University of Reading

Supporting evidence-based conservation for hedgehogs in urban areas: the importance of residential gardens and householder actions

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Abstract

Urban-dwelling wildlife face a wide range of challenges including, but not limited to, habitat loss, habitat fragmentation and the mortality risks associated with roads, domestic animals and human activities. Nonetheless, urban areas can provide critical refuge for a range of species, including some of conservation concern; detailed knowledge of how these species persist in human-modified landscapes is necessary for the development of sound conservation strategies.

The West European hedgehog (*Erinaceus europaeus*) is a small (<1.5kg), nocturnal, hibernating mammal that has declined markedly in Britain over recent decades most prominently within rural landscapes, and is nowadays more commonly found within urban habitats, including in residential gardens. Consequently, householders are urged by conservation groups to make their gardens more 'hedgehog friendly' by, for example, increasing accessibility through garden boundaries, providing artificial refugia and/or giving supplemental food. Current understanding of garden use by hedgehogs, the extent to which such 'hedgehog-friendly' initiatives have been adopted by householders and their subsequent impacts is, however, limited. Therefore, the current study aimed to quantify key factors relating to habitat use by urban hedgehogs and conservation actions within gardens.

First, 28 hedgehogs were radio/GPS tracked in a residential area in Reading, UK, and the data were used in combination with GIS and householder-supplied information to quantify habitat selection, the number of gardens visited and factors affecting the extent of individual garden use. Second, hedgehog occupancy in gardens during a hibernation period was monitored using footprint tunnels and assessed against within- and outside-garden variables. Finally, two online questionnaire surveys were undertaken to explore (i) factors affecting the use of artificial refuges (nest boxes) in gardens, and (ii) householder engagement with the 'hedgehog highways' campaign which aims to increase connectivity between gardens; collectively, >10,000 responses were received from householders in the UK.

Overall, it is evident that householders have the capacity to positively influence hedgehog activity patterns in gardens via the provision of key resources such as food and nesting opportunities, but that other biotic and abiotic factors also play a role. However, householder engagement with some conservation activities can be strongly impacted by, e.g., the need to coordinate with neighbours. Future studies are therefore needed to identify mechanisms to overcome such impediments to maximise the number of participating households. Fundamentally, future research needs to focus on quantifying the impacts, potentially both positive and negative, of conservation activities on hedgehog populations.

Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Abigail Gazzard

Papers

This thesis is formed by an introductory chapter, four manuscripts and a general discussion. Contributions to each of the four studies are outlined below, including the estimated percentage contribution made by the candidate.

1. **Gazzard, A.**, Yarnell, R.W. & Baker, P.J. (2022) Fine-scale habitat selection of a small mammalian urban adapter; the West European hedgehog (*Erinaceus europaeus*). *Mammalian Biology* 102, 87-403.

A.G. 70%: Conceptualisation, fieldwork and other data collection, data analysis, original draft, review, editing

R.W.Y.: Review, editing

P.J.B.: Conceptualisation, analysis of missing GPS fixes, writing, review, editing

2. **Gazzard, A.** & Baker, P.J. (2020) Patterns of feeding by householders affect activity of hedgehogs (*Erinaceus europaeus*) during the hibernation period. *Animals* 10, 1344.

A.G. 80%: Conceptualisation, fieldwork and other data collection, volunteer management, data analysis, original draft, review, editing

P.J.B.: Conceptualisation, review, editing

3. **Gazzard, A.** & Baker, P.J. (2022) What makes a house a home? Nest box use by West European hedgehogs (*Erinaceus europaeus*) is influenced by nest box placement, resource provisioning and site-based factors. *PeerJ* 10, e13662.

A.G. 80%: Conceptualisation, questionnaire design, data collection, data analysis, original draft, review, editing

P.J.B.: Conceptualisation, comments on questionnaire content , writing, review, editing

4. **Gazzard, A.**, Boushall, A., Brand, E. & Baker, P.J. (2021) An assessment of a conservation strategy to increase garden connectivity for hedgehogs that requires cooperation between immediate neighbours: a barrier too far? *PLoS ONE* 16, e0259537.

A.G. 70%: Conceptualisation, questionnaire design, data collection, data analysis, original draft, review, editing

A.B.: Initial questionnaire design, review

E.B.: Initial questionnaire design, review

P.J.B.: Conceptualisation, comments on questionnaire content, writing, review, editing

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Chapter 1

Introduction

Despite the small physical footprint of towns and cities totalling just 3% of all land globally (Liu *et al.*, 2014), over half of the world's human population currently live within urban settlements (Ritchie, 2018). This is projected to exceed more than two-thirds of the population by 2050 (Ritchie, 2018) and urban areas will expand three-fold within the same period (Angel *et al*., 2011). The transition from a predominantly rural global population to an urban one occurred as recently as 2007 (Ritchie, 2018) yet has already had a profound effect on the environment: approximately 75% of total global resource consumption, 70% of CO_2 emissions (Madlener and Sunak, 2011) and the generation of 3 million tonnes of waste per day (Hoornweg *et al*., 2013) can be attributed to cities alone. On an ecological level, urbanisation has caused declines in ecosystem services (Radford and James, 2013; Wang *et al*., 2020) and species richness (Reynaud and Thioulouse, 2000; Burton *et al*., 2005; Mangialajo *et al.*, 2008; Saito and Koike, 2013) and has had a homogenising effect on species assemblages (McKinney, 2006; Concepción *et al*., 2015). Consequently, urbanisation has been implicated as a threat to biodiversity worldwide (Seto *et al.,* 2012; Concepción *et al*., 2015).

Urban landscapes can, however, provide critical habitats for some species (Eyre *et al*., 2003; Goddard *et al*, 2013; Löki *et al*., 2019) and support populations that are otherwise becoming uncommon in rural areas (Carrier and Beebee, 2003; Goddard *et al*., 2010; Mayer and Sunde, 2020). Scientific interest in the importance of urban green spaces for native and endangered wildlife is, therefore, growing (Collins *et al*., 2021), with many conservation organisations and local authorities recognising this in their initiatives (Goddard *et al*., 2010; Kabisch *et al*., 2016; Aronson *et al*., 2017; Davies and Lafortezza, 2017). Towns and cities are also the settings in which many people experience much of their everyday contact with nature (Dunn *et al*., 2006; Richardson *et al.*, 2020), thereby creating opportunities for public engagement in urban conservation. Despite this, wildlife living within urban landscapes face significant, and often novel, challenges.

