Roads and Wildlife

Amy L. W. Schwartz (BSc, MSc)
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Statement of contributions

Chapter 1: Introduction to road ecology

Writing by Amy Williams Schwartz.

Chapter 2: The value of monitoring wildlife roadkill

Writing and data compilation by Amy Williams Schwartz.

Chapter 3: Temporal patterns of wildlife roadkill on UK roads

Data collected by volunteer contributors to roadkill recording scheme Project Splatter (project founder and co-ordinator: Dr Sarah Perkins). Chapter design, data analysis, and writing by Amy Williams Schwartz.

Chapter 4: Roadkill scavenging behaviour in an urban environment

Data collection by Harry Williams, data analysis and writing by Amy Williams Schwartz.

Chapter 5: The 'phantom road'; effects of artificial light and traffic noise on woodland wildlife

Experimental design, data analysis, and writing by Amy Williams Schwartz. Data collection by Amy Williams Schwartz with assistance from Stephen Lowe and Hannah Atkins.

Chapter 6: Discussion

Writing by Amy Williams Schwartz.

Thesis summary

Roads are an inevitable result of human expansion across the globe, but result in unintended consequences for the other species we share our planet with, both directly (e.g. through deaths due to wildlife-vehicle collisions), as well as indirectly (e.g. through habitat degradation, and providing a barrier to animal movement). These effects are so wide-reaching that a new term – road ecology – was coined in 1998 to describe the study of these ecological impacts.

The overall aim of this thesis is to increase our knowledge of road ecology and begins by reviewing the literature on the scientific value of monitoring wildlife roadkill (**Chapter 2**). Five continuous years of data from a citizen science roadkill recording scheme 'Project Splatter' is then used to examine temporal trends in wildlife roadkill in the UK (**Chapter 3**). Camera-trapping experiments were utilised to gain additional insight into the behavioural effects of roads on wildlife, namely the behaviour of scavengers of roadkill (**Chapter 4**), as well as the effects of light and sound pollution caused by roads on the behaviour of wildlife (**Chapter 5**).

A review of the existing literature in **Chapter 2** demonstrates how studying roadkill has enhanced our knowledge in several critical areas of ecological study, I also show how even with limited geographical and taxonomic estimates, in excess of 400 million vertebrates are killed on roads worldwide each year. **Chapter 3** shows that the temporal patterns of roadkill in the UK are peculiar to a given species, but are remarkably consistent between years, and poses the hypothesis that the observed temporal patterns are driven by species-specific seasonal changes in behaviour. In **Chapter 4**, I show how scavengers of roadkill can remove carcasses very quickly, potentially leading to an under-estimation of true roadkill numbers - 76% of experimentally placed carcasses were removed within 12 hours, and the number of scavenging events peaked in the first few hours of daylight. Finally, **Chapter 5** demonstrates how road traffic noise is likely to negatively influence wildlife behaviour by causing animals to avoid particularly noisy areas, as well as by altering

their behaviour to increase the amount of vigilance behaviour, leading to a reduction in time available to spend foraging.

The research presented within this thesis has expanded the current knowledge of road ecology, particularly within a UK context, and has continued to demonstrate how data collected by members of the public (through citizen science projects) can have important scientific value. This deeper understanding of the impacts of roads on wildlife is important if we wish to reduce the ecological impacts of our ever-expanding road system.

1

Introduction to road ecology

Roads and wildlife

Roads split the terrestrial surface of the Earth into ~600,000 individual patches (Ibisch et al., 2016), and it is expected that at least 25 million kilometres of new roads will be built globally by 2050, a 60% increase in road lengths since 2010 (Laurance et al., 2014). An estimated 15-20% of the United States is ecologically impacted by roads (Forman & Alexander, 1998), and this percentage is likely to be much higher in the UK, where road networks are even denser. As a result, both direct and indirect (Forman & Alexander, 1998) effects of roads are likely to cause significant impacts on wildlife. 'Direct' impacts of roads usually refers to wildlife-vehicle collisions (WVCs), which result in millions of wildlife deaths per year across many countries. 'Indirect' impacts can cover a variety of factors, from the 'barrier effect' (preventing animals from crossing) and habitat loss/degradation that roads cause, to road avoidance caused by artificial light and sound pollution, which can render many roadsides unsuitable for wildlife (Ware et al., 2015).

Direct impacts

Wildlife-vehicle collisions

Any time that an animal crosses a road, there is the potential for a collision to occur. We show (Chapter 2) that where estimates of WVC numbers have been made, every

country's estimates number in the millions per annum (Schwartz et al., 2020). The first organised citizen-science survey of wildlife roadkill in the UK was run by the British Trust for Ornithology during 1960-61, which calculated the number of birds killed on UK roads as 2.5 million per annum (Hodson and Snow 1965). There is no contemporary count of the number of vertebrates killed on UK roads, but yearly estimates of individual species/taxa deaths have been made. A study of the UK badger (*Meles meles*) population size combined with an estimate of the percentage of badgers that die due to collisions with vehicles determined that 50,000 badgers per year die on roads (Harris et al., 1992), although this number is likely to be even higher now as both the badger population and the numbers of vehicles on roads (Department for Transport, 2017c) have increased since that study took place. A recent study using roadkill count data estimated that at least 167,000 hedgehogs (*Erinaceus europaeus*) – 10% of the population (but potentially as many as 335,000 – 20%) are killed each year in the UK (Wembridge et al., 2016).

Indirect impacts

Habitat fragmentation and the barrier effect

Roads can act as a physical barrier to many species, preventing crossing from occurring. The surface of the Earth is split into ~600,000 patches by roads (Ibisch et al., 2016), which results in the available habitat for species to be drastically reduced, and subsequently fragmented as roads can act as a barrier, thus constraining the distribution and movement of many species (Corlatti et al., 2009). This fragmentation, in some cases, can result in a genetic 'bottleneck' effect when a population is contained within a small area – this has been shown to occur in a range of species, including mountain lions (*Puma concolor*) in the Santa Monica Mountains, California, which live alongside the 101 Freeway (Benson et al., 2016), common frog (*Rana temporaria*) populations separated by highways in Germany (Reh & Seitz, 1990), and in road-fragmented populations of bank voles (*Myodes glareolous*) in Europe (Gerlach & Musolf, 2000).

Road avoidance and anthropogenic disturbance

As well as being a barrier to crossing for some species, roads can also result in habitat degradation, two sources of which are particularly apparent; sound and artificial light disturbance from vehicles and streetlights, the effects of which are explored in more depth in Chapter 6. An experiment in the USA using a series of speakers playing road traffic noise to create a 'phantom road' in a previously undisturbed area found that a large proportion of the bird community avoided the noisy areas – a quarter decline in overall abundance, and almost complete avoidance by some species (McClure et al., 2013). Of birds that remained in the area despite the noise, there was a marked decline in body condition, hypothesised to be due to an increase amount of time spent performing vigilance behaviour, and therefore a reduction in time spent feeding (Ware et al., 2015) – younger birds were found to be more strongly affected by noise than the adults (McClure et al., 2017). Light pollution from streetlights poses a particular problem for nocturnal species such as bats; although some bats such as the *Pipistrellus* species may take advantage of feeding opportunities that insect aggregations around lights can offer (Stone et al., 2015), some, such as lesser horseshoe bats (*Rhinolophus hipposideros*), will actively avoid any artificially lit area (Stone et al., 2012).

Benefits of roads?

Provision of habitats

The negative effects of roads are numerous, but there are, however, some opportunities for roadside verges to become 'reserves' for some species. It is difficult to balance the positive effects (e.g. habitat/food provision) with the negative (increased sound/light disturbance, and vehicle collision risk), and, indeed, very little work has been done in this area. For example, leaving road verges uncut can provide habitat for many plants, pollinators (Valtonen et al., 2006), and small mammals (Bellamy et al., 2000), but could have the unfortunate effect of attracting predators to hunt in the area, resulting in an increased risk for collisions. Indeed, the presence of rabbits (*Oryctolagus cuniculus*) taking advantage of the food resources present in

road verges has been found to result in a significant increase in polecat (*Mustela putorius*) road mortality in the area (Barrientos & Bolonio, 2009). A study reviewing road effects on birds found that roads can provide foraging habitat, reduce predation pressure, and associated roadside structures such as fences and streetlights can provide perching opportunities for hunting and rest, but the number of documented negative impacts of roads on abundance outweighed the positives by a factor of five (Morelli et al., 2014). Some species can use road verges not only as habitat, but as their own transportation corridors, as has been shown for hedgehogs (Patrick et al., 2001).

Roadkill scavengers

As has been previously discussed, the number of animals estimated killed per year in many countries is in the millions, which then results in a widely available food source for a range of scavenging vertebrates. Although the only vertebrate obligate scavengers are vultures (Ruxton & Houston, 2004), there are many taxa that will take advantage of an easy carrion meal – some are even named for their propensity to do so, i.e. the carrion crow (*Corvus corone*). These scavengers are providing an important ecosystem service – removing carcasses from the environment and thus reducing the risk of disease, as well as removal of unsightly carcasses – and this can occur remarkably quickly (Schwartz et al., 2018; Chapter 4). However, in the UK, many of these common roadkill scavengers (such as magpies *Pica pica*, carrion crows, and foxes *Vulpes vulpes*) are generalist predators, and will also feed on other sources of food including eggs and chicks of songbirds, many of which are in decline (Baker et al., 2006). Therefore, there is a concern that the availability of a large biomass of roadkill can support an artificially inflated population of such scavengers/generalist predators, which in turn could impact other species. Certainly, this has already been shown to be the case with the pied crow (*Corvus alba*) in southern Africa, whose range-expansion (and subsequent abundance) has been shown to be directly linked with the availability of food in the form of roadkill, but the presence of this species may place additional predation pressure on other wildlife (Joseph et al., 2017).

Citizen science and potential issues of bias

'Citizen science' as a means for collecting data is on the rise, especially with the frequent use of smartphone apps which can provide an easy way to collect standardised data by utilising citizen scientists (Vercayie & Herremans, 2015). A 'citizen scientist' is defined as "a volunteer who collects and/or processes data as part of a scientific enquiry" (Silvertown, 2009). Citizen science projects have been widely used in the field of ecology to provide information on areas such as population trends, species' range shifts, and changes in phenology (Bonney et al., 2009). The majority of roadkill recording schemes use citizen science to collect roadkill data, many of which are opportunistic (or *ad-hoc*) records (Shilling et al., 2015). Although the use of citizen science is likely the only way to get large amounts of roadkill data over a broad geographic and time span (Vercayie & Herremans, 2015) it is important that the potential limitations and issues that could arise from using such data are examined.

Project Splatter and roadkill recording schemes

Part of the data used in this thesis have been collected by members of the public and submitted to UK roadkill recording scheme 'Project Splatter' (www.projectsplatter.co.uk). The project was founded in 2013, and began life as an undergraduate project, but it was quickly realised that collecting such data was of huge ecological importance, as no group had previously collected roadkill data for all vertebrates, across the entire United Kingdom, all year round. Project Splatter uses data primarily from 'citizen scientists' – members of the public who submit observations of wildlife roadkill that they observe on an ad-hoc basis, but also receives records from local councils, and other species-interest groups such as the Badger Trust, and the Cardiff University Otter Project. To date, the project has amassed over 72,000 individual wildlife roadkill records (as of January 2020).

Other contemporary groups record wildlife roadkill in the UK, but these are either done for a limited timeframe (e.g. People's Trust for Endangered Species' 'Mammals

on Roads' survey), or for a specific group (e.g. the Badger Trust receives *ad-hoc* records of badger roadkill). Globally, there are a number of organisations that record wildlife roadkill (Shilling et al., 2020; http://globalroadkill.net/index.html; Table 1), the majority of which rely on citizen scientists for the majority of their records (Shilling et al. 2015).

Table 1. Summary table of roadkill recording schemes worldwide that currently (as of October 2020) record data year-round, and for all vertebrate species – projects that focus only on certain species groups (i.e. ungulates) are omitted. An indication is given of whether the schemes accept roadkill records from the public (citizen science).

Project name	Location	Website/app	Citizen science?
Alberta Wildlife Watch	Alberta, Canada	https://albertawildlifewatch.ca/	No
Animal-vehicle Collisions	Czech Republic	http://srazenazver.cz/en/	Yes
Animals Under Wheels	Belgium	https://old.waarnemingen.be/vs/start	Yes
California Roadkill Observation System	California, USA	https://www.wildlifecrossing.net/california/	Yes
Cyprus Roadkill Observation System	Cyprus	https://cyroadkills.org/home/	Yes
LIFE LINES	Portugal	https://lifelines.uevora.pt/	Yes
Linking Landscapes for Massachusetts Wildlife	Massachusetts, USA	https://www.linkinglandscapes.info/wildlife-roadkill-database.html	Yes
Maine Audubon Wildlife Road Watch	Maine, USA	https://www.wildlifecrossing.net/maine/	Yes
Project Roadkill	Austria & Worldwide	https://roadkill.at/en/	Yes
Project Splatter	United Kingdom	https://projectsplatter.co.uk/	Yes
Road Kill Survey	Ireland	http://www.biology.ie/home.php?m=npws	Yes
Road Watch	South Africa	https://play.google.com/store/apps/details?id=com.ewt.ewtroadwatch&hl	Yes
ROad.kill	Romania	https://road-kill-registration.green-web.eu/?lang=en	Yes

Roadkill Reporter	Australia	https://play.google.com/store/apps/details?id=au.com.ionata.roadkillreporter&hl=en_GB&gl=US	Yes
Roadkills India	India	https://www.roadkills.in/	Yes
Viltolycka	Sweden	https://www.viltolycka.se/	No

Data collection methods

There are two broad methods of citizen science roadkill data collection (Heigl & Zaller, 2016); standardised and opportunistic data collection. Standardised roadkill monitoring involves a participant recording the length of road surveyed, as well as the presence of any roadkill animal that is encountered along the journey - such data are sometimes more valuable than opportunistic records as recorder effort is recorded and the data therefore includes information on both the presence and absence of roadkill. However, due to the rigorous nature of such data collection, this method is significantly more time-consuming for the citizen scientist, and there can be much lower uptake of participants as a result (Vercayie & Herremans, 2015), resulting in reduced amounts of data recorded overall. Opportunistic data collection can see very large datasets being compiled (Isaac et al., 2014), but the records are presence-only, usually with no recorder effort included. The lack of recorder effort means that opportunistic roadkill records cannot be used to, for example, estimate the number of animals killed on a particular road over a given time period. However, due to the large size of many citizen science datasets, the ratio of signal to noise is favourable, resulting in strong patterns (Bonney et al. 2009), and volunteer-based recording schemes usually provide reliable data, with an increased sampling effort (and therefore statistical power) with an increasing number of participants (Schmeller et al., 2009).

Species bias

The species that are recorded by a citizen science roadkill recording scheme can be biased by several factors. Firstly, many participants record roadkill that they see whilst in a moving vehicle (either as a passenger or later when the journey has

concluded), and this can result in a bias towards the larger or more easily identifiable species (e.g. badger would be much easier to identify at speed than a small passerine bird) – previous work has shown that searching for roadkill on foot is significantly more effective than searching from a car (Slater, 2002). Secondly, even if a participant is searching for roadkill on foot, a lack of records of smaller species may come about due to the fact that smaller species are more quickly and easily removed from the road by scavengers. The majority (62%) of small carcasses (the size of a large field vole *Microtus agrestis* or common swift *Apus apus*) have been found to be removed within just two hours in urban areas (Schwartz et al., 2018, Chapter 4). Finally, a bias that may be either conscious or unconscious can lead to larger and more charismatic species being more likely to be recorded. For example, a bias has been found in the recording of more eye-catching species in a citizen science roadkill recording dataset based in Austria (Heigl & Zaller, 2016), and personal communication with Project Splatter participants has revealed that some reporters do not record all species that they observe frequently, for example ring-necked pheasant (*Phasianus colchicus*) and rabbit. Occasional observers in a South African citizen science roadkill recording scheme were found to be more likely to report easily identifiable and/or charismatic species more often than regular reporters or trained observers (Périquet et al., 2018).

Participant distribution

The spatial distribution of participants in a citizen science study can have an impact on the types of roadkill data that are collected. For example, a given participant may report every roadkill animal they see, but they may only drive one particular commuting route, and not venture into the wider countryside. This could have an impact on both the overall number of animals, as well as the species assemblage that is observed as roadkill. However, work in South Africa comparing roadkill data from trained road patrols to citizen science data found that the broad spatial and taxonomic patterns were similar between the two groups, and that citizen scientists

can provide reliable and robust data for roadkill studies looking at general patterns across spatial and temporal scales (Périquet et al., 2018).

Citizen science & temporal patterns

Citizen science data can be used to detect trends in species occurrence and/or abundance, both in the long and short term. Data from eBird (a citizen science-based database of bird observations) has been used to describe the seasonal patterns of relative abundance shown by the eastern phoebe (*Sayornis phoebe*) in the USA by computing seasonal abundance as an average of daily abundance estimates (Bonney et al., 2009). Long-term trends of some species have also been calculated using citizen science data as a proportion of total records of all species that are recorded within the same time frame (Callcutt et al., 2018). Temporal trends in disease have also been identified through the use of citizen science; in the UK, a database of opportunistic reports of mortality and morbidity in garden birds was found to have a significant peak in the number of reports of avian pox during August and September, and a spatial spread was also observed for one type of pox (Lawson et al., 2012).

Temporal patterns in wildlife roadkill have traditionally been identified through the use of standardised roadkill counts along a given road transect e.g. for vertebrates in Spain (D'Amico et al., 2015; Garriga et al., 2017), mammals in Ireland (Haigh, 2012) and Colombia (Meza et al., 2019), carnivores in Portugal (Grilo et al., 2009), birds in southern Brazil (Rosa & Bager, 2012) and barn owls (*Tyto alba*) in France (Massemin et al., 1998). However, such targeted studies are costly in both time and finances, and are limited in the spatial area that can be covered, due to logistical restraints (Périquet et al., 2018).

The use of existing databases to examine temporal roadkill trends, however, such as Government records of vehicle-ungulate collisions in Spain (Lagos et al., 2012), and a police database of animal-vehicle collisions in Belgium (Morelle et al., 2013), as well as citizen science roadkill databases can offer an opportunity to study such patterns across broader spatial and temporal scales than traditional roadkill surveys (Périquet et al., 2018).

A study on pheasant (*Phasianus colchicus*), mortality that included data from a citizen science roadkill recording scheme (Project Splatter) used both measures of the proportion of roadkill birds that were pheasants, as well as the proportion of annual records of pheasants that were killed in a given month to overcome issues with temporal biases (Madden & Perkins, 2017). Using the proportion of birds killed that were a given species allows for sampling effort and traffic pressure to be corrected for over long-term data, however this particular approach can be vastly distorted by mortality of other species – for example, the relative decrease of one species' reports could be due to an increase in reports of another species, rather than reflecting true patterns (Madden & Perkins, 2017). However, using the proportion of a species' yearly records that were killed in a given month controls for year-on-year variations in population sizes of that species, as well as fluctuations in mortality of other species, but is more susceptible to biases caused by sampling effort (Madden & Perkins, 2017).

Thesis overview

This thesis aims to fill gaps in knowledge of wildlife/road interactions in the UK by presenting novel data, both from long-term data collection by Project Splatter, as well as from separate field experiments. The thesis begins with a literature review that synthesises and provides examples on the ways in which collecting data on wildlife roadkill can contribute to a variety of ecological fields (Chapter 2). The following chapters use Project Splatter citizen science data to examine temporal (Chapter 3) patterns of wildlife roadkill, followed by empirical experiment using camera traps to study wildlife behaviour related to road ecology, namely looking at roadkill scavenging behaviour (Chapter 4) and wildlife behavioural changes during light and sound disturbance (Chapter 5).

Objective 1: To review the benefits of monitoring wildlife roadkill (Chapter 2 – The value of monitoring wildlife roadkill).

In this chapter I provide a review and synthesis of the literature of the ways in which consistently, systematically, and extensively monitoring roadkill facilitates five critical areas of ecological study: 1) monitoring roadkill numbers, 2) estimating population sizes, 3) mapping native and invasive species distributions, 4) animal behaviour, and 5) monitoring of contaminants and disease. Additionally, I explore how the collection of such data also offers a valuable opportunity for members of the public to be directly involved in scientific data collection and research (citizen science).

Objective 2: Determine the variation in temporal patterns of wildlife roadkill (Chapter 3 – An overview of temporal patterns of wildlife roadkill on UK roads).

In this chapter, I used six years of data (2014-2019 inclusive) collated by Project Splatter to examine the temporal patterns of wildlife roadkill for a variety of species. The most common species/taxa (referred to hereafter as 'taxa') reported to the project were used in the analysis (amounting to 18 taxa). Most (17 out of 18) taxa showed one of two distinct yearly patterns of roadkill abundance; unimodal (one peak), and bimodal (two peaks), with only one species (the red fox) showing no seasonality. These patterns differed markedly between taxa but were usually remarkably consistent between years for each given taxon. In the majority of cases, the between-taxa variation is driven predominantly by animal behaviour. For example, polecats show a strongly bimodal peak in spring and autumn, driven by males dispersing in spring to find mates, and then juveniles dispersing in autumn, whereas the peak for hedgehogs is unimodal, occurring in the summer due to higher activity levels and an inflated population size due to the presence of juveniles.

Objective 3: Investigate the extent to which scavenging of roadkill could lead to under-estimations of numbers of animals killed on roads (Chapter 4 – Roadkill scavenging behaviour in an urban environment).

This chapter uses data from a field experiment using baited camera-traps at a variety of locations (both residential and parkland) within the city of Cardiff, Wales, to look at roadkill scavenging behaviour in urban areas. We found that the 'roadkill' was scavenged remarkably quickly, usually within two hours, and that scavenging behaviour peaks at around sunrise. The majority of bait was removed by corvids; of 90 incidences of bait removal, 18 were performed by carrion crows (*Corvus corone*), and 20 by Eurasian magpies (*Pica pica*) – the other species observed were gulls (both herring *Larus argentatus* and lesser black-backed *Larus fuscus*), foxes (*Vulpes vulpes*), and domestic cats and dogs. We found that removal of corpses by scavengers could mean that the actual number of road deaths is six times more than that observed during surveys.

Objective 4: To look at whether artificial light and road noise affects wildlife behaviour (Chapter 5 – How does the creation of a 'phantom road' affect wildlife behaviour?).

This chapter involved setting up a 'phantom road' in an area of previously undisturbed woodland. The 'road' consisted of a deployed LED street light and a speaker which played a looped recording of traffic noise. Behaviour was monitored using camera-traps, baited with food. The study used a before-during-after design to look at whether overall animal activity, as well as individual behaviour types, varied during four different treatments on the 'during' day – either a control (where no equipment was turned on), sound only, light only, and both light and sound disturbance. We found a significant reduction in animal activity during sound-on treatments, as well as proportionally more time spend performing anti-predator 'vigilance' behaviour.

