Spatial and temporal trends in western polecat road mortality in Wales

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Roads have considerable ecological effects that threaten the survival of some species, including many terrestrial carnivores. The western polecat is a small-medium sized mustelid native to Asia and Europe, including Britain where its historical stronghold is in Wales. Polecats are frequently killed on roads and road casualties represent the most common source of data on the species in the UK. However, little is known about the factors that increase the risk of collision. We used Generalized Linear Mixed Models to explore seasonal patterns in collisions as well as using Principal Component Analysis and regression modelling to identify landscape characteristics associated with polecat road casualties in Wales. Polecat road casualties had a bimodal distribution, occurring most frequently in March and October. Casualties were more frequently associated with road density, traffic volume, presence of rabbits, habitat patchiness and the abundance of proximal improved grassland habitat. Casualties were negatively associated with elevation and the abundance of semi-natural grassland habitat. The results of this study provide a framework for understanding and mitigating the impacts of roads on polecats in their historic stronghold, hence has considerable value to polecat conservation as well as broader applicability to ecologically similar species.

1 **Spatial and temporal trends in western polecat road mortality in Wales**

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24   **Abstract**

25   Roads have considerable ecological effects that threaten the survival of some species,

26   including many terrestrial carnivores. The western polecat is a small-medium sized

27   mustelid native to Asia and Europe, including Britain where its historical stronghold is in

28   Wales. Polecats are frequently killed on roads and road casualties represent the most

29   common source of data on the species in the UK. However, little is known about the

30   factors that increase the risk of collision. We used Generalized Linear Mixed Models to

31   explore seasonal patterns in collisions as well as using Principal Component Analysis

32   and regression modelling to identify landscape characteristics associated with polecat

33   road casualties in Wales. Polecat road casualties had a bimodal distribution, occurring

34   most frequently in March and October. Casualties were more frequently associated with

35   road density, traffic volume, presence of rabbits, habitat patchiness and the abundance

36   of proximal improved grassland habitat. Casualties were negatively associated with

37   elevation and the abundance of semi-natural grassland habitat. The results of this study

38   provide a framework for understanding and mitigating the impacts of roads on polecats

39   in their historic stronghold, hence has considerable value to polecat conservation as

40   well as broader applicability to ecologically similar species.

Introduction

41   **Introduction**

42   There are currently almost 500,000 kilometres of road in the United Kingdom, over

43   3,000 kilometres of which has been built in the last 10 years (Department for Transport

44   2020). As road networks continue to expand, it is critical to understand the impact that

45   they have on wildlife populations (Schwartz, Shilling and Perkins 2020). Roadways pose

46   a serious risk to wildlife and can have a substantial impact on populations (Department

47   for Transport, 2019; Hill, DeVault and Belant, 2019; Schwartz, Shilling and Perkins,

48   2020). For example, barrier effects caused by linear features in the environment - such

49   as roads – can restrict animal movements (Forman and Alexander, 1998; Schwartz,

50   Shilling and Perkins, 2020), potentially fragmenting populations into smaller, isolated

51   subpopulations that may be more vulnerable to stochastic events (Trombulak and

52   Frissel, 2000; Jaeger and Fahrig, 2004; Riley *et al.,* 2006; Klar *et al.*, 2009).

53

54   Roads also have more direct effects in the form of injury and mortalities associated with

55   wildlife-vehicle collisions (WVC). WVCs have been subject to increasing scrutiny in the

56   last 20 years (e.g. Gomes *et al.* 2009; Langen, Ogden and Schwarting 2009; Patrick,

57   Gibbs and Popescu 2012; Schwartz, Shilling and Perkins 2020; Wright *et al.* 2020) and

58   are acknowledged as one of the most important sources of anthropogenic mortality of

59   terrestrial vertebrates worldwide (Hill, DeVault and Belant 2019). Road characteristics

60   such as road class (Clevenger, Chruszcz and Gunson, 2002), traffic volume (Jaarsma,

61   van Langevelde and Botma, 2006) and speed limit (Barrientos and Bolonio, 2009), as

62   well as surrounding land cover (Wright *et al*., 2020), roadside topography (Clevenger,

63   Chruszcz and Gunson, 2002), species ecology and behaviour (Grilo, Bissonette and

64 Santos-Reis, 2009; Jacobson et al., 2016) and resource abundance (e.g. prey in

65 roadside verges, Planillo *et al*. 2013) affect the frequency of WVCs. WVC 'hotspots' (i.e.

66 areas with high numbers of collisions) are often identified and used to target mitigation

67 measures aimed at reducing the frequency and severity of WVCs (Langen, Ogden and

68 Schwarting, 2009; Patrick, Gibbs and Popescu, 2012; Schwartz, Shilling and Perkins,

69 2020; Wright *et al.*, 2020). The efficacy of this approach may be dependent on road

70 age, however (Zimmermann Teixeira *et al.* 2017). Road mortality data can also further

71 our understanding of species distributions and movements (Schwartz, Shilling and

72 Perkins, 2020). Threatened mammal taxa include felids (Parchizadeh *et al.* 2018;

73 Blackburn *et al.* 2021), ursids (Ha 2021), ungulates (Putman 1997; Riginos *et al.* 2022),

74 and mustelids (Clarke, White and Harris 1998; Russo *et al*. 2020). Carnivore

75 populations may be particularly susceptible to the negative effects of roads due to their

76 unique life-history traits. For example, predators tend to be highly mobile, occur at low

77 densities and have low reproductive rates (Grilo, Smith and Klar 2015; Ceia-Hasse *et al.*

78 2017). Hence, they are and more likely to interact with a road network and a single

79 mortality will have a greater impact on the population than would be the case for a more

80 fecund species.