Risks associated with urban areas

Urbanisation – which, in the broadest sense, refers to both land-cover change and growth in urban populations (McGranahan and Satterthwaite, 2014) – results in physical, chemical and biological changes that can create a range of unfavourable conditions for wildlife. Changes in environmental parameters such as the volume and flow of runoff (Berry *et al*., 2008), surface temperatures (Arnfield, 2003; Yuan and Bauer, 2007) and rates of soil compaction (Wei *et al*., 2013) resulting from urban development have been linked to poor body condition of wild animals and reduced survival rates (Campbell, 1994; Gillis, 2012; Wei *et al*., 2013; Dale and Frank, 2014; Hall and Warner, 2018; Johnson *et al*., 2019). Crucially, urbanisation causes a direct loss, degradation and/or fragmentation of natural or semi-natural habitats which leads to a range of ecological consequences, including local species extinctions (McKinney, 2002; Preston *et al*., 2003; Hahs *et al*., 2009; Hamer and McDonnell, 2010; Fattorini, 2011).

Habitat fragmentation creates small, isolated patches. The size of fragmented habitat patches and patterns of inter-connectivity between them have been found to decline as cities expand (Liu *et al*., 2016), and as housing density and areas of hardstanding increase (Germaine and Wakeling, 2001). This limits dispersal opportunities and/or decreases access to sites that may be critical for survival through means of nesting, breeding or foraging (Hamer and McDonnell, 2010). The subsequently divided and isolated sub-populations are potentially susceptible to genetic isolation and at increased risk from stochastic events which may, ultimately, lead to local extinctions (Lande, 1993; Noël *et al*., 2007; Reed *et al*., 2007).

One major driver of urban habitat fragmentation is the development of urban road networks (Moore *et al*., 2020) which often exist in higher densities than those in rural areas and experience markedly greater daily traffic flow (Department for Transport, 2020). Subsequently, urban habitat is a strong predictor of road mortality for some species (Glista *et al*., 2007; Wright *et al*., 2020); vehicle-animal collisions are a major source of wildlife mortality worldwide (Tigas *et al*., 2002; Coffin, 2007) and have driven declines in the abundance and richness of a range of taxa (Huijser and Bergers, 2000; Fahrig and Rytwinski, 2009; Summers *et al*., 2011). In addition to direct mortality, roads can also trigger behavioural aversions to e.g., traffic volume, road type or road width (Jaeger *et al*., 2005) thereby enhancing their 'barrier effect' and further impeding dispersal. This barrier effect has been linked to increased genetic differentiation within populations of both vertebrate and invertebrate species (Bhattacharya *et al*., 2003; Jaeger *et al*., 2005; Coffin, 2007; Noël *et al*., 2007; Delaney *et al*., 2010; Holderegger and Di Giulio, 2010). One possible solution to road-related genetic fragmentation is to install underpasses, culverts or wildlife bridges at strategic locations along road networks to facilitate road crossings (Moore *et al*., 2020) but, for many species, it is not known to what extent road-crossing structures may facilitate dispersal or gene flow (Soanes *et al*., 2017).

Roads are not the only barriers to movement within urban areas. Other problematic barriers include buildings, footpaths, kerbs, drains, property boundaries and artificial lighting (Cooke, 2000; Amphibian and Reptile Conservation, 2009; Stone *et al*., 2009; Riley *et al*., 2013; Froglife, 2020; Hedgehog Street, 2020a). These barriers can limit connectivity pathways or create 'pinch points' within urban landscapes (Braaker *et al*., 2014) yet, compared to roads, are generally unmapped or undocumented (Jakes *et al*., 2018). For example, fences – whether they are installed to e.g., protect the public or delineate property boundaries – are often impenetrable to wildlife and limit access to valuable resources (Abu Baker *et al*., 2015). In some locations, fences can be more prevalent than roads, yet research into their impact upon animal movements and populations is significantly lacking (Jakes *et al*., 2018).

Artificial lighting is another prominent feature of urban landscapes that can disrupt habitat connectivity. Some mammal species, for instance, will avoid using commuting routes when they are illuminated (Bliss-Ketchum *et al*., 2016) and may reduce their activities in lit-up areas all together (Stone *et al*., 2009; Hoffmann *et al*., 2019; Voigt *et al*., 2020; Barré *et al*., 2021). The presence of artificial light can also trigger behaviour modifications that may in turn drive higher energy demands: for example, American robins (*Turdus migratorius*) initiate their morning chorus and sing for longer in areas that are artificially illuminated (Miller, 2006). Furthermore, artificial light alters foraging patterns (Hoffmann *et al*., 2019), reproduction (Kempenaers *et al*., 2010) and migratory behaviour (La Sorte and Horton, 2021). The ways in which species respond to artificial light are variable (Bliss-Ketchum *et al*., 2016), and relatively little is known about the local- or population-level effects of these impacts (Sanders and Gaston, 2018). Nevertheless, as a ubiquitous feature of urban landscapes, artificial lighting should be considered carefully within urban planning (Schroer *et al*., 2020).

Government strategies commonly urge regional or local planning authorities to enhance habitat connectivity and introduce additional habitat patches as part of urban development (Kabisch *et al*., 2016; Aronson *et al*., 2017; Davies and Lafortezza, 2017) but, in many countries, implementation rates of these strategies are low (Boulton *et al.*, 2018; Wang *et al.*, 2020). Of the public green spaces that are created, many are designed to prioritise human recreational use rather than provide opportunities for wildlife (Boulton *et al.*, 2018), and management of these patches often involves practices that homogenise habitats, e.g., intense mowing or pruning regimes (Aronson *et al*., 2017). Government authorities are, of course, further restricted in their ability to implement or regulate management schemes on privately-owned land. Private land constitutes a major proportion of urban green space (Loram *et al*., 2007; Davies *et al*., 2009) but, given that landowners' management preferences do not always align with nature-friendly practices (Clayton, 2007; Kendal *et al*., 2012), can be subject to similarly intensive management regimes resulting in, for example, significant losses of trees (Croeser *et al*., 2020) and native grasslands (Williams *et al*., 2005).

Despite the loss of biodiversity opportunities observed in urban green spaces (Williams *et al*., 2005; Perry and Nawaz, 2008; Aronson *et al*., 2017; Croeser *et al*., 2020), it is within these areas where many people experience their everyday interactions with nature (Dunn *et al*., 2006; Richardson *et al.*, 2020). Encounters with urban wildlife are often positive and enjoyable for people (Soulsbury and White, 2015), yet human presence can create a landscape of fear for wild animals, driving declines in foraging efficiency and general activity (Suraci *et al*., 2019), even when animals exhibit a preference for urban habitat (Nickel *et al*., 2020). General human disturbance (e.g., pedestrian traffic or gardening activities) sometimes has acute consequences including the abandonment of young or diminished nutritional intake (Fernández-Juricic and Tellería, 2000; Ditchkoff *et al*., 2006).

