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Life in the fast lane: roadkill risk along an urban–rural gradient

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Abstract

Wildlife-vehicle collisions are a major cause of mortality in animal populations and can cause significant population-level effects. Urban areas are typically associated with higher road densities and unique wildlife communities in comparison to rural areas, and therefore have the potential to be associated with high numbers of collisions, and roadkill risk. Here, we use a citizen science database of wildlife roadkill and species distribution models to assess how roadkill risk (probability of roadkill observation per km^2) varied along an urban–rural gradient for British wildlife. Roadkill risk was positively associated with road density, until around 5000 m/km^2, a value representing villages or the outskirts of towns and cities. Beyond 5000 m/km^2, risk remained high for some species (hedgehog, fox, pigeons and gulls) but reduced for other species (badger, rabbit, pheasant). Roadkill risk was a function of live species distribution for badger, hedgehog and rabbit, with significant overlap between spatial patterns of roadkill risk and the species' live distribution. This was not the case for fox, pheasant, pigeons and gulls. Fox roadkill risk was underrepresented in rural areas, possibly due to low road density, while pheasant risk was overrepresented. For pigeons and gulls—well-known urban exploiters—roadkill risk was overrepresented in urban areas given their live distributions, possibly due to risks associated with foraging, particularly roadkill scavenging by gulls. Our results highlight the dangers of the UK's dense road networks to wildlife, even to species considered adapted to urban environments and human disturbance.

Key words: wildlife-vehicle collisions, urban ecology, citizen science

Introduction

Roads make an important contribution to the global human footprint. Currently, a fifth of the Earth's terrestrial surface is located within 1 km of a road (Ibisch et al. 2016), and their effects can permeate far into the surrounding habitat (Forman 2000; Jaeger et al. 2005; Ibisch et al. 2016). Globally, 25 million km^2 of road is expected to be built by 2030, along with a doubling of the number of cars being used by 2050 (Alamgir et al. 2017; Leonard and Hochuli 2017). As a universal characteristic of human development, roads are found across many habitat types, including along the entire urban–rural gradient (Forman 2000; Lawton 2018). It is predicted that an additional 1.2 million km^2 of land will be urbanised by 2030, with a bias towards development in biodiversity hotspots and the tropics (Seto et al. 2012).

As road networks and urban areas grow, a pressing issue is how this infrastructure is affecting wildlife. Wildlife-vehicle collisions are a major source of mortality, estimated to be in the millions annually in many countries (Schwartz et al. 2020). The population-level effects of this anthropogenic mortality are significant for some species and can lead to major population declines (Coffin 2007; Fahrig and Rytwinski 2009; Lawton 2018). Three critically endangered Amur leopards (*Panthera pardus orientalis*) killed on roads, for example, accounted for approximately 5–10% of the population (Lawton 2018). Indeed, roads have been described as a significant contributor to current widespread biodiversity declines (Yue et al. 2019). Similarly, urban infrastructure has profound effects on habitat quality, with knock-on effects for population sizes, community structures

and animal behaviour (Lowry et al. 2013; Aronson et al. 2014; Beninde et al. 2015; Saari et al. 2016), with animal abundance generally seen to decrease (Saari et al. 2016). Towns and cities also support high densities of roads and high traffic levels, both of which are likely to increase wildlife-vehicle collisions (Ditchkoff et al. 2006; Ha and Shilling 2018; Fabrizio et al. 2019).

Rural areas, conversely, are typically characterised by low road densities and traffic levels, factors that are expected to lower wildlife-vehicle collisions (Ha and Shilling 2018; Fabrizio et al. 2019). However, where major roads, such as motorways, intersect rural habitat, the associated high traffic levels could be a wildlife mortality factor. In addition, rural roads tend to have high-speed limits, lighting is poor and wildlife habitats are likely to abut road edges, all factors that may increase roadkill risk (Caro et al. 2000; Burgin and Brainwood 2008; Visintin et al. 2016; Tejera et al. 2018; Kreling et al. 2019). Road characteristics, habitat quality and disturbance levels not only vary between rural and urban areas but also within and between urban areas. Thus, classifying entire cities and towns as one habitat type – 'urban' misses this environmental heterogeneity (McDonnell and Hahs 2008; Beninde et al. 2015). Dense collections of buildings and areas of high human activity are often interspersed with green spaces and less disturbed habitats (Ramalho and Hobbs 2012). Additionally, patterns of human activity differ within cities and towns, with industrial, residential and commercial areas all having different disturbance regimes (Hahs and McDonnell 2006; Schwartz et al. 2018). Therefore, we need to examine the urban–rural gradient at a fine spatial scale to capture this heterogeneity and to assess its role in wildlife roadkill risk.

Despite the negative ecological impacts of urbanisation for some species, others known as 'urban exploiters', can reach large population sizes and densities within towns and cities, for example, house sparrows (*Passer domesticus*; Ditchkoff et al. 2006; McKinney 2006; Lowry et al. 2013), brown rats (*Rattus norvegicus*; McKinney 2006) and raccoons (*Procyon lotor*; Ditchkoff et al. 2006). High population sizes of urban wildlife species can be driven by exploitation of anthropogenic food sources, the use of artificial structures for roosting and nesting and higher temperatures relative to rural areas that act to increase overwinter survival (Chace and Walsh 2006; Ditchkoff et al. 2006; McKinney 2006; Lowry et al. 2013; Shwartz et al. 2013).

