple projects across Britain was used to assess when, where and why hedgehog roadkill are more likely to occur. Seasonal trends were assessed using a Generalized Additive Model (GAM). There were few casualties in winter — the hibernation season for hedgehogs — with a gradual increase from February that reached a peak in July before declining thereafter. A sequential multi-level Habitat Suitability Modelling (HSM) framework was then used to identify areas showing a high probability of hedgehog roadkill occurrence throughout the entire British road network (~ 400,000 km) based on multi-scale environmental determinants. The HSM predicted that grassland and urban habitat coverage were important in predicting the probability of roadkill at a national scale. Probabilities peaked at approximately 50% urban cover at a 1 km scale and increased linearly with grassland cover (improved and rough grassland). Areas predicted to experience high probabilities of hedgehog roadkill occurrence were therefore in urban and suburban environments, i.e. where a mix of urban and grassland habitats occur. These areas covered 9% of the total area within the national British road network. Used alongside evidence on the persistence with which hedgehog roadkill are recorded in a given location over time, the HSM framework can help to identify priority areas for mitigation measures.

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16   **Abstract**

17   Road vehicle collisions are likely to be an important contributory factor in the decline of the

18   European hedgehog (*Erinaceus europaeus)* in Britain. Here, a collaborative roadkill dataset

19   collected from multiple projects across Britain was used to assess when, where and why

20   hedgehog roadkill are more likely to occur. Seasonal trends were assessed using a Generalized

21   Additive Model (GAM). There were few casualties in winter — the hibernation season for

22   hedgehogs — with a gradual increase from February that reached a peak in July before declining

23   thereafter. A sequential multi-level Habitat Suitability Modelling (HSM) framework was then

24   used to identify areas showing a high probability of hedgehog roadkill occurrence throughout the

25   entire British road network (~ 400,000 km) based on multi-scale environmental determinants.

26   The HSM predicted that grassland and urban habitat coverage were important in predicting the

27   probability of roadkill at a national scale. Probabilities peaked at approximately 50% urban cover

28   at a 1 km scale and increased linearly with grassland cover (improved and rough grassland).

29   Areas predicted to experience high probabilities of hedgehog roadkill occurrence were therefore

30   in urban and suburban environments, i.e. where a mix of urban and grassland habitats occur.

31   These areas covered 9% of the total area within the national British road network. Used

32   alongside evidence on the persistence with which hedgehog roadkill are recorded in a given

33   location over time, the HSM framework can help to identify priority areas for mitigation

34   measures.

Introduction

36 **Introduction**

37 Growing human populations and associated urbanisation have led to an expansion of road

38 networks and traffic volumes globally. In Europe, an average of 70,000 km of roads are built

39 every year, while in Britain, traffic on major roads has increased by 9.5% since 2000 and is

40 expected to grow an estimated 17% - 51% by 2050 (UK-Gov, 2018).

41 Road traffic has both direct and indirect impacts on wildlife (van der Ree *et al.*, 2011; Rytwinski

42 & Fahrig, 2015; Bennett, 2017). These include the loss and fragmentation of habitat (Andrews,

43 1990; Eigenbrod, Hecnar, & Fahrig, 2008; Ibisch et al., 2016), disturbance via elevated noise and

44 pollution levels (Berthinussen & Altringham, 2012), and direct mortality through wildlife-

45 vehicle collisions (WVCs), which can in turn drive population declines (Fahrig & Rytwinski,

46 2009). Several studies have been undertaken to understand the threats posed by roads to wildlife,

47 and to identify potential mitigation measures, although most published evidence is derived from

48 regional case studies (van der Ree *et al.*, 2011).

49 WVCs are known to occur for a wide range of mammal species (Barthelmess & Brooks, 2010).

50 Numerous studies have shown the negative impact of roadkill on populations of large carnivores,

51 such as tigers (*Panthera tigris altaica*; Kerley *et al.*, 2002), grizzly bears (*Ursus arctos*; Waller

52 & Servheen, 2005) and servals (*Leptailurus serval*; Williams *et al.*, 2019). Collisions likely to

53 pose a risk to human safety (e.g. with large mammals such as deer) are also a focus of research

54 (Girardet, Conruyt-Rogeon, & Foltête, 2015). The frequency of these collisions appears to be

55 increasing, possibly owing to the global increases in traffic volume (e.g. Madsen, Strandgaard, &

56 Prang, 2002). Small mammal species (< 1 kg in body mass), however, often go under recorded in

57 roadkill surveys due to their lower detectability (Slater 2002; Ford & Fahrig, 2007; Langen *et al*.,

58 2007) and the fact that their carcasses are rapidly scavenged (Slater, 2002; Barthelmess & Brooks,

59   2010; Schwartz *et al*., 2018). This hinders the ability to identify factors that are associated with

60   roadkill and the development of targeted and effective mitigation measures that aim to limit the

61   impact of roads on wildlife populations through either a modification of motorist behaviour

62   and/or the modification of animal behaviour (Glista, DeVault, & DeWoody, 2009). These

63   measures are often species- or genus-specific, and vary in their forms (e.g. wildlife warning

64   signs, wildlife crossings, fencing, under- & overpasses) and effectiveness in different situations

65   (Clevenger & Waltho, 2000; Glista, DeVault, & DeWoody, 2009; Rytwinski *et al.,* 2016).

66   The likelihood of WVCs is often linked to local road characteristics and the surrounding

67   landscape (Neumann *et al.*, 2012; Grilo *et al.*, 2016; Santos *et al*, 2018). Habitat Suitability

68   Models (HSMs) can predict and examine the relationship between animal observation data and

69   environmental variables through mathematical algorithms (Guisan & Zimmermann, 2000; Elith

70   & Leathwick, 2009). These models can be used to identify high quality habitat and derive

71   information on the underlying environmental drivers (Phillips, Anderson, & Schapire, 2006;

72   Elith *et al.*, 2011). Although HSMs are typically used to identify and predict species' habitat

73   requirements (e.g. Razgour, Hanmer & Jones, 2011; Croft, Chauvenet & Smith, 2017), they have

74   also been used previously to identify the environmental variables that explain and predict

75   roadkill occurrence (e.g. Malo, Suarez & Diez, 2004; Santos *et al*., 2013; Fabrizio *et al*., 2019).

76   For example, Ha and Shilling (2018) successfully identified the impact of forest cover and road

77   density on ungulates roadkill in Central California.