Interactions with wildlife can also involve the provision of artificial food, albeit sometimes non-intentionally; it has been estimated that approximately 51% of UK households supply food for garden birds (Davies *et al.*, 2009) and, in one study of Swiss urban residents, 85% of residents were found to provide food for wildlife, primarily via refuse (Contesse *et al*., 2004). Anthropogenic food sources can form a major component of animal diets (Ditchkoff *et al*., 2006) but sometimes lead to malnutrition and pathogen transmission (Bradley and Altizer, 2007; Becker *et al.*, 2015; Murray *et al.*, 2016; Moyers *et al*., 2018), or even contain dangerous chemicals (Murray *et al*., 2016). Furthermore, they may stimulate changes in animal behaviours (Krofel *et al*., 2017). For example, in built-up areas in the US, black bears (*Ursus americanus*) consuming large amounts of artificial food subsidies have been found to undergo shorter hibernation periods, which in turn has implications for rates of cellular aging (Kirby *et al*., 2019).

An abundance of food resources has also been linked to the presence of vertebrate pest species such as the brown rat (*Rattus norvegicus*) (Shetlar, 2002; Traweger *et al*., 2006). Management actions against vertebrate pests could have extensive ramifications for urban wildlife. Despite attempts to exclude them with e.g., bait boxes, it is not uncommon for non-target species to directly access these boxes if they are small enough, or for predators to catch and kill moribund individuals that have consumed poisoned baits, or consume their carcasses once they have died (López-Perea *et al*., 2019; Lettoof *et al*., 2020). High levels of exposure to anticoagulant rodenticides can have lethal consequences for non-target species, but the effects of low-level exposure are difficult to determine (Sánchez-Barbudo *et al*., 2012). Anticoagulant rodenticides are used widely in towns and cities, and urban land cover and human population density are significant predictors of their presence in tissues of non-target wildlife (López-Perea *et al*., 2015; López-Perea *et al*., 2019). Other chemicals such as insecticides and herbicides are also commonly applied around residential areas (Md Meftaul *et al.*, 2020) to the point that, historically, homeowners may have used 10 times more pesticides per acre on garden lawns than that used on agricultural crops (US Fish & Wildlife Service, 2000). Household pesticides are likely to be dangerous to human health, non-target fauna and the wider environment, yet studies of their impact in urban settings are limited (Md Meftaul *et al*., 2020).

Urban wildlife may also commonly encounter companion animals. Domestic cats (*Felis catus*) and dogs (*Canis familiaris*) can be more abundant in urban settings than rural (Campos *et al*., 2007; Ortega-Pacheco *et al*., 2007; Flockhart *et al*., 2016) and negatively impact wildlife through mechanisms such as predation, behavioural changes, pathogen transmission and hybridisation (Twardek *et al*., 2017). Additionally, the release or escape of domestic pets can lead to the establishment of populations of non-native invasive species in urban habitats which, in some cases, contributes to habitat degradation or a loss of native wildlife (Manchester and Bullock, 2000; Cadi and Joly, 2004; Teillac-Deschamps *et al*., 2009).

Undoubtedly, urbanisation creates a wide range of direct and indirect challenges for wildlife, resulting from significant threats that include habitat loss, degradation and fragmentation, as well as the mortality risks related to roads, humans and their pets. Despite such risks, however, some wildlife species persist, and even thrive, in towns and cities (Ditchkoff *et al*., 2006).

Surviving and thriving in towns and cities

Species that are able to acclimatise to urban environments are commonly referred to as urban adapters (i.e., those that are able to utilise both anthropogenic and natural resources) or exploiters (i.e., those that typically solely depend on anthropogenic resources: Blair, 1996; McKinney, 2002). Adapters and exploiters tend to be generalist species (Concepción *et al.*, 2015; Ducatez *et al*., 2018; Callaghan *et al*., 2019) exhibiting behavioural traits such as boldness, heightened tolerance or general behavioural flexibility (e.g., diet diversity or problem-solving skills), along with high reproductive outputs (Ditchkoff *et al*., 2006; Møller, 2009; Atwell *et al*., 2012; Lowry *et al*., 2013; Santini *et al*., 2019). Urban species can include common pests (Traweger *et al*., 2006) but also rarer species of conservation concern (Coleman and Barclay, 2012; Orros and Fellowes, 2015); almost one third of Australia's endangered plant species, for example, are found in cities (Ives *et al*., 2016). Additionally, declining species such as the song thrush (*Turdus philomeos*) in the UK and the European hare (*Lepus europaeus*) in Denmark can occur in higher densities in urban locations than rural sites (Mason, 2000; Mayer and Sunde, 2020), with urban areas also associated with improved body condition, recruitment and survival rates (Harveson *et al*., 2007; Maclagan *et al*., 2018). Subsequently, towns and cities have become important locations in which to focus conservation efforts.

Urban landscapes contain a variety of habitats including woodland, scrub, amenity grassland, parks, cemeteries, gardens, allotment plots, roadside verges, brownfield sites, wetlands and waterways (Angold *et al*., 2006; Li *et al*., 2019). The structure and diversity of these habitats typically varies with the level of urbanisation (Li *et al*., 2019), with moderately developed areas (e.g., residential areas) thought to support comparatively species-rich or abundant communities (McKinney, 2008; Parsons *et al*., 2018) due to greater habitat diversity and land-use practices, combined with lower levels of disturbance, relative to highly urbanised centres (see McKinney, 2008). For example, bird abundance appears to increase with housing density, but then declines at the highest levels (Tratalos *et al*., 2007). The value of different habitat types is likely to vary between species, management regimes and other site-based factors (Aronson *et al*., 2017). For example, some urban bat species appear to favour waterbodies over other habitat types (Gilioli *et al.*, 2020), but their presence around waterways can be influenced by artificial light levels (Barré *et al*., 2021), bankside vegetation and water smoothness (Warren *et al*., 2000). Within a conservation context, it is therefore important to consider habitat use across multiple species and at multiple spatial scales, including at local- and site-based levels (Garden *et al*., 2010).

A primary factor believed to influence space use in urban areas, and which contributes to the growth and size of some populations (Orros and Fellowes, 2015), is food sourced from humans as well as urban plantings (Lowry *et al*., 2013). For example, artificial food is a strong predictor of the occurrence of urban mammal species (Prange *et al*., 2004; Hubert *et al*., 2011; Bonnington *et al*., 2014) and, relative to their rural counterparts, the home ranges of mammalian carnivores tend to be smaller (Prange *et al*., 2004; Šálek *et al*., 2015). Consuming anthropogenic food has been linked to improved survival and growth rates of young and can provide critical sustenance during vulnerable periods, such as over winter (Robb *et al*., 2008). It is also possible that during winter, foraging opportunities may be greater than expected where the higher temperatures experienced in built-up areas (Yuan and Bauer, 2007) lead to thinner snow cover (Møller, 1983) or prolonged invertebrate prey availability (see Meineke *et al*., 2013). However, whilst urban-associated food resources are likely to help sustain dense populations (Robb *et al*., 2008; Hubert *et al*., 2011; Orros and Fellowes, 2015), additional research is needed to understand the complex, and sometimes disadvantageous, impacts of anthropogenic feeding.