The risk of wildlife-vehicle collision is often a function of a species' local abundance (Gehrt 2002; Morelle et al. 2013; D'Amico et al. 2015). By definition, urban exploiter species are more prevalent in cities and towns, and so we posit they may be more frequently observed as roadkill in urban compared with rural areas simply as a function of being locally abundant. Urbanisation is often synonymous with declines in native biodiversity, associated with habitat loss and/or fragmentation (Aronson et al. 2014). Species that are not adapted to, or have been excluded from urban environments and as a consequence suffer reduced survival and populations, are termed 'urban avoiders' (McKinney 2002) and include, for example, wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*; Croft et al. 2017). We may expect roadkill risk for urban avoiders to be a function of their local abundance, and so wildlife-vehicle collisions for these species be more frequently observed in rural than in urban areas.

In this study, we analysed a unique and extensive citizen science database of UK wildlife roadkill to create national species distribution models for the seven most commonly reported roadkill species, spanning both urban exploiter and avoider species. Using these models at a fine spatial scale (1 km²), we assessed how roadkill risk varied along an urban–rural gradient, and what abiotic factors underlie this risk. Additionally, because roadkill risk may simply be a function of a species being adapted to that particular habitat, and so present there, we also determined if risk was a function of a species' distribution or not.

Methods

Roadkill data

Records of date, location and species of wildlife roadkill across Great Britain were extracted from a citizen science project (https://projectsplatter.co.uk/) from January 2013 to the end of January 2019 and included 45 499 reports covering 148 species. Data constituted ad hoc records of wildlife roadkill submitted year-round and UK-wide by citizen scientists and by other organisations (e.g. local authorities and species interest groups, such as Cardiff University Otter Project https://www.cardiff.ac.uk/otter-project). Data were submitted to the project primarily by a bespoke smartphone app but were also collected via social media, an online form, and by email. Data were compiled weekly and filtered for quality, for example, through ensuring that records are within a species' known range. Reports from Northern Ireland were excluded due to low reporting coverage. The data used for this study are open access, available online via the NBN Atlas (https://registry.nbnatlas.org/public/show/dp205).

To allow for detailed investigation of spatial roadkill patterns of different species, the three most frequently reported mammal and bird species were selected as focal species to ensure large sample sizes and wide coverage. For mammals, these were badger (*Meles meles*, $n = 6877$), red fox (*Vulpes vulpes*, $n = 4564$) and rabbit (*Oryctolagus cuniculus*, $n = 4050$). Hedgehog (*Erinaceus europaeus*, $n = 3273$), the fourth most common mammal, was also included due to their conservation importance (Roos et al. 2012; Pettett et al. 2017). Frequently many *Laridae* and *Columba* were not identified to species level, and so species were grouped as 'gulls' and 'pigeons', respectively. Thus, the top three reported birds were pheasant (*Phasianus colchicus*, $n = 4050$), pigeons (Columbidae, $n = 2918$) and gulls (Laridae, $n = 826$).

Quantifying an urban–rural gradient

Great Britain was divided into 1 km² grid cells using Quantum GIS v3.4.4 (QGIS Development Team 2018). For each cell, we quantified two habitat variables, which have previously been shown to effectively represent an urban–rural gradient, these were road density and 'urbanity' (Hahs and McDonnell 2006; McDonnell and Hahs 2008; du Toit and Cilliers 2011). A third variable, 'urban green space', was also added to capture the heterogeneity in urban spaces associated with parks, allotments, etc. (Beninde et al. 2015).

Road density was calculated as the density of roads (metres) per km² using OpenStreetMap (Ordnance Survey 2018). To create the 'urbanity' and 'urban green space' variables, a principal components analysis (PCA) was used to combine data on human population density, people per urban fabric, proportion urban fabric and proportion urban green space. Human population density was calculated in each 1 km² cell using 2017 census data on Lower Layer Super Output Areas; these are geographic areas of varying size that contain a mean human population of 1500 (Office for National Statistics 2018). People per

urban fabric was calculated as human population density/(proportion urban fabric + 0.5) to distinguish between areas within cities with the same level of urban fabric that vary in usage and disturbance patterns, for example, industrial areas, where human activity is highest during work hours, and residential areas where human activity is highest in the early morning and evening (after Hahs and McDonnell 2006). A value of 0.5 was added to the denominator to avoid issues of division by 0 in areas without urban fabric. The proportion of urban fabric (built land) and the proportion of urban green space (e.g. public parks, allotments and sports grounds), for each 1 km^2 grid cell, were calculated from the 100 m resolution Land Cover Project 2018 maps (Copernicus Land Monitoring Service 2018) defined according to CORINE (Bossard et al. 2000).

The first two components of the PCA accounted for 89% of the variance and were used as the urbanity and urban green space variables. Principal component 1, 'urbanity', was similarly explained by proportion urban fabric (loading coefficient = 0.53), population density (loading coefficient = 0.59) and people per urban fabric (loading coefficient = 0.58). Principal component 2, 'urban green space', was mainly explained by the proportion of urban green space (loading coefficient = 0.99). Both PCA variables were positively loaded, so that higher values indicated greater urbanity or more green space.

How does roadkill risk vary along an urban–rural gradient?

Species distribution models were created in MaxEnt 3.4.1 (Phillips et al. 2006) for each of the seven focal taxa (badger, fox, hedgehog, rabbit, pheasant, pigeons and gulls) in order to calculate the relationship between road density, urbanity and urban green space (our urban–rural gradient) and the probability of roadkill presence within any given km^2, hereafter 'roadkill risk' (after Garrote et al. 2018). MaxEnt calculates these relationships by comparing urban-rural variables at the roadkill locations with those at random background points, known as pseudo-absences and visualises them in 'response curves' (Phillips et al. 2006). Post hoc jack-knife analyses of MaxEnt models were used to determine which variables most affected roadkill risk by assessing the relative contribution of each variable to the model's performance. Species distribution models were also used to produce distribution maps of roadkill risk in the UK.