2

The value of monitoring wildlife roadkill

A version of this chapter has been published in the European Journal of Wildlife Research:

Abstract

The number of wildlife-vehicle collisions have obvious value in estimating the direct effects of roads on wildlife, i.e. mortality due to vehicle collisions. Given the nature of the data – species identification and location - there is, however, much wider ecological knowledge that can be gained by monitoring wildlife roadkill. Here, we review the added value and opportunities provided by these data, through a series of case studies where such data have been instrumental in contributing to the advancement of knowledge in species distributions, population dynamics, and animal behaviour, as well as informing us about health of the species and of the environment. We propose that consistently, systematically, and extensively monitoring roadkill facilitates five critical areas of ecological study: 1) monitoring roadkill numbers, 2) monitoring population trends, 3) mapping native and invasive species distributions, 4) animal behaviour, and 5) monitoring of contaminants and disease. The collection of such data also offers a valuable opportunity for members of the public to be directly involved in scientific data collection and research (citizen science). Through continuing to monitor wildlife roadkill, we can expand our knowledge across a wide range of ecological research areas, as well as facilitating investigations that aim to reduce both the direct and indirect effects of roads on wildlife populations.

'Road ecology' - an emerging field

Major roads split the Earth's terrestrial surface into ~600,000 patches, of which more than half are <1km^2 in area, and only 7% are larger than 100km2 (Ibisch et al., 2016). Unsurprisingly, wildlife-vehicle collisions are subsequently numerous. Globally, second to legal harvesting, roads are the largest source of anthropogenic mortality for many vertebrates (Hill et al., 2019), with more than a million vertebrates estimated to be killed on roads in the USA per day (Erickson et al., 2005; Loss et al., 2014). Wildlife-vehicle collisions, and the related ecological effects of roads on

wildlife, for example the 'barrier effect' - linear infrastructure reducing animal movements (Forman & Alexander, 1998) - have led to the field of 'road ecology'; a term first mentioned in the literature twenty years ago (Forman, 1998). Since that time the field has burgeoned, with 'road ecology' peer-reviewed papers on Web of Science increasing dramatically (Figure 1), and organisations appearing that are dedicated to studying the field, for example, the Road Ecology Center at UC Davis, California (https://roadecology.ucdavis.edu/frontpage), as well as 'citizen science' projects worldwide that collate roadkill observations submitted by members of the public to collect data on road impacts on wildlife (http://globalroadkill.net/) (Shilling et al., 2015). It is expected that at least 25 million kilometres of new roads will be built globally by 2050, a 60% increase in road lengths since 2010 (Laurance et al., 2014), so wildlife-vehicle collisions are expected to increase with time (mammal-vehicle collisions have already been shown to have increased significantly since the 1970s: Hill et al. 2019), and with that we expect this discipline to continue to expand too.
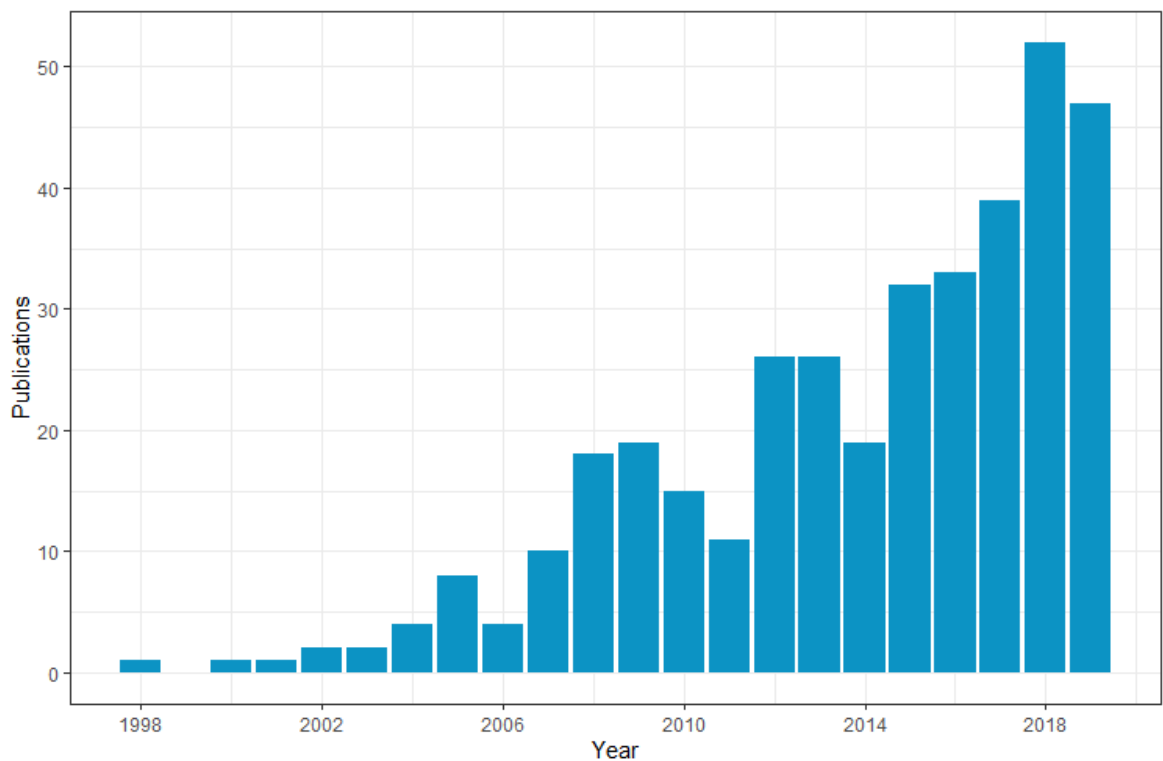

Figure 1. ISI peer-reviewed publications with "road ecology" as a topic on Web of Science from 1998 to 2019

In this review, we first provide context to the importance of collecting and collating data of wildlife vehicle collisions by providing a brief overview of how the collection of such data provides an essential framework for understanding and quantifying the 'direct' effects of roads on wildlife, i.e., wildlife mortality associated with roads. Reviews exist of the field of road ecology as a whole (Forman & Alexander, 1998; Coffin, 2007), the use of citizen science in monitoring wildlife roadkill (Shilling et al., 2015; Vercayie & Herremans, 2015), and the use and effectiveness of mitigation strategies (Grilo et al., 2010; Rytwinski et al., 2016). Here, we add to this rich literature by focusing on our second aim to describe how the growing systems for collecting wildlife-vehicle collision data also provides rich datasets of ecological data. These new and growing datasets can also inadvertently and sometimes opportunistically provide additional ecological insights, which are the focus of this review. Specifically, we describe how this opportunistic data collection may enable information on population trends and species distributions, non-native species invasions, as well as revealing novel animal behaviour. In addition, roadkill carcasses can be used as 'sentinels' for monitoring of environmental contaminants and diseases. Finally, the collection of roadkill data can offer a valuable opportunity for members of the public to get directly involved in scientific data collection and research (citizen science), and we outline ways in which 'citizen scientists' have been instrumental in contributing to roadkill data collection.

Monitoring wildlife-vehicle collision numbers

The first published count of wildlife-vehicle collisions took place in 1935, in which an individual observer recorded 940 avian mortalities over 4000 miles of road (Barnes, 1936). The first citizen science project to quantify wildlife mortality on roads in the UK, however, was organised by the British Trust for Ornithology during 1960-61 (Hodson & Snow, 1965). By extrapolating the number of casualties across a given length of road, the annual number of roadkill birds was calculated as approximately 2.5 million. It is important to note, however, that when this study occurred in the 1960s, the UK's roads supported fewer than 8 million vehicles compared to the current-day 38 million (Department for Transport, 2018). Present day national

roadkill surveys engage citizens across the world (Shilling et al., 2015), with millions of vertebrates estimated to be killed on the roads yearly (Figure 2). Worldwide, the direct effects of vehicles on population numbers are substantial, for example, estimates amount to 340 million birds killed on the roads annually in the US (Loss et al., 2014), and 13.8 million birds annually in Canada (Bishop & Brogan, 2013). Indeed, globally where annual estimates have been calculated there is not a country that does not have a wildlife-vehicle collision count that is estimated to be in the millions (Figure 2). Estimating the total number of animals killed on roads, and population impacts from this source of mortality is important in its own right, but as important is the use of wildlife-vehicle collision data to understand other aspects of ecology. Wildlife-vehicle collision data number in the millions and even with limited geographical and taxonomic estimates, in excess of 400 million vertebrate records per year could be generated using roadkill data (Figure 2). It is clear that the amount of data generated are high, and utility of such data could be extended beyond counts of deaths.
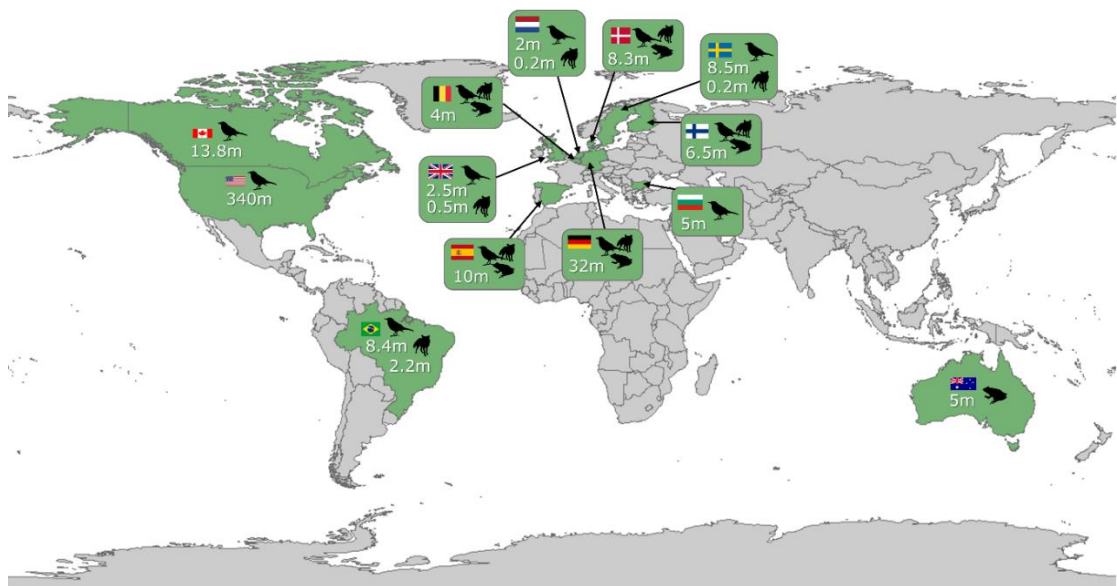
**Figure 2**. Available country-level estimates of vertebrate wildlife-vehicle collisions by major taxa (birds, mammals, and amphibians) in millions per year. No annual estimates were found for countries in grey. Data collated from Hodson & Snow, 1965; Harris et al., 1992; Seiler & Helldin, 2006; Langbein, 2007; Bishop & Brogan, 2013; Loss et al., 2014; Wembridge et al., 2016 & González-Suárez et al., 2018.

Using wildlife-vehicle collision data to inform about species distributions

Traditionally, species distribution data are collected in a variety of ways; by individual hobbyists and interest groups, through systematic monitoring of populations, professional surveys (e.g. scientific studies or surveys by ecological consultants), and increasingly through citizen science projects, all of which can consist of standardised surveys and/or opportunistic sightings (Berry, 1988; August et al., 2015; Pocock et al., 2015). These data are frequently, but not always, collated locally by biological records centres (Nelson & Ellis, 2018), and globally, into the Global Biodiversity Information Facility (GBIF - https://www.gbif.org/; Robertson et al., 2014). GBIF is the world's largest open source biodiversity dataset, and currently holds nearly 1.4 billion records, comprised of over 49,000 individual datasets (as of December 2019). Currently, there are 12 roadkill recording schemes worldwide (http://globalroadkill.net/programs.html), of which two submit their data to GBIF (UK's Project Splatter and Taiwan's Roadkill Observation Network), with many others offering open access to the data (Shilling et al., 2015).

It is important to understand species distributions both for inherent interest and knowledge gain, as well as for practical reasons, such as implementing conservation efforts, and management of invasive species (Guisan et al., 2013; Caley et al., 2015). Distribution data for species that are elusive (e.g. nocturnal) or in low densities can be difficult to collect (Kindberg et al., 2009) and such data have traditionally been collected through targeted surveys (e.g. Newman et al., 2003), which may only cover a given area, or time-frame. Such surveys are inherently high-cost (Jones, 2011). Wildlife-vehicle collision data, however, offers consistent and continuous insight beyond dedicated surveys, due to high geographical coverage and relatively low cost (Shilling et al., 2015).

The presence of a carcass offers incontrovertible evidence of the presence of a given species, leading to the discovery of populations in previously unknown locations. Roadkill monitoring has led to rediscovery of the Indochinese rat snake (*Pytas korros*) in Borneo from an incidental roadkill encounter; the first time the species had been recorded in the country for over 100 years (Auliya 2002). Such a contribution to

species' distribution data are particularly valuable for species that are difficult to monitor, such as a recovering species, one that is range-expanding and/or nocturnal animals (Calenge et al. 2015; see case study below). The nine-banded armadillo (*Dasypus novemcinctus*), for example, is an elusive species whose range expansion in the southern United States is being tracked via roadkill carcasses (Hofmann, 2005). In Wales, the first pine marten (*Martes martes*) in the country since the 1970s was discovered dead on the road in 2012 (Vincent Wildlife Trust, 2012). Prior to this, efforts to determine whether pine marten were still present in Wales had relied solely on the presence of scat (Vincent Wildlife Trust, 2012). Similarly, roadkill data have been used to monitor the recovery of the polecat (*Mustela putorius*) in the UK; over half of all records were road casualties (Croose 2016; see case study below).

New species have been described through monitoring roadkill - a decomposing roadkill bird was collected in the Nechisar National Park, Ethiopia, and on return to the Natural History Museum, London was confirmed as a new species to science; the Nechisar nightjar (*Caprimulgus solala*) (Safford et al., 1995). Roadkill can also provide information on the potential of some species to appear well outside their normal range (vagrancy). There are occasions of extremely rare vagrant birds being discovered dead on the road following a vehicle collision. One such example was a common nighthawk (*Chordeiles minor*) found dead on a road on St Mary's, Isles of Scilly in 2008, only the 21st record for Britain and Ireland (Hudson & the Rarities Committee, 2009). Additionally, the first record of golden nightjar (*Caprimulgus eximius*) for the Western Palearctic region occurred in 2015 on a road in Morocco after being struck by the observers' car (Dyczkowski, 2016).

It is, however, important to state that, as in all ecological surveys, absence of evidence is not evidence of absence. Animals may not be observed as roadkill for a variety of reasons; firstly, they may simply avoid the road completely – species categorised as road 'avoiders' face lower mortality than other species (Jacobson et al., 2016). Secondly, certain species may cross roads safely throughout their distribution, or in places where that is possible, for example via 'green bridges'. Thirdly, the lack of observed roadkill of a given species could be due to previous mass mortality events due to extensive wildlife-vehicle collisions (Ascensão et al., 2019),

i.e. a population has already become locally extinct due to traffic pressure. Finally, the persistence of carcasses on the road, and so the opportunity to be observed can differ due to a variety of factors such as traffic flow, animal taxon, size (Barrientos et al., 2018) and scavenging rates of the carcass (Barrientos et al., 2018; Schwartz et al., 2018).

Case study – monitoring polecat spread and recovery through roadkill observations

Although a formerly very widespread species, the polecat in the UK was persecuted almost to extinction in the 1800s, and was confined to a stronghold in mid-Wales (Costa et al., 2013). Following the cessation of widespread persecution in the second half of the 20th century, the population recovered, recolonising most of Wales and much of central England, with range expansion occurring in south-west England and East Anglia (Croose, 2016). As a fairly shy and nocturnal species, they can be difficult to monitor, and monitoring efforts can be further complicated by the presence of feral ferrets (*Mustela putorius furo*), certain morphs of which can be very difficult to tell apart from a 'true' polecat, with which they hybridize (Davison et al., 1999). Members of the public (citizen scientists) collect roadkill carcasses that are examined using morphological characteristics to determine whether they are 'true' polecats, or ferret hybrids (Birks, 2008; Croose, 2016) or report roadkill to map species recovery (Figure 3). Over half of polecat records received by Vincent Wildlife Trust were road casualties (Croose 2016), consistent with other distribution surveys, (Birks and Kitchener 1999; Birks 2008; Figure 3) demonstrating the importance of roadkill in recording species recovery.

Figure 3. Roadkill polecat. Physical characteristics of such casualties can be used to determine levels of hybridisation between polecats and feral ferrets, as well as to record their geographical distributions. Inset map shows distribution of polecat roadkill records in the UK as collated by wildlife-vehicle collision citizen science project 'Project Splatter' (photo: Barry Deakin)

Invasive species represent taxa for which roadkill data could be informative. Invaders cost billions in economic losses, create large-scale ecological perturbation, and displace native species (Vila et al., 2011; Dorcas et al., 2012). Monitoring their arrival and spread is critical, but expensive (Hauser, 2006). The spread, control efficacy and ecosystem impacts of invasive species can be informed through roadkill at a low cost. As species in the initial stages of invasion are usually at low densities, detection via surveillance can be difficult (Berry et al., 2007), but a roadkill carcass offers undeniable evidence of a species' presence and can trigger an increase in surveillance and control efforts in a given location, as was the case for the early stages of red fox (*Vulpes vulpes*) invasion in Tasmania (Berry et al., 2007; Caley et al., 2015). The large amount of biomass provided by (native) roadkill could facilitate expansion of invasive species; the non-native, generalist scavenger; pied crow (*Corvus albus*) in southern Africa was strongly associated with the presence of roadkill (Joseph et al., 2017). Roadkill animals can provide insight into how invasion is progressing, as observed for the established invasive raccoon dog (*Nyctereutes procyonoides*) in Poland, where

almost all (90%) of roadkill animals were dispersing juveniles, inferring a healthy breeding population (Kowalczyk et al., 2009). Where an invader is well established, for example, the invasive Burmese python (*Python molurus bivittatus*) in the Everglades National Park, southern Florida (Dorcas et al., 2012), roadkill provides insight into ecosystem impacts as the pythons' main prey item, the raccoon (*Procyon lotor*), has undergone a 99.3% reduction in roadkill observations since pythons became established (Dorcas et al., 2012).

Population trends and impacts

Biodiversity data collated as roadkill can be used to examine both long and short-term changes in population trends because roadkill numbers can accurately reflect live population densities (Gehrt, 2002; Baker et al., 2004; George et al., 2011). The data collated for roadkill can therefore be used to estimate species trends without the need for observations of the live animals (for example, rabbits (*Oryctolagus cuniculus*, George et al., 2011) and urban foxes (Baker et al., 2004)), or to evaluate spatial differences in population density (e.g. raccoons; Gehrt, 2002). The benefit of collating these data long-term are also apparent; it was roadkill records that revealed the long-term decline in hedgehog (*Erinaceus europaeus*) numbers in the UK (Wembridge et al., 2016; Pettett et al., 2017).

The greatest known cause of mortality for some species is vehicle collisions. Of a sample of 80 radio-tagged ocelots (*Leopardus pardalis*) in the US, collisions with vehicles were the largest single cause of mortality, causing 45% of deaths (Haines et al., 2012). Similarly, there are an estimated 50,000 badgers (*Meles meles*) killed on the roads per year in the UK, with vehicle collisions the highest single cause of mortality for this species (Harris et al., 1992). Roads are also the highest single cause of mortality for bobcats (*Lynx rufus*) in Illinois, US (Nielsen & Woolf, 2002), otters (*Lutra lutra*) in most European countries (Silke et al., 2006), and an important mortality factor for juvenile swift foxes (*Vulpes velox*) in Kansas, US (Sovada et al., 1998) and the Florida panther (*Puma concolor couguar*; McClintock et al. 2015), in Florida, US.

A meta-analysis of terrestrial vertebrate mortality has shown that, overall, 6.25% of mortality of adult animals is due to vehicle collisions (Hill et al., 2019). Roadkill data combined with population viability analyses can provide far more insight into the potential impacts of roads on a given species/population than roadkill counts alone; e.g. for small rodents in Spain, collisions cause a potentially insignificant mortality rate of around 6% each month (Ruiz-Capillas et al., 2015). Impacts of roads can, however, be significant; populations of Blanding's turtles (*Emydoidea blandingii*; Beaudry et al. 2008), spotted salamanders (*Ambystoma maculatum*; Gibbs and Shriver 2005), and jaguars (*Panthera onca*; Cullen et al. 2016) have been found to be under threat of extinction due to roads.

Why did the animal cross the road? Insights into behaviour

Wildlife-collision data can reveal broad behavioural patterns; annual peaks of roadkill in spring and late summer (Clarke et al., 1998; Haigh, 2012) for example, are indicative of seasonality in mating, dispersal, and foraging behaviours in badgers (Davies et al., 1987) and pheasants (Madden & Perkins, 2017). Variations in temporal reporting rates of roadkill of a wide range of other vertebrate species can also be explained by differences in their behaviour and ecology, for example searching for mates, or increased foraging activity at particular times of year (Clevenger et al., 2003; Erritzoe et al., 2003). Similarly, reporting rates of a given species or taxa (e.g. raccoon dogs; Kowalczyk et al. 2009, and other carnivores; Grilo et al. 2009) may increase at a time when juvenile dispersal is taking place, due to both an inflated population size and the presence of inexperienced young animals (Clevenger et al., 2003; Erritzoe et al., 2003; Grilo et al., 2009; Kowalczyk et al., 2009; Madden & Perkins, 2017). Polecats in the UK, for example, have a bimodal peak in roadkill observations; the spring peak being primarily adult males (mate searching), and the autumn peak mostly juveniles (dispersing), (Birks, 2015).

Although animal movement and foraging behaviour can be observed through other means (e.g. GPS tagging), roadkill can reveal changes in a species' behavioural patterns over time, without the need for costly equipment. For example, pheasant

(*Phasianus colchicus*) mortality on UK roads has significantly changed in pattern and increased in numbers from the 1960s (prior to mass release of pheasants for shooting at the current scale) to the 2010s, when in excess of 35 million birds are released per year (Madden & Perkins, 2017). Pheasants were formerly (during the 1960s) most-often reported as vehicle collisions during the breeding season in the spring, but roadkill now also peaks between September and November, when millions of birds are released for the shooting season, which begins in October. The change in temporal patterns is unlikely, in this specific case, to be related to other factors that have changed over time, for example an increase in traffic flow, as the same study found that patterns of woodpigeon (*Columba palumbus*) roadkill did not significantly differ over the same time period (Madden and Perkins 2017). An added risk factor for captive-bred animals (such as many UK pheasants) is their naivety to roads compared to wild-bred animals (Leif, 1994); a pattern also observed in released Tasmanian devils (*Sarcophilus harrisii*) over multiple generations of captive breeding (Grueber et al., 2017).