78   To create HSMs and other models to better understand WVC patterns, some prior, spatially

79   explicit species information is required. Biological records, consisting of incidences where a

80   species or other taxonomic group identification has been recorded alongside location, time and

81   other metadata, can be collected via bespoke surveys. However, this approach is resource

82   intensive and expensive. Biological records from citizen science studies, where volunteers

83   collect data as part of a scientific study and as ad hoc observations, represent a valuable source of

84   ecological data (Powney & Isaac, 2015). Recent technological advancements, such as online

85   reporting and smart phone apps, have facilitated a huge growth in the adoption of this approach

86   in various fields (Silvertown, 2009; Pocock *et al.*, 2015). Numerous citizen science approaches

87   have already been established for recording and surveying roadkill (e.g. Heigl & Zaller, 2014;

88   Vercayier & Herremans, 2015; Heigl *et al.*, 2016); the resulting data have been shown to provide

89   useful spatial information on roadkill clusters, despite varying slightly from data collected via

90   comparable surveys run by trained observers (Periquet *et al.*, 2018). However, biological records

91   from citizen science projects or as *ad hoc* observations are typically unstructured and prone to

92   biases and errors due to issues such as a lack of standardised survey protocols (Prendergast *et al.*,

93   1993; Isaac *et al.*, 2014). These biases can create noise in the data, which can hide or introduce

94   false trends and increase uncertainty in analyses (Kamp *et al.*, 2016). However, if records are

95   carefully filtered to remove those with geographic uncertainty, and if sampling bias is effectively

96   accounted for during analysis biological records represent a huge data resource (Kery *et al.*,

97   2010; Hill, 2012; van Strien *et al.*, 2013; Isaacs *et al.*, 2014).

98   The aim of this study is to investigate the spatial and temporal distribution of European

99   hedgehog (*Erinaceus europaeus*) roadkill records across the entire British road network and

100   between different road types. The European hedgehog is widespread throughout most of Europe,

101   but is thought to be in decline in many countries. In Britain, for example, population estimates

102   have reduced from 1.5 million individuals in 1995 to 522,000 in 2016 (Mathews *et al.*, 2018).

103   The causes for the species' dramatic decline remain unclear, but factors including the

104   intensification of agriculture resulting in a loss of habitat and prey (Hof & Bright, 2009),

105   predation and competition with badgers (Pettett *et al.*, 2018; Williams *et al.*, 2018), and road

106   collisions (Huijser & Bergers, 2000; Rondinini & Doncaster, 2002) are likely to contribute. It has

107   been estimated that approximately 100,000 to 300,000 hedgehogs are killed every year on roads

108   in Britain (Roos, Johnston, & Noble, 2012; Wembridge *et al.*, 2016), Belgium (Holsbeek, Rodts,

109   & Muyldermans, 1999) and the Netherlands (Huijser, Bergers, & De Vries, 1998). Yet, the

110   causal factors behind these large numbers of roadkill are still poorly understood.

111   We have analysed seasonal trends in hedgehog road casualties, and, using a multi-level HSM

112   framework, produced spatial predictions of the probability of hedgehog road casualties across

113   Britain, based on environmental variables. Furthermore, an analysis of temporal trends is used to

114   provide seasonal patterns of hedgehog roadkill risk and to highlight months when the majority of

115   roadkill are recorded. The outputs can inform targeted mitigation measures aiming at reducing

116   the impact of roads on the declining hedgehog population in Britain.

117   **Materials & Methods**
118   **Hedgehog roadkill data**

119   Data on hedgehog roadkill were obtained from multiple citizen science projects in Britain (Big

120   Hedgehog Map, Mammal Mapper, Mammal Tracker, Mammals on Roads, Project Splatter and

121   Suffolk Wildlife Trust), National Biodiversity Network (NBN) gateway, and national and local

122   monitoring schemes (Supplementary 1). These records were collections of both transect

123   associated and opportunistic records, collected using a variety of recording methods, including:

124   online recording forms, smart phone apps and email submitted records. A total of 12,684

125   hedgehog roadkill records were collected from 1959 to 2018.

126   Each record was subject to screening against inclusion criteria before being considered in the

127   models. Only confirmed roadkill records were used, for example live hedgehogs from projects

128   that did not specifically target roads were not included. Similarly, information on recorder effort

129   (e.g. transects) was not necessary and therefore not retained. Due to a very low number of

130   records before 2000, only records made between January 2000 and December 2017 were

131   included to coincide with the environmental data used. For each HSM level (1 km or 100 m),

132   only records with a spatial precision equal or finer to the model resolution were retained, and

133   only single record per grid cell was used. Similarly, the seasonality model only included records

134   that had dates with information on at least month and year.

135   **Modelling hedgehog roadkill seasonality**

136   A Generalized Additive Model (GAM) was used to characterize the seasonal trends in hedgehog

137   roadkill throughout the year using the 'mgcv' package (Wood & Wood, 2015) in the statistical

138   analysis software R (v. 3.4.3; R Core Team, 2018) and implemented in R Studio (v.1.1.456;

139   RStudio Team, 2018). The monthly number of hedgehog roadkill was modelled using a Poisson

140   family error distribution. Five candidate models were fitted using a cyclic cubic spline, with

141   twelve knots for the month variable. The best model was selected based on a generalized

142   likelihood ratio test. The autocorrelation function (ACF) and partial autocorrelation function

143   (pACF) were used to assess the residuals of all models. The first candidate model assumed that

144   all observations were independent. The next four candidate models included a correlation

145   argument for the month variable, within an extended mixed model framework of the GAM,

146   ranging from 1 to 4, to account for temporal non-independence.

147   **Modelling probability of hedgehog roadkill occurrence**

148   The probability of hedgehog roadkill occurrence on British roads was modelled using the

149   presence-only modelling software MaxEnt (Phillips, Anderson & Schapire, 2006). MaxEnt

150   determines occurrence probabilities by using a set of explanatory variables together with species'

151   presence data and expresses the suitability of each grid cell as a function of the explanatory

152   variables within that grid cell (Phillips, Anderson & Schapire, 2006). The filtered hedgehog

153   roadkill data were used as the presence data within all subsequent models (Figure 1). A suite of

154   candidate environmental explanatory variables was selected based on *a priori* expectations from

155   the literature that they influence the presence or behaviour of hedgehogs (e.g. Driezen *et al.*,

156   2007; Croft, Chauvenet, & Smith, 2017). The source and resolution of the candidate explanatory

157   variables is provided in Table 1 and further information on their preparation can be found in

158   Supplementary 2.

159   The MaxEnt models were created and integrated across two levels using a multi-level HSM

160   framework developed by Bellamy *et al*. (In Review). This framework models species'

161   distributions at multiple geographic levels in turn, from coarsest to finest resolutions, whilst

162   including habitat suitability indices (HSI) from the preceding coarser resolution level as an

163   explanatory variable in models at a subsequent model level. This sequential approach reduces

164   predictor collinearity and enables a species' response to the local environment at lower levels to

165   vary according to higher level conditions (Bellamy *et al*., In Review). The modelling process for

166   hedgehog roadkill was set out as below:

167   1)   A national-level model for the whole of Britain was constructed at a 1 km grid cell

168   resolution. It focused on percentage cover of habitat variables, road density and climatic

169   variables, which were measured at candidate resolutions of 1 and 3 km (Table 1 and

170   Supplementary 2).

171   2) Road-level models were constructed at a higher, 100 m grid cell resolution and covered

172   all areas in Britain within 200 m of the road. Road types considered were based on the

173   official and unofficial road type classifications of the Department of Transport

174   (Department for Transport, 2002; refer to Supplementary 3 for full description and

175   classifications of road types). Each individual road-level model was constructed

176   according to the following road types:

177   a) Minor roads (minor roads and local roads)

178   b) B-roads

179   c) Major roads (A roads and motorways)

180   d) All roads combined.