A common feature of *ad hoc* collected citizen science data is sampling bias (Dickinson et al. 2010; Shilling and Waetjen 2015; Mair and Ruete 2016). To control for the possibility of such bias in the public reporting of roadkill, a Gaussian kernel density map of all 45 499 roadkill reports was produced in R Version 3.5.1 (R Core Team 2018) using packages dismo (to interface R and MaxEnt), raster (to manipulate spatial data), maggrittr, MASS (to calculate kernel densities), maptools and GISTools (both to read shapefiles) (Venables and Ripley 2002; Brunsdon and Chen 2014; Hijmans et al. 2017; Bivand and Lewin-Koh 2019; Hijmans 2019). This map was then used as a bias file in MaxEnt; bias files are used to weight pseudo-absences so that they are equally biased to the roadkill reports, effectively 'cancelling out' variations in sampling effort (Phillips et al. 2006; Elith et al. 2011; Warton et al. 2013; Ha and Shilling 2018).

The statistical significance of variables related to roadkill risk was determined through comparison to null models using random locations (after Raes and ter Steege 2007; Gomes et al. 2018). Therefore, 99 null models were run using unique random locations produced in QGIS, using the 'Random Points Inside Polygons' tool with sample sizes equal to the number of reports for a given species (Raes and ter Steege 2007; Gomes et al. 2018). Sampling bias in roadkill reports could increase the likelihood of species distribution models performing better than null models (Raes and ter Steege 2007; Gomes et al. 2018). Therefore to avoid this, the random locations produced in QGIS were restricted to 1 km^2 grid cells where at least one roadkill occurrence of any species was reported (Raes and ter Steege 2007; Gomes et al. 2018). MaxEnt settings, urban–rural gradient variables and the bias file used for null models were identical to those used for focal species models. A one-sided 95% confidence interval (CI) was used to determine whether roadkill models performed significantly better than the null models; thus, if the roadkill model's area under the curve (AUC) was higher than the upper CI value, roadkill risk varied significantly along an urban–rural gradient (after Raes and ter Steege 2007; Gomes et al. 2018).

Is roadkill risk a function of species distribution?

Live sightings of all seven focal taxa were obtained from the National Biodiversity Network (NBN) Atlas (National Biodiversity Network 2019) from 2013 to 2019, to cover the same temporal distribution as the roadkill data, and used as presence data to produce species distribution maps, using MaxEnt species distribution models. Species distribution models of NBN data were run using the same variables and settings as the roadkill models, except for the bias file that was not used as it is specific to bias within the roadkill data.

To identify whether roadkill risk was a function of a species' distribution or not, Schoener's (1968) niche overlap statistic (D) was used to calculate the similarity between the distribution maps of live species and those of roadkill risk for each of the seven focal species. Niche overlap statistics were originally developed to quantify similarities in the utilisation of resources (such as space, time, or prey) between two populations (e.g. species, age classes or sexes) (Schoener 1968; Pianka 1973). Recently, niche overlap models have been adapted to compare species distribution model outputs in order to measure the overlap in spatial distributions between two populations (Warren et al. 2008). Using ENMTools (Warren et al. 2010) the overlap between the spatial distribution of wildlife roadkill and live species distribution from NBN was calculated for each species, giving a measure that ranges from 0 (no overlap; roadkill risk is not related to live distribution) to 1 (identical; roadkill risk is a function of live distribution) (Warren et al. 2008). The significance of the overlap between live species and the roadkill distributions was calculated using a niche equivalency test in ENMTools, which determined whether the overlap was greater than that expected by chance.

Results

How does roadkill risk vary along an urban–rural gradient?

Across an urban–rural gradient, road density was the most important variable for predicting roadkill risk for all focal species (Table 1), with risk increasing with increasing density of roads, rising sharply for all species up to a peak road density of c. 5000 m/km^2 (Fig. 1A and B). This road density is synonymous with villages and the outskirts of towns and cities. As an illustration of what a given road density equates to in the landscape, we have created an example with the city of Cardiff, UK and its surrounding settlements (Fig. 2A) where the peak road density (dark blue cells) is seen to be associated with peri-urban areas;

Table 1: Percentage contribution of urban–rural gradient variables to MaxEnt model performance of roadkill risk for the most common UK wildlife roadkill species

Species	Road density	Urbanity	Urban green space	Model AUC (upper CI)
Badger	94.9	5.1	0	0.67 (0.61)[*]
Fox	92.2	7.6	0.2	0.75 (0.64)[*]
Hedgehog	97.5	1.5	1	0.73 (0.66)[*]
Rabbit	89.5	10	0.5	0.68 (0.65)[*]
Pheasant	81.8	17.9	0.2	0.66 (0.61)[*]
Pigeon spp.	71.7	28.3	0	0.78 (0.67)[*]
Gull spp.	96.4	3.6	0.1	0.86 (0.74)[*]