Long-term roadkill data could be particularly useful to observe changes in temporal behaviour due to our current shifting climate. For example, climate-change driven changes in phenological patterns have already been observed through a 20-year dataset of roadkill snakes in the Mediterranean, with roadkill peaks shifting earlier in the year, corresponding with earlier warmer temperatures (Capula et al., 2014). As roads can have long-term effects on wildlife, it is perhaps unsurprising that selection for behaviours that promote survival is occurring. For example, adaption of shorter flight initiation distances on roads with higher speed limits has been observed in birds (Legagneux & Ducatez, 2013), and 'road-naïve' (immigrant) Florida scrub-jays (*Aphelocoma coerulescens*) experienced a yearly mortality rate of 50% in areas with roads, compared to 38% for 'road-experienced' birds (Mumme et al., 2000), showing the capacity for learning 'safe' behaviour around roads. Similarly, increased nocturnality among mammals is associated with human activity and presence, including roads and traffic (Morrison et al., 2014; Gaynor et al., 2018).

Roadkill as sentinels: contaminants and disease

Efforts to quantify environmental contaminants include monitoring of watercourses and soils through active sampling (Daughton, 2004). These abiotic samples, however, do not necessarily accurately represent contaminants that might be biologically relevant, i.e. those found in wildlife or humans due to bioaccumulation of contaminants in living tissues (van der Oost et al., 2003). Roadkill, instead, offers the opportunity to collect a carcass, which can be used as a 'sentinel' for environmental health and wildlife disease. Roadkill is relatively low cost to sample and is particularly useful in the case of rare and/or protected species where destructive sampling is not possible, or desired. The Eurasian otter, a wide-ranging species at the top of the aquatic food chain is an excellent sentinel for aquatic systems (Chadwick et al., 2011, 2013; Pountney et al., 2015). A long-term roadkill carcass collection project, the 'Cardiff University Otter Project' (https://www.cardiff.ac.uk/otter-project), has through post mortems of collected otters found high levels of flame retardants in otter tissue (Pountney et al., 2015), but also declining levels of lead over time, following tighter environmental regulations (Chadwick et al., 2011). A similar long-term carcass collection project that receives roadkill birds of prey, the 'Predatory Bird Monitoring Scheme', (https://pbms.ceh.ac.uk/) has found contaminants such as organochloride insecticides (Heys et al., 2017), flame retardants (Crosse et al., 2013), and anticoagulant rodenticides (Walker et al., 2008) in raptors, sampling that would not have been possible (due to legislative protection) without the collection of roadkill.

The health of a given species could itself be a study focus, for example, stoats, weasels, and polecats were subjects of the first examination for respiratory diseases in this family (Simpson et al., 2016) – over half of the carcasses examined were collected from the road. This study also identified the first records of *Angiostrongylus vasorum* (a parasitic nematode) in small mustelids. Some species are routinely monitored for infectious diseases, such as the collection and testing of roadkill deer carcasses for chronic wasting disease (CWD) in the USA (Arkansas Game & Fish Commission, 2018). Deer with CWD are highly susceptible to being struck by a vehicle compared to healthy individuals (Krumm et al., 2005), so although in this scenario roadkill may represent a biased sample in terms of assessing the proportion of the

population that is affected, it is, however particularly useful to map disease spread (Krumm et al., 2005) and prevents the need for destructive sampling outside of the deer hunting season. Indeed, new areas of CWD infection have been identified due to the collection and testing of roadkill (Arkansas Game & Fish Commission, 2018). Devil facial tumour disease (DFTD), one of only two transmissible cancers known in wildlife, causes high mortality in Tasmanian devils (Hawkins et al., 2006). Tasmanian devils are also highly vulnerable to collisions with vehicles (Jones, 2000) and collecting and testing of these roadkill devils assists in monitoring the spread of DFTD and has even identified a new strain of the pathogen (Pye et al., 2016).

Bovine tuberculosis (*Mycobacterium bovis*; bTB) is a disease of significant economic and welfare concern due predominantly to its effects on cattle herds (Independent Scientific Group, 2007). For these reasons, the levels of bTB in wildlife is of particular interest, and badgers are an important reservoir (Delahay et al., 2002). Testing roadkill carcasses offers a way of quantifying the levels of bTB in badgers as well as identifying spatial distribution. A dedicated survey in Wales, UK, collected 442 carcasses, of which 25 (7%) tested positive for bTB (Animal & Plant Health Agency, 2016). The largest systemic UK survey of bTB infection in mustelids other than badgers comprised of samples opportunistically collected samples from the South-West of England (Delahay et al., 2007) of which over a quarter (27.4%) were wildlife-vehicle collisions. This work was also the first to confirm stoat (*Mustela ermina*) and polecat as sylvatic reservoirs for bTB (Delahay et al., 2007).

Considering that over 70% of parasites and pathogens are zoonotic in origin, i.e., they have wildlife as a primary source (Jones et al., 2008), roadkill offers an excellent opportunity for screening infectious disease risk to humans. Raccoons are a reservoir for *Baylisascaris procyonis*, a parasite which has the potential to cause severe illness in humans, and of which >80% of roadkill raccoon carcasses were found to be infected (Weinstein, 2016). Roadkill raccoon carcasses have also been used to monitor the spread of rabies during an outbreak in Baltimore, Maryland (Anthony et al., 1990). Roadkill samples have provided the first evidence of the zoonotic disease *M. avium* ssp. *paratuberculosis* in a diverse range of wild carnivores in Portugal (Matos et al., 2014). Given sufficient and widespread samples, not only can wildlife

roadkill be used as sentinels of zoonotic pathogens, but also to shine light on their spatial distribution. Analysis of otter carcasses, for example, found that *Toxoplasma gondii* (a zoonotic parasite with the capacity to infect all endothermic vertebrates) was common (39.5% prevalence, n=271), and that infection was significantly higher on the east coast of the UK, potentially due to the drier climate leading to increased oocyst survival (Chadwick et al., 2013; Smallbone et al., 2017).

Roadkill monitoring as a tool for citizen science

So pervasive is wildlife roadkill, that one benefit is achieved in the surveying of its presence, so engaging the public as 'citizen scientists'; volunteer individuals who collect and/or process data as part of a scientific enquiry (Silvertown, 2009). All of the 12 roadkill recording schemes listed on globalroadkill.net engage citizen scientists to collect roadkill data, a process which can be 97% accurate in its identification of species (Waetjen & Shilling, 2017). The rise of smartphones and the popularity of social media platforms have greatly expanded the possibilities for wide-scale environmental data collection, including that of roadkill (Vercayie & Herremans, 2015). Although the practice of members of the public voluntarily gathering data for a project is not a new one, (the National Audubon Society started its annual Christmas Bird Count in 1900 (Droege, 2007)), technology has allowed many new 'citizen science' projects to emerge in recent years, which curate the collective observations of members of the public to record data, whilst being unconstrained by time and geographical locations (Bonney et al., 2009).

Globally, a network of roadkill recording systems exists (Shilling et al., 2015) spanning multiple countries, for example the Austria-based 'Project Roadkill' (https://roadkill.at/en/), and the 'Wildlife and Roads Project' in South Africa (https://www.ewt.org.za/WTP/road.html). In the UK, Project Splatter (www.projectsplatter.co.uk) is the only UK-wide and year-round project that aims specifically to collect data on all wildlife roadkill. Since the project's inception in 2013 to date it has received over 70,000 ad hoc records from the public. There are state-specific citizen science roadkill recording projects in the USA; for example, the

California Roadkill Observation System (http://wildlifecrossing.net/california, UC Davis); Maine Audubon Wildlife Road Watch; (http://www.wildlifecrossing.net/maine, Maine Audubon and UC Davis); and the Idaho Fish and Wildlife Information System (https://idfg.idaho.gov/species/roadkill, Idaho Department of Fish and Game). All projects receive roadkill observations from members of the public, which are submitted through websites, social media, smartphone apps, or a combination of channels (Shilling et al., 2015).

As well as the obvious benefits that a widespread network of volunteers offers, it is important to note that a citizen science project is a two-way interaction between project coordinators and members of the public, such that each group can benefit from interactions with the other (Haklay, 2015). Participating in citizen-science wildlife-recording projects has been shown to increase the amount of time that people spend observing wildlife, even after they finish participating (Bonney & Thompson, 2007). Most participants (90%) that took part in a citizen science project named 'Neighbourhood Nestwatch', recording birds in their gardens around Washington DC, reported learning from participating in the project, with even the most experienced birders reporting learning more about bird biology and behaviour (Evans et al., 2005).

Monitoring wildlife roadkill numbers
- Essential to monitor wildlife roadkill numbers to quantify population-level effects (Erritzoe *et al.*, 2003)
- Country-wide estimates of millions of animals killed per year (Seiler & Helldin, 2006)
- Globally, over 400 million animals killed per year, but estimates absent for most countries

Photo: Amy Schwartz

Species distributions
- Continuous insight into distributions beyond dedicated surveys (e.g. Hofmann, 2005)
- Monitoring of recovering species e.g. most polecat (*Mustela putorius*) records in the UK come from observations of roadkill animals (Croose, 2016)
- Also used for monitoring of invasive species progression and distribution (Berry *et al.* 2007; Caley *et al.* 2015; Kowalczyk *et al.* 2009)

Photo: Tony Hisgett

Population trends and impacts
- Roadkill reflects relative population trends over time (Baker et al. 2004; Gehrt 2002; George et al 2011)
- Longitudinal data have discovered species declines, for example, European hedgehog (*Erinaceus europaeus*) in the UK (Wembridge *et al.*, 2016)

Photo: Alexas_Fotos

Animal behaviour
- Long-term monitoring can provide information on a species' changing susceptibility to vehicle collisions, (e.g. pheasant seasonality) driven by changing human behaviour (Madden & Perkins, 2017)
- Insight into behaviour (e.g. movement) of species that can be otherwise difficult or expensive to monitor (Barrientos & Bolonio, 2009)

Photo: Andy Mackay

Contaminants and disease
- Use roadkill carcasses as 'sentinels' to monitor environmental health and wildlife disease, reducing the need for destructive sampling (e.g Delahay *et al.* 2007)
- Using >2500 roadkill *Lutra lutra* carcasses, Cardiff University Otter Project has studied contaminants (Pountney *et al.* 2015; Chadwick *et al.* 2011) and disease prevalence (Chadwick *et al.* 2013)

Photo: Amy Schwartz

Figure 4. Infographic outlining the five major areas where consistently, systematically, and extensively monitoring roadkill has facilitated our knowledge of five critical areas of ecological study

Roadkill monitoring and ecology – opportunities for the future

Roadkill monitoring can inform us about a diverse range of fields; as such the value of collecting these data is to facilitate the expansion of knowledge across a variety of research areas (Figure 4). Additionally, the use of 'citizen science' projects that record roadkill facilitate the inclusion of members of the public in scientific research (Heigl & Zaller, 2016). As roadkill numbers are strongly and positively associated with the local abundance of live animals (Gehrt, 2002; Baker et al., 2004; George et al., 2011; Pettett et al., 2017), roadkill monitoring can be used to track long-term changes in population dynamics (Capula et al., 2014). Roadkill records can be used to 'fill in the blanks' on species distribution maps when the live animal is rarely or infrequently seen, as well as for monitoring the spread of species that are both re-colonising and invading (Calenge et al., 2015; Caley et al., 2015; Croose, 2016), and this species tracking could also include monitoring of changing animal behavioural patterns (Sovada et al., 1998; Haigh, 2012; Madden & Perkins, 2017). Finally, collecting biological samples from roadkill carcasses can provide increasing ecological and geographic resolution for contaminant studies (Chadwick et al., 2013; Heys et al., 2017; Smallbone et al., 2017).

Although substantial roadkill data are collected globally, there remains a challenge to estimate the extent of the issue; only 13 countries globally have produced country-wide estimates of roadkill, but even these limited estimates amount to over 400 million vertebrates (Figure 2). Roadkill observation systems can be highly effective in collecting these data (Waetjen & Shilling, 2017) for low-cost, and more of such projects are needed globally to collect such data, which can then be deposited in global databases (i.e. GBIF). With improvements and standardization of the metadata associated with roadkill observations, a wide range of ecological studies can be supported. In many ways, roadkill observation is likely to become the most useful single wildlife observation and sampling approach available for ecology.

3

Temporal patterns of wildlife roadkill on UK roads

Abstract

Wildlife-vehicle collisions are a major cause of mortality for wild mammals and birds. Here, using a dataset of 54,000+ records collated by a citizen science roadkill recording scheme between 2014- 2019, we analyse and present temporal patterns of wildlife roadkill mortality and consequent biomass of the 18 most commonly reported taxa in the UK (comprising 84% of all roadkill). Most species (17 out of 18) showed significant but consistent seasonal variations in road mortality and fitted one of two seasonal patterns; bimodal or unimodal, with only one species (red fox *Vulpes vulpes*) showing no seasonality. The two observed temporal patterns are consistent with species-specific seasonal changes in behaviour. For bimodal patterns, typically mate-searching is followed by juvenile dispersal (e.g. European polecats *Mustela putorius* in spring and autumn), with unimodal patterns representing breeding in birds or a single pulse in foraging activity (e.g. grey squirrels *Sciurus carolinensis* in autumn). Additionally to behaviour-driven annual patterns, abiotic factors (temperature and rainfall) explained some variance in roadkill temporality. Notably, high rainfall was associated with decreased observations of three bird taxa (gulls, magpies *Pica pica*, and tawny owls *Strix aluco*) but an increase in the number of otters reported. The high number of wildlife-vehicle collisions creates substantial roadkill biomass in excess of 3900 tonnes each year, which represents a large and relatively stable food resource for scavenging species such as foxes and corvids. By quantifying seasonal patterns in roadkill and biomass we highlight how modern landscapes can interact with wildlife to shape their population dynamics. By highlighting temporal hotspots, such effects can be mitigated against to some extent, for example, via seasonally targeted awareness campaigns for drivers.

Introduction

Roads represent a significant source of mortality for wildlife. In the UK, for example, collisions with vehicles are the leading observed cause of mortality of barn owls (*Tyto*

alba) (Ramsden, 2003), European badgers (*Meles meles*) (Harris et al., 1992), and Eurasian otters (*Lutra lutra*) (Philcox et al. 2001). The impact of UK roads on wildlife has likely increased over the last 50 years due to expansion of road infrastructure and an increase in vehicle use. For example, there were only 4.2 million vehicles on the UK's roads in 1951, compared to 37.3 million by the end of 2016 (Department for Transport, 2017b). Over the same period, the overall length of the road network increased from 184,000 miles to 246,500 miles (Department for Transport, 2017a). National estimates of annual wildlife mortality due to roads in the UK includes 50,000 badgers (Harris et al., 1992), 74,000 deer (Langbein, 2007) and between 167,000–335,000 European hedgehogs (*Erinaceus europaeus*), representing 10-20% of the latter species' annual mortality (Wembridge et al., 2016). Up to 13% of captive-bred ring-necked pheasants (*Phasianus colchicus*) die due to collisions with cars following their release into the wild (Sage et al., 2018). With an estimated 35-50 million pheasants released for shooting yearly (BASC, 2015; Pringle et al., 2019), this therefore implies that around 4.5-6.5 million pheasants die on roads in the UK each year. The numbers of wildlife roadkill are certainly substantial, but they almost certainly vary temporally (within and between years) due to inter-specific variation in behaviour and ecology, and this variation may be important to mitigate against the direct negative impacts of roads on wildlife when a high rate of roadkill is detected in a short period of time (Garriga et al., 2017). In addition, roadkill represents an important food resource for a guild of scavengers and "meso-predators" (Schwartz et al., 2018; Pringle et al., 2019), which possibly has knock-on implications for scavenger populations and their impacts on prey populations (Pringle et al., 2019).

Previous studies (of small vertebrates in Canada (Clevenger et al., 2003); birds in Europe (Erritzoe et al., 2003); and vertebrates in Belgium (Morelle et al., 2013)) have shown that periods of searching for mates or increased foraging activity leads to peaks in road mortality. Likewise, the time of year at which juvenile dispersal occurs may also influence seasonal variation in road mortality, due to the increased abundance of free-ranging but inexperienced juveniles at the end of each species' breeding season (Clevenger et al., 2003; Erritzoe et al., 2003; Grilo et al., 2009; Madden & Perkins, 2017). Interestingly, there is evidence for adaptation to roads

with some bird species exhibiting learned avoidance behaviours around roads, specifically, adjusting flight initiation distance depending on expected vehicle speed (Legagneux & Ducatez, 2013). Increased seasonal mortality among birds might therefore be expected at fledging times, due to a lack of learnt behaviours and experience among younger individuals.

Seasonal variation in roadkill has also been linked to environmental variables; amphibian roadkill, for example, increases with rainfall events and increased humidity, due to increased activity in wet conditions (Clevenger et al., 2003; Glista et al., 2007; Carvalho & Mira, 2011;; Garriga et al., 2017). Conversely, increased humidity has been negatively associated with avian roadkill (Garriga et al., 2017). Increasing temperature has been linked to an increase in roadkill of many vertebrates, including mammals (Garriga et al., 2017), amphibians (Glista et al., 2007), and reptiles (Capula et al., 2014; Mccardle & Fontenot, 2016; Garriga et al., 2017), and reptiles may be particularly at risk of vehicle collision due to their attraction to warm road surfaces (Mccardle & Fontenot, 2016). Some species can also be negatively affected by roads due to seasonal weather conditions or short-term weather events; road mortality of Eurasian otters, for example is positively associated with increased river flow – an increase in water levels can cause otters to cross roads rather than utilise spaces underneath bridges (e.g. culverts) (Philcox et al. 2001).

In this study, we analyse over 54,000 data points to examine temporal patterns of wildlife roadkill in the UK. The majority of roadkill data are collated via citizen science schemes many of which are opportunistic (or *ad-hoc*) records (Shilling et al., 2015), as is the case with the current study. Although many studies examining temporal patterns have traditionally used standardised roadkill counts along a given road transect (see e.g. Massemin et al. 1998; Grilo et al. 2009; Haigh 2012; Rosa and Bager 2012; D'Amico et al. 2015; Garriga et al. 2017; Meza et al. 2019), such targeted studies are costly in both time and finances, and are limited in the spatial area that can be covered, due to logistical restraints (Périquet et al. 2018). The use of citizen scientists allows large amounts of roadkill data over a broad geographic and time span to be collected (Vercayie and Herremans 2015). Due to the large size of many

citizen science datasets, the ratio of signal to noise is favourable, resulting in strong patterns (Bonney et al. 2009). Volunteer-based recording schemes usually provide reliable data, with an increased sampling effort (and therefore greater statistical power) with an increasing number of participants (Schmeller et al., 2009).

Using this large dataset, we identify the seasonal variations in road mortality of wildlife in the UK and discuss the utility of the data for temporal mitigation as well the behavioural, ecological and abiotic factors that may drive this variation. Specifically, we aim to determine: 1) whether there is significant seasonal variation in roadkill, 2) whether this seasonality varies between species, and 3) to evaluate the potential biotic and abiotic factors underlying such variation. We also 4) test for the influences of seasonal temperature and rainfall on species-specific temporal variation in roadkill, in the context of species-specific behavioural and ecological mechanisms. Finally, 5) we model seasonal variation in the biomass of roadkill available to scavengers and examine the relative contributions of different species to this important trophic resource across the annual cycle.

Methods

Roadkill Data

The data used for this study were compiled by a citizen science roadkill recording scheme hosted at Cardiff University (www.projectsplatter.co.uk). Data were *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) (Bíl et al., 2020). Data were submitted to the project primarily through the use of a specially built smartphone app, but were also collected via social media, an online form, and email. Data are compiled weekly and filtered for quality, i.e. through ensuring that records are within a species' known range. Studies of species identification skills by participants in other citizen science roadkill recording schemes have shown data collection to be very reliable (Waetjen & Shilling, 2017; Périquet et al., 2018). Dates,

locations, and species identification of roadkill were collected for 5 years from January 1st, 2014 until December 31st, 2019, forming a dataset of ca. 54,000 records. The data used for this study are available online via the NBN Atlas (https://registry.nbnatlas.org/public/show/dp205).

Seasonal variation in wildlife roadkill in the UK

Taxa included in this study

Taxa for which species-level identification was not frequently reported were grouped. Specifically, all gull species (Laridae) were grouped as 'gulls'; brown hare (*Lepus europaeus*) and mountain hare (*Lepus timidus*) were grouped as 'hares', and all six UK breeding deer species (both native: red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, and non-native: fallow deer *Dama dama*, Reeves' muntjac deer *Muntiacus reevesi*, sika deer *Cervus nippon*, and Chinese water deer *Hydropotes inermis*) were grouped as 'deer'. Any roadkill reported simply as 'rat' or 'squirrel' was assumed to be brown rat (*Rattus norvegicus*) and grey squirrel respectively, due to the relative rarity of black rat (*Rattus rattus*) and red squirrel (*Sciurus vulgaris*) in the UK. For analysis of seasonal variation in total roadkill, all species/taxa (hereafter referred to as taxa/taxon) were included. For taxon-specific analyses, taxonomic groups with fewer than fifty records in any given year were excluded, leaving taxa for which data were considered sufficient to produce robust estimates of seasonal variation. The resulting dataset included ten taxa of mammals ('deer', 'hare', brown rat, grey squirrel, Eurasian badger, red fox, West European hedgehog, Eurasian otter, European polecat, and European rabbit *Oryctolagus cuniculus*), and eight taxa of birds ('gull', barn owl, European blackbird *Turdus merula*, common buzzard *Buteo buteo*, Eurasian magpie, ring-necked pheasant, tawny owl, and common woodpigeon *Columba palumbus*).