81

82 Western polecats (*Mustela putorius*) are small-medium (600 – 1,500 g) mustelids native

83 to Europe and Asia. They are considered generalists in both diet and habitat, although

84 in the UK and Mediterranean regions they rely heavily on European rabbits

85 (*Oryctolagus cuniculus*) and their burrows for both food and shelter (Birks and Kitchener

86 1999; Barrientos and Bolonio 2009). Polecats were once abundant in Britain but were

87 hunted to extinction in Scotland and much of England in the 19th century, leaving

88 remnant populations in some English counties and a stronghold in mid-Wales (Langley

89 and Yalden 1977; Blandford 1987; Birks and Kitchener 1999; Packer and Birks 1999;

90 Birks 2008; Croose 2016). Aided by the start of the first World War and the associated

91 decrease in hunting and gamekeeping pressure, along with the recovery of the rabbit

92 population post-myxomatosis (Costa *et al.* 2013), the Welsh polecat population

93 rebounded (Langley and Yalden 1977). Polecats have been listed on schedule 6 of the

94 Wildlife and Countryside Act since 1981 (Wildlife and Countryside Act 1981, 2020),

95 which protects listed species from being killed or taken by certain methods, such as

96 self-locking snares. They are also a priority species on the UK Biodiversity Action Plan

97 (BAP) since 2007 (BRIG 2007). Polecats have now successfully repopulated every

98 county in Wales and much of southern England (Croose 2016). There is the threat,

99 though, of hybridisation with feral ferrets in England which may mask their true

100 distribution, making the Welsh population critical to maintaining the genetic legacy of the

101 species (Costa *et al.* 2013).

102

103 Polecats exhibit several of the life-history traits that make many carnivores vulnerable to

104 the impacts of roads (Grilo, Bissonette and Santos-Reis 2009; Ceia-Hasse *et al.* 2017).

105 They are also known to commonly consume carrion, which may put them at particularly

106 high risk of WVC as roads and roadsides provide ample opportunities for scavenging

107 (Forman and Alexander 1998; Grilo, Bissonette and Santos-Reis 2009; Barrientos and

108 de Dios Miranda 2012). Conversely, Grilo *et al.* (2008, 2009) suggest that polecats may

109 be less susceptible to WVC than other carnivores due to an observed tendency to

110   actively avoid roads. This type of discrepancy demonstrates the need for further,

111   focused research on the topic.

112

113   Little is known about landscape characteristics that might increase the likelihood of

114   WVCs involving polecats. The few studies that have been conducted thus far suggest

115   that relevant factors include the speed and density of traffic (Barrientos and de Dios

116   Miranda 2012), proximity to rabbit burrows (Barrientos and Bolonio 2009), presence of

117   arable land and human settlements, and proximity to water courses or other linear

118   features (Červinka *et al.* 2015). Here, we aimed to describe the temporal and spatial

119   distribution of polecat WVC in Wales and to identify landscape characteristics

120   associated with increased risk.

121

122   **Materials and Methods**

123   *Study area*

124   Wales is a small country (20,782 km^2) of varied geography, with coastal plains in the

125   south and west giving way to a largely mountainous interior dissected by deep rivers

126   and valleys (Smith, Carter and Gruffudd 2020). Elevation ranges from 200 meters

127   above sea level on the coast to 1,085 meters at the tallest peak. The landscape is

128   primarily a matrix of natural and improved grasslands and pastures, with the exception

129   of the mountainous areas in the centre and north of the country that are characterised

130   by a mosaic of woodland, heathland and wetlands. It has a maritime climate; rainfall is

131   common throughout the year, with an average of 1000 millimetres annually (Mayes

132   2013). The average daytime temperature ranges from 4˚C in the winter to 16˚C in the

133   summer (Smith, Carter and Gruffudd 2020), though there is substantial spatial variation.

134   *WVC data*

135   Observations of polecat road mortalities in Wales were provided by the Vincent Wildlife

136   Trust (VWT). Records were collected via a national monitoring survey carried out from

137   December 2013 to December 2015 (Croose 2016). The survey used a community

138   science framework to obtain reports of polecat casualties from members of the public,

139   volunteers, and VWT members. Where possible, reports were verified by professionals

140   with sufficient experience and expertise as polecats, feral ferrets or ferret-polecat

141   hybrids via photo, video, or evaluation of the carcass (Croose 2016). During the survey

142   period there were 85 observations in Wales verified as true polecats, no confirmed

143   records of hybrids or feral ferrets, and 86 unverified records. Both phenotypic and

144   genetic studies suggest that most polecats in Wales are true polecats, while

145   hybridisation is more common in England (Costa *et al.* 2013; Croose 2016). We did not

146   have access to carcass materials, hence further verification was not possible.