181   The explanatory variables associated with the individual road-level models were

182   primarily associated with distance to landscape features (e.g. distance from broadleaved

183   woodland). All explanatory variables were measured at two candidate scales: 100 and

184   500 m. Each variable was cropped within a 200 m buffer for each road type.

185   The national-level model was run first, and the HSI values for the probability of hedgehog

186   roadkill occurrence were calculated. These values were then incorporated as an explanatory

187   variable into the subsequent higher resolution road-level models, as described above, by

188   disaggregating them to the resolution of road-level models. The optimal resolution for each

189   variable was identified at each level by comparing the univariate MaxEnt model (default

190   settings). The resolution which resulted in the model with the highest measure of training gain

191   (interpreted as the likelihood of the presence points; Merow, Smith, and Silander , 2013), was

192   retained for the final model. For each level, highly correlated variables were removed using the

193   'vifstep' stepwise function in the 'usdm' package (Naimi *et al.*, 2014) based on a conservative

194   VIF threshold of three (Zuur, Ieno, & Elphick, 2010). The package 'ENMeval' (Muscarella *et*

195   *al.*, 2014) was used to identify the optimal MaxEnt model settings. Combinations of feature

196   types were tested with the threshold features disabled to reduce overfitting (L, linear; H, hinge;

197   Q; quadratic; P, product): L, H, LQ, LQH and LQHP. The regularisation multiplier was varied in

198   steps of 0.5, from 0.5 to 4. These optimal settings were then used to produce model predictions.

199   All analyses were carried out using R (v. 3.4.3; R Core Team, 2018) in R Studio (v.1.1.456;

200   RStudio Team, 2018) and using code adpated from Bellamy *et al*. (In Review).

201   The HSIs from each HSM were used to classify grid cells with the highest probability of

202   hedgehog roadkill occurrence. The predicted HSI values were partitioned into a binary response

203   (high and low probability of hedgehog roadkill occurrence) using the Maximum Training

204   Sensitivity and Specificity (MTSS) occupancy rule (Liu, White, & Newell, 2013).

205   In order to compare hedgehog roadkill probabilities between the different road types, the mean

206   HSI value of major roads, B-road and minor road-level models were extracted directly from the

207   'all roads' model. A high probability of hedgehog roadkill occurrence ratio was also calculated

208   to consider differences in total road type length. To take into account differences in the

209   availability of different road types, a ratio of the probability of occurrence relative to the length

210   of each road type was computed. The ratio was calculated as the number of 100 m^2 grid cells

211   classed as high probability of roadkill occurrence divided by the number of grid cells classified

212   as having a low probability of roadkill occurrence (based on binary model outputs).

213   To control for possible bias in the hedgehog roadkill records towards locations that were heavily

214   observed, pseudo-absence points (background points) were used for the HSMs based on the

215   combined roadkill records of seven other mammal species. The species used (*Vulpes vulpes,*

216   *Neovison vison, Mustela erminea, Mustela nivalis, Meles meles, Lutra lutra,* and *Capreolus*

217 *capreolus*) all shared a similar national distribution and are frequently recorded as roadkill.

218 These records were from the same time period and underwent the same inclusion criteria as the

219 hedgehog dataset. For the road-level models, subsets were created by including only records that

220 were within the 200 m road buffers. HSMs were also run using 10,000 (national model) and

221 2,500 (road models) random pseudo-absence points. The degrees of similarity between the

222 roadkill and random pseudo-absence HSMs were assessed using Schoener's index. HSM

223 performance was judged using the Area Under Curve (AUC) test statistic, with 1 being perfect

224 predictions and 0.5 representing a model that does not predict better than random.

225 To test for variations between the observed hedgehog roadkill records and the locations predicted

226 to have a high probability of occurrence, three maps were also produced:

227   1) The inter-annual persistence of observed roadkill was calculated based on the number

228   of years that at least one hedgehog roadkill per year was recorded in each 10 km

229   British National Grid cell.

230   2) Kernel density at a 10 km resolution of the number of roadkill presence records used

231   for the national-level model.

232   3) Kernel density at a 10 km resolution of grid cells classified as having a high

233   probability of hedgehog roadkill occurrence based on the 'all roads' HSM binary

234   results.

235 The correlation between all three outputs was then assessed using pairwise Pearson's correlation

236 between all three outputs.

237 **Results**

238 After the inclusion criteria were applied to all the hedgehog roadkill data, a total of 6,004 records

239 were available for all subsequent HSMs (Figure 1) and 3,777 for the seasonal analysis. Records

240 were spread throughout Britain and displayed distinct areas of high and low recording (Figure 1).

241 The seasonal analysis used the GAM model with a correlation argument of two, this being the

242 best candidate model based on the Generalised Likelihood Ratio Test. The inclusion of a

243 correlation argument took into account the temporal correlations between the monthly roadkill

244 records. The GAM indicated clear seasonal variations in the relationship between the months of

245 the year and the number of hedgehog roadkill recorded ($F_{9, 24}$= 124.98, p < 0.001). The

246 smoothing function indicated that roadkill was at its lowest in winter, gradually increased to a

247 peak in July, then subsequently decreased (Figure 2).

248 All models were adequate, based on the AUC scores, but some performed better than others did.

249 The national, minor, and all road level models performed well with AUC scores higher than

250 0.70, while the major roads and B-road models performed less well (AUC $\leq$ 0.6). High niche

251 overlap between models using roadkill and random pseudo-absence background data was

252 identified with all Schoener's D statistics being > 0.85 (Table 2).

253 The shape and strength of the species-environment relationships varied between HSMs. The

254 output response curves and permutation importance values varied between the different model

255 levels and the different pseudo-absence data used, roadkill or random (Figure 3; Supplementary

256 4 - 18). However, certain variables, such as those associated with urban cover, buildings and

257 grasslands, had a consistent importance throughout all models.