The AUC values of roadkill models containing all three variables and the upper 95% CI of null models are given.
[*]Models that are significant at the 5% level.
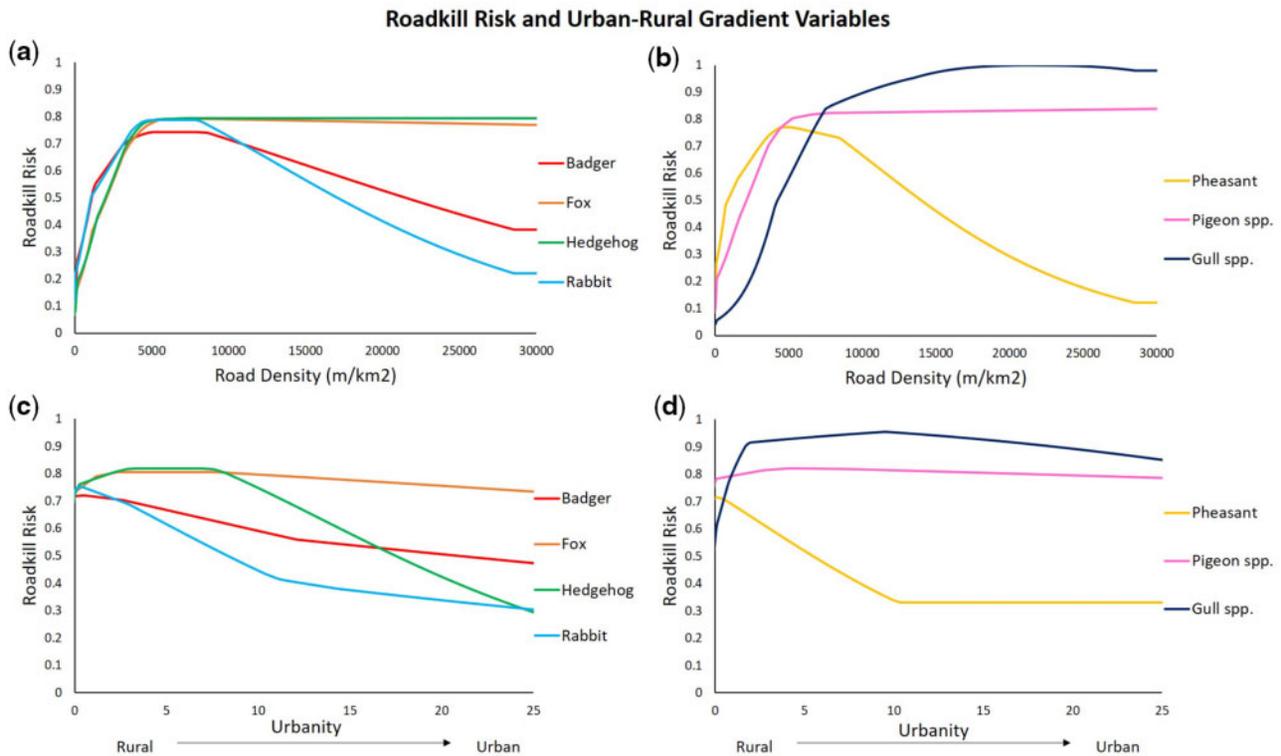
Figure 1: MaxEnt response curves describing the shape of the relationship between roadkill risk and road density (m/km^2) in (A) mammals and (B) birds and the relationship between roadkill risk and urbanity in (C) mammals and (C) birds.

effectively the habitat on the edge of and in-between towns and cities (Fig. 2B). For most species, roadkill risk remained high with increasing road density, but for pheasant, badger and rabbit roadkill risk decreased at road densities above c.5000 m/km^2 (Fig. 1A and B).

Urbanity was less important than road density in explaining variation in roadkill risk, contributing <10% of model performance for most species, but had a role to play in roadkill risk for pheasant (17.9%) and pigeons (28.3%). For pheasant, the risk reduced as urbanity increased (Fig. 1D), while for pigeons the roadkill risk initially rose with urbanity and remained high with increasing urbanity (Fig. 1D). A small amount of variation in urbanity contributed to roadkill risk in mammals, the species-specific patterns were similar to those with road density, but notably hedgehog roadkill risk reduced at high urbanity levels

(>10, synonymous with city centres). Urban green space did not play a role in explaining variation in roadkill risk for any species, contributing ≤1% of model performance (Table 1).

Is roadkill risk a function of species distribution?