Other important anthropogenic resources in urban areas include water – either provided purposefully as a drinking resource or in e.g., urban ponds – shelter, nesting structures and materials (Becker *et al*., 2015). Openings in buildings and manmade structures are known to be exploited by a variety of wildlife including roosting bats (Mering and Chambers, 2014), hibernating amphibians (Dervo *et al*., 2018) and nesting birds (Reynolds *et al*., 2019). As well as these 'opportunistic' nesting sites, purpose-built nest boxes or other artificial refugia are commonly installed in urban locations by householders and practitioners to supplement or replace naturally occurring nest sites (Beyer and Goldingay, 2006). Numerous designs of artificial refugia are commercially available for a variety of taxa (Mering and Chambers, 2014; Gaston *et al*., 2005; Dervo *et al*., 2018), although these have been studied most extensively in birds (Lambrechts *et al*., 2010): bird nest boxes are frequently installed in residential areas and there are an estimated 4.7 million bird boxes in gardens in the UK (Davies *et al*., 2009). Nest boxes are thought to increase breeding opportunities, thereby helping local populations to grow and colonise urban spaces (Lambrechts *et al*., 2010; Reynolds *et al*., 2019), but their conservation value varies between species (Griffiths *et al*., 2017) as well as between refugia designs (Goldingay *et al*., 2015). Some species also make use of anthropogenic materials such as plastics, papers, cigarette butts and other discarded materials in nest construction to the extent that, for birds, shifts in nest composition have been recorded along urbanisation gradients (Reynolds *et al*., 2019). Artificial materials in bird nests are known to risk entanglement, exert genotoxic effects and impact the nest's insulative properties (Corrales-Moya *et al*., 2021) but, alternatively, can provide anti-parasitic, anti-predatory and altered signalling effects (Reynolds *et al*., 2019). The use of such materials in nest-building has also been recorded anecdotally in mammals (e.g., Mohan and Singh, 2018), but the ecological and population-level impacts of this are unclear.

Developed areas can also provide refuge for prey species (Gering and Blair, 1999; Leighton *et al*., 2010; Møller, 2012; Guiden *et al*., 2019) as some predators are known to avoid urban landscapes (Guiden *et al*., 2019) and/or being in proximity to humans

(Møller, 2012). Consequently, predation pressure is perceived to be reduced; in fact, targeted disturbance by humans to actively encourage the displacement of predators could aid the survival and conservation of endangered prey in built-up areas (Leighton *et al*., 2010). Alternatively, some predators have adapted to and increased in abundance in urban environments (Stracey, 2011) without having an elevated impact on prey populations (Fischer *et al*., 2012). This may be because predators are less reliant on prey where alternative food sources, such as anthropogenic foods, are available (Stracey, 2011). For example, both domestic cats and many of their avian prey occur in high densities in urban settings (Sims *et al*., 2008), yet the diet of urban cats contains markedly less vertebrate prey in comparison to those living in rural areas (Piontek *et al*., 2021) as they may receive much of their daily nutritional requirements from anthropogenic foods.

In conclusion, despite the many challenges associated with living in urban areas, it is clear that towns and cities can be a source of many, sometimes novel, resources, whilst offering additional advantages such as the absence of some predators and competitors. Therefore, although often linked to the loss of wildlife and natural spaces (Williams *et al*., 2005; Perry and Nawaz, 2008; Aronson *et al*., 2017; Croeser *et al*., 2020), the creation of urban areas can be associated with diverse ecological communities (Kühn *et al*., 2004; Ives *et al*., 2016) including some species that are rare or declining (Mason, 2000; Ives *et al*., 2016; Mayer and Sunde, 2020). Despite the conservation value of urban spaces, however, there are significant knowledge gaps within the field of urban ecology (Miller and Hobbs, 2002; Magle *et al*., 2012; Martin *et al*., 2012), including a detailed understanding of how different species persist and thrive in these human-modified landscapes (Magle *et al*., 2019); such knowledge is necessary for the development of sound conservation management strategies.

Residents, research and conservation in urban areas

Implementing conservation strategies or studying biodiversity in areas of human habitation presents numerous opportunities but is equally associated with a range of logistical and practical challenges. The involvement of local citizens as participants contributing directly to data collection and/or the incorporation of their land as survey sites can help to maximise sample size and effort (Domroese and Johnson, 2017), but can be logistically difficult to manage as, for example, participants may not follow instructions or may simply cease collecting data (Dyson *et al*., 2019). Nonetheless, data collection by volunteers has become an increasingly popular tool in urban ecology research (Dickinson *et al*., 2012) with studies sometimes relying on the recruitment of urban residents to: report on incidental wildlife sightings (Scott *et al*., 2014); to conduct systematic surveys

(Williams *et al*., 2018a); or to obtain biological samples (Krabbenhoft and Kashian, 2020). In some cases – for example, where no training is required and/or where results can be submitted from their homes – citizen-based surveys have been conducted on national scales: well-established examples include the Garden BirdWatch (British Trust for Ornithology) and Living with Mammals (People's Trust for Endangered Species) surveys which have been running for over a decade in the UK, garnering thousands of records of wildlife sightings from urban spaces annually.

Some such studies can be operated via the use of questionnaire surveys. These provide a relatively cheap method of mass data collection if, for example, they are distributed online, and can be used to effectively evaluate stakeholder perceptions, human-nature interactions, and wildlife observations (White *et al*., 2005). From a conservation perspective, questionnaires are useful tools for examining public attitudes and engagement with schemes that directly involve community participation, or for projects physically based in areas of human habitation. In these situations, questionnaires can identify potential concerns or motivations (Hobbs and White, 2012; Maund *et al*., 2020), as well as assess the effectiveness of volunteer-based conservation work (Jordan *et al*., 2016). Such feedback could aid the adaptive management of conservation projects (Keith *et al*., 2011; Rist *et al*., 2012; Williams and Brown, 2016) where progress is assessed intermittently, and management plans subsequently adapted, or even abandoned, following these assessments (Rist *et al*., 2012). However, many modern conservation projects are not managed in this way and a lack of resources often means that there are no data to support adaptive decision-making nor demonstrate that conservation outcomes have been successful (Gaston *et al*., 2005; Sutherland and Wordley, 2017). Close collaborations between conservation practitioners, scientists and volunteers should therefore be considered a critical aspect of urban conservation schemes.