258 The probability of hedgehog roadkill occurrence in the national-level model using roadkill

259 pseudo-absences was characterised by medium to high urban cover (permutation importance: 68

260 % at a 1 km scale), with probability of occurrence reaching a peak at approximately 50 % urban

261 cover (Figure 3). Grassland cover was also important (permutation importance: ~ 10 % at a 1 km

262 scale for improved grassland and a 3 km scale for rough grassland) with the probability of

263 roadkill occurrence increasing with the amount of improved and rough grassland coverage

264 (Figure 3A; Figure 3C - Figure 3F). Similar results were also found with the national-level model

265 that used random pseudo-absences (Supplementary 4 & 7).

266 The road-level model with roadkill pseudo-absences identified distance from major roads, B

267 roads and buildings at a 100 m scale as important predictors, alongside distance from rough

268 grassland at a 500 m scale (Figure 3B; Figure 3G - Figure 3J). While the outputs of the different

269 road-level models showed high overlap (Table 2), the permutation importance of the national-

270 level HSI varied considerably according to which background dataset was used (roadkill or

271 random). The HSI variables from the national-level model had a high importance (~ 50%) when

272 using random points and very low importance (< 5%) when using the pseudo-absence roadkill

273 data (Figure 3 and Supplementary 5).

274 The mean HSI value extracted from the road-level model containing all roads (100 m resolution)

275 indicated a higher probability of hedgehog roadkill occurrence on major roads (0.48) compared

276 to minor roads (0.35) and B-roads (0.28). Major roads also had a higher probability of roadkill

277 occurrence ratio (0.52) than that of B-roads (0.38) and minor roads (0.11).

278 The binary response (high and low probability of a roadkill occurence) using the MTSS

279 identified a total of 9% of the 100 m^2 grid cells from the road network, based on the 'all roads'

offlow

0

280 level model, as having a high probability of hedgehog roadkill occurrence. These areas were

281 mainly in central Britain, southern Wales, the outskirts of London, and southern Scotland (Figure

282 4). The outputs also regularly identified large areas of small towns, while only the edges of large

283 cities had a high probability of roadkill occurrence (Figure 4).

284 High levels of correlation were identified between the persistence of records over time and the

285 kernel density of roadkill records (at 10 km resolution) (r = 0.93; Figure 5). However, the kernel

286 density of 100 m resolution grid cells predicted to have a high probability of roadkill occurrence

287 showed a lower correlation with both the persistence and presence data (r ≤ 0.55; Figure 5). The

288 HSM identified regions of high probability of roadkill that were not identified from the presence

289 records alone, such as the Central Belt (southern Scotland). It also helped identify that areas with

290 a high number of records do not necessarily identify areas with a high probability of hedgehog

291 roadkill occurrence on a national scale, e.g. eastern England (Figure 5).

292 **Discussion**
293 Vehicle collisions are a major threat contributing to the decline of hedgehogs in Britain. In this

294 study, roadkill data were analysed using GAMs and multi-level HSMs to understand seasonal

295 trends, assess the influence of landscape variables and to identify areas with a high probability of

296 roadkill occurrence. These analyses were conducted throughout the entire British road network

297 (~ 400,000 km) at a national scale but using a local resolution (100 m).

298 The seasonal trends in hedgehog roadkill, with low probability in the winter and higher

299 probability in summer, aligns with expectations from hedgehog biology and behaviour:

300 hedgehogs in Britain typically hibernate between October/November to March/April (Reeve,

301 1994), whereas they are active largely between March and October in England (Reeve, 1981).

302 The single peak of roadkill in July is similar to the findings of Canova and Balestrieri (2019) and

303 Orlowski and Nowak (2006), who found peak distributions of hedgehog roadkill in July and

304 August in Northern Italy and Poland respectively, and suggests that roadkill is likely to be linked

305 with breeding, rather than night length. The results could indicate that most British hedgehogs

306 have a single litter, as roadkill peaks are expected to coincide with population peaks and with the

307 dispersal of vulnerable juvenile hedgehogs from their natal area. Mitigation measures are

308 therefore likely to be most successful if they are implemented during these months when

309 hedgehogs are more vulnerable.

310 Hedgehog roadkill probability is linked to a combination of environmental and abiotic variables.

311 The following habitat variables were important predictors of hedgehog roadkill: the extent of

312 improved grassland; the extent of rough grassland; urban land use; and road density

313 (combination of distance from major and B roads). This aligns with studies of other wildlife that

314 suggest that collision probability increases where there is a combination of favourable habitat

315 and human dominated areas (Neumann *et al.*, 2012; Santos *et al.*, 2018).

316 The findings presented here cannot distinguish whether the probability of hedgehog casualties is

317 determined by habitat *per se*, by high hedgehog densities associated with these habitats, or a

318 combination of the two. The recent population review of British mammals (Mathews *et al.*,

319 2018) found that unimproved (rough) grassland and arable habitats made substantial

320 contributions to the total population estimate, with over 55% of the total estimated British

321 hedgehog population being associated with these two habitats. Croft, Chauvenet & Smith (2017)

322 also predicted that hedgehog abundance was highest in improved grassland and arable habitats,

323 supporting this study's findings that arable, improved, and rough grassland, were listed in the top

324 four influential habitats (Supplementary 9). Croft *et al.* (2017) also reported very high habitat

325   suitability indices for urban habitats, followed equally by suburban and broadleaved woodlands.

326   Almost 40% of the estimated population of hedgehogs in Britain was derived from broadleaved

327   woodland habitat (Mathews *et al*., 2018). However, it is not a notably influential factor in the

328   current hedgehog roadkill models. Recorder efficiency may be reduced in roads that pass through

329   woodlands as fallen leaves, shade, dappled light, and increased scavenging rates may reduce the

330   visibility of hedgehog roadkill. This study's finding of increased probability of hedgehog

331   roadkill occurrence on major roads corresponds with earlier research (Bright, George, &

332   Balmforth, 2005).

333   The models have predicted areas of the British road network that are likely to have high

334   probability of hedgehog roadkill. Both the national and road-level models identified central

335   Britain as being a large area where hedgehog collisions are highly probable. This is the region

336   where there is the most persistence (i.e. inter-annual records) of roadkill records since 2000.

337   Urbanisation levels are also known to be a significant barrier for the range expansion of both

338   polecats (*Mustela putorius*) and pine martens (*Martes martes*) in this region (Vincent Wildlife

339   Trust, 2019). At a local scale the prediction maps suggest that elevated roadkill probability

340   occurs throughout small villages and towns, but is restricted to the suburban areas of larger

341   cities, owing to the lack of grassland in the central parts of large cities. Similarly, Orlowski and

342   Nowak (2006) in a small scale and largely rural study found that most roadkill occurred inside

343   villages.

