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REVIEW

A systematic review into the suitability of urban refugia for the Eurasian red squirrel *Sciurus vulgaris*

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ABSTRACT

1. Urban growth and intensification are projected to increase as the global human population increases. Historically, urban areas have been disregarded as suitable wildlife habitat, but it is now known that these areas can be biodiverse and that wildlife species can adapt to the environmental conditions. One such urban-dwelling species is the Eurasian red squirrel *Sciurus vulgaris*, which has suffered population declines in several countries throughout its range in recent decades.
2. The current published literature was systematically reviewed to determine whether or not urban habitats are suitable refugia for red squirrels, through identifying and discussing key topics regarding the urban ecology of red squirrels.
3. Urban environments can support higher population densities of red squirrels than rural areas, probably due to the widespread and reliable provision of anthropogenic supplemental food alongside natural food sources. The availability and quality of urban greenspaces are important determinants of the suitability of urban habitats for red squirrels, as they provide natural food sources and nesting sites. Despite the barriers present in urban landscapes (e.g. roads), red squirrels can still disperse and maintain gene flow at the population level.
4. Road traffic accidents appear to be a significant cause of mortality in some urban red squirrel populations, and seasonal peaks of mortality occur during the autumn months. Diseases (e.g. squirrelpox virus) can also be a significant cause of mortality, although effects differ between populations and depend on whether grey squirrels *Sciurus carolinensis* are present. Many of the predation events that affect red squirrels appear to be due to free-ranging domestic and feral cats *Felis catus*, although there is currently little evidence to suggest that predation is a limiting factor for urban red squirrel populations.
5. We conclude that urban areas can be suitable refugia for red squirrels, provided that high-quality greenspaces are maintained. Mitigation measures may also be necessary to reduce population mortality and to prevent disease outbreaks.

INTRODUCTION

Currently, 55% of the global human population inhabits urban areas; the percentage is projected to increase to 68% by 2050 (United Nations 2019). The resultant urban growth and intensification are dramatic forms of habitat alteration, which present substantial challenges to wildlife conservation (McCleery et al. 2014). For instance, urban areas can lack sufficiently large and connected greenspaces to provide foraging resources, nesting sites, and dispersal for wild animals (Marzluff & Ewing 2001). The presence of roads has been identified as a mortality risk and a potential barrier to movement (Rondinini & Doncaster 2002). The urban environment may also support an increased abundance of predators, particularly free-ranging companion animals such as cats *Felis catus* and dogs *Canis lupus familiaris*, associated with higher numbers of human inhabitants (Baker & Harris 2007).

Urban developments have historically been ignored as potential wildlife habitat (McCleery et al. 2014). However, it has been demonstrated that urban areas can be biodiverse and, in some cases, support populations of endangered species (Alvey 2006). Environmental action plans now include the development of urban areas, particularly identifying the importance of greenspaces (e.g. DEFRA 2018), which highlights the urgent need to advance our understanding of urban wildlife ecology to inform appropriate management. Resources can be plentiful in urban habitats, resulting in higher population densities of wild animals than in rural locations. For example, peregrine falcons *Falco peregrinus* have significantly higher clutch sizes, brood sizes, and fledging success in urban areas (Kettel et al. 2018). Some species have the behavioural flexibility to adapt to the urban environment, resulting in urban populations having adaptations that are not shared by their rural counterparts. For instance, some urban mammals have been shown to alter their foraging patterns temporally and spatially, to avoid periods of peak human activity (Lowry et al. 2013).

This study focusses on the Eurasian red squirrel *Sciurus vulgaris* (hereafter referred to as the red squirrel), which is a diurnal, arboreal rodent that currently remains widespread throughout most of Eurasia. In the UK, the population has declined following extensive habitat loss and the introduction of the Eastern grey squirrel *Sciurus carolinensis* (hereafter referred to as the grey squirrel) from North America in the late 19th century (Bosch & Lurz 2012). Grey squirrels out-compete the red squirrel for resources (Wauters et al. 2002) and spread the squirrelpox virus (SQPV), which they carry asymptomatically but is often fatal to red squirrels (Rushton et al. 2006). Following the more recent introduction and subsequent spread of grey squirrels in Italy, the continental population of red squirrels is now also threatened (Bertolino et al. 2008, 2014).

In the UK, red squirrels are part of the natural heritage and an iconic species, which tourists specifically travel to reserves to see (Shuttleworth 2001). Red squirrels are highly charismatic, and interactions with them can encourage people to connect with nature and develop a wider interest in wildlife. This is particularly important in urban areas, where access to greenspaces may be limited, as contact with local wildlife has been shown to provide environmental education and improve mental well-being (Dearborn & Kark 2009, Irvine et al. 2010). People who live alongside red squirrels tend to have positive feelings towards the species and are aware of the conservation issues affecting the squirrels (Rotherham & Boardman 2006). Therefore, red squirrels have a high cultural value (Gurnell & Pepper 1991), but need conservation management in the UK and in other countries where populations are declining (e.g. Turkia et al. 2018). Towns and cities could potentially act as refugia for red squirrels, so understanding the species' urban ecology would help to inform effective management.