147   Therefore, unverified records were retained in analysis and assumed to be true

148   polecats, giving a total of 171 observations. Due to the lack of true absence data a total

149   of 1200 pseudo-absence points (Barbet-Massin *et al.* 2012) were generated across the

150   Welsh road network and at least 3 kilometres (i.e. the average home range size of

151   polecats in Britain (Birks and Kitchener 1999) distant from the nearest presence point

152   (Fig. 1).

153   *Environmental parameters*

154   Species abundance is an important driver of road-kill patterns (Barrientos and de dios

155   Miranda 2012; Husby 2016). While the range and overall, population-level abundance

156   and distribution of polecats in the UK has increased, suitable abundance or density data

157   are unavailable for polecats in Wales (Matthews *et al*. 2018). Simple population-

158   occurrence relationships, where changes in habitat quality and/or quantity impacted the

159   populations of associated species (Freckleton, Noble and Webb 2006) offer a potential

160   proxy for abundance. However, such models have never been applied to polecats in the

161   UK and the extent to which they may be (un)suitable is unknown. Hence, our models

162   did not capture local abundance or a proxy thereof.

163   Explanatory environmental variables were selected *a-priori*, based on previously

164   published literature and knowledge of the species' ecology. These included proportional

165   land cover, habitat patchiness, elevation, waterway density, road density, presence of

166   rabbits and traffic volume (Table 1). The percentage of each land class and the total

167   number of patches (where more patches = more fragmentation) were extracted from the

168   25m resolution Land Cover Map 2015 (UK Centre for Ecology & Hydrology 2017) within

169   a 1.5 kilometre buffer of each presence and pseudo-absence point, based on average

170   polecat home range size (Birks and Kitchener 1999). In order to evaluate the effect of

171   many land classes in fewer variables, classes of interest were combined using Principal

172   Component Analysis (PCA) with Box-Cox transformation, prior to analysis. Three

173   principal components (PCs) with eigenvalues >1 were retained for use in models.

174   Elevation was extracted in R using the *elevatr* package (Hollister *et al.* 2021). We

175   attempted to capture spatial autocorrelation using the *glmmPQL* function in the *MASS*

176   package (Venables, 2002), using a correlation structure (Dormann *et al.*, 2007).

177   However, all models returned zero-distance errors that resisted resolution. We also

178   explored the use of GAMMs via the *mgcv* package (Wood, 2003, 2011, 2017), where

179   spatial coordinates were included in a bivariate spline with a Markov random field

180   smoother. These models performed very poorly. Hence, spatial autocorrelation in the

181   data was captured by calculating Moran's I scores for each presence and pseudo-

182   absence point using the Anselin's Local Moran's I tool within the Spatial Analyst toolbox

183   in ArcGIS Desktop (ESRI 2011). All numeric variables were rescaled so that $\bar{x} = 0$, $\sigma = 1$

184   to facilitate direct comparison between covariates.

185

186   Prey abundance and availability are a key consideration when evaluating predator

187   occurrence (e.g. Šálek *et al.* 2010; Mougeot *et al.* 2019). Indeed, the proximity of rabbits

188   to roads may be a reliable indicator of polecat collision risk (Barrientos and Bolonio

189   2009). However, accurate, landscape-scale data on the presence or absence of many

190   UK mammals – including European rabbits - are sparse (Mathews *et al.* 2018b). We

191   therefore captured the potential influence of rabbits on polecat WVC using National

192   Biodiversity Network (NBN; https://nbn.org.uk/) rabbit data between 2010-2019 inclusive

193   and calculating the minimum distance between mortalities/pseudo-absences and rabbit

194   locations. The selected date range ensured national coverage and assumes that a

195   rabbit observation in a given year represents a population that was present during the

196   period 2013 – 2015 (i.e. when polecat data were collected).

197

198   *Modelling seasonal trends*

199   Seasonal trends in polecat WVC were analysed using a Generalized Additive Model

200   (GAM), following Wright *et al.* (2020). Five candidate models were created with the

201   number of roadkill observations as the response variable and month as the predictor.

202   Models used a Poisson family error distribution with a log-link function, and a cyclic

203   cubic spline with 12 knots applied to the month variable. Temporal non-independence in

204   the data was accounted for by including a correlation argument in four of the models

205   where the autoregressive order, *p* varied between 1-4. The fifth model assumed

206   independence between observations. Residuals of each model were evaluated using

207   the Auto-Correlation Function (ACF) and Partial Auto-Correlation Function, and the

208   best-approximating model was identified using Akaike's Information Criterion (AIC).