In comparison, other research questions are likely to necessitate the collection of data using more intensive field-based approaches. For example, tracking animal movements using Global Positioning System (GPS) or radio tags (e.g., Figure 1.1) can provide essential insights into patterns of habitat use, dispersal, and other ecological processes (Kays *et al*., 2015). Tracking animals in urban areas can, however, be problematic since tall buildings and artificial shelters may block or reflect the signals from GPS tags (Adams *et al*., 2013), thus reducing the rate at which location fixes are recorded successfully. In addition, the capture of animals for individual marking and subsequent identification, as well for fitting tags for tracking, can have ethical and welfare implications (Kays *et al*., 2015; Jung *et al*., 2020). Alternatively, information on animal presence/absence, abundance, distribution, activity and behaviour could be gathered using non-invasive survey techniques such as camera trapping (Wearn *et al*., 2019), monitoring the use of refugia (Beyer and Goldingay, 2006), or searching for field signs or footprints (Cooper *et al*., 2017). Footprint tracking tunnels (Figure 1.1), for instance, are a cost-effective tool used to record animal presence via prints left in ink or sand, and can be used by members of the public as well as professionals (Cooper *et al*., 2017; Melcore *et al*., 2020).

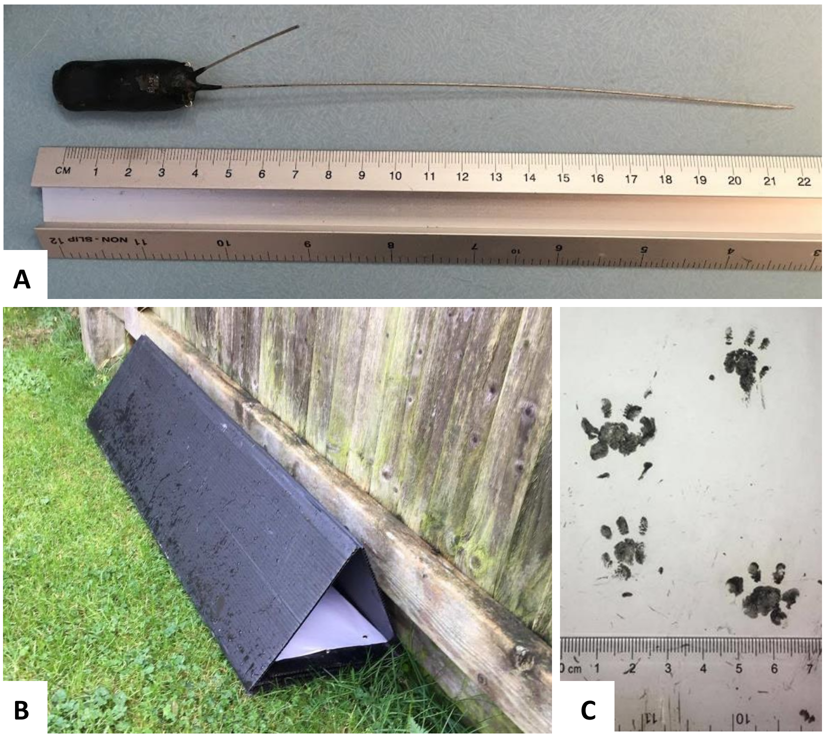

Figure 1.1. Examples of field-based tools for monitoring wildlife: a GPS tag suitable for use on birds and small mammals (A), and footprint tunnel (B), with an example of footprints belonging to *Erinaceus europaeus* (C). Photos by A. Gazzard.

Within urban settings, it is imperative that areas of privately owned land are incorporated in scientific studies (Dyson *et al*., 2019), as these can constitute a considerable proportion of urban green space (Loram *et al*., 2007; Davies *et al*., 2009); failing to consider such land types will inevitably lead to an incomplete understanding of a species' occupancy, density, habitat use and movement patterns throughout the urban landscape as a whole (Dyson *et al*., 2019). Obtaining permission from householders and other landowners to access their property is therefore an essential precursor for conducting fieldwork in urban areas, but is often time consuming, associated with safety considerations and/or made difficult by a lack of landowner interest. Site selection (and retention) can therefore be biased if permissions related to access are influenced by participant-level factors such as pre-existing environmental concerns (Dyson *et al.*, 2019), landowner availability or a lack of desire to take part in repeated surveys (Lesser, 2001).

Ultimately, biases related to the recruitment of surveyors and sites can also lead to biases in the data recorded. In recent years, several studies have, for example, recruited householders to survey their gardens for wildlife (Williams *et al.*, 2015; Domroese and Johnson, 2017; Dörler *et al.*, 2018; Williams *et al.*, 2018a; Finch *et al.*, 2020). To engage with as many ‘citizen scientists’ as possible, survey protocols tend to be simplified and often permit volunteers to choose their survey locations (Ditmer *et al.*, 2021). The latter may, however, inadvertently promote a lack of negative reporting and/or observer bias (Marks *et al.*, 2017) whereby volunteers are more likely to survey areas that are easily accessible (Tiago *et al.*, 2017) or where they believe they can obtain positive results; this is also likely to complicate long-term monitoring of species if volunteers are increasingly likely to ‘drop out’ if they do not detect the focal species. Such biases could be reduced by providing training, ensuring sampling protocols are standardised, and validating volunteers’ results (Gonsamo and D’Odorico, 2014) as well as ensuring that results are fed back to the volunteers (Cooper *et al.*, 2007). Thus, citizen science based approaches require a substantial effort from researchers in terms of recruiting volunteers, distributing equipment, providing training sessions or verifying results, but can, with due diligence, result in good quality data and large sample sizes which, ideally, incorporate private land (Newman *et al.*, 2003a; Crall *et al.*, 2011; Bonter and Cooper, 2012).

Engaging with householders and other landowners is also fundamental for successful conservation outcomes as the management of private property often lies outside of legislative control. As such, collaboration with private landowners is essential for protecting and enhancing existing habitats, as well as creating new areas for the benefit of flora and fauna (Goddard *et al.*, 2010). For instance, the UK’s Wildlife Trusts operate a scheme that awards landowning businesses for positively managing their property for wildlife (The Wildlife Trusts, 2021a). Often, conservation campaigns also focus on private residential gardens (Goddard *et al.*, 2010) and encourage householders to manage their gardens in nature-friendly ways by creating diverse habitat patches, providing resources for wildlife and avoiding damage to habitats or fauna. For example, the National Wildlife Federation's Certified Wildlife Habitat™ scheme in the US aims to educate homeowners on the benefits of wildlife gardening by operating a programme to “certify” gardens that fulfil a wildlife-friendly checklist (Widows and Drake, 2014). In the UK, garden-based actions commonly promoted by conservation groups include the addition of log piles and other refugia, ponds, wildflowers, structurally diverse vegetation, and artificial and natural food resources, as well as ensuring that garden boundaries are wildlife-permeable (e.g., Wildlife Gardening Forum, 2021a). An example of this is the Wild About Gardens campaign which encourages UK householders to 'pledge a patch' for wildlife for e.g., beetles, by building "a Beetle Bucket, Beetle Bank, or Dead Hedge" (Wild About Gardens, 2021). Gardens are the preferred habitat type for numerous urban animal species (Davison *et al*., 2008; Van Helden *et al*., 2020a) and managing them appropriately could have significant conservation benefits.