Modelling of seasonal variation

For each taxon, we examined seasonal variation in the occurrence of roadkill. To facilitate direct comparisons between species and overcome any inter-year biases in

number of animals reported (i.e. the inherent bias in data that is collected *ad hoc*), monthly totals for each species were scaled as a percentage of the given species' annual total records for that year (to the nearest 1%), as has been done in previous studies (e.g. Madden and Perkins 2017). Due to extremely high numbers of reports occurring in July and August 2019 due to national media coverage of the project (approximately 3x in July, and 2x in August the mean number of reports typical for this time of year as compared with previous years), records for these months were randomly subsampled to reduce the numbers of records by a third, and a half, respectively. Each taxon was analysed using a separate General Additive Model (GAM) (Poisson error family, log-link function) implemented using the R-package "mgcv" (version no. 1.8-15, Wood 2011). To determine whether there was significant seasonal variation for any given taxon, the monthly percentage of roadkill records in each given year was the dependent variable, month was a smoothed independent term (k-value = 6), and year was a categorical independent term. The two-way interaction between month and year was included in the model, to enable different seasonal patterns in different years to be modelled. For the purposes of this study, we define the seasons as follows; spring: March – May, summer: June – August, autumn: September – November, and winter: December – February.

Modelling abiotic factors

To examine the relative importance of possible drivers of interannual variation in the seasonal pattern of roadkill of different taxa, we collated monthly mean temperature and rainfall data from UK-wide databases published by the Meteorological Office, the UK's national weather service (https://www.metoffice.gov.uk). Using these data, we fitted a GAM to the number of roadkill reports per month for each taxon, using a Poisson error family and log-link function (except where high dispersion resulted in poor model fit, identified by an over-dispersion statistic value >2.0, in which cases we used a negative binomial family, and log-link function (Table 2; Thomas et al. 2017). Analyses were performed using the R-package "mgcv" (version no. 1.8-15; Wood 2011) to test whether there were linear effects of temperature and/or rainfall that explained variance in roadkill, while controlling for the overall non-linear

seasonal pattern of variation in roadkill using 'month' as a smoothed term (k-value = 6). These models test whether unseasonable temperature and rainfall had additional effects on observed roadkill, e.g. whether a particularly wet period influences the number of a given species that is observed as roadkill at that time.

Biomass of roadkill

To calculate total roadkill biomass, we used previously published records of mean species body mass in grams; bird species mass were taken from BTO Birdfacts (https://www.bto.org/about-birds/birdfacts), and mammals from the Mammal Society species hub (http://www.mammal.org.uk/species-hub/full-species-hub/discover-mammals/). For sexually dimorphic species, we used the mean mass of male and females. Combined body mass of each taxa (mass multiplied by the number of any given taxa recorded each month) was used as a dependent variable in a GAM (Gamma error family, log-link function), using month, year, and the two-way interaction between month and year as independent terms to test whether roadkill biomass varied seasonally, and to model the seasonal pattern of roadkill biomass in each year.

Results

Seasonal variation in overall abundance of roadkill

The total number of reported roadkill animals varied significantly across the annual cycle for all years (e.d.f. = 5, χ^2 = 44.27, *p* <0.001). Although specific patterns of seasonal variation in the total number of roadkill reports differed between years, typically there were fewer records during winter, and a peak in the spring / summer (Figure 5).
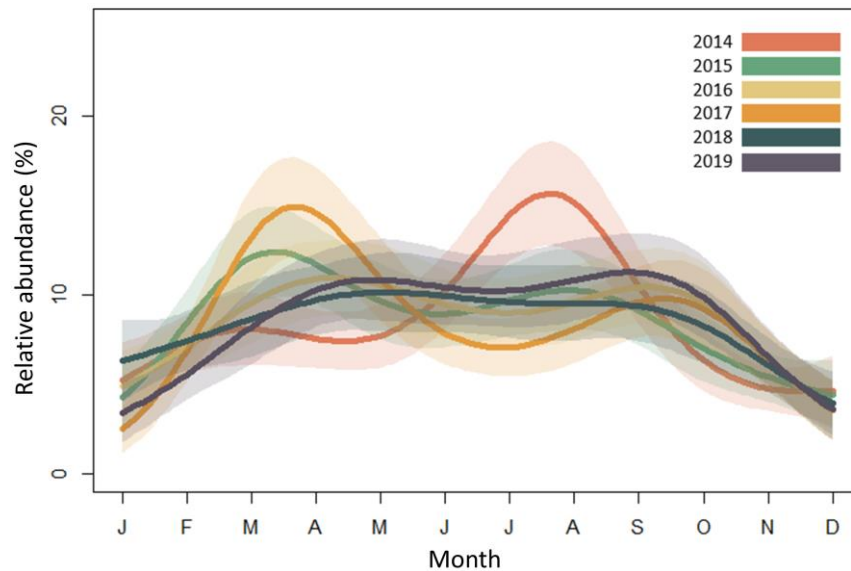
Figure 5. Seasonal variation in vertebrate roadkill in the UK. Abundance is quantified as the percentage of total number of roadkill per year, across all species/species groups. Records span 6 years, from 1st January 2014 to 31st December 2019. Shaded areas show 95% confidence intervals.

Seasonal variation in roadkill of mammals

Across all mammal species (except for red fox, which showed no seasonality), two broad temporal patterns were observed; bimodal and unimodal (Figure 6). Several mammal species demonstrated a statistically significant and bimodal distribution in monthly patterns of recorded roadkill; polecats showed the most distinctly bimodal distribution (Figure 6d), but badgers, deer, brown rats and hares also exhibited both a spring and autumn peak (Figure 6a, i, e, and g, respectively). Polecat roadkill records showed a large peak in both the spring and autumn (e.d.f. = 5, χ^2 = 121.1 p <0.001, Figure 6d). For badgers, the main peak was in late winter-early spring (February to April), with a smaller autumn peak in September to October (e.d.f. = 5, χ^2 = 140.3, p <0.001), although 2019 showed a marked and unusual late summer peak in mortality. Across all five years, December had the fewest reports of roadkill badgers (Figure 6a). Deer mortality showed a similar, but less marked seasonality (e.d.f. = 5, χ^2 = 44.33, p <0.001, Figure 6i), with a larger spring peak, and a small secondary peak in autumn; 2019 was the only exception to this pattern with no apparent bimodality. For brown rats, the highly consistent bimodal pattern differed from that for badgers and deer,

with the main peak in autumn and a smaller peak in spring (e.d.f. = 5, χ^2 = 118.3, p <0.001, Figure 6e). Peaks were seen for hares in spring, and also in late summer (e.d.f. = 5, χ^2 = 41.47, p <0.001, Figure 6g).

Otters were the only mammal species to exhibit a winter peak in roadkill records (e.d.f. = 5, χ^2 = 91.25, p <0.001, Figure 6c). Other taxa showing single peaks in records include hedgehogs in summer (e.d.f. = 5, χ^2 = 191.8, p <0.001, Figure 6j), rabbits and grey squirrels in summer-autumn (rabbits peaking in August, e.d.f. = 5, χ^2 = 113.4, p <0.001, Figure 6h; and squirrels peaking consistently in September each year; e.d.f. = 5, χ^2 = 183.8, p <0.001, Figure 6f). There was no statistically significant variation in the monthly reporting of foxes (e.d.f. = 5, χ^2 = 4.273, p 0.511, Figure 6b); the only observed species for which this was the case.
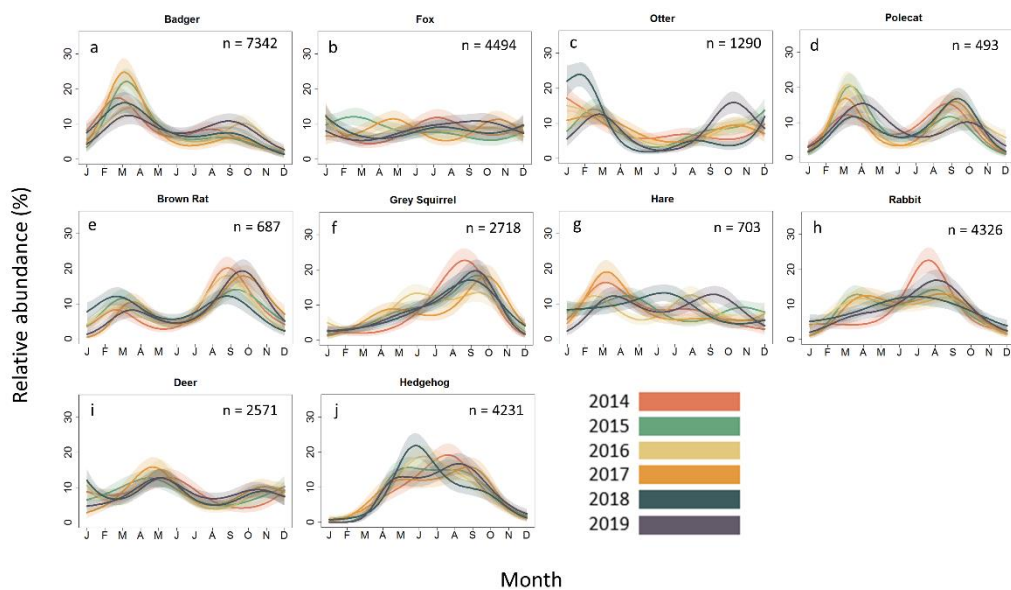

Figure 6. Seasonal variation in roadkill of mammals. Abundance (monthly percentage of annual total for each taxon) of the most common roadkill wild mammals in the UK. Records span 1st January 2014 to 31st December 2019. Shaded areas show 95% confidence intervals.

Seasonal variation in roadkill of birds

As for the patterns observed for mammals, all of the birds fitted two broad temporal patterns: bimodal or unimodal (Figure 7). The predatory birds examined in the present study (barn owl, tawny owl, and common buzzard) showed highly variable patterns of seasonal variation (Fig 7, a-c). Notably, the high between-year variance in temporal dynamics of the three predatory bird species is in sharp contrast with the non-predatory bird taxa, which have much more consistent patterns of seasonal variation, with low between-year variation. Within-year temporal variation in both barn owl and tawny owl roadkill reports, as well as for buzzards was statistically significant (e.d.f. = 5, χ^2 = 79.24, p <0.001; e.d.f. = 5, χ^2 = 61.86, p <0.001; e.d.f. = 5, χ^2 = 13.33, p 0.021, respectively) (Figure 7, a-c).

Pheasants showed a strongly bimodal seasonal distribution in roadkill reports (e.d.f. = 5, χ^2 = 198.6, p <0.001, Figure 7d). The first and most prominent peak in reports of roadkill pheasants occurred in spring, around March/April, followed by a lull in reports during the summer, and another smaller but distinct peak during the autumn. This bimodal distribution pattern of pheasant roadkill reports was consistent across all six years of the study. Half of the eight taxa of birds showed a single, statistically significant peak in roadkill records, occurring during the spring and summer months (Figure 7, e-h). The highest number of reports of roadkill gulls usually occurred in July (e.d.f. = 5, χ^2 = 356.4, p <0.001, Figure 7e), woodpigeon roadkill reports peaked in the summer months of June/July/August (e.d.f. = 5, χ^2 = 280.8, p <0.001, Figure 7f), and magpie roadkill peaked in June or July (e.d.f. = 5, χ^2 = 490.3, p <0.001, Figure 7g). Blackbird roadkill exhibited a broader peak compared to the other unimodal species and were reported abundantly as roadkill throughout the spring and summer (e.d.f. = 5, χ^2 = 168.8, p <0.001). In 2015-2018, blackbird roadkill usually peaked in May, whereas the peak was slightly shifted to July in 2014 and 2019 (Figure 7h).
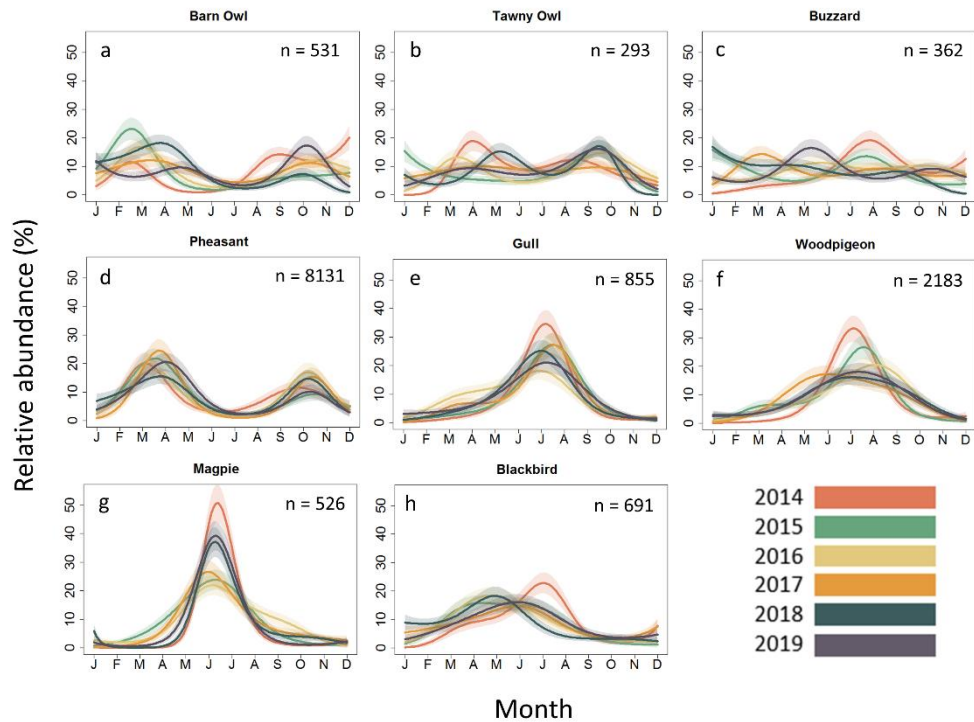
Figure 7. Seasonal variation in roadkill of birds. Abundance (monthly percentage of annual total for each taxon) of the most common roadkill wild birds in the UK. Records span 1st January 2014 to 31st December 2019. Shaded areas show 95% confidence intervals.

Abiotic factors

Country-wide seasonality in mean temperatures was highly consistent between 2014-19, whereas the seasonal pattern of mean monthly rainfall was much more variable (Figure 8). The between-year variation in the seasonal pattern of roadkill (total abundance of all taxa combined) was not significantly associated with either temperature or rainfall (Table 2, 'all taxa'). However, for specific taxa, some differences between years were explained at least in part by abiotic factors (Table 2). Fewer barn owls and gulls were reported when temperatures were higher (χ^2 = 8.159, d.f. = 1, p 0.004; χ^2 = 6.639, d.f. = 1, p 0.010); hares, in contrast, were reported more frequently at warmer temperatures (χ^2 = 5.580, d.f. = 1, p 0.019). Significantly fewer roadkill reports were received with high rainfall for three of the 18 taxa; gulls (χ^2 = 12.953, d.f. = 1, p 0.010), magpies (χ^2 = 4.787, d.f. = 1, p 0.029), and tawny owls (χ^2 =

4.759, d.f. = 1, *p* 0.029). Otters, on the other hand, were observed as roadkill significantly more often with increased rainfall (χ^2 = 3.812, d.f. = 1, *p* 0.051).
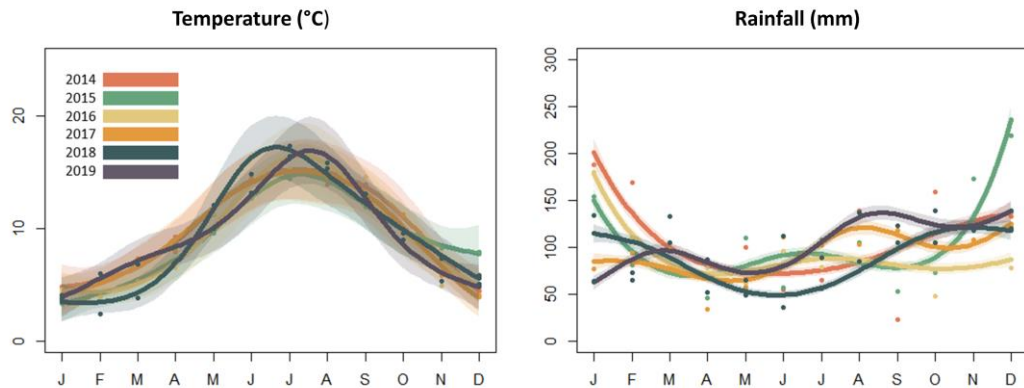
Figure 8. Variations in temperature and rainfall. Smoothed plots showing variation in mean temperature and rainfall across the UK during the six years that we report roadkill data from; 2014-2019.

Table 2. Summary table of statistical values (χ^2 and p-value) for Generalised Additive Model examining relationships between seasonal roadkill patterns and two abiotic variables; mean temperature and rainfall. Statistically significant values are shaded, with the direction of the relationship indicated by font style; italics indicating a significant negative relationship, bold a significant positive relationship. In all instances, the degrees of freedom were 1.

Species	Mean Temperature		Rainfall		Model family
	χ2	p-value	χ2	p-value	
All taxa	0.038	0.844	0.875	0.350	Poisson
Badgers	0.371	0.543	1.050	0.305	Poisson
Foxes	0.396	0.529	0.013	0.909	Poisson
Otters	3.387	0.066	**3.812**	**0.051**	Poisson
Polecats	1.354	0.245	0.130	0.710	Neg. binomial
Brown Rats	1.304	0.253	0.361	0.548	Poisson
Grey Squirrels	0.357	0.550	1.008	0.315	Poisson
Hares	**5.580**	**0.019**	0.557	0.455	Poisson
Rabbits	0.000	0.999	2.990	0.084	Poisson
Deer	0.166	0.684	1.604	0.205	Poisson
Hedgehogs	0.003	0.957	1.550	0.213	Poisson
Barn Owls	*8.159*	*0.004*	1.523	0.217	Neg. binomial
Tawny Owls	0.774	0.379	*4.759*	*0.029*	Neg. binomial

Buzzards	0.367	0.545	0.354	0.552	Neg. binomial
Pheasants	0.022	0.881	3.482	0.062	Poisson
Gulls	*6.639*	*0.010*	*12.953*	*<0.001*	Poisson
Woodpigeons	0.013	0.908	0.090	0.765	Poisson
Magpies	0.001	0.972	*4.787*	*0.029*	Neg. binomial
Blackbirds	0.063	0.802	2.501	0.114	Neg. binomial

Seasonal variation in roadkill biomass

The reported monthly mean biomass of all roadkill was estimated at over 3 tonnes (equivalent to the body mass of a female African elephant *Loxodonta africana*), or 39 tonnes annually. We currently estimate reporting coverage in our citizen science project to be ca. 1% of all roadkill, due to rapid scavenging of roadkill by many animals (Schwartz et al., 2018), and the variable coverage typical of citizen scientist projects (Heigl et al., 2016). Scaling up to account for under-recording, the actual roadkill biomass is likely to be in the region of 3900 tonnes annually (the equivalent of 1300 female elephants). The biomass of roadkill did differ significantly between months, (e.d.f. = 5, F = 5.322, *p* <0.001), but there was a supply of roadkill available to scavengers throughout the year and between years (Figure 9). In 2017, there was a spring peak in roadkill biomass, which was primarily due to a large number of badgers reported at that time.
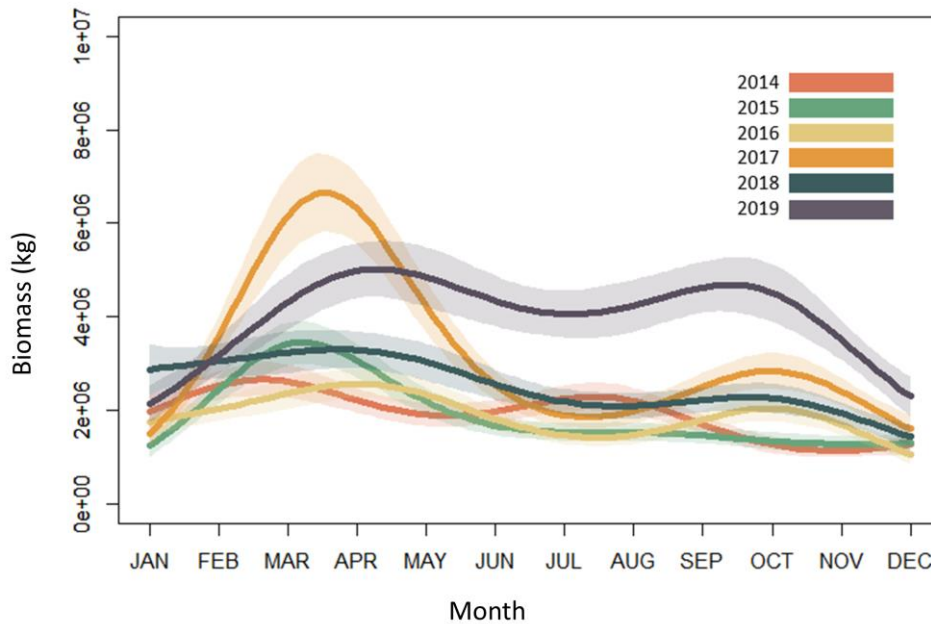
Figure 9. Seasonal variation in roadkill biomass of the most common roadkill species in the UK. Records span 6 years, from 1st January 2014 to 31st December 2019. Shaded areas show 95% confidence intervals.

Discussion

This study is the first to consider temporal variation across multiple mammalian and avian species in the UK using data collected by citizen scientists, and indicates species-specific differences in the nature of that seasonal variation. Across taxa, two broad temporal patterns of seasonality were found; bimodal or unimodal. Where seasonality was present (i.e. for all taxa except foxes), peaks in roadkill reports are likely linked to periods of increased activity, such as mate-searching, foraging, feeding young, and dispersal (Davies et al., 1987; D'Amico et al., 2015; Garriga et al., 2017). Understanding these patterns can provide valuable insights into the behaviour and ecology of the species recorded (and by extension, that of scavengers using roadkill as a food resource), as well as opportunities to implement effective mitigation on roads to reduce both wildlife mortality, and to reduce the risk of injury to drivers as a result of a wildlife-vehicle collision (Garriga et al., 2017). The use of

temporary warning signs, for example, has been shown to reduce deer collisions by 50% (Sullivan et al. 2004), and temporary drift fences in hotspots of chelonian roadkill have reduced roadkill by 98% (Aresco 2005). There is limited evidence to show long-term effectiveness of permanent animal warning signs (Huijser et al. 2015), but temporary signs can help to overcome the habituation effect of 'sign-blindness' that occurs when signs are used long-term. In addition to intrinsic biotic drivers of temporal wildlife roadkill, we find that between-year patterns for some taxa can be affected by abiotic factors (temperature and rainfall, Table 2); notably of which, high rainfall was associated with reduced road mortality for 3 of the 18 taxa (gulls, magpies, and tawny owls), and of increased mortality of one species (otters).

The total biomass of the roadkill of all species was estimated at an annual mean of 39 tonnes (although this could be as high as 3900 tonnes due to ca. 1% reporter coverage). Although the absolute biomass is difficult to estimate, it is clear that it represents a fairly stable, year-round resource (Figure 9) that could sustain an artificially high density of meso-predators. Corvids and red foxes are common scavengers of roadkill in the UK (Schwartz et al., 2018); these and other scavenger species may negatively impact other wildlife species e.g. by prey-switching to eating eggs and chicks of native birds when these are available (Pringle et al., 2019). Scavengers, however, may also provide an important ecosystem service by removing carcasses from the environment, resulting in health benefits for humans (Inger et al., 2016; Peisley et al., 2017; Schwartz et al., 2018).