209   *Modelling environmental relationships*

210   The relationship between polecat road WVC and percent land cover classification

211   ('habitat model', hereafter), was explored using a Generalized Linear Model (GLM)

212   using a binomial error distribution with logit link function. Presence/pseudo-absence of

213   polecats was the dependent variable and the proportional land cover, patchiness,

214   elevation, road density, road class, distance to rabbits, and Moran's I were fixed

215   explanatory variables. All variables had Variance Inflation Factors (VIF) ≤ 2 and were

216   retained (Zuur *et al*. 2010). All possible model permutations of the resulting GLM were

217   generated using the *MuMIn* package (Barton 2020) and Akaike weights were calculated

218   for each model within the top subset of models (Δ AIC ≤ 2). Both the best-approximating

219   model (Δ AIC = 0) and the full average model (i.e. averaged across the top subset of *n*

220   models) were subsequently identified. Using both approaches accounts for uncertainty

221   in model selection and produces more robust results than using the best-approximating

222   model alone (Grueber *et al.* 2011).

223

224   A second GLM was produced using the same method and based on the subset of the

225   data that included traffic volume ('traffic models', from hereon). Traffic volume data for

226   2015 (point locations) were obtained from the Department for Transport (Department for

227   Transport 2019), but data was not available for every road and, by extension, every

228   presence/pseudo-absence location. However, traffic volume has frequently been

229   reported as an important factor in determining risk of WVC (Forman and Alexander

230   1998; Jaarsma, van Langevelde and Botma 2006; Jacobson *et al.* 2016). Therefore, a

231   second set of models was constructed using a reduced dataset (n = 150 presence;

232   1,058 pseudo-absence) containing only presence/pseudo-absence points on roads that

233   were also associated with traffic volume data. WVC data did not necessarily directly

234   overlap roads due to imprecision in location information, hence presence data were

235   aligned with the nearest road, according to a 1.5-kilometer threshold. Code are

236   available at https://zenodo.org/record/7025191 (Barg *et al.,* 2022).

237   All analyses were conducted in R (v.3.6.3; R Core Team 2019).

238   **Results**

239   Of the 171 road mortalities identified and included in these analyses, 85 were

240   considered to be true polecats and 86 were unverified (i.e. plausible but not confirmed).

241   WVC were most frequently recorded on trunk roads (28%), followed by unclassified

242   roads (18%), primary roads (15%), and secondary roads (15%). Only one carcass was

243   recorded on a motorway (Fig. 2).

244

245   Out of five candidate seasonal models, the model that performed best was the one that

246   did not include a correlation argument. This model showed significant temporal variation

247   across months (Intercept β = 1.90 ± 0.16; s(month) F = 2.78, p = 0.006). WVC had a

248   bimodal distribution, peaking in March and October. Winter WVC was substantially

249   lower than summer WVC (Fig. 3).

250

251   PC1 accounted for 24% of total variance in the data and was positively associated with

252   semi-natural grassland, and negatively associated with improved grassland. The

253   loadings of PC2 (14%) described a negative association with improved grassland and a

254   positive association with urban cover. PC3 (13%) was associated positively with

255   wetland and heathland, and negatively with broadleaf and coniferous forest (Table 2).

256

257   The best-approximating habitat model suggested that polecat WVC occurred with

258   greater frequency in landscapes that were more fragmented (habitat patchiness; β =

259   11.57 ± 1.84 [95% Confidence Interval]) and had greater road densities (β = 0.4.20 ±

260   1.63) than areas where WVC were not recorded. Polecat WVCwere also more likely

261   where rabbits occur (distance to rabbits; β = 3.63 ± 1.31), at lower elevations (β = -2.09

262   ± 1.03) and in areas with more semi-natural grassland and less improved grassland

263   (PC1; β = -1.17 ± 0.31). Polecat WVC also exhibited spatial autocorrelation; carcasses

264   were found nearer to other polecat carcasses than would have been expected by

265   chance (Moran's I; β = 4.92 ± 4.19). The top subset of models within ≤2 ΔAIC used to

266   create the average model consisted of six models. Six variables occurred across all six

267   models (weight = 1.00): road density; habitat patchiness; distance to rabbits; PC1;

268   elevation; and Moran's I. PC2 occurred in three models (weight = 0.57), and waterway

269   density and PC3 both occurred in two models (weight = 0.37 and 0.19, respectively;

270   Table 3).

271

272   Traffic models behaved similarly to habitat models. Polecat WVC were again associated

273   with a more fragmented landscape (β = 1.14 ± 0.19); greater road densities (β = 4.585 ±

274   1.70), proximity to rabbits (β = 3.80 ± 1.39), lower elevations (β = -2.42 ± 1.13), and

275   semi-natural grassland and less improved grassland (β = -1.12 ± 0.32). There was a

276   positive association between traffic volume and WVC, with more carcasses being

277   recorded on more active roads (β = 2.77 ± 1.99). Similar results were observed in the

278   average model, in which six variables - distance to rabbits, elevation, habitat

279   patchiness, road density, traffic volume, and PC1 - occurred in all 14 models (i.e.

280   importance = 1) across the top subset of models. Waterway density (weight = 0.43),

281   Moran's I (weight = 0.38) and PC3 (weight = 0.33) each occurred in six models (Table

282   4). It should be noted that our thinned traffic dataset was biased towards trunk road and

283   primary roads, both meant for high volumes of traffic. Almost all records associated with

284   these road classes were retained, compared to only 10% of records from unclassified

285   roads, 15% from service roads and 30% from tertiary roads.