Review objective

Systematic reviews using strict methodologies were pioneered in the field of medicine to overcome the selection and interpretation biases that can occur in traditional literature reviews (Haddaway et al. 2015). In recent years, systematic reviews have been promoted within conservation biology, due to the associated benefits of increased transparency and objectivity, in order to inform evidence-based management decisions (Cook et al. 2013).

This systematic review aimed to evaluate the current published literature regarding the urban ecology of red squirrels, in order to determine whether urban areas are suitable refugia for red squirrels. The initial broad literature search aimed to ensure an objective approach to the review and to overcome any potential selection bias. Following the screening process and based on the final dataset of articles, this review aimed to identify and synthesise key topics regarding the urban ecology of red squirrels.

METHODS

Definitions

Interpretation of the term 'urban' is complicated, with definitions based upon different factors (e.g. density of buildings or the human population) and varying between scientific disciplines (McIntyre et al. 2000). Therefore, for the purpose of this review, 'urban' is broadly classified as any area characterised by a collection of buildings, including houses and shops, and associated infrastructure, such as gardens, roads, and parkland (Baker & Harris 2007).

In the context of this study, we define anthropogenic food sources as food provided by humans for wild animals; this includes supplemental feeding, which is the deliberate provision of food (e.g. through bird feeders or squirrel boxes), as well as the accidental provision of food (e.g. through garden allotments or rubbish, which can be scavenged). In addition, we define natural food sources as food that would be available without human intervention, regardless of whether those items are available through artificial planting and management by humans. For example, in the context of squirrels, this would include a range of coniferous and broad-leaved tree species growing naturally in rural woodlands, as well as those being managed by humans in forestry plantations and urban areas.

Literature search

A systematic literature review was undertaken in December 2019 following the PRISMA protocols (Moher et al. 2009). The PRISMA protocols aim to improve reporting of systematic reviews by following a process of screening and assessing the identified literature using clearly defined inclusion and exclusion criteria.

A literature search was conducted on Scopus, Web of Science, and Google Scholar using the following search terms: (‘red squirrel*’ OR ‘Eurasian red squirrel*’ OR ‘European red squirrel*’ OR ‘Sciurus vulgaris’) AND (urban* OR town OR city). All the results listed on Scopus and Web of Science were collected. Only the first 200 articles of Google Scholar were collected, following the threshold used in other reviews (e.g. Lisón et al. 2020); after this point, the results become less relevant. There were no restrictions regarding the year of publication.

Inclusion criteria

Articles were excluded if they were not published in a peer-reviewed journal or not written in English. The articles were then screened for inclusion using the following criteria: 1) the title, abstract, or keywords specified ‘(Eurasian) red squirrel’ or ‘*Sciurus vulgaris*’, and 2) the keywords included, e.g. ‘urban ecology’ or ‘urbanisation/urbanization’, or 3) the abstract specified that the study was conducted in an urban environment, including comparisons with rural areas, or 4) the abstract specified that the study investigated the impact of an anthropogenic activity (e.g. road traffic mortality, supplemental feeding). Any articles that did not meet the screening criteria were excluded from the review.

For the articles that passed the initial screening process, the full text was then assessed for eligibility. The articles were required to meet all three of the following inclusion criteria; otherwise, they were excluded: 1) Eurasian red squirrels were the focal study species; 2) the research had been conducted on an urban population, including if compared with a rural population; and 3) the study investigated at least one aspect of red squirrel biology (e.g. behavioural ecology, genetics, population mortality) or conservation (e.g. reintroductions). Assessment of the scientific quality (e.g. identification of causal relationships, empirical evidence, replication, and wider application) was not used to exclude articles at this stage, but instead informed later evaluation in this systematic review. Only the key findings from the final dataset of articles were collated and reported.

RESULTS

The initial literature search returned 226 articles once duplicates were removed (Fig. 1). During the screening process and eligibility assessment, 201 articles were excluded in total, resulting in a final dataset of 25 articles

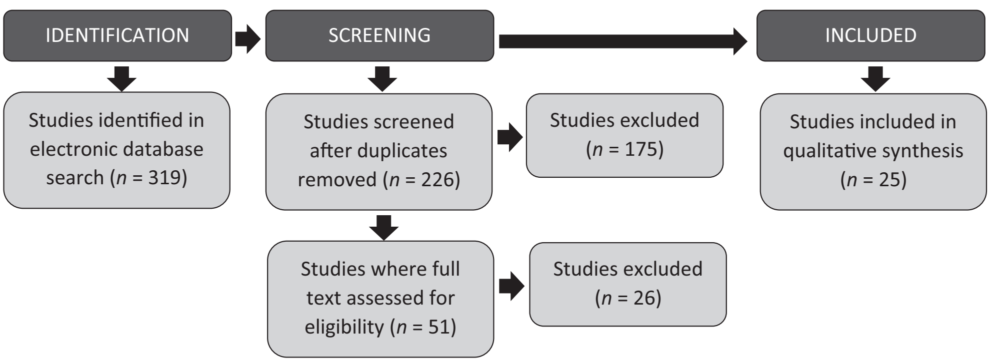

Fig. 1. PRISMA literature search and screening flow diagram of articles included and excluded from systematic analysis. Each article describes one study.

describing 25 studies (Appendix S1). Of the 25 articles, 76% were published since 2014, whilst the remaining articles were published between 1986 and 2009, often with large gaps between years (Fig. 2). The majority of the published research was conducted in mainland Europe (n = 16); five studies were conducted in the UK and Republic of Ireland, three studies were conducted in Japan, and one study was carried out in both Poland and the UK (Appendix S1).