General temporal patterns across all species

Combining all roadkill data shows the highest number of animals are reported over the summer months (Figure 5). There is, however, significant temporal variation within the year for individual species, with the exception of foxes (Figures 6 & 7). The broad summer mortality pattern of all roadkill could be due to breeding activity in temperate regions, where many species produce young during the spring and early summer (e.g. Cramp 1972; Davies et al. 1987), and therefore by late summer population sizes are high, boosted by the abundance of young of the year. Not only

does this mean more individuals, so increasing the probability of a vehicle collisions, but also an abundance of inexperienced juveniles which have to disperse and may not yet have learned to avoid vehicles. Birds, for example, learn to adjust their flight initiation distance depending on the traffic speed (Legagneux & Ducatez, 2013), a skill that recently fledged birds may lack. Further evidence that juveniles may be more vulnerable to vehicle collisions comes from captive-bred (and therefore road naïve) Tasmanian devils (*Sarcophilus harrisii*), which when released to the wild are more likely to be struck by vehicles than their wild-bred counterparts (Grueber et al., 2017). In addition, some adult animals may also be more vulnerable to vehicle collisions at this time as parents will be actively provisioning dependent juveniles in the spring and summer, which may require more frequent or longer foraging trips (Grilo et al., 2009), which may increase the frequency with which they encounter roads.

Whilst intra-annual changes in general patterns of animal behaviour were apparently a major factor associated with many of the temporal patterns, abiotic factors also played a role, but these patterns were not evident across all species. Rainfall had the greatest consistent effect on roadkill occurrence with three bird taxa (gulls, magpies, and tawny owls) having significantly fewer roadkill individuals reported during wetter conditions. This pattern is likely due to reduced activity during rainfall (Garriga et al., 2017), although reports by citizen scientists could also be low in bad weather due to poor visibility. If that were the case, however, we could expect the temporal dynamics of all species to be affected by rainfall, which does not occur. Clearly, some biology inherent to the species must underlie the pattern. Temperature also has some effect on the temporal dynamics of roadkill – with hares, barn owls, and tawny owls affected (Table 2) - a pattern that again likely reflects the underlying biology of the species affected. Between-year variation in barn owl roadkill, for example, was negatively associated with unseasonably high temperatures (Table 2) potentially because in unseasonably warmer periods rodents, the owls' main prey are abundant (Pucek et al., 1993), meaning owls do not have to travel as far to hunt, and will therefore encounter roads less frequently. However, an increased number of otters were observed in wet weather (Table 2), in line with previous studies (Philcox et al. 2001).

Bimodal seasonal patterns

Bimodality was the most common temporal pattern across all species, although the peak in observations were not coincidental across species in the months in which they occurred (Figures 6 and 7). Wildlife-vehicle collisions are strongly correlated with the number of road crossings made (Grilo et al., 2009), and therefore increased movement and population size likely produces seasonal peaks. In the current study the bimodal patterns are likely to arise as a result of increased activity and large-scale movement related to breeding for the first peak, followed by juvenile dispersal for the second peak, and the troughs a function of reduced activity levels, e.g. as food becomes scarce in winter (Cresswell & Harris, 1988). Lending weight to this interpretation, as an example, is that polecat roadkill collected in spring was found to consist primarily of adult males, and of juveniles in autumn (Birks, 2015). Badger roadkill (Figure 6a) usually peaks in February-April, as has been widely observed by others (Davies et al., 1987; Harris et al., 1992; Grilo et al., 2009; Haigh, 2012) and again in July to September (Davies et al., 1987). Notably, some species have mating season and juvenile dispersal reversed; for deer (Figure 6i), May is when young male roe deer disperse, with the autumn increase in deer collisions likely due to increased mobility during the autumn rut (Langbein, 2007).

We propose anthropogenic activities due to land and/or species management may drive the seasonal peaks in in brown rats and pheasants. Rats are capable of breeding throughout the year if conditions are suitable (Macdonald et al. 1999), and it is therefore unlikely that the consistent September peak (Figure 6e) was due to mate-searching or juvenile dispersal. The majority of farms in the UK have usually completed their harvest by the end of September (Defra, 2017), which we hypothesise will remove an important source of cover and food for this species, subsequently leading to increased levels of movement, and so increased contact with roads. For pheasants, the autumn peak coincides with the release of captive-bred birds onto shoots (Figure 7d). The highest peak in pheasant roadkill, however, is in the spring (Figure 7d); the shooting season ends in February, at which time supplementary feeding (designed to keep birds in close proximity to the shoot) tends

to cease (Madden & Perkins, 2017). Cessation of feeding causes the pheasants to travel larger distances in search of food, which may account for the large spring peak in reports of roadkill pheasants (Madden & Perkins, 2017).

Unimodal seasonal patterns

Unimodal peaks in roadkill were more commonly observed for birds than mammals, and the timing of the peak within the year was species dependent (Figures 6 and 7). Similar to factors underlying bimodal peaks, we propose that mate searching, increased activity of adults while provisioning their young and juvenile dispersal create the peaks. In birds, however, the time period of adults breeding to juvenile dispersal is usually much shorter comparatively than in mammals (Dawson et al., 2001), so we propose that this explains the common unimodal mortality patterns in birds.

Four of the eight bird taxa examined here (gulls, woodpigeons, magpies and blackbirds) demonstrated a single consistent peak in roadkill numbers centred around the summer months, contrasting with the weak patterns shown by the birds of prey, and the strongly bimodal peaks of pheasant roadkill. Gull chicks usually hatch in June in the UK (Parsons et al., 1976), and many are unable to fly when they leave the nest in July, consistent with the peak in roadkill observations (Figure 7e). Although many pigeon species can breed all year round, the main nesting season for the woodpigeon is between March and September, with peak egg-laying taking place in April and May (Cramp, 1972). The temporal distribution of road mortality in woodpigeons then exhibits a single seasonal peak centred on July, when the young pigeons fledge (Figure 7f). For most of the year, records of roadkill magpies were relatively scarce. However, during the summer reporting rates increased substantially (Figure 7g). For example, in 2014, 84% of all records (n=92) occurred in June and July; magpie chicks usually fledge in June (Vines, 1981). Blackbirds have a more variable, drawn-out and less prominent peak compared to most of the other birds (Figure 7); likely due to their extended breeding; they can successfully rear two or more broods in a year depending on weather conditions (Magrath, 1991).

For some mammals, mate searching is unlikely to play a large role in road-associated mortality risk, due to their social structure. Rabbits live in large and dense social systems within a warren (e.g. 113 individuals per km^2 in northern Italy; Pérez et al., 2009), and can reach very high densities especially near roads, due to an abundance of suitable vegetation and 'predator release' resulting from road avoidance/roadkill of predators (Rytwinski & Fahrig, 2012; Planillo & Malo, 2013) so it is unlikely that mate-searching would require large scale movements. Peak reproductive activity in both hares and rabbits occurs in March and April (Lincoln, 1974; Trout & Smith, 1995), but with a unimodal summer peak in rabbits (Figure 6h), juvenile dispersal represents the most parsimonious explanation for this species. Other drivers of a unimodal peak include behaviour peculiar to a given species. Otters showed a single peak during the winter months – the only mammals in our study to do so (Figure 6). In the UK, river flow is generally higher in winter than in summer (Hannaford & Buys, 2012). Otters often travel on land alongside watercourses, rather than swimming upstream, and may be unable or unwilling to swim through structures such as bridges and culverts during periods of high flow and be forced to continue its journey by crossing a road (Philcox et al. 2001), and increase mortality risk. Indeed, 65% of otter roadkill mortalities occur within 100m of a watercourse, and of these, around 34% occur at bridges and 44% at culverts (Grogan et al., 2001). In addition, our investigation of abiotic variables showed a significant positive relationship between otter mortality peaks and rainfall (Table 2).

Foraging can increase movement of animals, and so increase the probability of vehicular collision. Hedgehog roadkill reports peaked in July and August of each year, and was lowest in the winter months (Figure 6j), as has been found in other countries (Italy; Canova and Balestrieri 2019 & Poland; Orłowski and Nowak 2004). Hedgehogs are the most active during the summer (Morris, 2014), when they may travel several kilometres in a night (Patrick et al., 2001) in search of food – population numbers are also highest around July, when juveniles begin to leave the nest (Morris, 2014). Similarly, foraging may be the underlying cause of the September peak in grey squirrels (Figure 6f). This is the time of year when squirrels perform food-caching behaviour, ready for consumption in the winter (Hopewell et al., 2008). Caching

involves squirrels spending a lot of time on the ground, and frequently several minutes of travel time (Hopewell et al., 2008), when they may cross roads in order to find or bury their food. It is also at this time of year that the density of grey squirrels will be the highest; females can produce one or two litters of pups per year, in the spring (March/April) and summer (July/August) (Dubock, 1979; Kenward et al., 1998). Therefore, by autumn there will be high densities of squirrels, including many inexperienced juveniles, travelling to forage and store food (Kenward et al., 1998).

No seasonality

No seasonality in roadkill was not common, with only the red fox lacking seasonal peaks. This observation is in contrast to studies from other countries; for example, in Portugal, where spring and early summer are peak periods for red fox road mortality, with one study recording 42% of the entire annual mortality occurring between May and July (Grilo et al., 2009), when juveniles are dispersing (Baker et al., 2007). We propose that the lack of seasonality could reflect the road-adapted nature of this species in the UK. The red fox is well adapted to and found in reasonably high population sizes in urban areas in many parts of the UK (Saunders et al., 1993; Scott et al., 2014) and the species has acquired 'road sense' in urban areas compared to its rural counterparts (Baker et al., 2007). Alternatively, urban foxes in the UK scavenge more frequently in winter (Saunders et al., 1993), potentially leading to more road crossings (and mortality) so masking any summer mortality peak.

Biomass of roadkill as a resource for scavengers

Scavenging is a prevalent behaviour among nearly all carnivorous vertebrates (DeVault et al., 2003), many of which are generalist foragers (facultative scavengers), for whom scavenging on carcasses (including roadkill) can be a profitable foraging strategy (Kane et al., 2017). It is possible that the wide availability of roadkill carcasses available for scavenging could be supporting artificially inflated populations; 'anthropogenic' (human-sourced) food, including roadkill, is implicated in the increased range of red foxes (Scott et al., 2014) and gulls (Rock, 2005). In some

cases, this could be positive, for example by supporting scavenging species that are recovering (e.g. buzzards) or declining (e.g. many gull species in the UK). Scavenging species could also provide important ecosystem services by removing such carcasses from the environment (Inger et al. 2016a, b; Peisley et al. 2017; Schwartz et al. 2018). Conversely, when scavenging from roads, the scavengers could risk becoming roadkill themselves. The extent to which the year-round availability of roadkill as a food resource influences scavenger populations is currently unknown but is expected to depend both on the total amount of roadkill biomass available, and the magnitude of variation in this biomass across the annual cycle. The present study has shown that this resource is large and usually stable across the annual cycle, implying that it is capable of sustaining elevated scavenger populations.

Overall conclusions and applications

Reducing wildlife-vehicle collisions is clearly desirable in terms of wild animal welfare and conservation, but it would also pay dividends in terms of improved safety for vehicle drivers. The insights provided by this study could provide ways of minimising roadkill, for example by installing temporary road warning signage at times of greatest risk, at roadkill blackspots for species of conservation concern (e.g. otters). Here, by long term monitoring of wildlife roadkill, we reveal insight into the behaviour of wild vertebrate populations, but also the large extent to which wildlife and infrastructure are interacting. Given the extent of roadkill mortality across multiple taxa, and the large biomass of roadkill available to scavengers, we propose that roads are likely to exert a strong selective pressure on many species, which is likely to lead to behavioural adaptations in response.

4

Roadkill scavenging behaviour in an urban environment
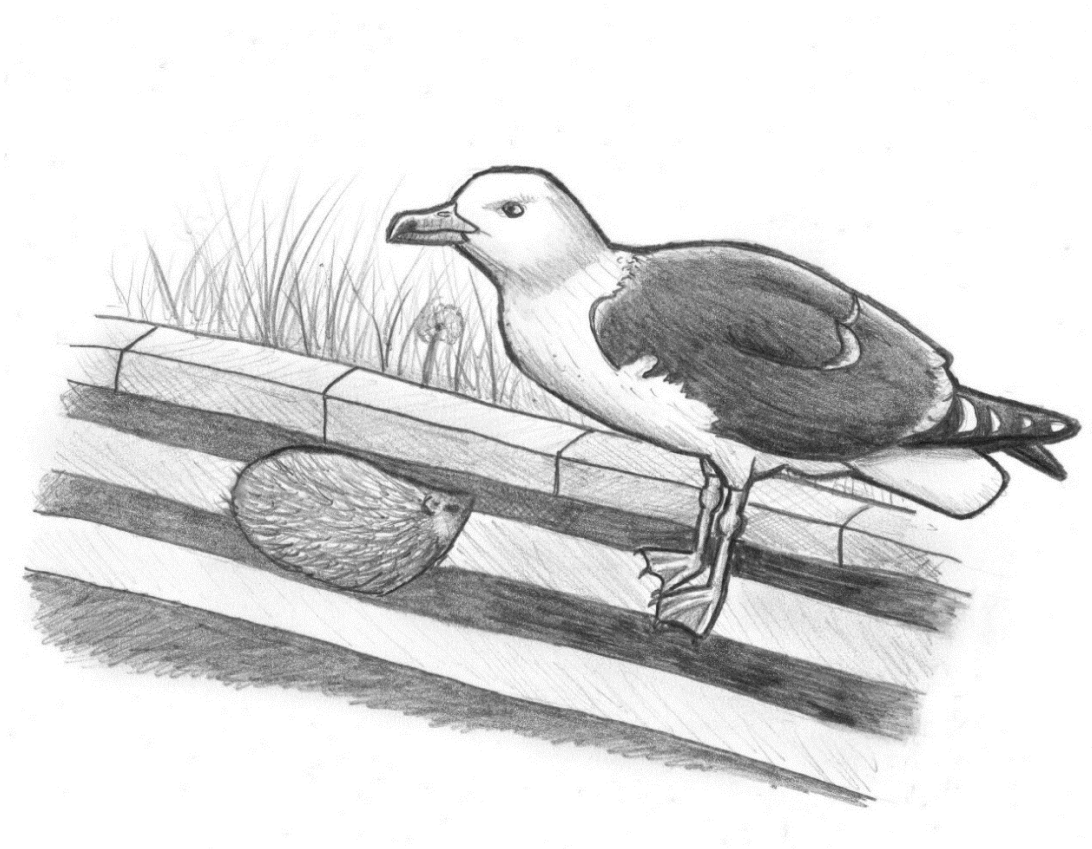
Abstract

Roads can have negative impacts on wildlife through indirect effects such as fragmentation of habitat, or through direct effects such as fatal collisions with vehicles. Wildlife deaths on British roads number in the millions per year, so the resulting carcasses represent a substantial carrion biomass available as food for scavengers. By removing roadkill in urban areas, scavengers perform a valuable ecosystem service, but the rapid removal of these carcasses by scavengers could bias estimates of the impacts of roads on wildlife. In order to evaluate the scale and context of urban roadkill scavenging, we examined: (i) which species scavenge on roadkill in urban areas; (ii) the likelihood of roadkill being removed by scavengers, and (iii) whether spatial and temporal factors (habitat type and time of day) influenced the rate of removal. Camera traps baited with chicken heads as simulated 'roadkill corpses' were deployed in six residential and six parkland sites in the city of Cardiff, UK. Seven species were observed removing the roadkill, with corvids being the most common scavengers, responsible for 42% of removals. Of the 120 corpses, 90 (76%) were removed within 12 hours. Time of day had a significant effect on the rate of removal, with the number of carcass removals peaking in the first few hours of daylight. Of roadkill placed at 9am, 62% of carcasses had been removed after only 2 hours. Removal of corpses by scavengers could mean that the actual number of road deaths is six times more than that observed during surveys.

Introduction

Fragmentation and alteration of habitat due to the presence of roads can force animals into close contact with vehicular traffic, which frequently causes mortality as a result of wildlife-vehicle collisions (Ibisch et al., 2016). It has been estimated that approximately 80 million birds are killed on roads each year in the USA (Erickson et al., 2005), and with more than a million vertebrates estimated to be killed per day, roadkill is now a higher cause of death for vertebrates in the USA than hunting

(Forman & Alexander, 1998). In other countries where annual roadkill mortality estimates are available, the figures are also high; 159,000 mammals and 653,000 birds killed per annum in The Netherlands; seven million birds in Bulgaria; and five million frogs and reptiles in Australia (Forman & Alexander, 1998).

The impact of roads on wildlife has probably increased over the last 50 years due to expansion of the road infrastructure and increased vehicle use. In the UK, for example, there were only 4.2 million vehicles in 1951, compared to 37.3 million by the end of 2016 (Department for Transport, 2016a). Over the same time period, the overall length of the road network has increased from 184,000 miles to 246,500 miles (Department for Transport, 2016b). The direct impact of roads on wildlife in the form of wildlife-vehicle collisions is clear, and given worldwide roadkill estimates of millions of animals per annum (Forman & Alexander, 1998; Erickson et al., 2005) roadkill carcasses represent a very large biomass available as a food source for scavenging animals.

Scavenging is not a behaviour restricted to a particular taxon or guild of animals. Although scavenging is prevalent among nearly all carnivorous vertebrates (DeVault et al., 2003), many vertebrate scavengers are generalist foragers (facultative scavengers), and scavenging enables them to maximise energy gained while minimising energy used (Kane et al., 2017). Vertebrate scavengers feed opportunistically on carrion, and can therefore be expected to be strongly affected by the presence of anthropogenic food, which includes roadkill (Oro et al., 2013). 'Anthropogenic foods' are those that are only accessible to wildlife due to human activity, and in the urban environment includes refuse, direct supplementary feeding (e.g. at bird tables), and roadkill. Indeed, the increase in gull (*Larus* spp.) populations in cities has been attributed in part to the increase in availability of anthropogenic food, including roadkill, which these opportunistic birds exploit (Rock, 2005). Some carnivores are able to exploit the urban environment and its anthropogenic resources through dietary generalism and flexible behavioural traits. One such example of an 'urban exploiter' is the red fox (*Vulpes vulpes*), the most globally widespread terrestrial carnivore (Scott et al., 2014). In England and Wales the distribution of red foxes has changed dramatically over the last 25 years, with red

foxes now present in 91% of urban areas that were previously predicted to have few or no urban red foxes; anthropogenic food sources are cited as one of the main reasons for this increase (Scott et al., 2014).

Scavengers perform important ecosystem services by removing potentially hazardous biomass from human contact (Inger et al., 2016a). While removal of carcasses by scavenging is an important 'service', one outcome of the removal of carcasses is that studies aiming to quantify the amount of roadkill using census data could underestimate counts. It follows that if carcasses are removed then the likelihood of scavenging and the rate and temporal variation of carcass removal are likely to be important factors for inducing bias in roadkill studies (Coelho et al., 2008). Quantifying the number of wildlife-vehicle collisions is useful, not only to estimate the direct impact of roads and vehicles on wildlife, but as a method to estimate species distributions and abundances (Gehrt, 2002) and for guiding mitigation, such as the siting of 'green bridges' over roads to allow safe passage of wildlife (Bissonette & Adair, 2008). Given the large geographical scale of roadkill, 'citizen science' is frequently used to collect data on roadkill and to supplement other sources of data, for example records submitted to police or held by local councils (Shilling et al., 2015; Heigl et al., 2016).

In the current study, baited camera traps were used in residential and parkland sites within the city of Cardiff, UK, to determine which urban species scavenge roadkill, and the likelihood of scavenging occurring in different urban contexts. In addition, we looked at temporal and spatial variation in the time taken for 'roadkill' to be removed, in order to quantify the extent to which scavenging might lead to underestimation of the scale of roadkill by surveys

Methods

To observe scavenging behaviour, remotely activated camera traps (Bushnell Trophy Cam Model: 119436) were deployed at 12 different sites within the City of Cardiff, UK, (51.4816° N, 3.1791° W). The City of Cardiff has an estimated human population

of around 361,468, with a population density of 2,564 people per square kilometre (Office for National Statistics, 2017). The study took place in the city centre between January 27th and February 18th, 2014. Six sites were 'residential', consisting of randomly selected streets within 10m of housing, and the other six were parks and public gardens ('parkland' areas, none of which were smaller than 2.5ha). Mean sunrise during the study period was at 07:40 (ranging between 07:21 - 07:58) and mean sunset at 17:14 (16:53 - 17:33). Two camera-trapping sessions of the same length took place, one from 9am-9pm (the '9am session'), and one from 9pm-9am (the '9pm session').

Setting camera traps

Cameras were deployed at 20cm above ground level, and were strapped to a tree, lamppost, or signpost. To simulate roadkill, the cameras were baited with a de-feathered chicken (*Gallus gallus domesticus*) head placed 1m in front of the camera, on the pavement in residential areas, and on grassy areas in the parkland. The chicken heads weighed approximately 50g – equivalent to the body mass of a large field vole (*Microtus agrestis*), or a common swift *(Apus apus).* Using this easily obtained domestic species as 'roadkill' allowed for the standardisation of size and species of carrion used, and ensured that olfactory cues and palatability remained broadly the same across all samples. The cameras were programmed so that once triggered they would film continually for 20 seconds, to provide sufficient time for identification of the scavenger species. Care was taken to minimise the number of 'accidental' triggers of the camera by humans or vehicles, by positioning them facing away from roads in the residential study areas, and away from areas with high footfall such as paths and benches in the parkland areas.

During the survey period, each of the 12 survey sites were baited and filmed for ten 12-hour periods, resulting in a total of 120 12-hour filming sessions. Of the 10 baiting and filming replicates on each site, five were '9pm' sessions (9pm-9am), and five were '9am' sessions (9am-9pm). To ensure random sampling of each site, and to reduce any bias due to external sources (e.g. weather), the date on which the 9pm

and 9am camera-trapping sessions occurred at each site was randomized. Randomisation of the filming dates was also chosen due to the risk of theft if cameras were sited in a predictable manner. Camera traps were first set and baited at 9pm, and checked and re-baited again at 9am. Re-baiting was carried out whether or not the chicken head was scavenged, in order to reduce any bias based on olfactory cues potentially changing over time.