The spatial pattern of roadkill risk was closely related to a given species' live distribution for badger, hedgehog and rabbit, as indicated by significant live distribution-roadkill overlap (Table 2), with differences between the distributions limited to areas of Scotland and Mid-Wales where urban measures predicted moderate to high roadkill but these species are scarce (Fig. 3). For fox, pheasant, pigeons and gulls, roadkill risk was not a function of known species presence although distributions of live and roadkill risk overlap were high, they were not significant
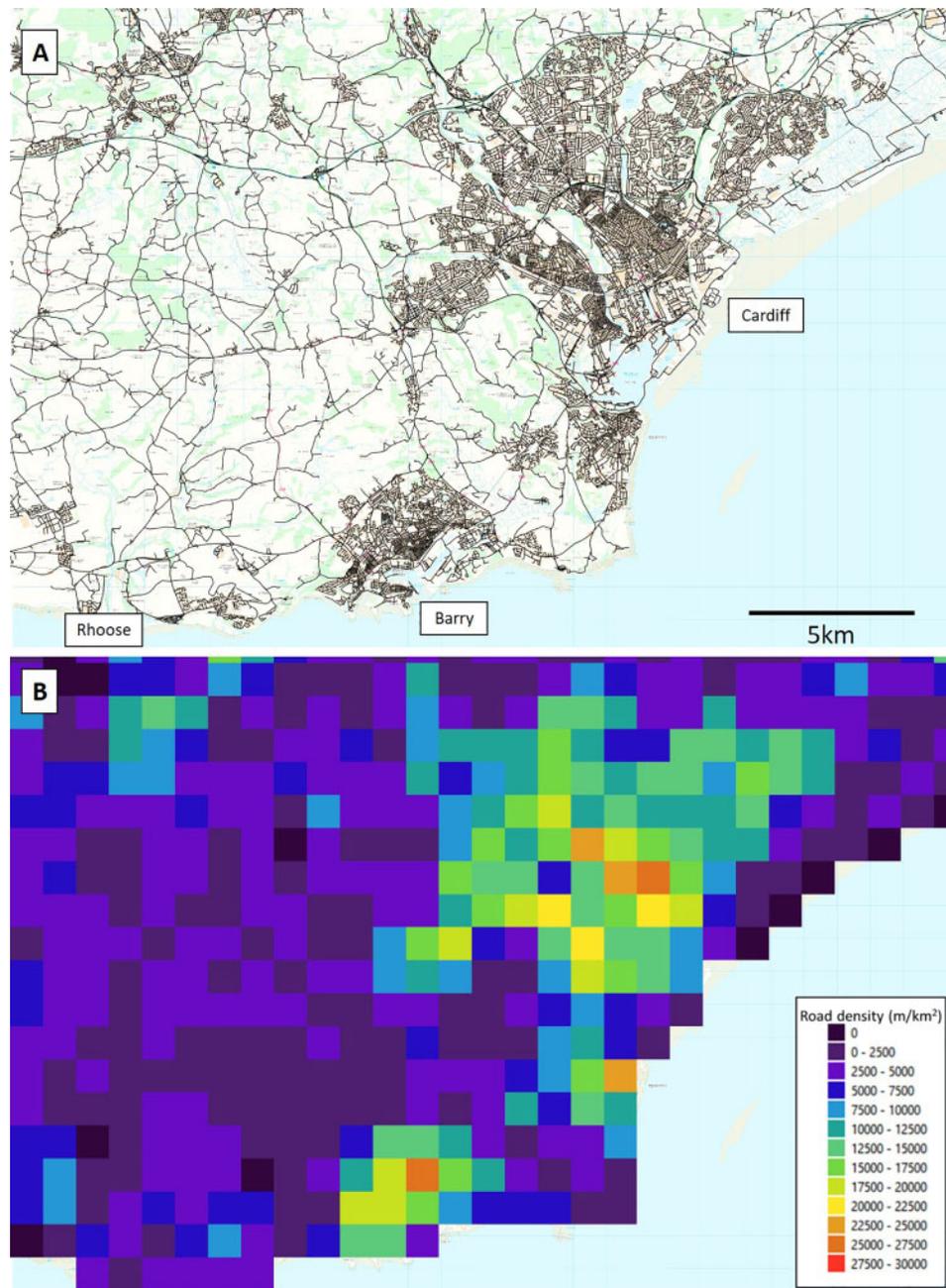
Figure 2: An illustrative example of road density around different sized settlements, showing that the 5000 m/km^2 density at which roadkill risk peaks is associated with peri-urban habitats. (**A**) A map of South Wales overlayed with the road network showing a city (Cardiff—population size of c.478 000), a town (Barry—population size of c.55 000) and a village (Rhoose—population size of c.5000). (**B**) The corresponding road density (coloured cells) at 1 km^2 resolution.

([Table 2](), [Fig. 4](https://)). Gulls and pigeons had the lowest levels of overlap, with roadkill being more concentrated in urban areas than expected, given their live distributions ([Fig. 4C and D]()).

Discussion

Along an urban–rural gradient, road density had the greatest influence on roadkill risk for all focal species, in agreement with previous studies ([Philcox et al. 1999]; [Ha and Shilling 2018]; [Fabrizio et al. 2019]). Roadkill risk increased sharply with road density until it reached approximately 5000 m/km^2, a value common in villages and on the outskirts of towns and cities.

There were, however, mixed effects as road densities increased above this value, and two patterns emerged; either roadkill risk remained high (for hedgehog, fox, pigeons and gulls) or it reduced (badger, rabbit and pheasant). A small amount of variation in roadkill risk was also attributed to urbanity, which followed the same species-specific patterns as road density. The inter-specific difference in roadkill risk associated with road density and to a lesser extent urbanity could simply be a reflection of a given species' presence (or absence), as has been observed previously ([Gehrt 2002]; [Morelle et al. 2013]; [D'Amico et al. 2015]). Our overlap tests, however, found that this was not the case for fox, pheasant, gulls and pigeons. We find that

Table 2: Similarity in spatial distribution between roadkill and live species distributions of the most common wildlife roadkill taxa in the UK, as measured by Schoener's D, where 1 implies total congruence and 0 entirely different

Species	Schoener's D	Lower 95% CI
Badger	0.93	0.81[*]
Fox	0.85	0.85
Hedgehog	0.87	0.86[*]
Rabbit	0.89	0.86[*]
Pheasant	0.87	0.88
Pigeon spp.	0.80	0.88
Gull spp.	0.66	0.90

The lower 95% CI of null models are given.
[*]Distributions that had significant live distribution-roadkill overlap at the 5% level.

pigeons and gulls have much higher roadkill risk in urban areas than expected by their distributions, whereas fox roadkill risk is underrepresented in very rural areas and pheasant risk is overrepresented in some rural areas.

What determines roadkill risk?