286

287   **Discussion**

288   Polecat WVC occurred most frequently in March and October, coinciding with the

289   seasons that polecats are most mobile (Birks 2012). Prior research suggests that

290   carnivores are particularly vulnerable during specific life-history stages (Grilo *et al*.,

291   2009). Polecats typically occupy fixed home ranges throughout the year, with two

292   exceptions - the breeding season (March and April) and during the period of kit

293   dispersal in autumn (Birks 2012). Polecats are polygynous (Lodé 2001) and males

294   travel outside of their home-range to find and mate with several females each year,

295   likely increasing their interactions with roads. Moreover, juveniles leaving their natal

296   home range may be particularly susceptible to WVC as they are likely naïve to the

297   variable dangers of roads (Grilo, Smith and Klar 2015; Carvalho *et al.* 2018). High

298   juvenile WVC in the autumn has the potential to negatively impact recruitment and

299   perturb population age- and genetic structure (Holderegger and Di Giulio 2010). We

300   recommend that future WVC studies aim to collect age and sex information whenever

301   possible with the goal of exploring potential population-level impacts.

302

303   There was a strong relationship between polecat WVC and the presence of European

304   rabbits adjacent to the road. In Wales, as well as other countries with large rabbit

305   populations, rabbits make up the majority of polecat diet, and polecats frequently use

306   rabbit warrens as daytime resting sites (Birks and Kitchener 1999; Barrientos and

307   Bolonio 2009; Birks 2012). Prey availability in roadside verges has been linked to

308   increases in predator roadkill, especially in heavily agricultural or developed areas

309   where verges may provide refuge for small and medium sized mammals (Barrientos

310   and Bolonio 2009; Silva *et al.* 2019). The presence of rabbits near roads may also lead

311   to higher rabbit road mortality, offering scavenging opportunities which may prove

312   dangerous (Silva *et al.* 2019).

313

314 Habitat analysis showed that WVC was positively associated with areas of improved

315 grassland, and negatively with semi-natural grassland. Grassland is the most prominent

316 land classification in Wales, and is the preferred habitat for European rabbits (Birks

317 2012; Mathews *et al.* 2018b). The split between improved and semi-natural grassland is

318 likely an effect of elevation, as semi-natural grassland is found primarily in upland areas

319 and improved grassland in lowland areas. The negative relationship with elevation also

320 appeared in the models. Several past distribution surveys have reported that polecats in

321 the UK are less common in upland areas than lowlands, potentially due to a reduction in

322 available resources at higher elevations (Birks and Kitchener 1999; Croose 2016). Birks

323 and Kitchener (1999) made the connection that roadways tend to follow valley bottoms

324 and suggested the increased road density in lowland areas as a potential reason that

325 polecats have been slow to recolonise parts of the South Wales valleys, the most

326 densely populated part of the country. The lack of density estimates for polecats, or a

327 reliable proxy, meant that this variable was not included in the model. However, polecat

328 densities are thought to be uniform across habitats in Wales, with the exception of

329 urban areas (Mathews *et al.* 2018; Mathews *et al.* 2020) so the trends observed here

330 are unlikely to be due to differing densities across habitat types. Still, we recommend

331 further surveys focused on determining polecat population metrics to inform future

332 models.

333

334 The influence of habitat patchiness evident herein suggests that polecats are at greater

335 risk in heavily fragmented landscapes. Several studies on polecat habitat use have

336 shown a preference for heterogeneous landscapes with a high number of habitat

337 patches (Zabala *et al.* 2005; Mestre *et al.* 2007). Indeed, fragmentation to some degree

338 can be beneficial for a generalist predator such as the polecat as it may provide a

339 higher variety of food resources and a large amount of edge habitat, which can increase

340 landscape-scale connectivity (Zabala *et al.* 2005). However, fragmentation and

341 interactions that increase WVC risk can create barriers to movement and impede

342 functional connectivity (Forman and Alexander 1998; Grilo *et al.* 2011). Further, the

343 influence of road density on polecat WVC risk is clear. It has been suggested that

344 polecats actively avoid roads (Grilo *et al.* 2008, 2009). However, roadside vegetation

345 may provide cover for polecats as well as ample opportunities for scavenging roadkill

346 (Schwartz *et al.* 2018). Polecat population density may also play a role, as high

347 densities of impacted wildlife species have been shown to be important predictors of

348 WVCs in some studies (e.g. Rolley and Lehman, 1992; Mayer *et al*. 2021). Thus, active

349 avoidance is unlikely to be possible where roads or polecats occur at sufficient densities

350 that interactions are inevitable.