344   The identification of regions with elevated probability of hedgehog roadkill occurrence provides

345   the opportunity to target mitigation and to test its effectiveness. The finding that only 9% of the

346   whole road network is identified as presenting a high probability of hedgehog roadkill provides

347   an initial focus for interventions, and we recommend wider-scale collection of data at high

348   spatial resolution could help improve the models further. For example, at a national scale,

349   mitigation may be best targeted on Central Britain, as this includes many areas of high

350   probability of occurrence and with repeated records across multiple years. At a local scale, high

351   resolution models of roads can help identify those roads — possibly even locations within roads

352   — where mitigation measures may be the most effective (See supplementary 19 for Chesterfield

353   case study). It is notable that in this example nearly all areas that have multiple reports of

354   hedgehog roadkills across time coincide with the areas predicted to have a high probability of

355   roadkill.

356   Mitigation measures have been shown to be a cost effective tool in reducing the number and

357   effect of roadkills, e.g. with large ungulates in the United States and Canada (Huijser *et al.*,

358   2009). Many measures will work best when engaging with communities and influencing

359   national policies, through increased awareness and effectively implemented management plans

360   (Dickman, 2010). There are a variety of mitigation options that could be used to lower the

361   probability of hedgehog roadkill (Glista, DeVault & DeWoody, 2009; Rytwinski *et al.*, 2016).

362   Although hedgehog roadkill probability was positively associated with good habitat, it is

363   important to ensure that mitigation measures ensure safe crossing of roads rather than dissuading

364   hedgehogs to use such habitats. Road signs and speed reductions can be used to alert drivers

365   when approaching areas of high risk. Although this type of intervention does not affect all

366   species equally (Dique *et al.*, 2003), they were found to decrease overall roadkill (including

367   echidna, a species with similar ecological traits to the European hedgehog) in Tasmania by ~50%

368   through a speed reduction of 20% (Hobday & Minstrelle, 2008). Fencing could help channel

369   hedgehog movement away from roads, although other structures that improve connectivity by

370   providing safe corridors across roads, such as overbridges, underpasses and culverts, may be

371   preferred (e.g. van Vuurde & van der Grift, 2005). It must be emphasised that the effectiveness

372   of many of these structural mitigation measures still remains unclear (Rytwinski *et al.,* 2016) and

373   are largely determined by a few successful examples (Glista, DeVault & DeWoody, 2009). The

374   continued recording of roadkill at high spatial resolution, before and after the implementation of

375   mitigation measures, can provide important evidence on the effectiveness of the measures taken.

376   It is vital that future monitoring is conducted at a high spatial resolution: a large number of data

377   points supplied to this project had to be discarded prior to analysis based on precision filtering (>

378   50 % of records of the records used for the national model were discarded for the 'all roads'

379   model and > 85% of records were discarded for the major and B-road models). This may in turn,

380   result in the low performance of models, low AUC values, as observed with the B-road and

381   major road models. Moreover, citizen science records should be supplemented by data from

382   dedicated surveys, so that true absence data, rather than pseudo-absence, can be used to construct

383   models (e.g. Brotons *et al*., 2004; Fiedler *et al*., 2018). The HSMs could also be refined in the

384   future by separating major trunk roads from motorways, and by incorporating potentially

385   important variables such as traffic speed (these data are not currently available at a national level

386   for Britain).

387   During the model selection process various candidate models were run with different spatial

388   scales and pseudo-absence (roadkill and random) points and each provided slightly different

389   variable importance and outcomes (Supplementary 5-18). Grilo *et al.* (2016) also found the

390   relative importance of variables in the model outputs were not materially altered by changes in

391   sample units and spatial scales. However, the use of different types of background data did affect

392   the importance of certain variables. The national-level HSI, for example, had a high permutation

393   importance (> 50%) when using random pseudo-absence data and a low importance (< 10%)

394   when using roadkill pseudo-absence data. The random pseudo-absence data were spread

395   throughout the width of the road buffer and were consequently further from roads than the

396   roadkill pseudo-absence data. This could have adjusted the effect of distance from roads on

397   hedgehog roadkill and subsequently help better target the effect of specific roads. Future

398   monitoring programmes can be used to ground truth the model results by supplying an

399   independent training dataset against which the model predictions and independent observations

400   can be compared.

401   The use of different types of background data helps to avoid potential recorder bias generating

402   erroneous conclusions. For example, it is uncertain whether roadkills were most recorded in

403   areas with a high probability of hedgehog roadkill occurrence, or whether certain individuals or

404   local citizen science projects, gathering numerous records at a local scale generate 'clusters' of

405   records (Isaac & Pocock, 2015). Therefore, the use of random pseudo-absence data was expected

406   to be somewhat biased towards heavily sampled areas, while the roadkill pseudo-absence data

407   would spread predictions to unsampled areas where conditions are similar to sampled areas

408   (Phillips *et al.*, 2009). The low correlation found between the density of roadkill records and

409   roadkill predictions indicates that predictions were not exclusive to highly sampled areas and,

410   therefore, accounted for recorder effort.

411   **Conclusions**
412   This work has shown how the collection of roadkill data can provide large datasets that can be

413   used to understand the seasonal variations, environmental determinants, and spatial distribution

414   of hedgehog roadkill. Our findings suggest that drivers should be most vigilant for hedgehogs in

415   July on roads surrounded by a mix of urban and grassland cover. Areas with high probability of

416   roadkill occurrence and persistent reports of roadkill were identified across the entire road

417 network at a spatial resolution fine enough to contribute to local planning and mitigation. Using

418 this information to target roadkill mitigation efforts should improve our ability to alleviate the

419 impact of projected increases in road cover, traffic levels and urbanisation on the size and

420 potential viability of already declining local and national hedgehog populations in Britain.

421 **Acknowledgments**

422 We are extremely grateful to the teams involved in the setup of Big Hedgehog Map, Mammal

423 Mapper, Mammal Tracker, Mammals on Roads, Project Splatter and Suffolk Wildlife Trust and

424 the citizen scientists involved in the collection of hedgehog roadkill records over the years. We

425 would also like to thank Emily Wilson and Emily Marnham for collating the roadkill data for this

426 project.

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666

667

Figure 1

Location of the hedgehog roadkill presence data used for the sequential multi-level Habitat Suitability Modelling (HSM).

(A) the national scale model. (B) Major roads. (C) B-roads. (D) Minor roads. (E) All roads.