Data analysis

To determine whether the number of times a species was recorded scavenging across the two habitat types (residential or parkland) was evenly distributed, a Fisher's exact test for count data was performed on a contingency table (as per Table 3). For analytical purposes, among the scavenging species the two observed gull species; herring gull (*Larus argentatus*) and lesser black-backed gull (*Larus fuscus*) were treated together as 'gull', as many of the juvenile *Larus* species are difficult to identify to species-level given the available video quality.

To investigate the effect of habitat type and time of day on the likelihood of a scavenging event occurring, a generalised linear mixed model (GLMM) with binomial error distribution and a complementary log-log link function, was implemented using R (R Core Team, 2013), and validated following Thomas et al. (2017). The occurrence or absence of a scavenging event (roadkill removed vs. not removed) was the dependent variable, with habitat (residential/parkland), trapping session time (9am/9pm), and their two-way interaction as independent variables. To account for spatial replication, 'site' was included in the model as a random effect.

To examine the effect of habitat type and time of day on the rate of roadkill removal (i.e. time taken until a scavenging 'event' occurred), a GLMM with Gamma error distribution and 'identity' link function was performed. In this model, time to removal (minutes) from baiting at either 9am or 9pm was the dependent variable, habitat type (residential/parkland) and time of session start (9am/9pm) and their two-way interaction, were fixed independent variables and 'site' was included as a random effect to account for spatial replication. In all analyses, an 'event' involved the

complete removal of the roadkill, and not just any apparent feeding behaviour. To visualise the "survival" of the roadkill baits (i.e. the time taken until their removal by scavengers), survival graphs (Figure 11) were drawn using the R package "survival" (Therneau, 2015)

Results

Seven species were observed removing the roadkill (Table 3); two species of gull; herring gull and lesser black-backed gull, carrion crow (*Corvus corone*), Eurasian magpie (*Pica pica*), red fox (*Vulpes vulpes*), domestic dog (*Canis familiaris*), and domestic cat (*Felis catus*) (Table 3). Corvids were the most common scavengers, responsible for 42% of roadkill removals. It is not known what species removed the roadkill in 11 of the 90 incidences of removal, as the scavenger did not remain in front of the camera for long enough for it to be triggered. In addition to the observed removals, mice, likely wood mice (*Apodemus sylvaticus*)*,* and a brown rat (*Rattus norvegicus*) were observed scavenging on the bait, but did not remove it. Furthermore, one experimental replicate was lost due to removal by a human. Of the known bird and mammal scavenging taxa, birds scavenged most frequently, with 51 incidences of roadkill removal, compared to 28 by non-human mammals. There was a significant difference between residential and parkland habitats in the relative frequencies of the different taxa scavenging the baits (Fisher's exact test, $p < 0.005$) showing that the likelihood of a particular taxon scavenging the bait was dependent on the type of habitat (Table 3). For example, gulls fed predominantly in residential areas (12 incidents compared to only once in parkland), whereas corvids mostly fed in parkland areas (28 incidents compared to 10 in residential areas).

Table 3. Frequency of simulated roadkill removal by different taxa in 'residential' and 'parkland' areas in Cardiff, Wales. Data taken from camera-trapping observations, with cameras baited using chicken heads. There was a significant association between species and habitat (Fishers exact test, $p < 0.005$).

Species	Residential	Parkland	Total
Carrion Crow	5	13	18
Eurasian Magpie	5	15	20
Gull spp.	12	1	13
Domestic Cat	3	1	4
Domestic Dog	4	11	15
Red Fox	4	5	9
Unknown	10	1	11
Total	43	47	90

In this study, only the red fox and domestic cats performed exclusively nocturnal scavenging behaviour, with domestic dogs showing both diurnal and nocturnal scavenging behaviour (Figure 10). All four recorded bird species scavenged during dawn and daylight hours, except for one instance of a carrion crow scavenging after sunset.

Figure 10. Frequency of scavenging in hourly periods for different species at camera traps baited with chicken heads (to simulate roadkill) within residential and parkland areas within the city of Cardiff, UK. Shaded areas represent times between sunset and sunrise

Of the 120 simulated roadkill carcasses, 90 (76%) were removed within the 12-hour recording period. There was a large peak in scavenging activity commencing just after 7am, and finishing just before 11am (Figure 10); more than half of the carcasses (53%) were removed by scavengers during this 4-hour period. The likelihood of carcass removal did not differ significantly between the two habitat categories, (LRT = 0.390, d.f. = 1, p 0.532), or between the trapping sessions, (LRT = 3.477, d.f. = 1, p 0.062), and there was no significant interaction between these two factors (LRT = 0.835, d.f. = 1, p 0.361).

There was a significant effect of time of day on time taken for roadkill to be removed (LRT= 36.377, d.f. = 1, p <0.001); roadkill was removed significantly faster when bait was placed at 9am (mean = 136 minutes, SD = 185 minutes), compared to when bait

was placed at 9pm (mean = 523 minutes, *SD* = 206 minutes). This faster removal time following 9am baiting is due to the higher level of activity of many of our observed scavenging animals in the first few hours following sunrise (Figure 11). The mean time elapsed before removal of a carcass, across all samples, was 310 minutes (*SD* = 274 minutes). There was no significant difference in time taken for roadkill removal between the residential and parkland habitats (LRT = 0.207, d.f. = 1, *p* 0.649), nor was there a significant two-way interaction between time of day and location (LRT = 0.074, d.f. = 1, *p* 0.786). The categorical variable "Species" also was not significantly associated with the time taken for roadkill to be removed (LRT = 1.892, d.f. = 6, *p* 0.929).
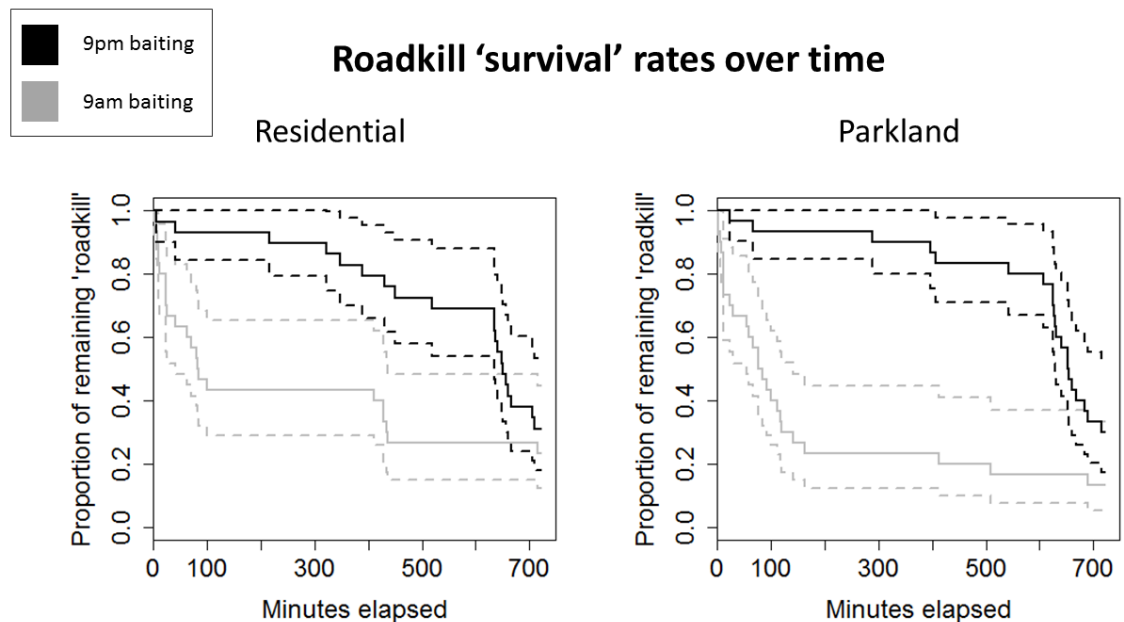
Figure 11. 'Survival' of roadkill (solid lines) with 95% confidence intervals (dashed lines) from baited cameras showing scavenging in 'residential' compared to 'parkland' areas. Minutes elapsed are from the beginning of a trapping session, from either 9pm (black lines) or 9am, (grey lines), respectively.

Following the 9pm-9am survey, 30% (around 1/3rd) of carcasses were still in place. At the end of the 9am-9pm survey sessions, only 18% of carcasses – approximately 1/6th – remained. Assuming that removal of chicken heads is a reasonable model for the

removal of other carcasses, our findings show that there could be as at least three times, but potentially up to six times as many incidents of wildlife roadkill as current estimates suggest.

Discussion

Seven species were observed scavenging the chicken heads representing simulated roadkill in this urban study, with corvids (carrion crow and Eurasian magpie) the most common scavengers, being responsible for 42% of carcass removals. This figure is in line with other studies of carcass scavenging in the UK that also show corvids are important for carcass removal (Slater, 1994, 2002; Inger et al., 2016a,b). There was a significant difference in scavenger species assemblages between the residential and parkland areas; for example, gulls fed more frequently in the residential areas, whereas corvids scavenged more frequently in parkland. Diurnal scavenging was primarily carried out by birds, whereas red foxes and domestic cats were only recorded scavenging nocturnally. The majority of mammalian mortality on roads occurs at night (Caro et al., 2000), and scavenging behaviour primarily occurs at night or early in the morning (Figure 10). These patterns may lead to underestimates of roadkill events by a factor of up to six in urban areas, due to the rapid rates of removal of carcasses by scavengers, occurring mainly in the first few hours of daylight (Figures 10 & 11).

Scavenging species provide valuable ecosystem services through the removal of carcasses from the environment, with associated hygiene benefits for humans (Inger et al., 2016a; Peisley et al., 2017). Before their population decline, Old World vultures (Family Accipitridae) in India provided health-based ecosystem services through scavenging that was valued at $34 billion US dollars during the period of 1993-2006 (Markandya et al., 2008). Although the UK does not have any resident obligate scavengers, many species that show dietary flexibility will still provide these valuable ecosystem services by removing roadkill, as well as other carcasses and anthropogenic food sources.

In the UK, corvids have previously been found to be the major category of scavengers active during daylight hours (Slater, 1994, 2002). This finding is mirrored by the results of the current study, where corvids (Eurasian magpie and carrion crow) were the most common scavengers. Carcass removal has been found to be directly related to the activity of carrion crows (Inger et al., 2016b), and corvids can frequently scavenge small mammal and bird carcasses in under an hour (Edwards & Slater, 1981). Carrion crows, Eurasian magpies, and red foxes were the only vertebrate scavengers in a UK urban camera-trapping study using carcasses of brown rats (*Rattus norvegicus*) as bait; 73% of the rat carcass biomass was removed by these three species (mean loss of 194g per carcass, compared to a mean loss of 14g per carcass when vertebrate scavengers were absent; Inger et al., 2016a). In addition, food items scavenged by red foxes in the city of Bristol, UK, accounted for a yearly average of 64% of the total diet of the foxes, by volume (Saunders, et al., 1993). Although many of these food items are likely to represent deliberately provisioned meat or other anthropogenic foods as well as carcasses, this represents a significant removal of unsightly refuse by urban red foxes, but because this scavenging activity is performed primarily nocturnally it is perhaps an under-appreciated, or rarely noticed, service.

Despite the valuable ecosystem services that scavenging taxa such as corvids, gulls and foxes provide in urban environments, they are frequently seen as 'vermin' or pests and are often persecuted as such. All of the wild species observed scavenging during the course of this study are treated as 'pests' in towns and can be culled, under specific circumstances. In the UK, all corvids except red-billed chough (*Pyrrhocorax pyrrhocorax*) and common raven (*Corvus corax*) can be shot under a general license available for any landowner or person acting with the landowner's permission to use (Wildlife and Countryside Act, 1981). Similarly, there are no restrictions on the shooting of red foxes, as long as the permission of the landowner is obtained. Although a nationwide program of fox culling by local authorities formerly took place, this has now been abandoned by councils due to its excessive cost and ineffectiveness (Harris, 2013), but culling of foxes in towns and cities of the UK still occurs, either by individuals or by contracted pest-control companies. Gulls,

however, are protected under the Wildlife & Countryside Act (1981) from deliberate interference with nests and eggs, as well as from injury and deliberate killing, except to 'preserve public health or public safety', for example around airports. This protection has not, however, prevented local authorities from obtaining licenses to kill gulls in cities, or destroy their eggs and nests; for example, in 2017, Bath & North East Somerset Council allocated £57,000 to tackle the 'gull problem' of aggression and noise in the breeding season (Bath & North East Somerset Council, 2017).

The guild of species which scavenge on carcasses can vary greatly from one region to another, and between habitat types. Scavenging experiments on deer (*Cervus* sp.) carcasses in Devon, UK, found that in woodland environments, the most common scavenging species were common buzzard (*Buteo buteo*), carrion crow (*Corvus corone*), wood mouse (*Apodemus sylvaticus*), and grey squirrel (*Sciurus carolinensis*); squirrels only scavenged during the later stages of decomposition, when the skeleton was exposed (Young et al., 2014). Our results show that habitat type can have a major influence on the assembly of species that perform scavenging behaviour, even within the city boundaries of Cardiff. The species that performed scavenging behaviour differed significantly between the residential and parkland areas. Herring / lesser black-backed gulls, for example, foraged more frequently in the residential areas than in parkland (Table 3). However, in our study, the overall number of scavenging events did not differ between the two habitat types (residential/parkland). In other words, the habitat types influenced which species scavenged within them, but this did not affect the total number of carcasses removed.

Eleven scavenging events occurred that were not captured on camera, but it is likely that these could be gulls, as both the habitat and rapidity of carcass removal fit the behavioural pattern that is generally shown by the gulls. When reviewing camera-trap footage, gulls removed the roadkill faster than corvids, which were more cautious in their approach. Gulls, especially in urban areas, are notoriously bold and aggressive (Rock, 2005), whereas cautious and hesitant feeding behaviour is typical of corvids (Heinrich, 1988; Kijne & Kotrschal, 2002). In experimental situations where common ravens (*Corvus corax*) were offered meat close to a novel object; the ravens preferred to take small pieces of meat over larger ones. By taking only small amounts,

this reduced their chances of having the food stolen by other ravens when they then moved away from the novel object (Kijne & Kotrschal, 2002). In the current experiment, there was at least one incident in which a carrion crow began to feed on the roadkill, which was then subsequently taken from it by a herring gull. This cautious behaviour could explain why corvids did not forage as much as the gulls in the residential areas, where there was more potential disturbance in the form of conspecifics, people, and cars.

The observed peak in scavenging activity shortly after sunrise reflects a typical peak in bird activity at this time (Robbins, 1981), and matches the temporal pattern observed by Slater (2002). Camera-trap observations of bird scavenging activity in this study were almost exclusively during daylight hours, except for one incidence in which a carrion crow fed on a piece of roadkill at 20:56 GMT in an artificially-lit residential area. During this study, red foxes and domestic cats scavenged exclusively at night; post-sunset and pre-sunrise - behaviour to be expected of these largely nocturnal mammals (Alterio and Moller, 1997). Scavenging activity by domestic dogs in this study occurred nocturnally as well as diurnally, but these behavioural patterns are likely dictated by when the domestic dogs are exercised by their owners, as they are the only scavenging species present in this study that is not generally free-roaming.

Most road casualties occur between dusk and two hours after dawn (Slater 2002). The majority of mammal road mortality also occurs at night or early in the morning, and there are two factors that are suggested to cause this: the bright headlights of vehicles can cause animals to 'freeze' (become immobile) on the road, and the more difficult driving conditions, which may lead to decreased driver awareness (Caro et al., 2000). Mortality of diurnal birds is most likely to occur around dawn, due to the greater activity of diurnal birds around sunrise (Robbins, 1981). The results of the current study suggest that roadkill is likely to be removed overnight by nocturnal mammalian scavengers, or by avian scavengers at first light. Nocturnal scavenging by birds may be facilitated by artificial street lighting, as birds are primarily visual foragers (Jones et al., 2007). In the current study, gulls (both herring gulls and lesser black-backed gulls) were only recorded scavenging during the daytime, but both

species do occasionally show nocturnal foraging behaviour when facilitated by artificial lights in cities (Rock 2005). Nocturnal scavenging by gulls has also been observed at sea, where gulls feed on discards from trawlers in the North Sea; behaviour, which will also likely be facilitated by artificial lights aboard such ships (Garthe and Hüppop 1996). It is likely, therefore, that street lights alongside roads could offer opportunities for nocturnal scavenging that would not otherwise be available to predominantly diurnal species such as gulls and corvids.

The rate of removal of carcasses can be driven by the assemblage of scavenging species, but is also often influenced by the carcass size - smaller carcasses could be under-estimated in roadkill data because they are more easily and more quickly removed by scavengers (Teixeira et al., 2013). In one study, between 60 and 97% of relatively small snake and bird carcasses disappeared within the first 36 hours of being placed on roads (Antworth et al., 2005). Similarly, 89% of carcasses of day-old domestic chicks (*Gallus gallus domesticus*) which were placed alongside a highway in Brazil were scavenged within 24 hours (Ratton et al., 2014). Within urban environments, similarly high scavenging rates of small carcasses can be seen; experimentally placed rat carcasses in green spaces in several UK cities had a likelihood of removal by vertebrate scavengers of 67% during a 2-4 day deployment period (Inger et al., 2016a). In the current study, 76% of chicken heads were removed within 12 hours, a similar time frame to that shown by other studies using small carcasses as bait. However, larger carcasses can remain on roads for a longer time compared to smaller carcasses (Slater 2002). For example, amphibians and small birds in Portugal were scavenged very quickly: 77% of toad corpses and 63% of small bird corpses were removed from roads within one day, compared with 49% of lagomorph and 20% of carnivore corpses (Santos et al., 2011). More specific scavenging times were measured in Brazil; on average, bird carcasses were removed the fastest, in an average (mean) of 0.51 days, followed by amphibians which took 0.96 days for removal, and large animals which took 5.2 days (Teixeira et al., 2013). Of 529 roadkill animals of 53 vertebrate species in New South Wales, Australia, only approximately 40% of those left on the roadside disappeared within seven days

(Taylor & Goldingay, 2004), but this is likely to be partly due to the relatively large size of many Australian vertebrates featuring in this roadkill survey.

Removal rates by scavengers can vary depending on the position of carcasses in the road. Previous studies have shown that carcasses placed in the centre of roads disappear significantly faster than carcasses at road edges (Antworth et al., 2005), despite the risk that roads pose to scavenging animals (Lambertucci et al., 2009; Cook & Blumstein, 2013). House sparrow (*Passer domesticus*) carcasses placed on the road were often crushed by oncoming traffic, and subsequently removed within 24 hours, while the carcasses placed at the side of the road where they were not crushed, were not removed for approximately 120 hours (Stewart, 1971). Slower removal of carcasses on road edges could be due to the difficulty of feeding on intact carcasses for many scavengers, as many scavenging birds such as crows and magpies lack the hooked beak that is needed to break through the layer of fur/feather and skin. As a result, some scavengers need to wait until more of the innards have been exposed, either by other, larger, scavengers, or by a car (Heinrich 1988). Corvids such as American crows (*Corvus brachyrhynchos*), blue jays (*Cyanocitta cristata*), and common ravens (*Corvus corax*) do not scavenge on intact ungulate carcasses (except for ravens removing eyes), but carcasses which have been cut open either by human hand or by coyotes (*Canis latrans*), attracted large groups of these three corvid species (Heinrich 1988). As the chicken heads used in the present study already had feathers and skin removed, this could have contributed to faster removal times, due to ease of feeding for many scavengers.

The rapid removal of roadkill, as well as the variety of species observed feeding on carcasses, demonstrates that many species are behaviourally adapted to scavenge on roadkill in urban environments. The rate of scavenging that occurred could lead to a significant underestimation of the impacts of roads on wildlife, by as much as a factor of 6, depending on time of day. Much small roadkill could be removed before it can be observed during daytime roadkill surveys, especially if such surveys were undertaken in the hours after which most scavenging occurs (after sunrise), as shown by Figures 10 & 11. Therefore, studies that aim to estimate the number of wildlife-vehicle collisions must consider the rate of carcass removal by scavengers –as by

failing to do so, estimates of roadkill numbers will be too conservative. Performing roadkill surveys shortly following sunrise (when light allows accurate recognition of carcasses) could be one way to gain a more accurate representation of true amounts of roadkill, before much is removed by scavengers. Biases in roadkill estimates that are introduced through the activities of scavenging animals could also negatively impact studies wishing to use road surveys to help inform wildlife conservation, or explore patterns in abundance of species (e.g. Gehrt, 2002). However, carcasses are an important source of food for scavenging animals, and by removing these carcasses from the environment (alongside other anthropogenic food sources), scavengers provide valuable ecosystem services. It is ironic, perhaps, that such a vital yet often overlooked ecosystem function is performed by some of the most heavily persecuted native species in the UK.

5

The 'phantom road'; effects of artificial light and traffic noise on woodland wildlife

The 'phantom road'; effects of artificial light and traffic noise on terrestrial woodland wildlife

Abstract

Roads can have direct negative impacts on wildlife such as wildlife-vehicle collisions and habitat destruction, but can also cause indirect negative effects, for example by being a barrier to animal movement. The artificial light and noise resulting from road systems can result in their ecological footprint extending far beyond the carriageway; some species begin to avoid roads and the surrounding habitat at very low traffic flow levels due to the light and sound pollution permeating the environment. To examine behavioural changes in vertebrates when exposed to such disturbances, we created a 'phantom road' in a roadless area. Temporary light and sound systems were installed to imitate the streetlights and traffic noise that can be found adjacent to roads. Animal behaviour was monitored in a two way factorial experimental design such that activity was monitored using remote movement-triggered camera-traps, baited with a food source, at 5, 10, and 15m distances away from the treatment (control, light plus sound, sound only, or light only). We observed a significant reduction in animal activity when sound treatment took place, as well as an increase in vigilance behaviour of 144.6% during light plus sound treatment, and 93.7% during sound treatment, compared to controls. The significant reduction in activity levels in response to road traffic noise as well as observed changes in behaviour demonstrates that the anthropogenic noise and light associated with roads could alter wildlife behaviour.

Introduction

The human population is ever-expanding, and so is the infrastructure that supports this growth; for example, the total length of road in the UK at the end of 2016 was 246,500 miles; 6,000 miles more than in 1996 (Department for Transport, 2017a). As

a result, land that is not affected by the presence of roads is growing ever-smaller; a recent estimate suggested that only 7% of land patches on Earth created by roads are larger than 100 km^2 (Ibisch et al., 2016). A meta-analysis of 49 studies of 234 bird and mammal species determined that the presence of human infrastructure (including roads) caused population declines that extended up to 1km from infrastructure for birds, and 5km for mammals (Benítez-López et al., 2010), and bird species richness has been found to increase with increasing distance from a road (Summers et al., 2011). Roads can act as a barrier to animal movement even when the risk of vehicle collisions is low; some species begin to avoid roads at very low traffic flow levels due to light and sound pollution (Jacobson et al., 2016). Clearly, it is important to understand the effects that roads – and the accompanying artificial light and traffic noise - can have on wildlife if we hope to mitigate for and reduce their ecological impacts.