The role of residential gardens in urban conservation

In many countries, much of the privately-owned green space consists of residential gardens: for example, it is estimated that gardens constitute 47%, 59% and 86% of urban green space in Leicester (UK; Loram *et al*., 2007), Melbourne (Australia; Marshall *et al*., 2019) and León (Nicaragua; González-García and Gómez Sal, 2008), respectively. In the UK, total garden space exceeds 430,000ha and collectively contains 28.7 million trees, 4.7 million bird boxes and 3.5 million ponds (Davies *et al*., 2009). As such, gardens represent a fundamentally important space for wildlife and sympathetic management by garden owners has the capacity to influence local assemblages (Daniels and Kirkpatrick, 2006; Plummer *et al*., 2019) by encouraging the presence of certain species (Van Helden *et al.*, 2020a) or even preventing or delaying the extinction of others (Maunder *et al*., 1998).

Residential gardens appear to provide key resources for some species of conservation concern. For example, radio tracked Critically Endangered Western ringtail possums (*Pseudocheirus occidentalis*) have been found to reside exclusively within gardens regardless of proximity to natural habitats (Van Helden *et al*., 2020b); declining species such as the house sparrow (*Passer domesticus*) are likely to occur in denser populations in urban areas when residential gardens are present (Chamberlain *et al*., 2007); and gardens act as hotspots for some arthropod groups (Vilisics and Hornung, 2009). Additionally, certain garden features may serve as key resources within the wider landscape, e.g., garden ponds as breeding sites for the common toad (*Bufo bufo*) (Carrier and Beebee, 2003) and great crested newt (*Triturus cristatus*) (Zakaria, 2017), both of which are considered to have become increasingly rarer in the UK (McKinnell *et al*., 2015; Petrovan and Schmidt, 2016).

The way in which animals use gardens *per se*, and the relative value of individual gardens, are likely to be dependent on a range of factors including garden dimensions, the quantity or quality of certain garden features including the extent of vegetation coverage and provision of food, but also prevailing environmental conditions (which may affect prey availability) and features in the wider landscape such as proximity to other nearby habitats (Baker and Harris, 2007). For example, Van Helden *et al*. (2021) found that the occupancy of arboreal and ground-dwelling mammals in residential gardens in Australia was associated with canopy cover and the presence of dogs, respectively, although the significance of these factors varied between seasons. Baker and Harris (2007) observed that frequency of presence of some urban mammal species in UK gardens, as reported by householders, was positively associated with increasing distance to natural or semi-natural habitats. Conversely, in a Swedish study, visitation frequency by urban fauna was either unaffected, or in some cases, negatively affected, by the proportion of natural habitat within a 1km radii of gardens (Anderson, 2021). However, such studies typically rely on information of animal presence/absence and are unable to distinguish between gardens based on how intensively they are used, nor assess patterns of behaviour within gardens.

Identifying patterns of behaviour within gardens can pose its own particular challenges, as animals cannot typically be viewed directly from publicly accessible spaces. Consequently, researchers may be reliant on data submitted by householders based on their own direct observations, although these are likely to be significantly diminished for nocturnal species since householders tend to be asleep when said animals are active. As a result, studies of within-garden behaviour require the use of technologies such as GPS and radio tracking, though these only indicate the amount of time spent at individual sites which may not easily reflect the relative importance of that site to an individual; for example, artificial food sources with a high calorific content could be accessed and consumed rapidly compared to foraging for invertebrate prey. Other approaches that could be used to quantify animal behaviour in residential gardens could include motion-activated cameras (Wearn *et al*., 2019), triaxial accelerometers (Barthel *et al*., 2019), animal-mounted cameras (Moll *et al*., 2007) and constant-monitoring video systems (Jumeau *et al*., 2017). To date, however, these have not been used extensively in urban areas. As such, the value of gardens to various fauna has been seldom studied (Van Helden, 2020) and the impacts of conservation actions in gardens remain largely unassessed (Wildlife Gardening Forum, 2021b) despite the wide range of existing garden-focussed conservation schemes (e.g., Widows and Drake, 2014; The Conservation Foundation, 2021; Wild About Gardens, 2021).

On the contrary, scientific understanding of the benefits of gardens for human health is growing. Access to a private garden is positively linked to wellbeing (de Bell *et al*., 2020) and lower cortisol levels (Rodiek, 2002), and participating in gardening activities may improve cognitive ability (Park *et al*., 2019). Spending time in urban green spaces is also related to pro-environmental attitudes and behaviours (Whitburn *et al*., 2018; Alcock *et al*., 2020). For instance, gardening during childhood can strongly influence positive environmental attitudes in adulthood as well as the likelihood of participating in gardening classes or programmes in later life (Lohr and Pearson-Mims, 2005). Thus, conservation campaigns focusing on urban garden biodiversity will likely benefit human health and wellbeing whilst also amplifying peoples' general interest in nature.

Irrespective of the potential benefits of garden-based conservation strategies, implementing such projects on scales appropriate for wildlife can be challenging. This is in part because residential gardens tend to be owned individually, and because individual gardens may only comprise a fragment of an animal's range such that success is often reliant on engaging multiple householders in close proximity to one another (Borgström *et al.*, 2006; Goddard *et al.*, 2010). For example, a study of the Certified Wildlife Habitat™ programme in the US found that, whilst uptake is considered to be generally high (>100,000 certified gardens; Goddard *et al*., 2010), benefits to wildlife could be far greater if participating gardens were in closer proximity to one another rather than one or two per neighbourhood (Widows and Drake, 2014). Willingness to participate in such schemes depends on the needs, opinions, and preferences of individual householders (van den Berg and van Winsum-Westra, 2010). Moreover, it is not uncommon for householders to choose to manage their land in a way that limits opportunities for biodiversity. For example, vegetated areas are often paved over (Perry and Nawaz, 2008) or replaced by synthetic lawns (Francis, 2018), and native plants are frequently substituted by non-native ornamentals (Burghardt *et al*., 2010). The presence and diversity of invertebrates, plants and other wildlife may be regulated by pesticide applications (Politi Bertoncini *et al*., 2012; Muratet and Fontaine, 2015) or the permeability of garden boundaries (Froglife, 2020; Hedgehog Street, 2020a). Motivations surrounding such management practices are tied to aesthetic preferences (Goddard *et al*., 2013), neighbourhood and social norms (Clayton, 2007), and the level of maintenance required (Beumer, 2018).