351

352 We found that higher traffic densities were associated with increased frequencies of

353 polecat WVC. This corresponds with previously published literature on WVC in polecats

354 and other species (Grilo, Bissonette and Santos-Reis 2009; Červinka *et al.* 2015;

355 Jacobson *et al.* 2016). The relationship between WVC and traffic volume (traffic flow

356 theory) suggests that collisions will increase in accordance with traffic volume to a

357 certain threshold, after which high traffic activity causes animals to avoid roads entirely

358 (van Langevelde and Jaarsma 2004; Moore *et al.* 2020). Jacobson *et al.* (2016)

359   expanded on the traffic flow model using species-specific behavioural responses to

360   traffic to better predict the effect of WVC and barrier effects on populations. Within their

361   framework species are categorized into four categories: nonresponsive, pausers,

362   speeders and avoiders. Polecats most likely fit into the pauser category along with

363   skunks and porcupines. This group tends to respond to perceived risk using by reducing

364   their speed or freezing, increasing the time spent on the roadway and increasing risk of

365   WVC especially in high traffic areas (Jacobson *et al.* 2016).

366

367   WVC were most often reported on trunk roads and primary roads, both road classes

368   meant for long-distance travel and associated with high traffic volume and high speed

369   limits (Department for Transport 2012). There is likely an element of observational

370   frequency bias in these results, where a greater number of people using a road leads to

371   a greater number of roadkill reports. However, the relationship between WVC and roads

372   with high traffic volume and speeds is well documented (van Langevelde and Jaarsma,

373   2004; Jaarsma, van Langevelde and Botma, 2006; Pagany and Dorner, 2016; Canal *et*

374   *al.*, 2019; Russo *et al.*, 2020). Second to trunk roads, the greatest number of

375   observations came from unclassified roads, which are small roads connecting rural and

376   suburban areas that make up approximately 60% of the roads in the UK (Department

377   for Transport 2012). While this may appear to contradict the result that WVCs increase

378   with traffic volume, the sheer number of unclassified roads likely contributed to the

379   comparatively high number of recorded collisions. Reports may also be somewhat

380   biased towards unclassified roads as, although WVC are less frequent, they may be

381   more likely to be reported when they do occur. Unclassified roads generally have slow

382   speed limits and little traffic, making it easier to spot roadkill while driving and more

383   convenient to stop, examine, and report the carcass than it would be on a busy road.

384   **Conclusion**

385   This paper is the first to describe factors influencing polecat WVC in Wales, the historic

386   stronghold for the species in Britain. As polecat populations continue to recover after

387   near extirpation, addressing potential risks to their survival is crucial. The Welsh polecat

388   population is important to maintaining the genetic legacy of polecats in Britain, as it has

389   been shown that they have higher rates of hybridisation with feral ferrets elsewhere in

390   their range. Further research on this topic should look at population-level effects of

391   WVC and spatial variation thereof and seek to identify appropriate mitigation measures.

392   This research has implications for polecat protection in Wales as well as applicability to

393   the rest of Britain, and throughout their European range, where they are thought to be in

394   decline in several countries.

395

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400

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Summary of the environmental covariates used for modelling polecat road mortality. TC = Land Class Map 2015 target class.

Description	Type	Source	Reference
Broadleaf woodland (% cover)	Raster, non-composite; TC 1	Land Cover Map 2015	Baghli *et al.,* 2005
Coniferous woodland (% cover)	Raster, non-composite; TC 2	Land Cover Map 2015	Zabala *et al.,* 2005
Arable (% cover)	Raster, non-composite; TC 3	Land Cover Map 2015	Birks, 2008
Improved grassland (% cover)	Raster, non-composite; TC 4	Land Cover Map 2015	Baghli *et al.,* 1005
Semi-natural grassland (% cover)	Raster, composite; TC 5, 6, 7	Land Cover Map 2015	Baghli *et al.,* 2005
Heathland (% cover)	Raster, composite; TC 9, 10	Land Cover Map 2015	Fournier *et al.,* 2007
Wetland (% cover)	Raster, composite; TC 8, 11	Land Cover Map 2015	Birks, 2008
Urban (% cover)	Raster, composite; TC 20, 21	Land Cover Map 2015	Baghli *et al.,* 2005
Number of habitat patches	Raster, non-composite	Land Cover Map 2015	Zabala et al., 2005
Density of roads	Spatial line	Open Street Map	Forman and Alexander, 1998
Density of water features	Spatial line	Open Street Map	Bahgli *et al.,* 2005
Distance to rabbits	Spatial point	National Biodiversity Network	Barrientos and Bolonio, 2009
Road type	Spatial line	Open Street Map	Barrientos and de Dios Miranda, 2012
Traffic volume	Spatial point	Department for Transport	van Langevelde and Jaarsma, 2004
Elevation	Spatial point	Calculated with Elevatr in R	Birks, 2012

Principal Component Axes loadings showing variation in the habitat classes used in roadkill models and retained within the top subset of models (Δ AIC ≤ 2; see Supplementary Information for PCs 4-8).

The percentage of total variation explained by each component is given in parentheses.

Loadings that explain the largest proportion of each PC are in bold.

Habitat type	Principal Component Axes		
	PC1 (24%)	PC2 (14%)	PC3 (13%)
Arable	-0.297	0.012	-0.360
Broadleaf woodland	-0.277	**0.392**	**0.427**
Coniferous woodland	0.351	0.126	**0.496**
Heathland	0.263	0.070	**-0.467**
Improved grassland	**-0.566**	**-0.411**	0.054
Semi-natural grassland	**0.540**	-0.186	0.051
Urban	-0.115	**0.787**	-0.173
Wetland	0.129	0.057	**-0.435**

Results of habitat models (n = 171 presence, 1200 pseudo-absence) investigating habitat and road characteristics in relation to polecat road mortality.