Impacts of light

Animal behaviour can be negatively altered by artificial lighting, either through avoidance of lit areas (Stone et al., 2012; Stone et al., 2015; Rydell et al., 2017) or through disorientation (DeCandido & Allen, 2006; Rodríguez et al., 2015); other animals may be attracted to lights for the feeding opportunities they provide (DeCandido & Allen, 2006; Stone et al., 2015). Light can disorient migrating birds (DeCandido & Allen, 2006; Rodríguez et al., 2015), which can be particularly harmful in cities with tall, lit buildings; birds can either collide with such buildings, or circle them, which leaves them vulnerable to predation and exhaustion (DeCandido & Allen, 2006). Even artificial lighting some distance from a species' breeding grounds can have significant negative effects on animals. Seabirds, for example, specifically Balearic shearwater (*Puffinus mauretanicus*), Scopoli's shearwater (*Calonectris diomedea*), and European storm-petrel (*Hydrobates pelagicus*), are frequently rescued after their navigation becomes disoriented by artificial lighting on land (Rodríguez et al., 2015).

Some birds can take advantage of periods of artificial light; during observations from the Empire State Building in the autumn bird migration period, resident peregrine falcons (*Falco peregrinus*, usually a diurnal hunter) were seen hunting at night, facilitated by the city lights (DeCandido & Allen, 2006). Similarly, during a study of peregrine diet in three cities in the UK, prey remains were found of species that are primarily nocturnal migrants such as common quail (*Coturnix coturnix*) and little (*Tachybaptus ruficollis*) and black-necked grebes (*Podiceps nigricollis*), suggesting that urban peregrines were able to hunt successfully at night (Drewitt & Dixon, 2008). Gulls have also been observed taking advantage of lights on fishing boats to allow them to feed nocturnally in the North Sea (Garthe & Hūppop, 1996).

Along roadsides in the UK, LED lights are gradually replacing the previously ubiquitous sodium lights, due to their reduced energy demands (Stone et al., 2012; Wakefield et al., 2016). LED lights emit very little heat as waste energy, and neither do they emit light on the UV spectrum, and are, as a result, less attractive to insects than sodium lights (Barghini & Medeiros, 2012; Wakefield et al., 2016). A combination of reduced insect attractiveness, as well as low energy use has led to a widespread belief that the ecological impacts of LED lights will be less than that of more traditional artificial light sources (Spoelstra et al., 2015; Wakefield et al., 2016). However, it has been shown that LED lighting can still have strong negative impacts on some bat species such as lesser horseshoes (*Rhinolophus hipposideros*, Stone et al., 2012), since some bats are actively avoiding any lit areas, regardless of lighting type. As well as street lights, car headlights can be a source of light pollution on roads – some species can be dazzled by lights of oncoming traffic, causing them to 'freeze' in the carriageway rather than fleeing, thus increasing their chance of being hit by a vehicle (Mazerolle et al., 2005).

Impacts of sound

It is estimated that 30% of the human population within the European Union is exposed to traffic noise exceeding 55 decibels at night, 15db higher than recommended to prevent adverse health effects; the World Health Organisation

estimates at least 1,000,000 healthy life years are lost in Europe each year due to traffic noise (Theakston & World Health Organisation, 2011). Anthropogenic noise interferes with acoustic communication in birds; great tits (*Parus major*) adjust the frequency of their calls to avoid acoustic masking by surrounding urban noise (Slabbekoorn & Ripmeester, 2008) and European robins (*Erithacus rubecula*) in cities change the timing of their singing to correspond with quieter periods (Fuller et al., 2007). However, not all species are as acoustically flexible, and the lack of ability to change song pitch or volume to compete with noise could render some species 'unsuitable' for life in noisy environments (Slabbekoorn, 2013).

Anthropogenic noise could cause a behavioural shift in wildlife; one hypothesis is that noise could be distracting animals and making them more susceptible to predation due to decreased vigilance. An alternative hypothesis is that noise could result in increased anti-predator vigilance behaviour (Quinn et al., 2006), which would give the animals less time to forage, potentially decreasing their fitness (Ware, et al., 2015). A series of experiments of road traffic noise on dwarf mongooses (*Helogale parvula*) found that artificial noise decreased responses of individuals to alarm calls from a sentinel, with individual animals instead increasing the time spent vigilant (Kern & Radford, 2016) - juveniles were particularly slow to resume foraging following noise disturbance (Eastcott et al., 2020). With mongoose there is also evidence of reduced responses to olfactory cues in the presence of road traffic noise compared to no road noise – they took longer to detect predator faeces when road noise occurred, and subsequently interacted less with this predator cue, did not show increased vigilance, and spent less time in a burrow compared to when the same cue was detected when no artificial traffic noise was present (Morris-Drake et al., 2016).

Some species may avoid anthropogenically noisy areas altogether; bird species richness increases with increasing distance from a road (Summers et al., 2011). To test the effect of road noise McClure et al. (2013) developed a 'phantom road'; a location in the environment in which an artificial treatment is used to mimic the anthropogenic effects associated with roads. They found a 25% decline in bird abundance, and complete avoidance of noisy sites by some species (McClure et al., 2013). Mammals have also been shown to be susceptible to road noise effects,

another phantom road style experiment found the number of recorded passes of five species of bat was significantly reduced (up to a distance of 20 metres away), and that feeding behaviour of both common pipistrelles (*Pipistrellus pipistrellus*) and soprano pipistrelles (*Pipistrellus pygmaeus*) was negatively affected (Finch et al., 2020).

Light and noise associated with roads are stressors that often do not occur independently of one another, as human habitations using artificial lights at night often also have high levels of anthropogenic noise, e.g. in cities. Although some research has been done into the effect of one or the other (either light OR sound, as outlined above), little is known about the effects of the presence of simultaneous anthropogenic stressors associated with roads on wildlife behaviour and ecology, and there is a need for additional case studies (Munns, 2006), particularly considering the emphasis on the importance of multiple stressors in other systems, for example freshwater (Ormerod et al., 2010) and marine (Hughes & Connell, 1999) ecosystems.

We aim to determine the extent to which terrestrial woodland wildlife activity and behaviour is altered by artificial light and traffic noise, in order to learn more about the indirect and combined effects that roads may have on wildlife. We investigate the effect of light and noise both separately, and in combination as a dual stressor. We assessed: a) whether animal activity differed during treatment compared to the pre-treatment period, b) whether activity levels return to pre-treatment level following cessation of treatment, c) whether distance away from treatment affects activity, and, finally, d) whether the type of behaviour animals exhibit differs before, during, and after the different forms of treatment.

Methods

Study site

The 'phantom road' was established at Nant Bran woodland, a sessile oak woodland located near the village of Llanfihangel Nant Bran, mid-Wales (52.003650, -3.5478559). The wood is privately owned and is held in trust for ecological research

and conservation by Eco-explore CIC (www.eco-explore.co.uk). The wood has a minor classification single-track road running adjacent to the edge of its south-western border. Before experimental treatment began, a bat survey took place to identify the presence of any potential roost features and locations, in order to avoid disturbance to bat roosts by the experimental protocol. Data collection occurred August - September 2018.

Creating a phantom road

We used a 2x2 factorial design with four treatments; (control, sound, light, and light combined with sound). Twelve replicated transects were chosen at random locations throughout the woodland, with stratified random allocation of experimental treatments to each location, such that each treatment type had 3 replicates. At each transect, three bait stations (baited with ~400g of a mixed seed, dried mealworm, and peanut mixture spread across a 30cm^2 area) were deployed at 5 metre intervals from the treatment (Figure 12). Bait stations were first placed 24 hours prior to treatment and data collection beginning, as an acclimatisation period, and to allow animals sufficient time to locate the bait stations. After 24 hours animal activity and behaviour were monitored via camera-traps for three days: one day pre-treatment, one day during experimental treatment, and one day post-treatment. Monitoring the day following the treatment period allowed us to determine whether activity levels returned to pre-treatment levels following the cessation of treatment.
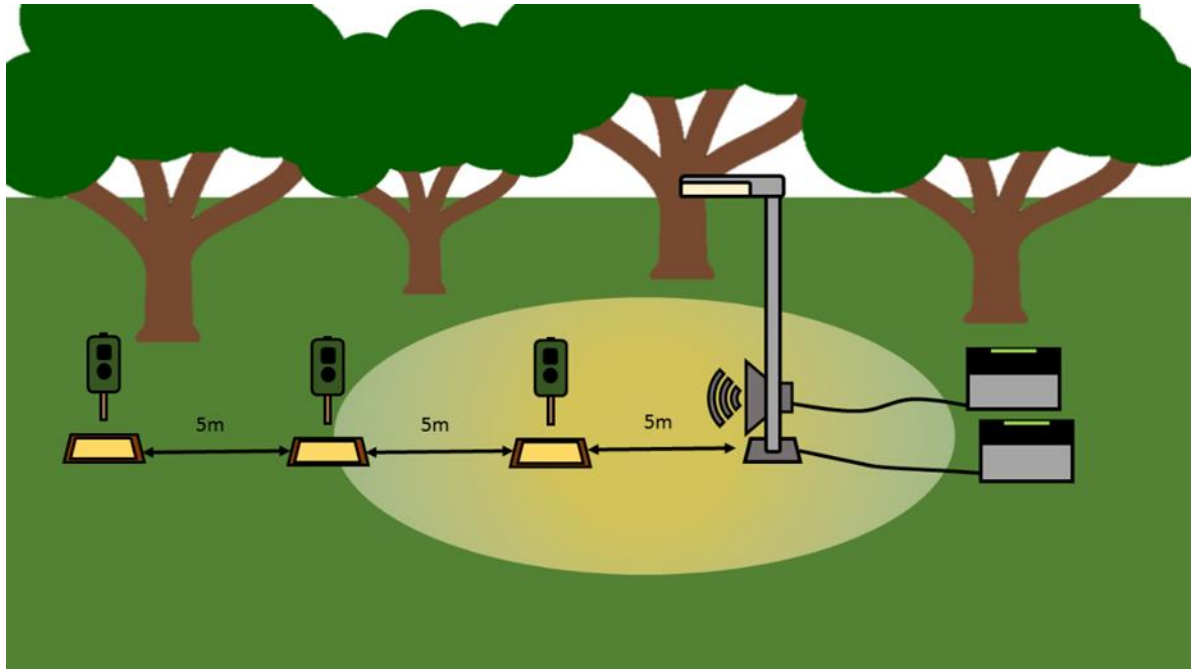
Figure 12. Experimental setup for typical transect of the 'phantom road', featuring a street light and speaker (the 'treatment site'), powered by a pair of Goal Zero Yeti 400 power packs, and three bait station at increasing 5 metre intervals from the treatment site, each monitored by a 'Ltl Acorn' camera-trap.

Experimental treatments constituting a 'phantom road', included temporary light and sound systems installed in the woodland to imitate the light spill from streetlights and traffic noise that can be found adjacent to roads. To mimic street lighting, an LED streetlight ('Kirium Mini', DW Windsor) was used, mounted on top of a 2m metal pole. The streetlight consisted of 5 LEDs producing light at 4000 Kelvin (temperature colour) and emitted a maximum of 1200 lumens. Although many street lighting systems in the UK are still low-intensity sodium lights, these are gradually being phased out and replaced with low-energy, low-cost LEDs, and LED lighting systems are now used on all new road builds in the UK (Stone et al., 2012). The streetlight turned on automatically once the inbuilt photocell registered light levels of 35 lux or below, as is standard for all streetlights in the UK, and off again in the morning when the ambient light levels exceeded 35 lux.

Road noise was generated by a speaker system which replayed sound recordings of road noise at a volume of 55-60dB measured at a distance of 5 metres from the speaker (after McClure et al., 2003). The speaker was placed in waterproof housing,

with an MP3 player connected with an AUX cable. The traffic noise recording was obtained online as an MP3 (from www.zapsplat.com); the 53s recording featured passes of 10 vehicles driving at speeds of around 40mph; this MP3 recording was looped to produce a continuous sound file which played for a 24-hour period. Although the streetlight was on for <24 hours, this mirrors a natural environment in which streetlights only turn on at night, but road traffic noise can be present at any time of day. Both light and sound systems were powered by a pair of Goal Zero Yeti 400 silent power packs, to avoid noise interference caused by a motorised generator. At 'control' sites, all equipment was still deployed, but not turned on, in order to control for any neophobic behaviours that the equipment might cause.

Recording behaviour

To record any changes in wildlife activity and/or behaviour, three movement-sensitive camera traps (Ltl Acorn 5210A) were placed at 5 metre intervals along each transect for each replicate, facing the bait to record both overall activity and the behaviour of any visiting animal (Figure 12). Once the cameras were triggered, they filmed for 30 seconds to allow adequate time for species identification and classification of behaviour types (feeding', 'collecting food', 'active', 'vigilance', and 'social behaviour'). Behaviour was assigned to one of five discrete categories: 'feeding', 'collecting food', 'active', 'vigilance', and 'social behaviour'. An animal was only assigned to be performing one behaviour at a time, and the time spent performing each behaviour was recorded. 'Feeding' was defined as any time the animal was actively eating the bait. 'Collecting food' was time spent collecting and removing the bait (including time spent travelling to and from bait that was captured on camera). 'Active' was any time the animal was moving around, walking, grooming etc. without involving food collection. 'Vigilance' was either when an animal actively looked around its surroundings from a standing position or if remained immobile on the spot. Finally, 'social behaviour' was any interaction (positive, negative, or neutral) taking place between one or more animals.

Camera interval times were set to 0 seconds, allowing continuous recording if the camera continued to be triggered by activity following the 30-second filming. Batteries and SD cards were changed daily in all cameras at 12 noon each day. The camera-traps had a built-in infra-red light, allowing monitoring to continue even during the night, whilst minimising disturbance to wildlife. This method of observation is non-invasive and does not require the presence of a human observer, which could bias results, and may not pick up particular groups which are more difficult to observe, such as small rodents, and/or nocturnal species. The use of camera-traps also facilitates continual observations, allowing us to pick up activity around-the-clock, which is important as many of the UK's mammal species are primarily nocturnal.

We recorded the number of individual visits to the food bait (an individual 'visit' being defined when the time since an animal was last seen was >30 seconds), the time at which each visit took place, the distance away from the source of light/sound, the amount of time animals spent in front of the camera (in seconds, defined as 'activity'), and then identified and categorised the activity time of each animal into a sub-set of behavioural types.

Statistical analysis

To investigate the effect of treatment type (control, light, light & sound, and sound), and the effect of distance away from the treatment site on animal activity, a generalized linear mixed-effects model with Gamma distribution and "log" link function, was implemented using R version 3.5.2 (R Core Team, 2013) and package *lme4* (Bates et al., 2015), and validated following Thomas et al. (2017). To ensure model stability, the data were first sub-set into treatment types (control, light, light & sound, and sound), with each treatment type modelled separately. There was not sufficient data to investigate species-specific effects, therefore observed activity (of all behaviours, pooled and measured in seconds) of all species was the dependent variable, with the day treatment ('before', 'during', or 'after' treatment), and distance away from treatment site (and its interaction with the treatment) as

independent variables, plus the site location within the wood (sites 1-12) as a random effect term to account for the differing locations.

Results

Observed species

Across all treatments eleven species/taxa of mammal were recorded; mice (*Apodemus* sp.), bank voles (*Myodes glareolus*), grey squirrels (*Sciurus carolinensis*), shrews (*Sorex* sp.), badgers (*Meles meles*), foxes (*Vulpes vulpes*), and a domestic cat (*Felis catus*). The mice were not identified to species level as it is not possible to distinguish wood mice (*A. sylvaticus*) and yellow-necked mice (*A. flavicollis*) from the views obtained, and both species have been previously recorded at the site. Similarly, the shrews were grouped simply as 'shrew', but were likely to have been a mixture of common shrews (*S. araneus*) and pygmy shrews (*S. minutus*), both of which have previously been recorded at the study site. Only two bird species were recorded on camera: a European robin (*Erithacus rubecula*) and a wren (*Troglodytes troglodytes*).

Effect of treatment type on activity

Sound significantly reduced animal activity time (before-during comparison), with activity post-treatment not significantly different to pre-treatment levels (Table 4; Figure 13), meaning the effect on behaviour was short-lived. Light alone did not alter activity levels (Table 4; Figure 13). When this light treatment model was re-run only including the potentially more light-sensitive nocturnally-active animals (by removing all records occurring within daylight hours), there was still no significant difference in activity levels during treatment when compared to the pre-treatment 'before' period (Estimate = -0.872, Std. Err. = 0.718, t = -1.214, Pr(>|z|) = 0.225). Finally, light plus sound together significantly decreased activity compared to the period when neither occurred, but returned to pre-treatment levels once the treatment period finished, illustrating the effect was ephemeral (Table 4; Figure 13).

There was, however, a statistically significant reduction in activity time for the control sites between both the "before" and "during" time periods and the "before" and "after" ones (Table 4; Figure 13).

Table 4. Summary results table of statistical analysis showing effects of differing treatment types on animal activity times (in seconds), comparing activity during treatment compared to the pre-treatment period, as well as activity post-treatment, compared to pre-treatment levels. Significant results are indicated by shading.

Treatment	Comparison	Estimate	Standard error	t	Pr(>|z|)
Sound	Before – During	-4.699	1.168	-4.022	<0.001
	Before – After	-1.416	1.101	-1.286	0.198
Light	Before – During	-0.328	0.511	-0.643	0.520
	Before – After	0.247	0.263	0.938	0.348
Light plus sound	Before – During	-1.388	0.282	-4.924	<0.001
	Before – After	0.629	0.211	2.977	0.003
Control	Before – During	-1.781	0.379	-4.700	<0.001
	Before – After	-0.899	0.304	-2.963	0.003
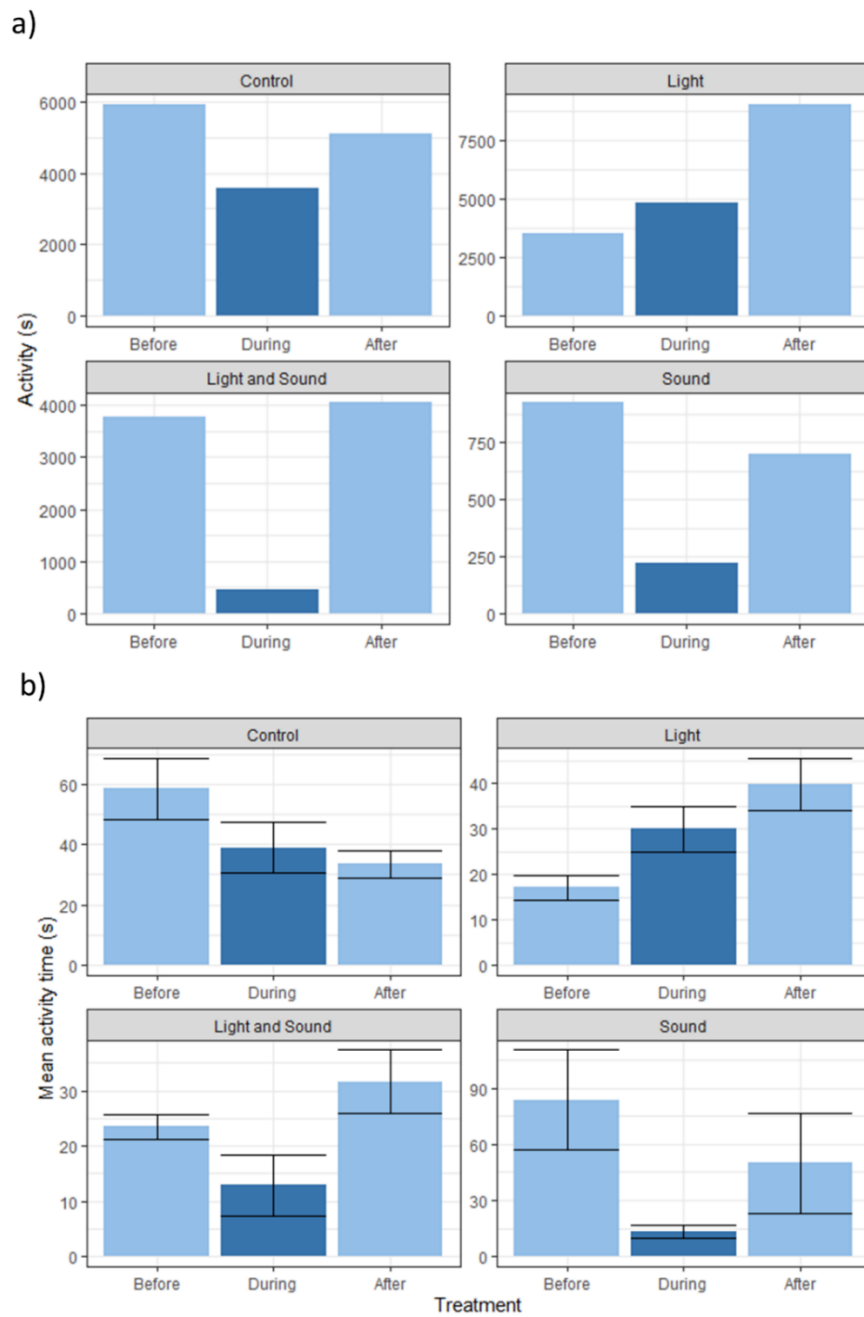
Figure 13. Summary of (a) cumulative and (b) mean (±SE) time (seconds) that animals were recorded for across all four treatment types (control, light, sound, and light & sound) before, during, and after each treatment.

Effect of distance from treatment on activity

Animal activity was consistently significantly higher for every treatment at 15 metres away from the treatment site, compared to 5 metres away (Figure 14; Table 5), and was still higher at 10m than 5m away from the treatment site for two of the treatments; light plus sound, and control.

