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Short note

SHORT NOTE

Roadkill scavenging behaviour in an urban environment

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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 h. 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 9 am, 62% of carcasses had been removed after only 2 h. Removal of corpses by scavengers could mean that the actual number of road deaths is six times more than that observed during surveys.

Key words: scavengers, camera-trapping, road ecology, wildlife–vehicle collisions, ecosystem services

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 ~80 million birds are killed on roads each year in the USA (Erickson, Johnson, and Young 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 and 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 and 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 with 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 (Erickson, Johnson, and Young 2005; Forman and Alexander 1998) 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, Rhodes, and Shivik 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, Kindel, and Coelho 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 and 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 (Heigl et al. 2016; Shilling, Perkins, and Collinson 2015).

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 2564 people per square kilometre (Office for National Statistics 2017). The study took place in the city centre between 27 January and 18 February 2014. Six sites were 'residential', consisting of randomly selected streets within 10 m of housing, and the other six were parks and public gardens ('parkland' areas, none of which were smaller than 2.5 ha). Mean sunrise during the study period was at 07:40 (ranging between 07:21 and 07:58) and mean sunset at 17:14 (16:53 and 17:33). Two camera-trapping sessions of the same length took place, one from 9 am to 9 pm (the '9 am session'), and one from 9 pm to 9 am (the '9 pm session').

Setting camera traps

Cameras were deployed at 20 cm 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 1 m in front of the camera, on the pavement in residential areas, and on grassy areas in the parkland. The chicken heads weighed ~50 g – 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 s, 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-h periods, resulting in a total of 120 12-h filming sessions. Of the 10 baiting and filming replicates on each site, five were '9 pm' sessions (9 pm to 9 am), and five were '9 am' sessions (9 am to 9 pm). To ensure random sampling of each site, and to reduce any bias due to external sources (e.g. weather), the date on which the 9 pm and 9 am 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 9 pm, and checked and re-baited again at 9 am. 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 were performed on a contingency table (as per Table 1). 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',

Table 1. Frequency of simulated roadkill removal by different taxa in 'residential' and 'parkland' areas in Cardiff, Wales[a]

Roadkill removal by species across habitats			
Species name	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

[a]Data taken from camera-trapping observations, with cameras baited using chicken heads. There was a significant association between species and habitat (Fisher's exact test, $P < 0.005$).

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 and The Guidebook Team (2017). The occurrence or the absence of a scavenging event (roadkill removed vs. not removed) was the dependent variable, with habitat (residential/parkland), trapping session time (9 am/9 pm), 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 9 am or 9 pm was the dependent variable, habitat type (residential/parkland) and time of session start (9 am/9 pm) 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 (Fig. 2) were drawn using the R package 'survival' (Therneau 2015).

Results

Seven species were observed removing the roadkill (Table 1); two species of gull; herring gull (*L. argentatus*) and lesser black-backed gull (*L. fuscus*), carrion crow (*Corvus corone*), Eurasian magpie (*Pica pica*), red fox (*V. vulpes*), domestic dog (*Canis familiaris*), and domestic cat (*Felis catus*) (Table 1). 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 with 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 1). For example, gulls fed predominantly in residential areas (12 incidents compared with only once in parkland), whereas corvids mostly fed in parkland areas (28 incidents compared with 10 in residential areas).

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 (Fig. 1). All four recorded bird species scavenged during dawn and daylight hours, except for one instance of a carrion crow scavenging after sunset.

Of the 120 simulated roadkill carcasses, 90 (76%) were removed within the 12-h recording period. There was a large peak in scavenging activity commencing just after 7 am, and finishing just before 11 am (Fig. 1); more than half of the carcasses (53%) were removed by scavengers during this 4-h 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, $P \leq 0.001$); roadkill was removed significantly faster when bait was placed at 9am (mean = 136 min, $SD = 185$ min), compared to when bait was placed at 9 pm (mean = 523 min, $SD = 206$ min). This faster removal time following 9 am baiting is due to the higher level of activity of many of our observed scavenging animals in the first few hours following sunrise (Fig. 2). The mean time elapsed before removal of a carcass, across all samples, was 310 min ($SD = 274$ min). 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, $P = 0.929$).

Following the 9 pm to 9 am survey, 30% (around one-third) of carcasses were still in place. At the end of the 9 am to 9 pm survey sessions, only 18% of carcasses—approximately one-sixth—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 (Inger et al. 2016a,b; Slater 1994, 2002). 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