The conditional average model was created from the top subset (Δ AIC ≤ 2) of six models. Regression coefficients (β) and 95% confidence intervals (+/- 95% CI) are given as well as the significance of each variable where *P < 0.05, ** P < 0.01, and *** P < 0.001. The weight of variables included in conditional average model is also given, with the importance (number of candidate models that contain the variable) in parentheses.

Variable	Best-approximating model		Full average model		
	β	+/- 95% CI	β	95% CI	Weight
Habitat patchiness	11.57	1.84***	11.47	1.83***	1.00 (6)
Elevation	-2.09	1.03***	-2.09	1.06***	1.00 (6)
Moran's I	4.92	4.19*	4.89	4.16*	1.00 (6)
Road density	4.20	1.63***	4.19	1.63***	1.00 (6)
Distance to rabbits	3.63	1.31***	3.66	1.33***	1.00 (6)
PC1	-1.17	0.31***	-1.17	0.31***	1.00 (6)
PC2	-0.18	0.22	-0.10	0.23	0.57 (3)
Waterway density	-	-	0.47	1.67	0.37 (2)
PC3	-	-	-0.02	0.03	0.19 (2)

Results of traffic models analyzing habitat and road characteristics related to polecat road casualties using only data points associated with traffic counts (n = 150 presence, 1,058 pseudo-absence).

The conditional average model was created from the top subset (Δ AIC ≤ 2) of fourteen models. Regression coefficients (β) and 95% confidence intervals (+/- 95% CI) are given as well as the significance of each variable where *P < 0.05, ** P < 0.01, and *** P < 0.001. The weight of variables included in conditional average model is also given, with the importance (number of candidate models that contain the variable) in parentheses.

Variable	Best-approximating model		Full average model		
	β	95% CI	β	95% CI	Weight
Road density	4.58	1.70***	4.05	0.83***	1.00 (14)
Distance to rabbits	3.80	1.39***	3.86	1.39***	1.00 (14)
Elevation	-2.42	1.13***	-2.41	1.13***	1.00 (14)
Traffic volume	2.77	1.99**	2.49	2.02*	1.00 (14)
Patches	1.14	0.19***	1.13	0.19***	1.00 (14)
PC1	-1.12	0.32**	-1.13	0.32***	1.00 (14)
PC2	-0.20	0.26	-0.11	0.28	0.55 (7)
Waterway density	-	-	0.56	0.90	0.43 (6)
Moran's I	-	-	1.12	4.11	0.38 (6)
PC3	-	-	-0.05	0.20	0.33 (6)

Figure 1

Maps of Wales showing locations of (a) mortalities (n = 171) and (b) pseudo-absences (n = 1200).

Country shapefiles were extracted using the *maps* (Becker and Wilks, 2021) and *mapdata* (Becker and Wilks, 2018) packages in R.
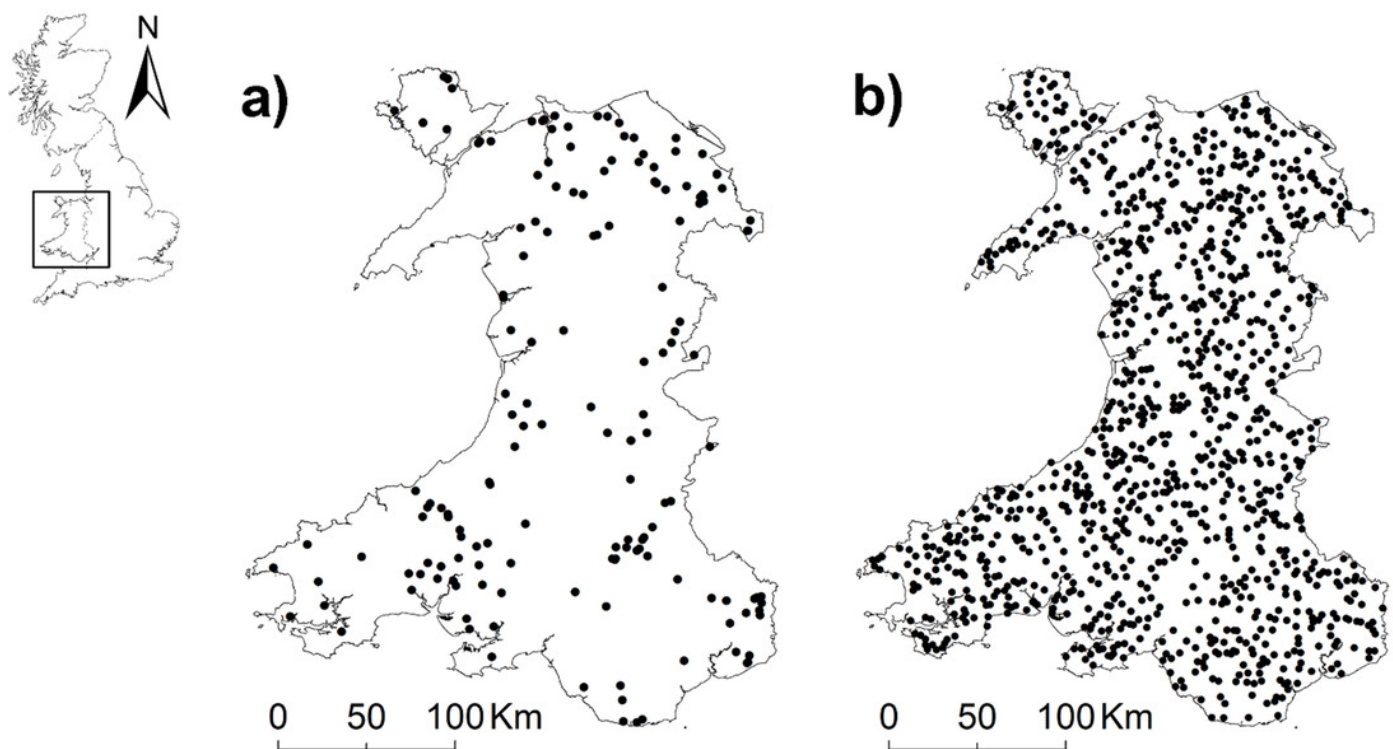
Figure 2