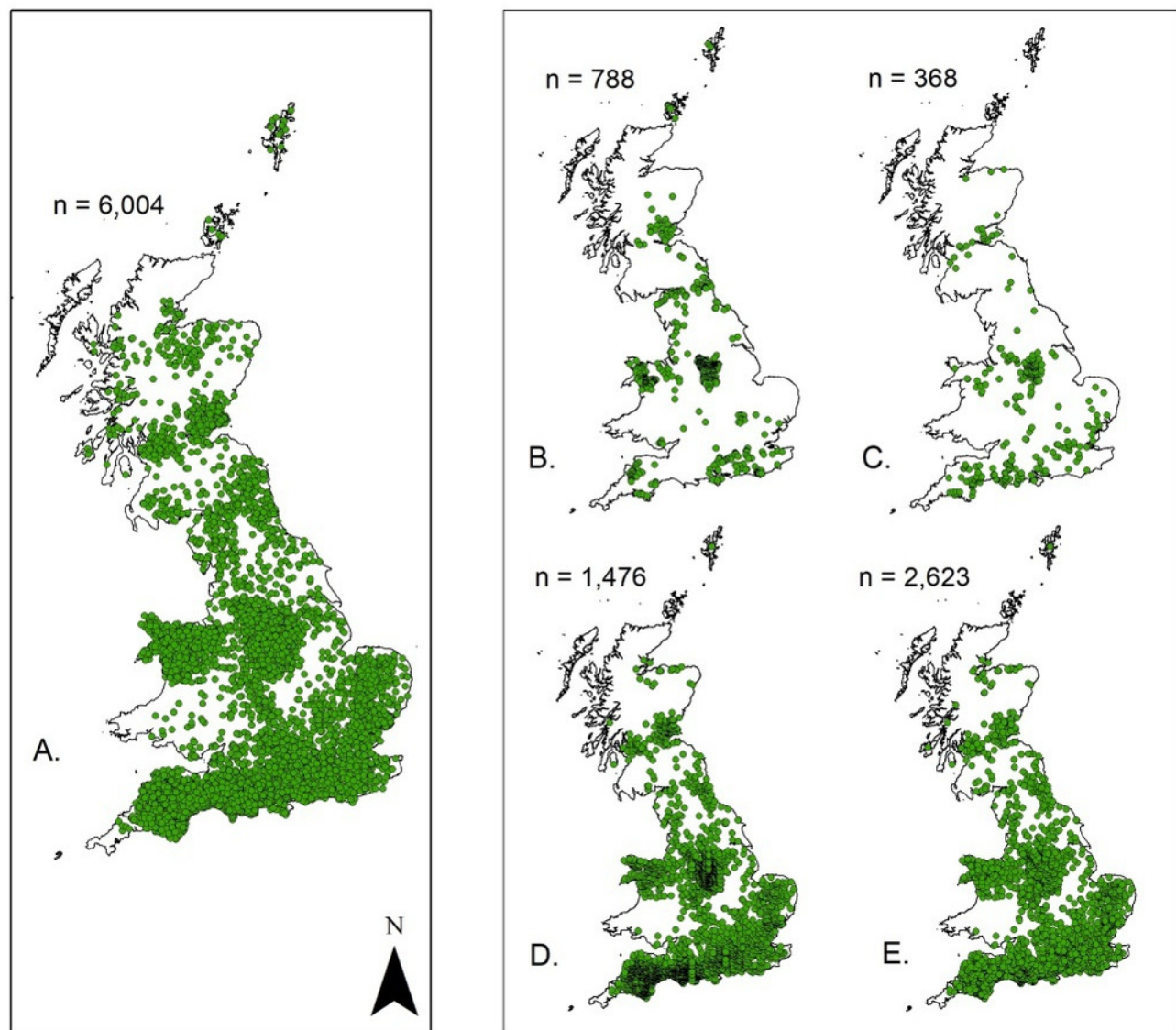



Figure 2

Seasonal variations in the number of hedgehog roadkill using a smoothing function (S) obtained by a generalized additive model (GAM).

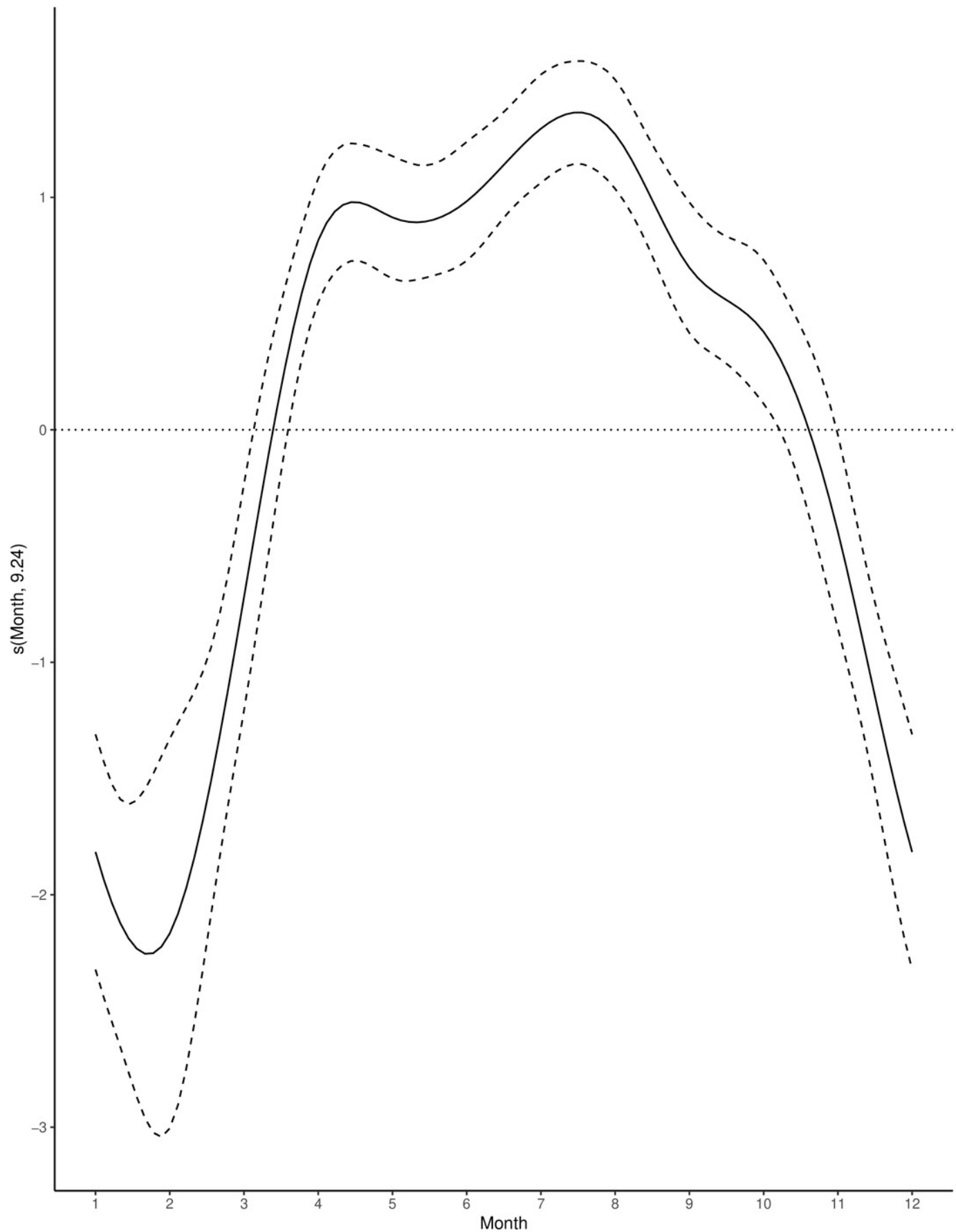



Figure 3

Mapped logistic habitat suitability indices (HSI) for *E. europaeus* roadkill at a countrywide level and road level using all roads.