Two possible explanations for reduced roadkill risk at high road densities and urbanity exist; behavioural adaptations and/or changes in population density mitigated by wildlife-vehicle collisions, although the two are not mutually exclusive. Animals can adapt to the presence of roads by exhibiting behavioural avoidance; disturbance created by vehicle noise and light may cause animals to change their home ranges in order to avoid roads (Jaeger et al. 2005; Fahrig and Rytwinski 2009; Berthinussen and Altringham 2012; Leblond et al. 2013; D'Amico et al. 2015) and could contribute to a reduction in roadkill risk as avoidance leads to reduced road crossing behaviour (Jaeger et al. 2005; Leblond et al. 2013). Such disturbance is known to affect badgers, pheasants and rabbits (Huck et al. 2008; Serrano Perez et al. 2008; Bosch et al. 2016; Madden et al. 2018). The second explanation is that populations have been suppressed due to historic wildlife-vehicle collisions (Ascensão et al. 2019). However, this explanation is very unlikely for pheasants, that are an artificially managed and inflated population due to release of an estimated number of 35 million individuals per year (Madden et al. 2018). Population declines may also occur indirectly by reducing both habitat availability (through destruction, fragmentation and 'barrier effects' that restrict animal movement), and habitat quality (due to vehicle emissions and edge effects) (Laurance et al. 2004; Jaeger et al. 2005; Coffin 2007; Fahrig and Rytwinski 2009; Berthinussen and Altringham 2012; Leblond et al. 2013; D'Amico et al. 2015).

Previous studies have suggested that behavioural adaptations in urban animal populations could reduce roadkill risk in urban areas with high road densities. For example, predator species including bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) have been documented to increase activity levels at times of low human disturbance, including reduced traffic loadings (Riley et al. 2003; Ditchkoff et al. 2006). Additionally, some birds can adapt directly to the risk of vehicle collisions; by adapting their flight initiation distance to the speed limit of the road (Legagneux and Ducatez 2013), and foxes learn to selectively cross roads when there is less traffic (Baker et al. 2007). While such behaviours should reduce roadkill risk, our results indicate that roadkill risk remains high in urban areas for fox, hedgehog,

gulls and pigeons. This unexpectedly high risk may be because such adaptations are balanced by other behavioural changes that are common in urban populations, for example, increased boldness and habituation, including longer response times to threats, such as oncoming vehicles, which could increase roadkill risk (Atwell et al. 2012; Lowry et al. 2013).

Urban green space made negligible contributions to roadkill risk for all species (Table 1). This variable, as calculated, quantifies parks and leisure facilities (e.g. golf courses). As such, city centres without this type of green space could have the same value as rural areas and agricultural land. As a result, urban green space does not fully account for the effects of these areas and means we may not have a full picture of roadkill risk within the urban environment. Managed parks can have positive effects on biodiversity and can change community composition within urban areas, sometimes supporting urban avoider species (Chace and Walsh 2006; Shwartz et al. 2013), thus potentially acting as high-risk habitat for rural species, which are otherwise absent from the urban environment. Alternatively, due to the lack of roads in parks, they could act as low-risk areas for urban exploiter species with small home ranges, as they can move within the park without needing to navigate roads.

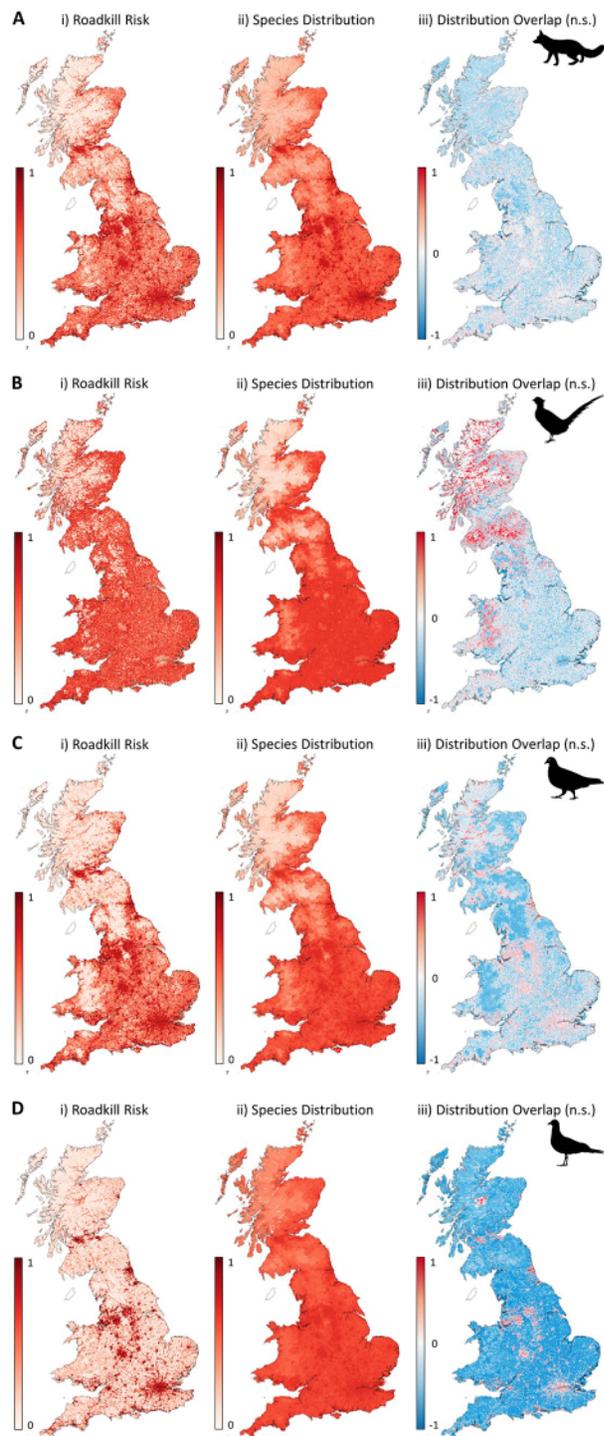## Is roadkill risk a function of distribution or adaptation?