Total numbers of polecat road casualties associated with certain road types in Wales.
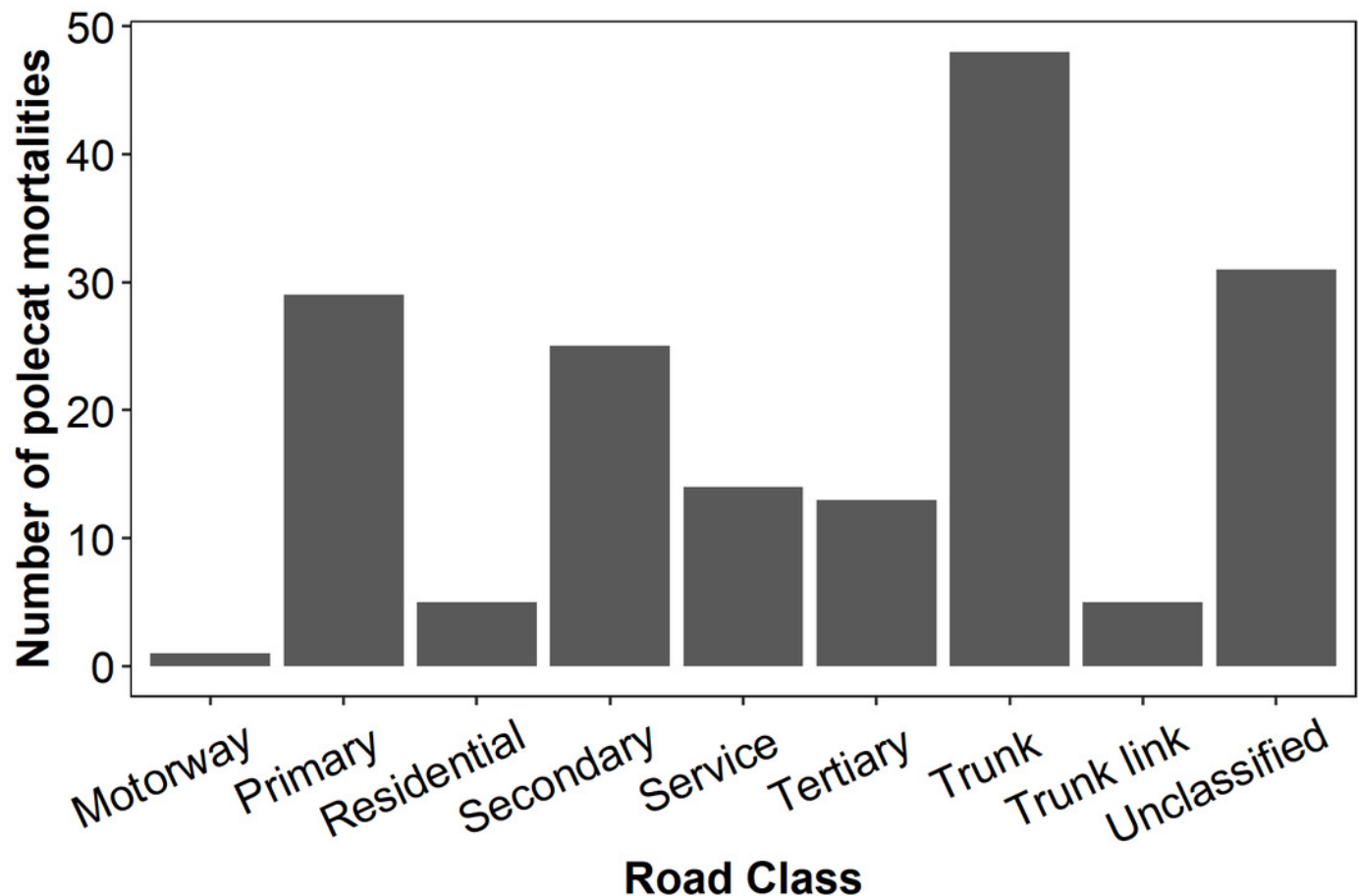
Figure 3

Seasonal fluctuation in polecat WVC showing smoothed numer of detections with 95% confidence intervals.