Of the 25 articles identified for this review, 84% provided evidence that urban areas can be suitable habitat for red squirrels, whilst the remaining 16% highlighted the potential risks of urban environments, such as mortality threats (Appendix S1). Five broad topics regarding the urban ecology of red squirrels were categorised from the studies, with each article evaluating at least one of the identified topics (Fig. 3).

Supplemental feeding

Supplemental feeding appears to be widespread in urban areas throughout the red squirrel's geographic range (Appendix S1) and can help to increase the viability of small, isolated populations (Bertram & Moltu 1986, Rézouki et al. 2014, Vieira et al. 2015). Reher et al. (2016) found that red squirrels' home ranges in a cemetery in Hamburg,

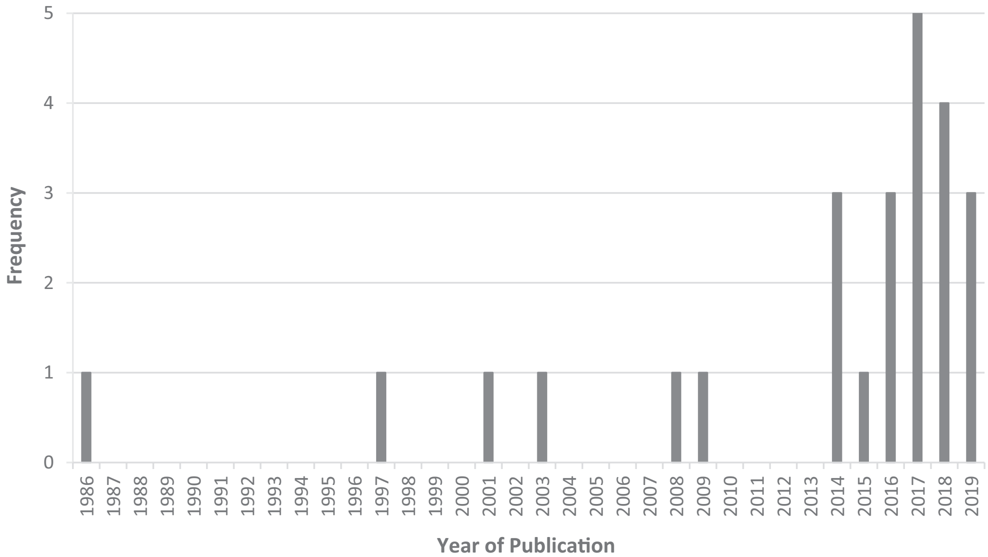

Fig. 2. The number of red squirrel urban ecology studies, based on the final dataset of articles (n = 25), published each year from 1986 to 2019.

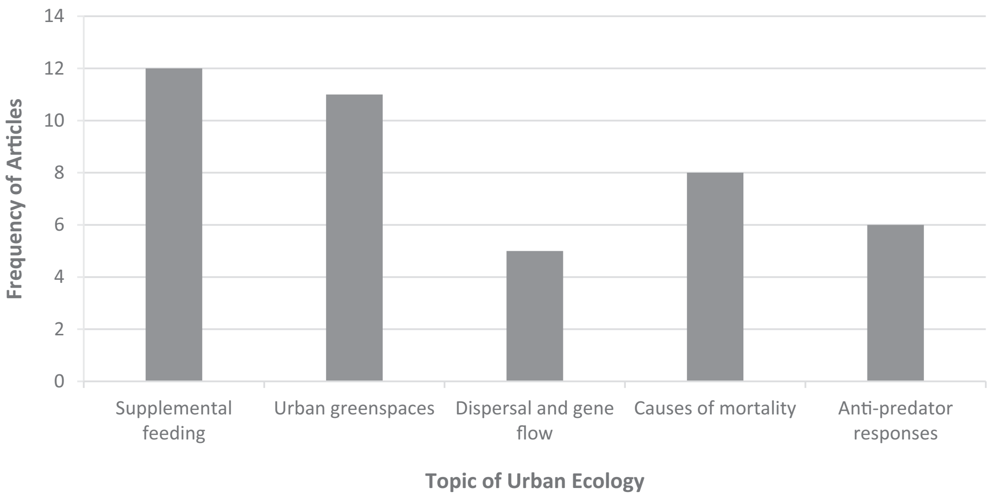

Fig. 3. The number of articles evaluating each topic regarding the urban ecology of red squirrels, as identified and categorised by this review. Each article can include information on more than one topic.

Germany, always incorporated stable natural food sources, but squirrels responded to seasonal changes in the provision of supplemental food by relocating their core areas. Core areas were shifted closer to reliable supplemental food sources in the autumn, when availability was highest, and moved to locations with natural food supplies in spring and summer when supplemental food became limited. Therefore, anthropogenic food sources had a measurable effect on patterns of space use, despite the abundance of natural food (Reher et al. 2016).