Mapped logistic habitat suitability indices (HSI) for *E. europaeus* roadkill at a national level (A), and road level using all road data (B) according to the hierarchical, multi-scale model using roadkill background data. The response curves with the highest permutation importance are represented for the countrywide level (C), (D), (E) & (F) and the model using all road data (G), (H), (I) & (J).

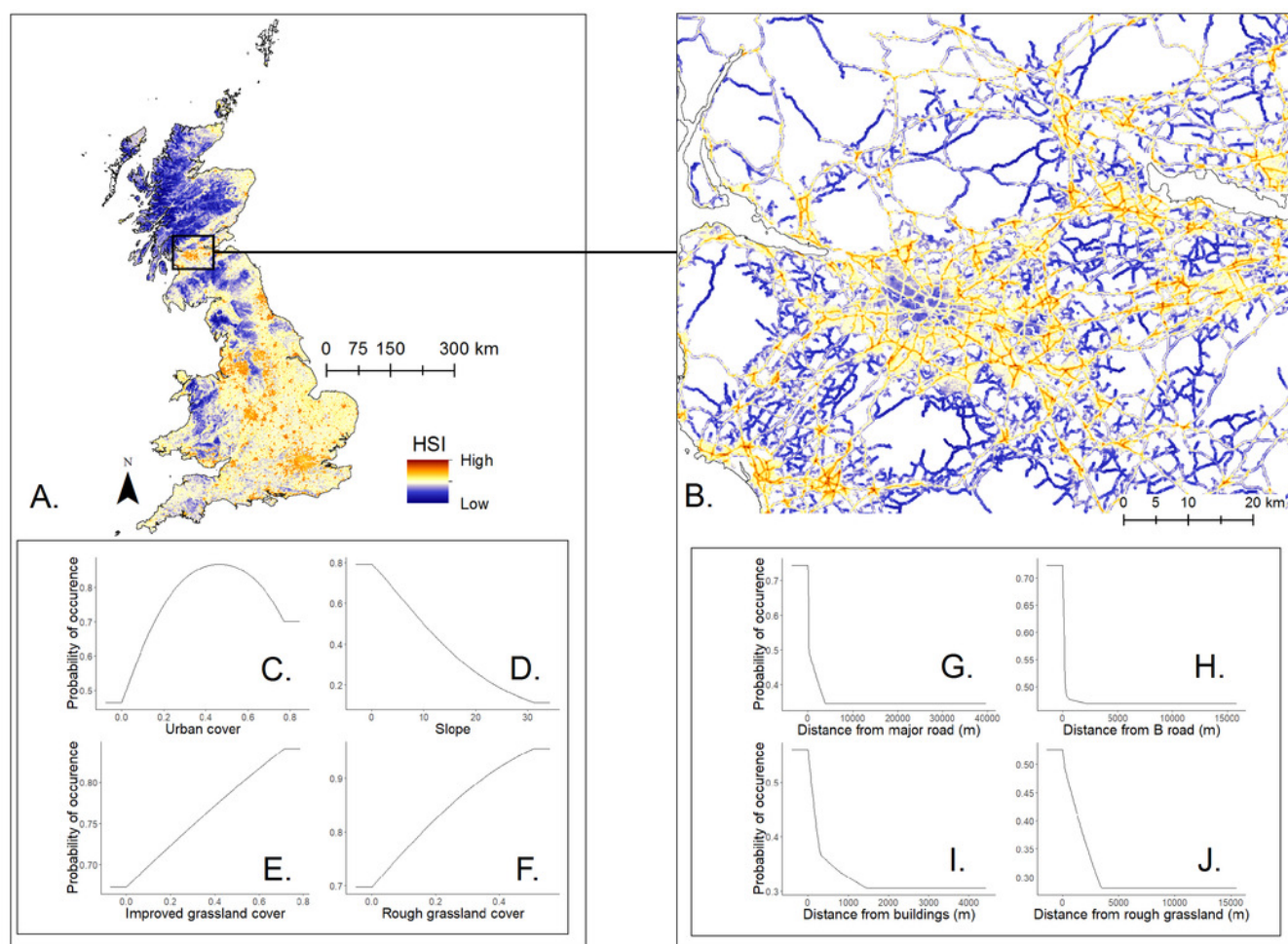



Figure 4

Binary output of logistic habitat suitability indices (HSI) for *E. europaeus* roadkill using all road data.

Red indicates areas with high probability of hedgehog roadkill occurrence and grey lines indicate all roads.