Table 5. Summary results table of statistical analysis showing effects of distance on animal activity times during treatment periods. Comparisons are made with the closest data recording station, situated 5 metres from the treatment site. Significant results are indicated by shading.

| Treatment	Distance	Estimate	Standard error	*t*	Pr(>|z|)
Sound	10m	1.688	1.041	1.620	0.105
	15m	3.032	1.123	2.699	0.007
Light	10m	-0.485	0.523	-0.927	0.354
	15m	1.062	0.478	2.222	0.026
Light plus sound	10m	-1.395	1.049	-1.330	0.184
	15m	2.727	0.500	5.459	<0.001
Control	10m	1.153	0.351	3.288	0.001
	15m	1.020	0.370	2.759	0.006
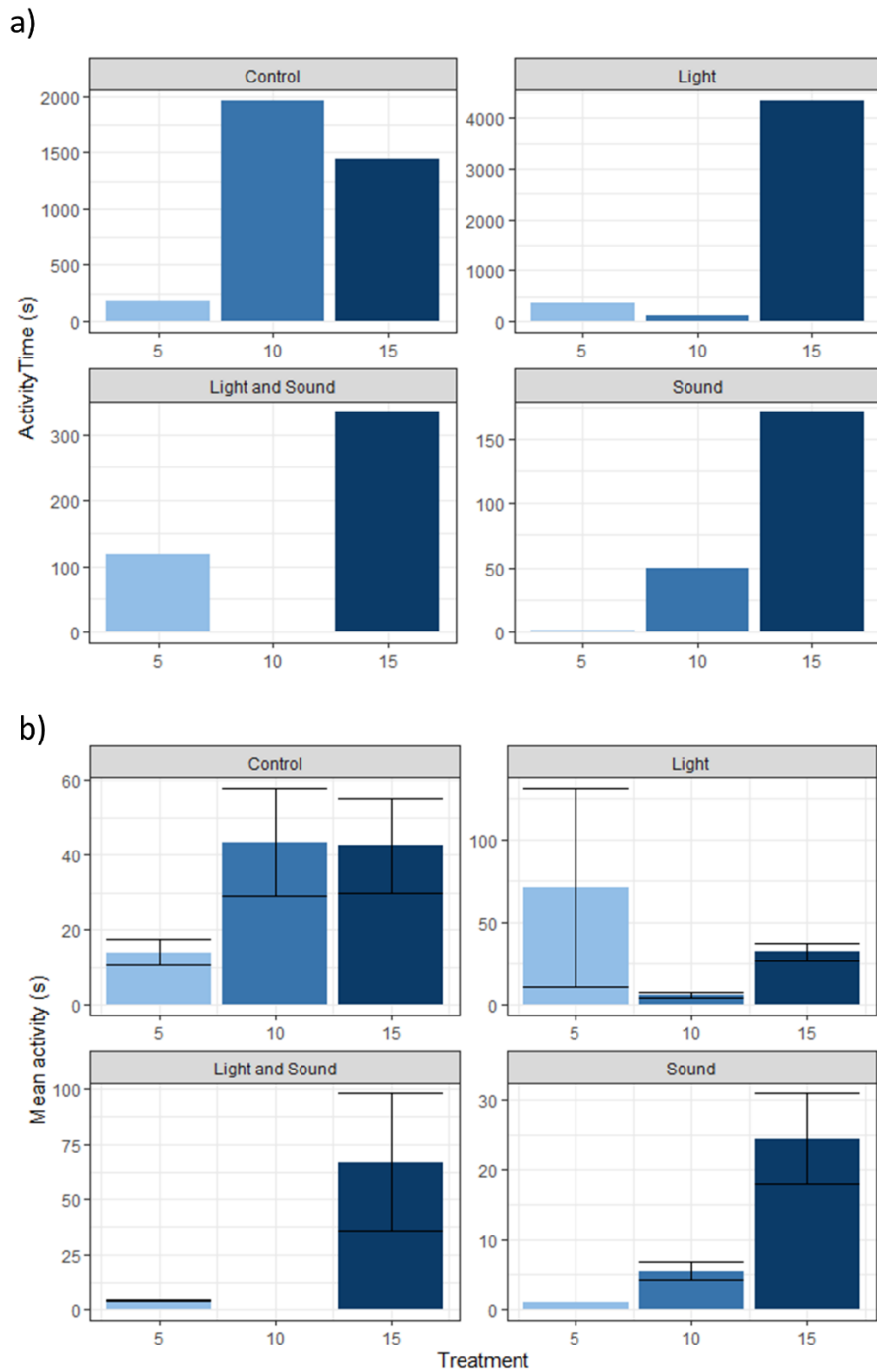
Figure 14. Summary of (a) cumulative and (b) mean (±SE) time (seconds) that animals were observed across all four treatment types on "during" days (when treatment is active), by distance away from treatment site (in metres).

Effects of treatment on animal behaviour

Behavioural effects were taxon dependent, for example, the two small rodents, mouse spp. and bank vole, spent a mean of between 55% and 60% of the time feeding, respectively, and between 19% and 24% of the time collecting food (Table 6). Grey squirrels, on the other hand, spent an average of 92% of the time feeding, and only 1% of the time collecting food. Shrews spent proportionally the highest amount of time collecting and caching food compared to all other species, at 43%. However, within species, time spent performing different behaviours differed depending on which treatment is occurring at the time (Table 6).

Table 6. Activity time (in seconds) of observed species/taxa during the course of the experiment, and percentage of time that each species/taxa spent performing each of five designated behavioural activities across all treatment types. Species for which fewer than 10 minutes of footage was obtained were excluded (cat, fox, robin, and wren). Treatment type codes: C = control (no treatment), L = light treatment, S = sound treatment, L+S = light plus sound treatment.

Species	Treatment	Activity time (s)	Percentage time spent performing given behaviour				
			Feeding	Active	Collecting food)	Vigilance	Social behaviour
Mouse (*Apodemus* sp.)	C	4655	61%	22%	10%	7%	<1%
	L	7666	74%	12%	8%	5%	<1%
	S	87	57%	33%	-	9%	-
	L+S	4399	34%	10%	50%	6%	<1%
Bank vole (*Myodes glareolus*)	C	142	54%	37%	6%	3%	-
	L	1459	69%	4%	16%	9%	2%
	S	63	-	19%	52%	29%	-
	L+S	735	34%	10%	40%	16%	<1%
Grey squirrel (*Sciurus carolinensis*)	C	5070	89%	<1%	<1%	9%	-
	L	6271	97%	<1%	<1%	2%	-
	S	1552	93%	<1%	-	6%	-
	L+S	1109	79%	5%	13%	4%	-
Shrew (*Sorex* sp.)	C	295	17%	61%	22%	-	-
	L	1748	43%	12%	43%	2%	<1%
	S	123	11%	28%	56%	5%	-
	L+S	830	35%	16%	47%	1%	-

Badger (*Meles meles*)	C	4021	86%	11%	<1%	3%	-
	L	2	-	100%	-	-	-
	S	-	-	-	-	-	-
	L+S	1162	91%	3%	-	6%	-

The percentage of time that species spent performing 'vigilance' behaviour (either when an animal actively looked around its surroundings from a standing position or if remained immobile on the spot) differed depending on the treatment. Prior to any treatment, the percentage of time that animals spent performing vigilance behaviour was a maximum of 7.9% of the time; however, during sound treatment, this increased to an average of 15.3% of the time (Table 7). There was no increase in time spent vigilant during light treatment, but a large increase in vigilance during sound treatment; an increase of 144.6% of the time during light plus sound treatment, and 93.7% during sound treatment.

Table 7. Percentage of time that animals were recorded performing vigilance behaviour across the four different treatment types, both before, during, and after treatment.

	Percentage of time spent 'vigilant'			
	Control	**Light**	**Light plus sound**	**Sound**
Before	6.7%	4.5%	5.6%	7.9%
During	4.9%	3.4%	13.7%	15.3%
After	7.5%	3.6%	6%	5.7%

Discussion

We have shown that for the observed taxa of woodland wildlife, the presence of artificial lights does not prevent feeding behaviour from taking place, nor significantly reduce activity levels. Sound treatment (including when combined with lighting), however, significantly reduced activity levels, even with the presence of a high-energy food bait. Although we did also observe a significant difference in activity

levels during control treatments the effects were certainly not as strong as the clear patterns shown during sound-on treatments (Figure 13), and this may be within the natural variation of animal behaviour. Species filmed during our experiment were predominantly mammalian - very limited avian activity was observed; with less than a minute combined activity of robin and wren, but previous work has shown that birds are indeed negatively affected by road traffic noise (McClure et al., 2013; Ware et al., 2015; McClure et al., 2017).

Effect of treatment type on activity

Overall, we observed no significant effects of light on overall levels of animal activity (Estimate = -0.328, Std. Err. = 0.511, t = -0.643, Pr(>|z|) = 0.520). Our findings are in contrast with previous research which found that experimental illumination of a natural habitat suppresses activity of wood mice (*Apodemus sylvaticus*) (Spoelstra et al., 2015). Other taxa are affected by the presence of artificial lighting; much work has been done examining the responses of bats to artificial lights, and responses to such lights differs across species depending on their feeding strategies and flight styles (G. Jones & Rydell, 1994). For example, fast-flying *Pipistrellus* species have been shown to be attracted to lights due to the feeding opportunities they offer (Lacoeuilhe et al., 2014; Spoelstra et al., 2015; Azam et al., 2018). However, broad-winged, slow-flying or bats that feed by gleaning, such as horseshoe bats (*Rhinolophus* spp.), *Myotis* spp., and long-eared bats (*Plecotus* spp.) have been shown to actively avoid artificial light sources (Rydell et al., 1996). Reasons suggested for this behaviour include predator avoidance; being illuminated would increase the chance of being eaten by nocturnal predators that feed on bats, such as tawny owls (*Strix aluco*) (Jones & Rydell, 1994). Variance in activity of the species we observed in the presence of light could be too high for us to detect any real change as it included diurnal species such as grey squirrels. However, when the analysis was re-run using only nocturnal species, there was still no significant effect of light on overall levels of animal activity (Estimate = -0.872, Std. Err. = 0.718, t = -1.214, Pr(>|z|) = 0.225).

There was, however, a significant reduction in activity time at the bait stations during sound treatment (Estimate = -4.699, Std. Err. = 1.168, t = -4.022, Pr(>|z|) = <0.001). As opposed to light treatment, which may disproportionately affect nocturnal species, sound has the potential to affect any vertebrate species; previous work has found significant effects on distribution and fitness of bird species following exposure to road noise – one study found a one-quarter decline in bird abundance, and almost complete avoidance by some species during a 'phantom road' experiment (McClure et al., 2013). Such road noise pollution could negatively impact species by preventing them from being able to detect predators using auditory cues, resulting in a reduction in time spent feeding. If these auditory cues are being masked by the sound of traffic noise, then more time must be spent being vigilant, looking around to detect predators, and therefore less time is available for foraging. Our experiment showed that animals may avoid noisy areas even if the habitat is suitable and there are significant feeding opportunities (through the provision of bait stations).

There was also a significant reduction in observed activity during the treatment combining both light and sound disturbance (Estimate = -1.388, Std. Err. = 0.282, t = -4.924, Pr(>|z|) = <0.001). As the treatment using solely sound also showed a significant decrease in activity, it is unclear whether the addition of light (which had no significant influence on its own) in this treatment has influenced the results in any way. However, we also observed a significant reduction in activity during the control treatment where the lighting and sound equipment were installed at the treatment site but not turned on (Estimate = -1.781, Std. Err. = 0.379, t = -4.700, Pr(>|z|) = <0.001), which may point to some of the observed effects on animal activity simply being a result of natural variation in animal activity and distributions in the woodland.

Effect of distance from treatment site on activity

We observed a consistent and significant increase in activity at 15m away from the treatment site compared to 5m away, as well as an increase in activity at 10m away compared to 5m for two of the treatments (Table 5; Figure 14) – perhaps unsurprising as the volume would have decreased at an increasing distance from the treatment

site, and animals generally avoid noisy areas (e.g. Slabbekoorn & Ripmeester, 2008; Summers et al., 2011; McClure et al., 2013; Ware et al., 2015; McClure et al., 2017). However, the control sites (where the light and sound equipment were present, but not switched on) also showed a significant increase in activity further away from the treatment site at both 10 metres (Estimate =, Std. Err. =, t =, Pr(>|z|) =), and 15 metres (Estimate = 1.020, Std. Err. = 0.370, t = 2.759, Pr(>|z|) = 0.006), indicating there may be some influence of neophobia of the lighting rig and speaker (e.g. Travaini et al., 2013), despite an acclimatisation period.

Effects of treatment on animal behaviour

During our study, the percentage of time that species spent performing 'vigilance' behaviour increased by 83.9% of the time during light plus sound treatment, and 63.8% during sound treatment (Table 7).This increased vigilance behaviour during sound treatment has been observed previously during laboratory experiments on captive chaffinches (*Fringilla coelebs*) and white-crowned sparrows (*Zonotrichia leucophrys*) (Quinn et al., 2006; Ware et al., 2015). It is hypothesised that this behavioural change is to do with predator avoidance; during 'sound-on' periods, less time was spent feeding, and more time performing vigilance behaviour. As animals can rely less on their hearing to detect predators if the noise is being masked by sound from a different source, they must rely more on other senses such as vision and smell, which may be difficult to use when the head is down in a feeding position. During a previous 'phantom road' experiment in the USA, it was shown that for individual birds that remained in a landscape despite the traffic noise disturbance, that overall body condition of these resident birds significantly decreased, and some migratory species showed an inability to improve body condition during stopovers (Ware et al., 2015).

Conclusions

It has long been observed that roads have negative effect footprints reaching far beyond the road itself (Forman & Alexander, 1998). The observed significantly reduced activity during the 'sound-on' periods, as well as increased anti-predator vigilance behaviour, could have potential for negatively impacting species on a wide level in the UK; as has been observed in previous studies (McClure et al., 2013; Ware et al., 2015; McClure et al., 2017). We also consistently observed significantly higher activity levels at the site that was the furthest away from the treatment site, which could still be an indication of animals avoiding these areas despite the presence of a food source, which could have implications for feeding, and subsequent fitness of populations, but would require further investigation to untangle potential effects of neophobia. The significant reduction in activity levels in response to road traffic noise, as well as a reduction in the time animals spent feeding or collecting food (with an increase in vigilance behaviour) demonstrates more ways in which simply the presence of roads can be detrimental to wildlife.

6

Discussion

Overview

Although the research field of 'road ecology' was only named as such in the last 25 years (Forman, 1998), observations on the ecological effects of roads have been taking place for considerably longer, with the first published count of wildlife-vehicle collisions taking place in 1935, in which an individual observer recorded avian mortalities over 4000 miles of road in the UK (Barnes, 1936). Monitoring of the ecological effects of roads (particularly of wildlife-vehicle collisions) has grown substantially over the last two decades, particularly with the widespread availability of personal GPS systems in the form of smartphones (Olson et al., 2014; Vercayie & Herremans, 2015). However, there are still many ecological questions that remain unanswered within the field – and the aim of this thesis has been to answer some of these questions, and to increase the pool of knowledge on the interactions between roads and wildlife, with a particular focus on wild vertebrates in the UK.

Through a literature review (Chapter 2) it is summarised how monitoring wildlife roadkill can contribute to five key areas of ecological research; 1) monitoring roadkill numbers, 2) monitoring population trends, 3) mapping native and invasive species distributions, 4) providing insights into temporal and spatial patterns of animal behaviour, and 5) monitoring of contaminants and disease. The collection of such data can also offer valuable opportunities for 'citizen scientists' to get involved in scientific data collection and research.

Chapter 3 (Temporal patterns of wildlife roadkill on UK roads) showed that there are distinct, but usually highly consistent temporal patterns in roadkill shown by the most common taxa found as roadkill in the UK. Only one species examined (the red fox) did not show any significant variation in temporal reporting patterns. Although for some species, these temporal patterns are driven at least in part by variable abiotic factors (temperature and rainfall), most of the variation is due to a given species' behaviour and ecology giving rise to seasonal patterns of vulnerability to being killed on roads.

In Chapter 4 (Roadkill scavenging behaviour in an urban environment) it is demonstrated how quickly removal of roadkill by scavengers can take place in urban areas - 76% of experimentally placed carcasses were removed within 12 hours. The number of carcass removals peaked in the first few hours of daylight, and of roadkill that was placed at 9 am, most (62%) of carcasses were removed in two hours or less. This quick removal of corpses by scavengers suggests that the actual number of road deaths of small vertebrates is up to six times more than that observed during surveys.

Finally, another camera-trapping experiment described in Chapter 5 (The 'phantom road': effects of artificial light and traffic noise on woodland wildlife) showed there was a significant reduction in wildlife activity in the presence of traffic noise, whether or not this was accompanied by artificial light or not. It was also shown how wildlife behaviour can be altered by the presence of this noise – there was an increase in the percentage of time that animals displayed vigilance behaviour (and therefore a reduction in the time available for other activities including feeding) – it is hypothesised that this is due to the road noise effectively masking the noise of potential predators, resulting in animals needing to spend more time searching for predators visually.

Benefits of long-term citizen science data collection

One of the chapters of this thesis (Chapter 3) was based entirely on data collected by citizen science roadkill recording scheme Project Splatter based at Cardiff University,

which collects data UK-wide on all wild vertebrates, at all times of year. Worldwide, there are many similar projects collecting such data, many of which also rely largely on records from members of the public (Shilling et al., 2020). Although there are concerns about the validity of results from such monitoring schemes as they rely on largely untrained volunteer contributors, most of these fears are shown to be unfounded (Périquet et al., 2018), and in fact can allow recording at larger spatio-temporal scales, and contribute to the recording of many more species than can usually be achieved by professional scientists alone (Bíl et al., 2020).

The collection of large, long-term datasets not only allows us to generate greater statistical power to monitor impact, but can also be used to examine any possible changes in patterns of roadkill occurrence over space and time over a long time-scale. This is particularly relevant with our current shifting climate – for example, a change in species' activity levels at different times of year due to climate change could be discovered through a shifting peak in roadkill numbers. Indeed, this has already been the case, in some contexts – for example, there has been a documented shift in the annual mortality peak for Western whip snakes (*Hierophis viridiflavus*) over a >20 year period, corresponding with increasingly higher temperatures earlier in the year over time (Capula et al., 2014).

Citizen science & spatial patterns

Although the focus of citizen science data in this thesis has been to examine temporal patterns of wildlife roadkill, such data have also been used widely to map species' distributions across a broad taxonomic range. There are two broad ways in which spatial patterns in wildlife roadkill can be analysed; firstly, the use of species distribution models which are capable of detecting potential roadkill risk, including in areas without existing data, as these models use additional information on environmental variables that can explain the presence of roadkill. Secondly, hotspot analysis is used to find spatial clusters in data but do not usually also include environmental or landscape variables in the analysis, so can only be used to look at existing clusters in areas where data already exist.

Species distribution modelling

Many roadkill recording schemes collect opportunistic data, but species distribution models exist to deal with such biases in presence-only data, one of the most commonly used being MaxEnt (Gomes et al., 2018). MaxEnt models use a machine-learning algorithm to estimate the distribution of a species using environmental knowledge from known (presence-only) occurrence sites, that is, using conditions at a known species presence site to infer whether a species may be present at another, similar, location (Gomes et al., 2018). MaxEnt has been used by researchers from the California Road Observation System to model the effects of various environmental factors and human population densities on wildlife roadkill (Ha & Shilling, 2018).

Hotspot analysis

Kernel Density Estimation (KDE) is a commonly-used technique in software such as ArcGIS to identify 'hotspots' of wildlife roadkill – that is – areas where higher-than-expected numbers of animals are killed in a particular area (spatial clustering). KDE+ analysis is built on the same principles as KDE but uses additional software (http://www.kdeplus.cz/en/) to allow for the hotspots to be ranked in terms of their significance. KDE+ analysis was first used in 2013 (Bíl et al., 2013), and has been subsequently widely used to analyse roadkill hotspots including across the entire Czech road network (Bíl et al., 2017), for amphibians and reptiles in Austria (Heigl et al., 2017), ungulate collisions in Northern Italy (Favilli et al., 2018), roadkill in South Africa (Périquet et al., 2018), as well as being combined with temporal data to form a STKDE+ (spatiotemporal KDE+) analysis (Bíl et al., 2019).

Directions for future work

As well as using the Project Splatter data for an in-depth examination of spatial patterns of wildlife roadkill in the UK, I propose the following additional research

priorities (expanding on the contents of this thesis) through which road ecology can most effectively be continued and furthered:

Continuation and spread of citizen science roadkill recording schemes

Firstly, as outlined above in the section 'Benefits of long-term citizen science data collection', the continued collection of long-term data on wildlife roadkill where such projects exist, and the creation of new monitoring projects in areas which do not currently collect such data is imperative if we are to continue to further our understanding of the impacts of roads on wildlife worldwide. For example, in Chapter 2, it was shown that even with a very limited number of countries with estimates (with many of the world's most biodiverse regions not represented), there is still estimated to be over 400 million (or over a million a day) wild vertebrates killed on the world's roads each year. Although the scale of this limited estimate is huge, it is likely that this is still a gross under-representation of the true cost of roads on our wildlife.

Long-term studies of shifts in temporal patterns

Although the work of Chapter 3 included data from over 6 years of roadkill monitoring, there is still potential for the same analysis to be repeated in the future over a longer time period, to examine whether there were any long-term shifts in patterns that could be identified, which may indicate phenological changes in wildlife behaviour, such as might be predicted under climate warming scenarios. Additionally, it would be of great interest for a similar study to be undertaken in other countries that collect year-round data on a variety of taxa, to see whether such patterns differ (within species as well as between species) on a country-by-country basis.

Roadkill scavengers

Chapter 4 showed just how quickly scavenging of small roadkill carcasses can take place in urban areas. However, there are several ways in which the study design could be adapted and repeated in a variety of different situations, for example in less urban habitats, on different road types (with differing speed limits), at different times of year, and with different carcass sizes. Although similar studies have taken place in countries other than the UK, these may not be as relevant to scavenging of roadkill in this country, due to a different assemblage of scavenger species. Consideration is given in Chapter 3 to the potential impacts of such a widely available resource for scavenging species over the year, but further work is needed to determine whether this resource has a significant impact on the survival of these scavengers.

Effects of artificial light and traffic noise on wildlife behaviour

Finally, in Chapter 5 it was found that the addition of road noise to a previously quiet area of woodland results in a reduction in animal activity, as well as a shift in behaviour. However, we did not detect any significant change in activity or behaviour due to artificial light emitted by a streetlight. The study design was necessarily focused on detecting the immediate effects of light and noise. A longer period of data collection would allow any longer term effects of light (as well as noise) to be uncovered, and would allow for more in-depth analysis, for example species-specific reactions to artificial light at night and traffic noise, as well as long-term effects (for example, whether there is any habituation shown by the animals to the changes in their light- and noise-environment.

Conclusions

The research presented in this thesis has provided further, novel evidence of the impacts that roads can have on wildlife, as well as identifying what can be learned by monitoring and studying incidences of wildlife roadkill. New roadkill monitoring

schemes are founded each year in countries across the world, and therefore collection of data around wildlife/road interactions are likely to only continue to increase over time. Roads frequently represent an interface between areas of human habituation and the natural world, and it is therefore our collective responsibility to understand and attempt to mitigate for their impacts.

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