Supplemental feeding can support high red squirrel population densities in urban areas (Babińska-Werka & Żółw 2008, Kopij 2014, Jokimäki et al. 2017), as urban home ranges were found to be smaller, with a greater degree of overlap, than those in more rural populations (Reher et al. 2016, Thomas et al. 2018). Thomas et al. (2018) also reported that the urban squirrels in Hamburg city centre were less active throughout the day (mean activity rate of 25% per one-hour time slot) than the individuals inhabiting a nearby semi-natural site (mean activity rate of 58%). Furthermore, Turner et al. (2017) found that the red squirrels' body mass in the same cemetery site in Hamburg was relatively constant throughout the year, with only minimal physiological changes (e.g. metabolic rate) in response to seasonal fluctuations. These studies indicate that the widespread and abundant supplemental food sources available in urban environments allow red squirrels to satisfy their energy requirements whilst minimising energy expenditure, by reducing the need to travel as far or as often for foraging excursions (Reher et al. 2016, Turner et al. 2017, Thomas et al. 2018). Supplemental feeding may further increase population sizes, by allowing females to start breeding at the earliest opportunity and enhancing juvenile survival (Rézouki et al. 2014).

However, there are also risks associated with encouraging squirrels to travel between gardens whilst foraging and caching human-provided food items. Red squirrels have been shown to spend more time foraging on the ground when supplemental food is available, which may lead to more encounters with road traffic or predators; red squirrels usually spend 67–90% of their active time foraging for natural food in the canopy, but this is reduced to 50–53% when foraging for supplemental food (Shuttleworth 2001). Reproductive rates are density-dependent, so artificially high population densities can reduce fecundity in some females and therefore decrease breeding success (Kopij 2014, Stirkė 2019). Excessive consumption of supplemental food (e.g. peanuts) can also cause nutritional deficiencies, which may have health implications in highly urbanised environments where squirrels may not be able to compensate for such malnutrition if there is limited availability of natural food sources (Thomas et al. 2018). Finally, feeders may facilitate the spread of parasites and diseases, such as SQPV, by encouraging interactions both between red squirrels and with grey squirrels (Chantrey et al. 2014, Kopij 2014, Stirkė 2019).

Size, quality, and connectivity of urban greenspaces

Of the articles identified for this review, 44% highlighted the importance of size, quality, and/or connectivity of urban greenspaces for the persistence of red squirrel populations (Appendix S1). For example, Verbeylen et al. (2003) found that woodland patches within an urban landscape had a higher chance of red squirrel occupation if they were larger (>5 ha), higher quality, and well connected to nearby populations.

Using visual transects, Babińska-Werka and Żółw (2008) and Kopij (2014) recorded higher densities of red squirrels in city parks (1.8 and 0.26 individuals/ha, respectively) than in woodlands located on the outskirts of the cities (0.004–0.033 and 0.01 individuals/ha, respectively). Similarly, Jokimäki et al. (2017) found that relative squirrel abundance was higher in urban habitats (4.24 individuals/10 km transect) than in forests (1.43 individuals/10 km transect).

Babińska-Werka and Żółw (2008) and Kopij (2014) also found a significant positive correlation between the density of red squirrels and the size of the urban park, with higher densities in the larger parks, where diverse and mature trees provided ample natural food sources and which were connected to other nearby parks via habitat corridors. Conversely, smaller and more isolated urban parks with immature and few tree species had lower squirrel densities. For example, Kopij (2014) reported densities of 0.31–1.0 individuals/ha in the larger urban parks of 15 to 75 ha, compared with 0.0–0.4 individuals/ha in the parks less than 12 ha in size. Kopij (2014) also reported that parks that were close to allotment gardens, which provided anthropogenic food sources, supported higher densities of squirrels (0.55 individuals/ha) than similar-sized parks that were not bordered by allotments (0.1 individuals/ha).

The importance of high-quality habitat, specifically the availability and diversity of natural food sources, was further emphasised by Wauters et al. (1997), Vieira et al. (2015), and Jokimäki et al. (2017). Wauters et al. (1997) found that female reproductive rates and subsequent juvenile recruitment improved as the tree seed crop abundance increased. Jokimäki et al. (2017) also found that squirrel abundance increased as the spruce *Picea* cone crop increased. Vieira et al. (2015) reported that two red squirrel populations, which had been reintroduced into urban parks, were suffering from long-term declines due to the poor-quality habitat. Tree species composition in urban greenspaces is also important for providing suitable nesting sites (Kopij 2009, Stirkė 2019).

Although red squirrels seem to prefer areas with more trees available than in the surrounding urban landscape, they have been observed using very small groups or even lone trees, encircled by buildings and with no connectivity to other greenspaces, for dispersal and exploration (Hämäläinen et al. 2018). Urban red squirrels were found to travel in closer proximity to buildings than would be expected at random, with some instances of squirrels travelling along roofs and using buildings as nesting sites. This indicates that they are not confined to using only the available greenspaces (Hämäläinen et al. 2018, 2019).

Dispersal and gene flow

Fey et al. (2016) found that dispersing and non-dispersing red squirrels responded differently to the presence of roads. Non-dispersing individuals seemed to avoid roads during routine daily activities (e.g. foraging) within their home ranges, and perceived large roads (average daily traffic of 2000–7000 vehicles) as more dangerous than smaller roads (average daily traffic of 500–2000 vehicles). Conversely, roads did not act as barriers for dispersing individuals, who crossed them regardless of their size. Hämäläinen et al. (2019) also found that the landscape structure typically did not affect red squirrels' final straight-line dispersal distances, although it did alter their movement paths, with individuals favouring woodland patches whilst attempting to avoid more unsuitable habitats (e.g. open fields or buildings). In other words, individuals were likely to bypass barriers by travelling longer distances, but this did not impact how far they settled from their natal site. However, the overall dispersal distances of urban individuals were shorter than those of rural individuals (Fey et al. 2016, Selonen et al. 2018, Hämäläinen et al. 2019).