Some species had a sustained roadkill risk with increasing road density and urbanity (fox, hedgehog, pigeons and gulls), while for others risk declined (badger, rabbit and pheasant). In the current study foxes, hedgehogs, pigeons and gulls are all species that have successfully colonised urban environments and can be described as urban exploiters (Brousseau et al. 1996; Maciusik et al. 2010; Hubert et al. 2011; Scott et al. 2014; Spennemann and Watson 2017). The comparatively high population numbers of these species in urban areas likely combine with high traffic levels and an increased need to cross roads, keeping roadkill risk high in urban environments (Visintin et al. 2016). Thus, roadkill risk could be expected to be high as a result of each species' distribution, as previously observed (Gehrt et al. 2002; Morelle et al. 2013; D'Amico et al. 2015). Indeed, in the current study, we find significant overlap between live species and roadkill risk distributions for some species, for example, hedgehog (Table 2, Fig. 3), that is for some species roadkill risk is closely associated with species presence. Roadkill risk increases in urban areas but reduces again at the highest levels of urbanity, particularly found in city centres. Wright et al. (2020) found a similar pattern in hedgehog roadkill risk in the UK, which reflected the availability of suitable grassland habitat, further suggesting that for this species roadkill is a function of distribution.

Species distribution for foxes was similar to their roadkill risk distribution (Fig. 4B), with high overlap although this was narrowly non-significant (Table 2). The difference between the live and roadkill distributions was limited to very rural areas where roadkill risk was slightly lower than expected. While foxes are able to colonise urban areas, they are just as common in rural areas with similar estimates of population densities across urban and natural habitat types in the UK (Croft et al. 2017). Thus, risk closely reflects variation in road density and is low in these very rural areas due to the limited amount of roads and traffic, rather than low density of fox populations.

For urban exploiters, notably pigeons and gulls, roadkill risk was not a function of their known presence (Fig. 4C and D). While these species typically have dense populations in cities (Brousseau et al. 1996; Belant et al. 1998; Maciusik et al. 2010; Spennemann and Watson 2017), roadkill risk was much higher
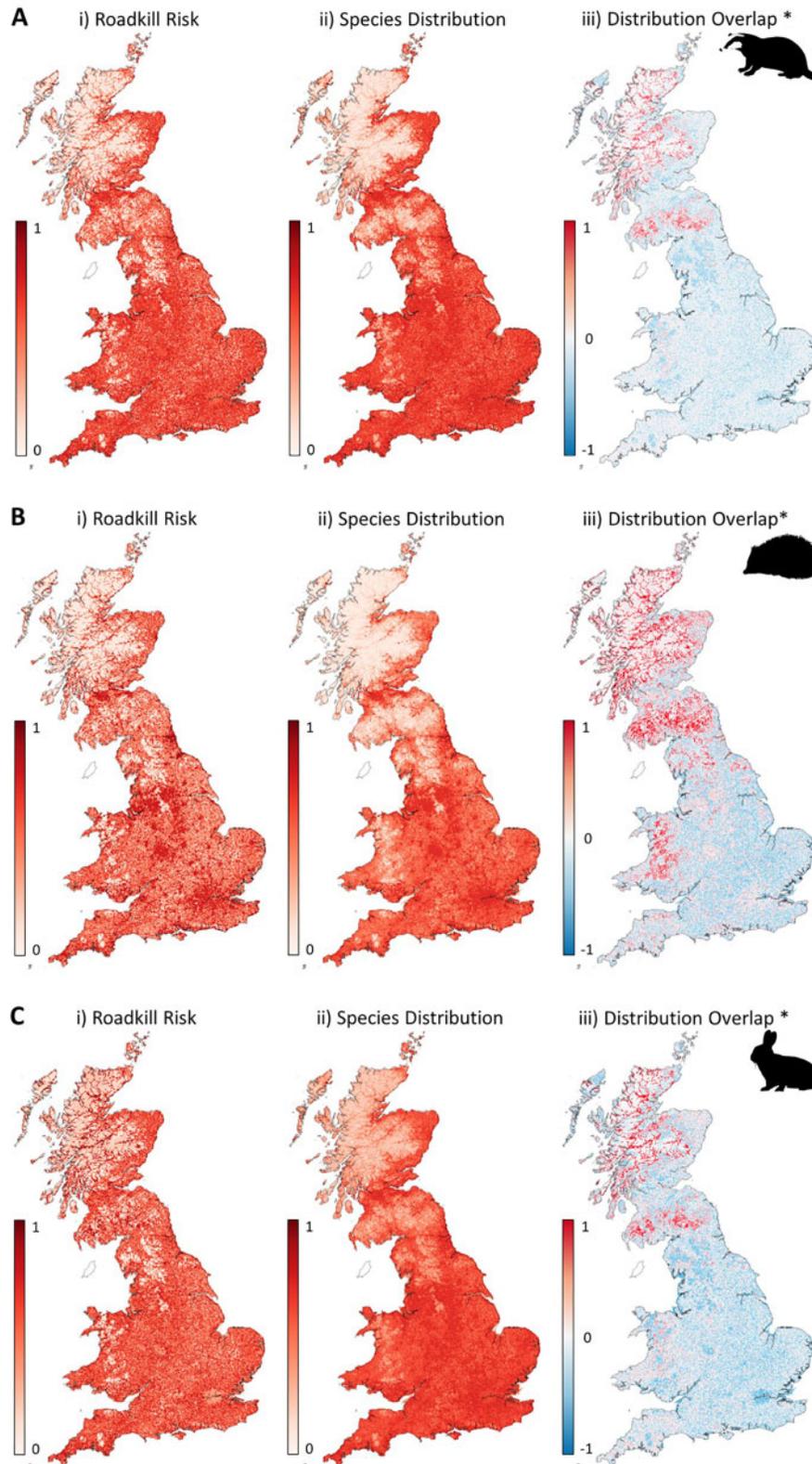
Figure 3: (**A**) Badger, (**B**) Hedgehog and (**C**) Rabbit—(i) roadkill risk and (ii) live species distribution plotted at a 1 km² scale across the UK, ranging from 0 (low) to 1 (high) roadkill risk/probability of species presence and (iii) the overlap between roadkill risk and a given species live distribution. Zero values (white areas) indicate no difference, negative values (blue) are areas where roadkill risk was lower than species presence, while positive values (red) are areas where roadkill risk was higher than species presence. Asterisks identify significant overlap for a given species across the UK, at the 5% level.