Even when householders do wish to participate in garden conservation, their willingness could vary between gardening activities as these differ in terms of the associated expenses, time commitments, permanence and visual appearance (see van Heezik *et al*., 2020). The likelihood of achieving positive conservation outcomes within a timeframe suitable to the householder can also be a guiding factor (Gaston *et al*., 2005). In one study conducted by van Heezik *et al*. (2020) with householders in New Zealand, participants were presented with various garden wildlife improvements/activities to choose from, and the majority opted to install bird feeders rather than the potentially more labour-intensive additions such as planting and maintaining native shrubs or monitoring mammal presence with a tracking tunnel; bird feeding is typically perceived to be a relatively simple practice (Cox and Gaston, 2016). Motivations behind bird feeding have been reasonably well-studied and are often associated with demographic factors as well as a sense of connectedness with nature (e.g., Davies *et al*., 2012; Goddard *et al*., 2013; Clark *et al*., 2019). However, engagement with other specific wildlife-gardening activities remains largely unexplored.

Overall, the challenges associated with studying garden fauna have resulted in a relatively limited understanding of gardens as a conservation resource. In particular, it is not clear which garden features are most important for individual species or for ecological communities in general (see Williams *et al.*, 2018a; Van Helden, 2020), nor how they might affect animal behaviour, survival or the abundance of local populations. In addition, there are gaps in knowledge relating to the motivations of engaging with wildlife-friendly gardening practices, and how householders may be encouraged to undertake pro-environmental behaviours. Residential gardens are nonetheless likely to be important conservation settings in the face of ongoing rapid urban expansion.

The West European hedgehog (*Erinaceus europaeus*)

The West European hedgehog (hereafter 'hedgehog') is a member of a primitive family of ground-dwelling, spiny insectivorous mammals found throughout Europe, Asia and Africa (Sommer, 2006; Pfäffle *et al*., 2014; Amori, 2016). It is native to and generally common throughout Western Europe (Figure 1.2) (Reeve, 1994), and can be found in a wide range of habitats up to the treeline, including in urban areas (Morris, 2018). It has also been deliberately introduced to the Azores (Witmer *et al*., 2004), the Outer Hebrides (Jackson and Green, 2000) and New Zealand (Jones *et al*., 2005); in the latter two locations, hedgehogs are considered pests due to their impacts on internationally important breeding bird populations and other fauna (Jackson, 2001; Department of Conservation, 2022). Otherwise, public attitudes towards hedgehogs are generally positive (Morris, 1987; Bjerke *et al*., 2003; Bjerke and Østdahl, 2004; Baker and Harris, 2007; Borgi and Cirulli, 2015) and, in the UK, there exists numerous community groups and wildlife organisations that are dedicated to this species (e.g., Hedgehog Street (hedgehogstreet.org); Hedgehog Friendly Campus (facebook.com/HogFriendly); Hedgehog Republic (hedgehogrepublic.org)).

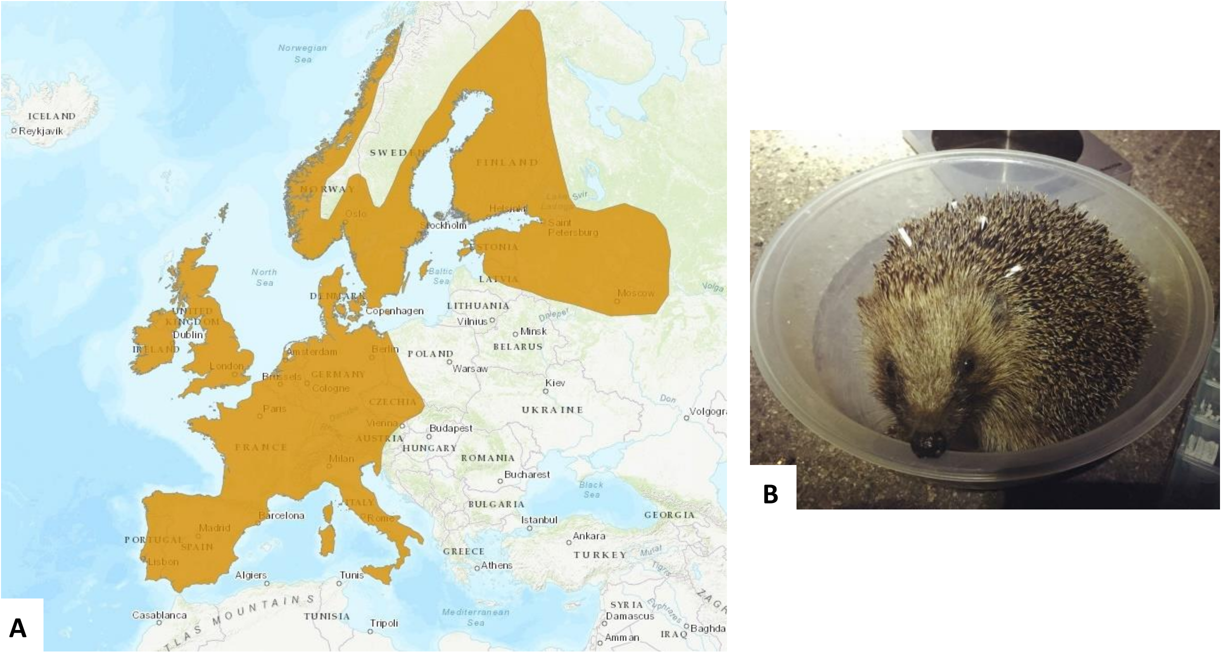

Figure 1.2. (A) The distribution, shown in orange, of the West European hedgehog in Europe (from IUCN, 2008), and (B) a hedgehog captured and marked in Reading, UK under licence (A. Gazzard).

Throughout most of its native range, hedgehogs typically hibernate between November and April, although the exact timing depends on climate, sex, body size and physical condition (Reeve, 1994; Morris, 2018). The factors which trigger hibernation are somewhat unclear but are likely to involve environmental and hormonal cues related to reduced natural prey availability, shorter days and lower ambient temperatures (Morris, 2018). Hedgehogs are otherwise active between spring-autumn during which they may breed at any point (Dowler Burroughes *et al*., 2021). The majority of litters in the UK are produced early in the annual cycle (May-June: Deanesly, 1934; Jackson, 2006; Haigh, 2011), although 'late litters' may be produced in August-October (Dowler Burroughes *et al*., 2021); occasionally a female might produce two litters in one year (Jackson, 2006). Litter size is typically 3-6 (Morris, 1977; Kristiansson, 1981; Walhovd, 1984), with the young becoming independent by approximately six weeks of age (Morris, 2018).