Despite shorter dispersal distances in urban populations, Fey et al. (2016) and Hämäläinen et al. (2019) suggest that the dispersal process still maintains the potential for gene flow at the population level. This is supported by Rézouki et al. (2014), who found that a red squirrel population in an urban park had relatively high levels of genetic diversity and minimal levels of inbreeding, despite being comparatively small, due to immigration from the surrounding woodlands. Similarly, Selonen et al. (2018) found no evidence to suggest that squirrels in their urban study site had been genetically isolated from the adjacent rural population.

Causes of mortality

Of the articles identified for this review, 24% discussed causes of recorded deaths. Instances of road traffic accidents were reported in 16% of the articles, ranging from 20% (n = 10; Bertram & Moltu 1986) and 33% (n = 12; Wauters et al. 1997) to 51% (n = 337; Blackett et al. 2018) and 65% (n = 188; Shuttleworth 2001) of recorded deaths. In some individual habitats, 88% of recorded deaths were attributed to road traffic accidents (Shuttleworth 2001). Further in-depth analysis of road traffic mortality by Shuttleworth (2001) determined that there was a distinct seasonal pattern, with a clear peak in the autumn months accounting for 54% of the total number of recorded deaths. Although there was no overall significant difference in the sex ratio of road traffic casualties, breeding adult males were more likely to be killed during the winter months.

Predation incidents were reported in 20% of the articles, ranging from 5.3% (n = 188; Shuttleworth 2001), 7.1% (n = 337; Blackett et al. 2018), and 10% (n = 10; Bertram & Moltu 1986) to 22% (n = 32; Fey et al. 2016) and 25% (n = 12; Wauters et al. 1997) of recorded deaths. Many of the mortality events were attributable to predation by free-ranging domestic or feral cat attacks (Bertram & Moltu 1986: 10%, Wauters et al. 1997: 8.3%, Blackett et al. 2018: 5.0%). Shuttleworth (2001) and Fey et al. (2016) did not specify the predator species, although the latter suggested they were most likely to be free-ranging cats and red foxes *Vulpes vulpes*.

Only two of the studies discussed the potential impact of accidental anthropogenic poisoning on red squirrel populations. Blackett et al. (2018) reported that 1.2% of red squirrels found dead displayed signs of poisoning, most likely by anticoagulant rodenticides. Lurz et al. (2017) conducted a pilot study investigating levels of industrially produced mercury in an urban red squirrel population in the city of Warsaw, Poland, and in two rural populations on the islands of Arran and Brownsea, UK. The results indicated that red squirrels have high levels of mercury, even individuals from rural UK islands where industrial activities are minimal, with currently unknown health implications. However, there is little evidence to suggest that accidental anthropogenic poisoning is a limiting factor for urban red squirrel populations.

Finally, Blackett et al. (2018) reported that 34% of recorded casualties on Jersey in the Channel Islands, UK, were attributed to diseases and that many individual red squirrels found dead were suffering concurrently with multiple conditions. The confirmed diseases included the following: amyloidosis (19%), where deposits of an abnormal protein can result in renal or hepatic failure; fatal exudative dermatitis (FED) associated with *Staphylococcus aureus* infection (15%); and parasitic infections of *Capillaria hepatica* (34%), *Hepatozoon* species (16%), and *Toxoplasma gondii* (2.1%). Amyloidosis and FED were determined to be major contributors to red squirrel mortality on the island. Amyloid deposits were often found alongside co-existing FED or *Capillaria hepatica* infections, suggesting there may be some association between the diseases. In squirrels on Jersey, there was no evidence of SQPV, which is visually similar to and often confused with FED (Blackett et al. 2018). SQPV can be a significant cause of red squirrel mortality, as occurred in Merseyside, UK, where the red squirrel population was reduced by over 80% (Chantrey et al. 2014). Despite this, Chantrey et al. (2014) found that 8.4% of red squirrels exposed during an SQPV outbreak survived the infection. Analyses supported the prediction that grey squirrels were responsible for initiating the outbreak, but once the disease had been introduced, the main driver of SQPV infections was red squirrels transmitting the disease to each other (Chantrey et al. 2014).

Anti-predator responses

Urban red squirrels had significantly shorter flight initiation distances and vertical escape distances than their rural conspecifics when approached by humans, which indicates strong habituation (Uchida et al. 2016, 2017). It is not clear whether urban squirrels are better at assessing risk (i.e. they tolerate human presence, until humans are in close proximity) or have reduced vigilance levels; if the latter, then they may not respond appropriately to predation threats (Uchida et al. 2016). As described by Uchida et al. (2017), alert distance (the distance at which an animal first detects a potential threat) represents vigilance, whilst flight initiation distance and vertical escape distance represent risk assessment. Uchida et al. (2019) found that both alert distance and flight initiation distance were significantly shorter in urban squirrels than in their rural conspecifics, which implies that, although urban individuals have reduced vigilance, they are also able to evaluate risk levels.