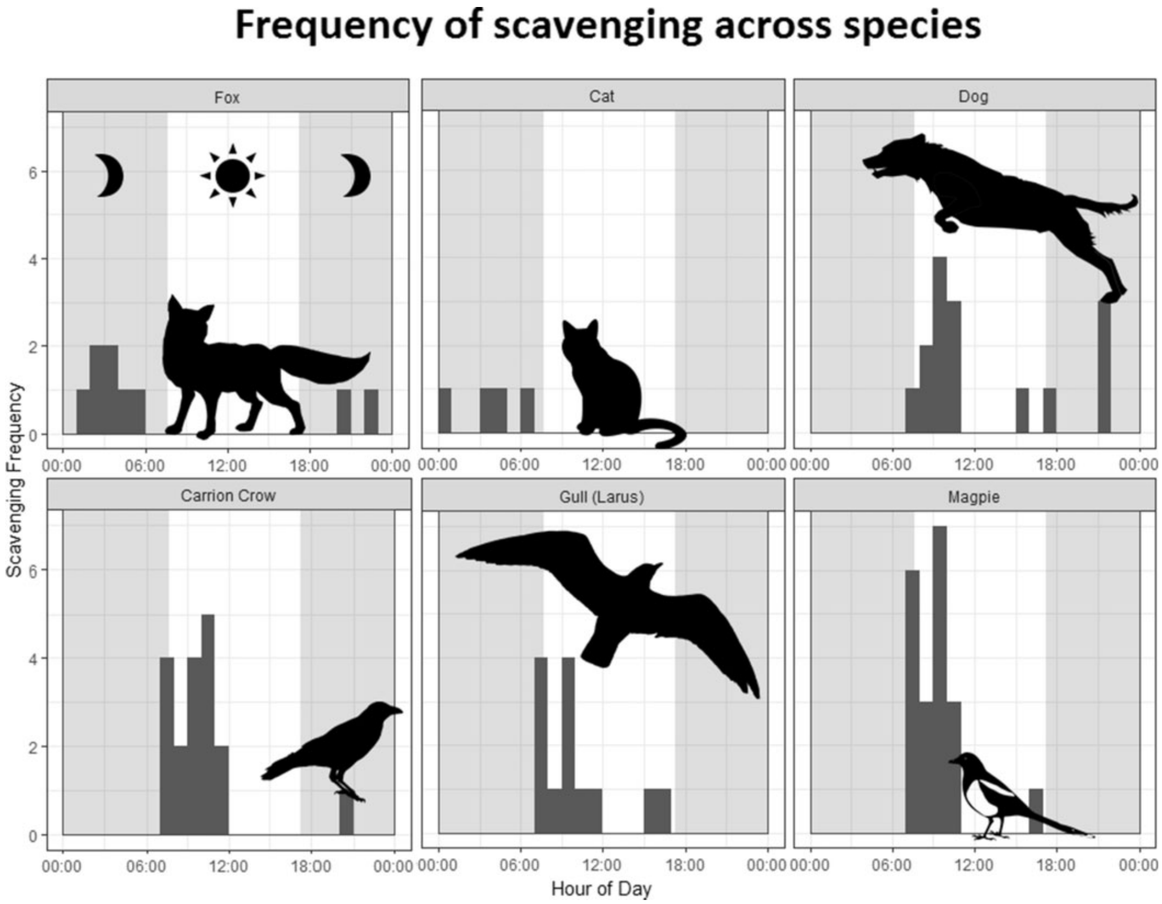

Figure 1. Frequency of scavenging in hourly periods for different species at camera traps baited with chicken heads (to simulate roadkill) within residential and parkland areas within the city of Cardiff, UK. Shaded areas represent times between sunset and sunrise.

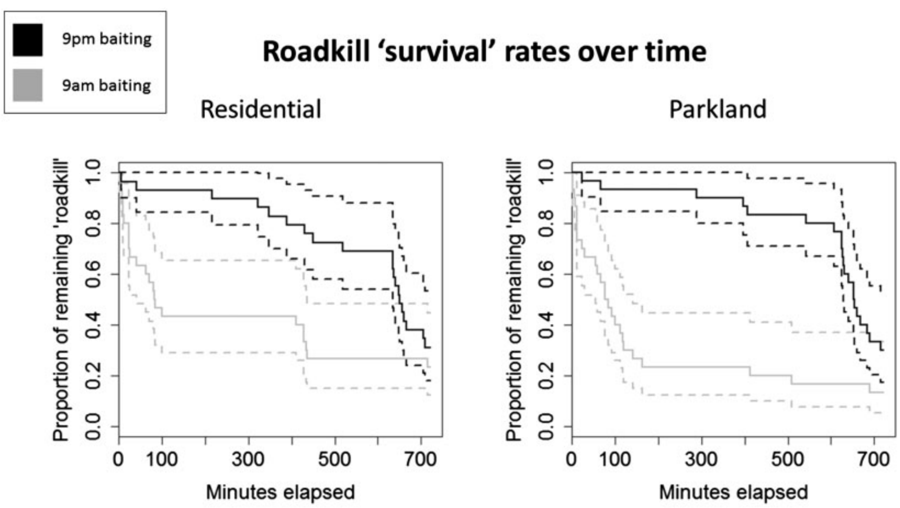

Figure 2. 'Survival' of roadkill (solid lines) with 95% confidence intervals (dashed lines) from baited cameras showing scavenging in 'residential' compared to 'parkland' areas. Minutes elapsed are from the beginning of a trapping session, from either 9 pm (black lines) or 9 am, (grey lines), respectively.

roads occurs at night (Caro, Shargel, and Stoner 2000), and scavenging behaviour primarily occurs at night or early in the morning (Fig. 1). 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 (Fig. 1).

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 and 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 (*R. norvegicus*) as bait; 73% of the rat carcass biomass was removed by these three species (mean loss of 194 g per carcass, compared to a mean loss of 14 g per carcass when vertebrate scavengers were absent; Inger et al. 2016a). In addition, carcasses 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 some of this is likely to represent deliberately provisioned meat, this still represents a significant removal of harmful carcasses and 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 (NBC Environment 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 (*C. corone*), wood mouse (*A. 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 1). 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 and 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 and 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, Shargel, and Stoner 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, Pierce, and Ward 2007). In the current study, gulls (both herring gulls and lesser black-backed gulls) were only recorded scavenging during the daytime, but both species 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 h of being placed on roads (Antworth, Pike, and Stevens 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 h (Ratton, Secco, and da Rosa 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 h, 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, Carvalho, and Mira 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 ~40% of those left on the roadside disappeared within seven days (Taylor and 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, Pike, and Stevens 2005), despite the risk that roads pose to scavenging animals (Lambertucci et al. 2009; Cook and Blumstein 2013). House sparrow (*Passer domesticus*) carcasses placed on the road were often crushed by oncoming traffic, and subsequently removed within 24 h, while the carcasses placed at the side of the road where they were not crushed, were not removed for ~120 h (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 Fig. 1. 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.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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