Figure 4: (**A**) Fox, (**B**) Pheasant, (**C**) Pigeons and (**D**) Gulls—(i) roadkill risk and (ii) live species distribution maps, plotted at a 1 km² scale across the UK, ranging from 0 (low) to 1 (high) roadkill risk/probability of species presence and (iii) the overlap between roadkill risk and a given species' live distribution. Zero values (white areas) indicate no difference, negative values (blue) are areas where roadkill risk was lower than species presence, while positive values (red) are areas where roadkill risk was higher than species presence.

pose. One other possibility is that the live distribution data (from NBN) for these species is positively biased towards reports from rural areas. Pigeons and gulls are considered pest species in urban areas and members of the public may be less likely to report them than in rural areas (Maciusik et al. 2010). The vast majority of gull roadkill reports, however, are clustered in and around large urban areas suggesting that this is a genuine ecological pattern.

Roadkill risk may be a function of the environment itself. The structure of urban habitats can affect airflow, and therefore change the use of airspace in urban birds (Shepard et al. 2016), for example. Gulls commonly use lines of buildings or trees to get lift, a strategy which is considered to be high risk; flying at low altitudes in cluttered environments increases the chances of losing control (Shepard et al. 2016). This strategy could bring birds into the path of vehicles, increasing roadkill risk. It is not clear, however, why this would have a stronger effect on gulls than pigeons, but it could be a function of species-specific wing loading differences as wing shape has an impact on manoeuvrability in flight, as well as take-off time (Warrick 1998). Alternatively, both pigeons and gulls commonly utilise anthropogenic food sources in urban environments (Brousseau et al. 1996; Belant et al. 1998; Ciminari et al. 2005; Rose et al. 2006; Maciusik et al. 2010)—in particular, gulls are heavily reliant on landfill and refuse (Brousseau et al. 1996; Belant et al. 1998; Maciusik et al. 2010), which may bring birds into close proximity with roads, for example, kerbside refuse collections, so increasing their risk of vehicle collisions. Gulls are also carrion scavengers in urban environments, including of roadkill (Schwartz et al. 2018), a feeding strategy that had been hypothesised to increase roadkill risk (Tejera et al. 2018; Kreling et al. 2019). Gull roadkill frequency peaks in July in the UK (Schwartz 2020), which coincides with their breeding season, and fledglings would be particularly at risk while scavenging near or on roads as they are unable to fly (Belant et al. 1998). These life history traits could explain why pigeons had a slightly weaker relationship between urban variables and roadkill risk as they do not commonly scavenge carrion and are more reliant on food sources that may be located away from roads and vehicles (Rose et al. 2006; Spennemann and Watson 2017; Schwartz et al. 2018). These results highlight that even for classic urban exploiter species, urban habitats are still associated with many risks to which they may not be well adapted.

In contrast to the urban exploiters, badgers, rabbits and pheasants represent typical urban avoiders, species that tend to avoid or are excluded from urban areas (Huck et al. 2008; Serrano Perez et al. 2008; Bosch et al. 2016; Madden et al. 2018). Thus, the low roadkill risk in urban areas for these species is likely driven by the species' presence, or lack thereof. Indeed, there was significant overlap between live species and roadkill risk distributions for badger and rabbit (Table 2, Fig. 3). Pheasants too had high levels of live distribution-roadkill overlap, but this was not significant (Table 2, Fig. 4), indicating that while roadkill risk is partly a function of their distribution, other factors play an important role in determining risk. One possible variable is that individuals raised for shooting may be at greater risk of road mortality than their naturalised counterparts, due to their lack of escape responses and underdeveloped flight muscles (Madden et al. 2018). Indeed, peaks in pheasant road mortality are reported in the autumn, when birds are released from pens, and in late winter when supplementary feed is withdrawn, causing dispersal from shooting estates (Madden and Perkins 2017).

in urban areas than their live distributions would predict (Fig. 4C and D). Such a pattern could suggest that even though the urban environment offers an optimum niche for these species, they are poorly adapted to the mortality risks that roads

With urbanisation, subsequent road building will be paired with large changes in habitat structure, and for many species, this may result in an increase in roadkill. While there are many examples of animals adapting to exploit or survive in the urban environment (Johnson and Munshi-South 2017), our study indicates that some species may not be well adapted to the hazards posed by dense road networks in urban environments and could be at a high risk of mortality. Further increases in the already high risk of road mortality could have significant negative impacts, especially for species such as gulls and hedgehogs that are endangered and for whom the urban environment is an important habitat (Roos et al. 2012; Eaton et al. 2015; Pettett et al. 2017). Increased roadkill in such environments poses particular challenges for conservation, as implementing post-hoc road mitigation strategies in dense urban road networks may be difficult and expensive.

Data availability

The data used for this study are open access, available online via the NBN Atlas (https://registry.nbnatlas.org/public/show/dp205).

Conflict of interest: None declared.

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