When reintroduced into an urban park, red squirrels that were used to human disturbance had a higher probability of survival and breeding than individuals initially taken from rural woodlands (Wauters et al. 1997). Wauters et al. (1997) suggested that squirrels that are familiar with receiving food from humans might adapt better to supplemental feeding, although red squirrels translocated from rural Fife in Scotland to Regent's Park in London still habituated to human disturbance and successfully adapted to using supplemental food hoppers (Bertram & Moltu 1986). However, these individuals had a period of captivity before release (Bertram & Moltu 1986), whereas the individuals described by Wauters et al. (1997) were released on the day of capture.

Another study monitored the impact of visitors to Fota Wildlife Park, Ireland, on the red squirrel population and found temporal avoidance of public areas (Haigh et al. 2017). The authors observed that, even though large numbers of squirrels continued to use the park, the squirrels only moved into the public areas when the park was closed, and instead were significantly more active in the non-public areas of the park when it was open. Despite this, there was no significant association between faecal cortisol metabolite levels (commonly used as a measure of stress) and visitor abundance.

DISCUSSION

The literature search highlighted the gradual increase in articles regarding urban ecology of red squirrels since 2014, which suggests that this is an area of growing research interest and most likely reflects the wider realisation of the need to understand the impact of increasing urbanisation on wildlife ecology (McCleery et al. 2014). Red squirrels have successfully adapted to urban environments, where their behavioural flexibility allows them to exploit the resources available whilst avoiding or adapting to the risks present.

Risks in the urban environment

Of the reviewed studies that reported instances of road traffic mortality, only Blackett et al. (2018) compared different causes of death. However, other comparative studies have also found that road traffic accidents accounted for 42% (n = 163; Simpson et al. 2013b), 43% (n = 245; LaRose et al. 2010), and 48% (n = 119; Shuttleworth et al. 2015) of recorded red squirrel deaths, comparable to the 51% reported by Blackett et al. (2018). This suggests that road traffic accidents are a significant cause of mortality in some urban red squirrel populations, although there are opposing arguments regarding whether records tend to be over- or underestimated (Shuttleworth 2001). Road kills tend to be more conspicuous, and may be more likely to be reported, than other causes of mortality (e.g. predation). On the other hand, cases could go unreported due to the carcasses being disposed of by roadkill removal services, eaten by scavengers, or degraded by road traffic and the weather. In some instances, squirrels injured by road traffic accidents shelter under nearby vegetation or in dreys before dying.

The seasonal pattern in road traffic mortality may be due to a combination of reasons. Red squirrels spend more of their active time engaging in foraging and scatter-hoarding behaviours on the ground, increasing from 32% in the summer months to 44% in the autumn due to the increased food availability, which could result in squirrels crossing roads more often as they travel to find and cache food items (Shuttleworth 2000, 2001). There are also typically lower red squirrel numbers in late spring and early summer, followed by a post-breeding increase in numbers in autumn and early winter, when the young are weaned (Bosch & Lurz 2012). As the juveniles then disperse, they are potentially more likely to encounter road traffic, although Shuttleworth (2001) found that the majority of autumnal road traffic casualties were adults. Similarly, Blackett et al. (2018) reported that only 2.9% of the 171 identified road traffic casualties were juveniles and 8.2% were subadults, although there was no further investigation into seasonal patterns of mortality. The male-biased winter mortality peak may be due to the breeding males searching for sexually active females (Shuttleworth 2001), as the start of the reproductive period tends to fall in December or early January (Bosch & Lurz 2012).

The presence of predators in urban environments appears to vary depending on the species and potentially the extent of urbanisation. Some studies suggest that predator abundance is decreased compared with rural areas, whereas others have suggested higher densities of predators in urban areas (e.g. Shochat et al. 2006, Bateman & Fleming 2012, Jokimäki et al. 2017). Similarly, predation risk varies between studies, ranging from less than 10% (Shuttleworth 2001, Blackett et al. 2018) to over 20% of recorded deaths (Wauters et al. 1997, Fey et al. 2016). When predation of red squirrels in urban environments does occur, it appears that free-ranging domestic and feral cats are generally responsible (Fey et al. 2016, Jokimäki et al. 2017, Blackett et al. 2018).

From the reviewed articles, there is currently little evidence to suggest that predation has significantly contributed to the decline of the red squirrel; this is consistent with other published studies (e.g. Petty et al. 2003, Turkia et al. 2018). However, the additional mortality pressure could have localised impacts in areas where predator densities are particularly high, as is the case with cats in urban environments, especially where red squirrel populations are already vulnerable. In addition, predation events may be underestimated as they can be difficult to identify, for instance if the squirrel carcass is mostly consumed or carried away by the predator. This implies that the impact of predation, particularly by free-ranging domestic and feral cats, on urban red squirrel populations may be greater than previously estimated and so may benefit from further investigation.

Red squirrels are susceptible to a range of diseases, some of which could potentially limit populations, such as SQPV (Chantrey et al. 2014). High concentrations of viral DNA have been found in the oral mucosa and exudative skin lesions of SQPV-infected individuals, which suggests that red squirrels may transmit the disease amongst themselves via social interactions (e.g. fighting, grooming, drey sharing) and scent marking (Fiegna et al. 2016). Local disease outbreaks may be exacerbated in urban environments, where red squirrel populations can often reach higher densities and the presence of supplemental feeders may act as sources for the spread of infection. Therefore, there is a need to identify any infectious individuals rapidly (Fiegna et al. 2016), ideally using non-invasive surveillance strategies such as those developed by Everest et al. (2019), to remove those individuals and reduce transmission of the disease.