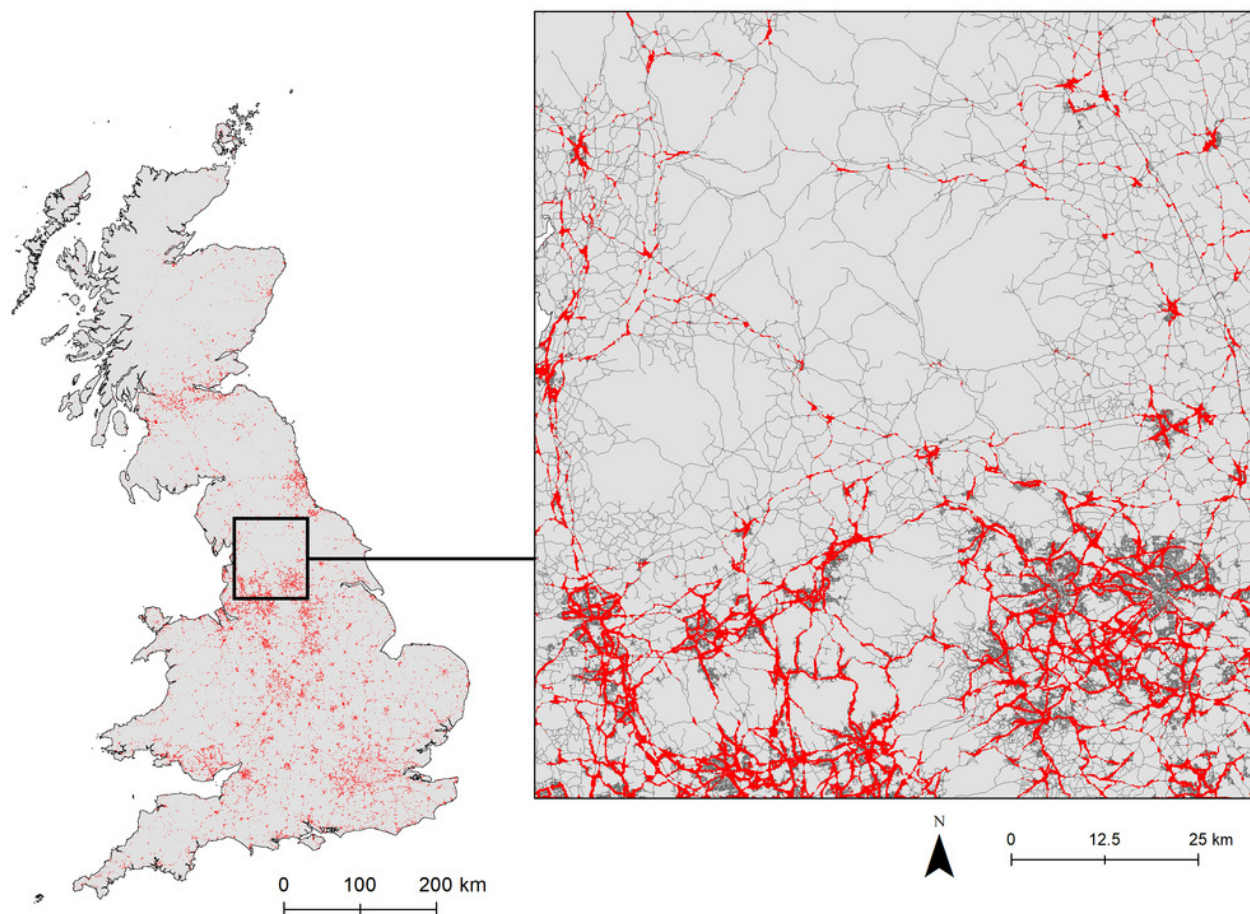
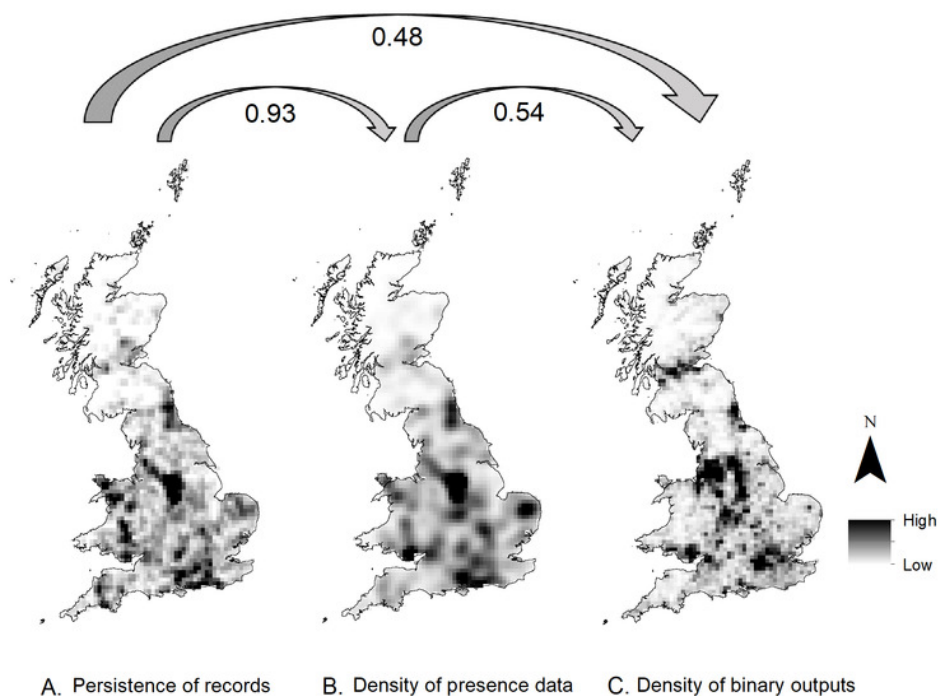



Figure 5

Map representing the correlation between the roadkill presence data and HSM model predictions.

(A) Persistence of records in 10 km grid cells since 2000. (B) Kernel density of roadkill records since 2000. (C) Density of cells predicted as having a high probability of hedgehog roadkill occurrence (binary outputs) from the all road model.

The Pearson correlation between each map is indicated by the arrows.

Model performance of the final national scale (1 km) roadkill HSM using roadkill background data and the road HSM's (100 m).

Schoener's D index scores represent the niche overlap between models using random and roadkill background data.

Explanatory variable	Resolution	Source
Arable (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Broadleaved (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Coniferous woodland (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Urban (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Improved grassland (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Rough grassland (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Freshwater (% cover)	1 - 3 km	Land Cover 2007 (LCM: Morton et al., 2011)
Greenspace (% cover)	1 - 3 km	OS MasterMap Topography Layer (2019)
Hedgerow density	1 - 3 km	Woody Linear Features (Scholefield et al. 2016)
Slope	1 - 3 km	SRTM Slope DEM (Pope, 2017)
All road traffic	1 - 3 km	data.gov.uk (2019)
B road density	1 - 3 km	OS Open Roads (2019)
Major road density	1 - 3 km	OS Open Roads (2019)
Major road traffic	1 - 3 km	data.gov.uk (2019)
Minor road density	1 - 3 km	OS Open Roads (2019)
Minor road traffic	1 - 3 km	data.gov.uk (2019)
Population density	1 - 3 km	EEA (Gallego, 2010)
Summer precipitation	1 - 3 km	WorldClim – Global Climate Data (Fick & Hijmans, 2017)
Summer temperature	1 - 3 km	WorldClim – Global Climate Data (Fick & Hijmans, 2017)
Distance from arable (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from broadleaved woodland (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from Greenspace (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from buildings (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from improved grassland (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from urban area (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from suburban area (m)	100 - 500 m	Land Cover 2007 (LCM: Morton et al., 2011)
Distance from major road*	100 - 500 m	OS Open Roads (2019)
Distance from B-road*	100 - 500 m	OS Open Roads (2019)
Distance from minor road*	100 - 500 m	OS Open Roads (2019)

Slope	100 - 500 m	SRTM Slope DEM (Pope, 2017)
HSM (1-3 km)	100 - 500 m	-

Model performance of the final national scale (1 - 3 km) and the road (100 - 500 m) roadkill HSMs using roadkill background data.

Schoener's D index scores represent the niche overlap between models using random and roadkill background data.

Model type	N	Feature types	Regularisation multiplier	AICc	Full AUC	Schoener's D
National (1 km)	6,004	LQ	1	138,246	0.72	0.85
Major road (100 m)	788	LQ	1	22,054	0.5	0.9
B road (100 m)	368	LQH	4	10,186	0.6	0.84
Minor road (100 m)	1,476	LQH	4	44,442	0.71	0.93
All roads (100 m)	2,623	LQHPT	4	79,724	0.74	0.92