There has been growing evidence that adenovirus may present a significant threat to red squirrel populations (e.g. Everest et al. 2014, 2018). Blackett et al. (2018) did not fully explore the potential for adenovirus infections within the Jersey population, having only tested 12 out of 337 individuals; however, 42% of those 12 tested positive for adenovirus. Another emerging disease is squirrel leprosy *Mycobacterium lepromatosis*, for which clinical cases have been diagnosed across the UK (e.g. Simpson et al. 2015, Avanzi et al. 2016), but which was not identified on Jersey (Blackett et al. 2018). In addition, there was no evidence of SQPV on Jersey (Blackett et al. 2018), which is likely due to the absence of grey squirrels on the island (McInnes et al. 2009), but the disease is likely to be a significant cause of red squirrel mortality where grey squirrels are present (Chantrey et al. 2014).

Blackett et al. (2018) highlighted FED and amyloidosis as causes of concern on Jersey. FED has also been identified as a potential cause of concern on the Isle of Wight (Simpson et al. 2010), although to a lesser extent than on Jersey, and there has been at least one possible case on Anglesey in North Wales (Shuttleworth et al. 2015). There have been no other published reports of amyloidosis, apart from one potential case on the Isle of Wight (V Simpson, unpublished observations, as cited in Blackett et al. 2018) and occasional cases in Lancashire, UK (J Chantrey, personal communication, as cited in Blackett et al. 2018). The origins and development of both FED and amyloidosis are currently unclear, although some evidence suggests that genetic predisposition (i.e. a heritable allele that increases an individual's susceptibility to a disease) and stress may be factors for amyloidosis (Caughey & Baron 2008, Simpson et al. 2013a). This may explain why the disease is so prevalent on Jersey, where the red squirrel population is small and isolated, and stresses associated with traffic, pets, and high local densities of squirrels lead to agonistic interactions at food sources (Blackett et al. 2018). As urban populations of red squirrels are often isolated and exposed to similar stressors, the impact of FED and amyloidosis requires further investigation in other locations.

Resources in the urban environment

Urban wildlife populations are reported to have higher numbers of bold individuals than rural populations (e.g.

Møller 2012, Díaz et al. 2013, Lowry et al. 2013), as demonstrated in urban red squirrel populations (Uchida et al. 2016, 2017, 2019), allowing them to exploit the available resources. Boldness is thought to result from repeated exposure to non-lethal stimuli from frequent human disturbance, resulting in a 'transfer of habituation' to other predator stimuli and an overall reduction in anti-predator response (McCleery 2009). This adaptive response helps to prevent urban animals repeatedly fleeing and expending energy unnecessarily, instead allowing them to spend more time foraging (Sol et al. 2013). Furthermore, Uchida et al. (2019) suggested that the capacity to assess varying risk levels effectively and respond accordingly may reflect higher cognitive abilities, which supports the proposition that learning in urban animals may be improved by the environmental complexity and unpredictability associated with urban areas (Griffin et al. 2017).

Urban environments appear to support higher population densities of red squirrels than rural areas (e.g. Babińska-Werka & Żółw 2008, Kopij 2014, Jokimäki et al. 2017). However, as highlighted by Jokimäki et al. (2017), the use of visual transects to count red squirrels in urban environments and woodlands may be affected by differences in habitat and habituation to people. For example, detectability may be higher in urban areas due to the increased visibility in more open greenspaces (e.g. parks) and more bold individuals (e.g. Uchida et al. 2016). On the other hand, detectability may be reduced due to obstructions by buildings (Jokimäki et al. 2017). The use of capture–mark–recapture can provide more accurate and reliable estimates of abundance (e.g. Turlure et al. 2018), but this invasive method requires time, resources, and experience. Alternatively, the use of baited visual transects may be a more effective method in future studies to improve detectability whilst maintaining the benefits of this non-invasive technique (Gurnell et al. 2011).

Many of the studies in this review have emphasised the importance of the availability and quality of urban greenspaces for red squirrel populations. For example, it is crucial to manage the tree species composition in urban greenspaces to ensure the availability of natural food sources (Vieira et al. 2015, Reher et al. 2016, Jokimäki et al. 2017) and the provision of suitable nesting sites (Kopij 2009, Stirkė 2019). However, it is difficult to unpick the relative importance of natural and supplemental food sources and habitat quality, as there often tends to be supplemental feeding wherever red squirrels are present in urban areas, as well as the availability of other anthropogenic food sources. For example, city parks with diverse and mature tree species had high densities of red squirrels, but of those parks, those that bordered allotments with anthropogenic food sources had the highest population densities (Kopij 2014). Clearly, high-quality natural food sources can support higher population densities, but it appears that the availability of supplemental food further increases the habitat quality. This is supported by the fact that supplemental feeding directly impacts patterns of space use, even when natural food sources are abundant (Reher et al. 2016).

Supplemental food is also typically available throughout the year and so can be relied upon when natural food is seasonally scarce, although supplemental food may not be nutritionally ideal: many people provide peanuts, which are high in fat and desirable to the squirrels, but can result in calcium deficiencies (Bosch & Lurz 2012). Natural food sources can help to provide a more nutritionally balanced diet and compensate for any malnutrition caused by eating supplemental food (Thomas et al. 2018).

Thomas et al. (2018) suggested that the smaller and overlapping home ranges observed in urban individuals may be because suitable habitat is sparse and movement between fragments is energetically costly, so red squirrels may simply occupy the remaining habitat fragments with available food sources. This is supported by Wauters et al. (1994), who found that the core areas of red squirrel home ranges in fragmented woodlands were smaller than those in larger, continuous woodlands, which suggests that home range size can be limited by the size of the woodland fragment.

The higher population densities in urban areas are likely to be due to the distribution and abundance of supplemental food, combined with the availability of natural food sources in the remaining greenspaces throughout the urban landscape, resulting in smaller home ranges with a greater extent of overlap between individuals (Reher et al. 2016, Thomas et al. 2018). This is supported by other studies that suggest that food availability is the main factor limiting abundance (Petty et al. 2003) and that squirrels alter their patterns of space use in response to changes in the distribution and abundance of food in rural woodlands (Wauters et al. 2005). The increased food availability also means that urban individuals can quickly attain the minimum body weight required to come into oestrus (Wauters & Dhondt 1989a), further increasing population sizes by allowing females to start breeding at the earliest opportunity (Rézouki et al. 2014), and can maintain stable body masses throughout the year (Turner et al. 2017). This differs in comparison with rural populations, where body weight is at a minimum in late summer and reaches a maximum in late winter, due to the limited provision or absence of supplemental food and the large seasonal changes in ambient temperature that affect natural food availability (Wauters & Dhondt 1989b).

Wauters et al. (2010) suggested that increasing habitat fragmentation when fragments are surrounded by an unsuitable or hostile matrix (e.g. barriers or urbanised areas) may inhibit dispersal, whereas when the matrix is not hostile (e.g. farmland or rural villages that are unsuitable for settling but not for movement), different degrees of habitat fragmentation appear not to affect dispersal behaviour. Contrary to the suggestion that urban areas could be considered a hostile matrix, the findings from this review indicate that movement ability does not appear to be restricted by built structures within the urban landscape. Instead, the shorter dispersal distances of urban individuals appear to be due to the stable resource availability reducing the need to disperse further (Fey et al. 2016, Selonen et al. 2018, Hämäläinen et al. 2019). This is supported by the fact that urban red squirrels travel in closer proximity to buildings than would be expected at random, as they move through the urban landscape to exploit supplemental food (Jokimäki et al. 2017, Hämäläinen et al. 2019).

Habitat loss and fragmentation are closely correlated with urbanisation (Liu et al. 2016) so it can be difficult to distinguish between the impacts of urbanisation and habitat fragmentation on red squirrel populations, as both can result in similar behavioural patterns. For example, similar effects of habitat fragmentation on spatial organisation and dispersal have been identified in both urban and rural woodland squirrel populations (Wauters et al. 1994, 2010, Thomas et al. 2018, Hämäläinen et al. 2019). However, the findings from this review suggest that habitat loss due to urbanisation has a greater impact on red squirrel populations than fragmentation, which is supported by Fahrig (1997). Therefore, increasing the availability and quality of greenspaces would be of most benefit to red squirrel conservation in urban environments, rather than improving connectivity between greenspaces.

CONCLUSION

The findings from this systematic literature review indicate that urban habitats can be suitable refugia for red squirrels, as their behavioural flexibility has allowed them to adapt successfully to the urban environment. However, it is desirable to manage urban habitats more effectively for both wildlife and people. For instance, the management of sufficiently large greenspaces and their tree species composition would ensure the availability of high-quality, reliable natural food sources and appropriate nesting sites for red squirrels, as well as benefitting the mental and physical well-being of the human residents. Furthermore, the provision of supplemental food can have substantial benefits, although mitigation measures may be required to minimise any negative impacts. For example, public engagement regarding suitable food items and appropriate hygiene practices may help to reduce nutritional deficiencies in the squirrels' diets and prevent disease outbreaks from sharing feeders. As is the case with existing red squirrel reserves, grey squirrel control within and around urban refugia would help to reduce SQPV outbreaks.

Mitigation measures may also help to reduce mortality; for instance, the use of non-invasive surveillance strategies could help to identify potential disease outbreaks, or rope bridges could be constructed to provide crossing points over busy roads to reduce road traffic casualties. In addition, the current evidence regarding the impact of predation by free-ranging domestic and feral cats is limited, but would benefit from further research to evaluate whether it has been previously underestimated. Mitigation measures may help to reduce instances of predation by pets; for example, owners could keep their cats inside during early morning when squirrels are most active and likely to be predated, but this would not address any potential impact of feral cats.

Red squirrels are well adapted to inhabiting urban areas, becoming strongly habituated to human presence, and being able to move through the built landscape to exploit the available resources. Therefore, urban refugia, if appropriately managed, may aid conservation efforts for this declining, native species whilst simultaneously benefitting the human inhabitants.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Key findings from the final dataset of published articles (n = 25), determined from the Abstracts and Discussions, and conclusions drawn regarding whether or not urban habitats are feasible refugia for red squirrels.