Other than when mothers are raising young, hedgehogs are solitary (Morris, 2018). They are not territorial, nor are they confined to the same nightly routes or ranges (Dowie, 1993; Riber, 2006; Schaus Calderón, 2021). Hedgehog nightly ranges – defined as the areas covered by an individual on a given night (Dowding *et al*., 2010a) – often overlap with those of other individuals' (Rautio *et al*., 2012) and appear to be markedly larger in rural environments, with males generally covering greater areas than females (Table 1.1).

Table 1.1. Estimates of areas ranged (ha) and distances travelled (km) by hedgehogs in rural and urban habitats. Data are provided as nightly averages unless denoted by *; corresponding ranges are shown in brackets. Method of range calculation is indicated in the reference column: [a] ranges were calculated using 100% minimum convex polygons; [b] ranges were calculated using 95% minimum convex polygons; and [c] ranges were calculated using 95% kernel range estimates.

Rural/ urban	Habitat type	Country	Sex	N	Area ranged (ha)	Distance travelled (km)	Reference
Rural	Pasture and woodland	New Zealand	M	4	2.5 (0.8-4.8)*	-	Parkes (1975)[a]
			F	10	3.6 (1.0-6.5)*		
	Disused farmland	Sweden	M	5	46.5 (25.0-67.7)	-	Kristiansson (1984)[a]
			F	6	19.7 (8.1-29.5)		
	Coastal scrub	Italy	M	9	57.1 (5.5-102.5)	-	Boitani & Reggiani 1984[a]
			F	5	29.1 (10.0-56.2)		
	Farmland	England	M	4	7.5 (1.54-14.69)	1.1 (0.5-1.8)	Morris (1988)[a]
			F	1	3.0 (3.0)	1.0 (1.0)	
	Mixed pasture and arable land	England	M	35	53.0	4.8	Doncaster *et al.* (2001)[a]
			F	33	25.6	3.2	
	Arable land, forests and grassland	Denmark	M	5	96.0	2.0	Riber (2006)[a]
			F	5	26.0	1.2	
	Farmland	Ireland	M	21	56.0*	-	Haigh (2011)[a]
			F	9	16.5*		
	Farmland	England	M	32	21.6	-	Pettett *et al.* (2017)[a]
			F		12.4		
	Farmland, woodland, rural	England	M	9	5.2	-	Schaus Calderón, 2021[b]
			F	14	2.0		
Semi-urban	Golf course	England	M	6	32.0 (15.5-41.5)	-	Reeve (1982)[a]
			F	7	10.0 (5.5-12.0)		
Urban	Residential area	England	M	4	5.0*	0.4	Rondinini & Doncaster (2002)[a]
			F	4			
	Residential area	England	M	11	1.9	0.6	Molony *et al.* (2006)[c]
			F	15			
	Residential area	England	M	19	2.9 (0.9-6.1)	0.9 (0.4-1.8)	Dowding *et al.* (2010a)[a]
			F	19	0.8 (0.3-2.1)	0.5 (0.2-1.0)	
	Campus, town centre, surrounding	Finland	M	11	97.9 (88.3-111.2)	-	Rautio *et al.* (2013)[a]
			F	10	55.2 (23.6-82.2)		
	City	Switzerland	M	40	17.32	-	

		F	0	-		Braaker *et al.* (2014)[a]
City park	Germany	M	8	4.7	-	Berger *et al.* (2020)[b]
		F	8	2.5		
Residential area(s)	England	M	13	3.3	-	Schaus Calderón, 2021[a]
		F	16	1.1		

*Average cumulative ranges (not average nightly ranges) were estimated for periods of 1-2 months (Rondinini and Doncaster, 2008), 1 year (Reeve, 1982), ~1.5 years (Parkes, 1975) and ~2 years (Haigh, 2011).

Nightly activity is dominated by foraging (sometimes almost continuously; Riber, 2006) before returning to a resting place for the subsequent day (Morris, 2018). Summer day nests are built for short-term use and are loosely formed compared to denser and more insulating hibernacula (Morris, 2018). Nests primarily contain leaf litter, grass and other natural materials (Reeve and Morris, 1985; Rautio *et al*., 2014) and are constructed in a variety of sheltered locations such as under hedgerows, scrub, log piles or in artificial (typically wooden) nest boxes (Morris, 2018). Hedgehogs will make use of multiple nests throughout all seasons, including the hibernation period (Haigh *et al*., 2012; Rautio *et al*., 2014; Morris, 2018; Yarnell *et al*., 2019; Bearman-Brown *et al*., 2020).

Both within-season (i.e., April–November) and over-winter survival estimates are variable, having been gathered during assorted lengths of study, in different seasons and habitats, and range from 0.31–1.0 for juveniles and 0.65–1.00 for adults (Kristiansson, 1990; Haigh *et al*., 2012; Rasmussen *et al*., 2019a; Yarnell *et al*., 2019; Bearman-Brown *et al*., 2020). Nonetheless, it is evident that survival rates are likely to be highest over winter (Kristiansson, 1990; Rasmussen *et al.*, 2019a; Yarnell *et al*., 2019) when hedgehogs are least active. This is despite a perceived heightened risk of mortality during hibernation, associated with the depletion of fat reserves (Morris, 2018). Other major mortality risks for hedgehogs include misadventure (e.g., drowning in ponds, entanglement in netting), road traffic accidents, severe parasitic burdens and predation (Morris, 2018). Known predators of hedgehogs are the Eurasian eagle owl (*Bubo bubo*), red fox (*Vulpes vulpes*), badger (*Meles meles*) and domestic dog (Doncaster, 1994; Martínez and Zuberogoitia, 2001; Morris, 2018; Rasmussen *et al.*, 2019a).

Conservation status of the West European hedgehog

On a global scale, the West European hedgehog is classified by the International Union for Conservation of Nature (IUCN) as a species of Least Concern (Amori, 2016). However, data suggest that hedgehogs have undergone a marked decline in Europe in recent decades (see Rasmussen *et al*., 2019a). In the UK, historical population estimates have been based upon relatively little information: Burton (1969) produced the first British hedgehog population estimate of 36.5 million individuals in the 1950s based upon an extrapolation of 1 hedgehog/acre derived from personal observations in southern England. In 1995, however, a review of British mammal populations by Harris *et al*. (1995) using data gathered from published studies and across varying land classes estimated that hedgehog numbers were in the region of 1.6 million. More recently, figures of 0.7-1.2 (Croft *et al*., 2017) and 0.5 million (Mathews *et al*., 2018) have been published. In all cases, the population estimates have been hindered by a lack of up-to-date density data available for different habitat types. Despite the limitations associated with these national estimates, a range of nationwide surveys have demonstrated a clear downward trend in numbers (Roos *et al.*, 2012; Table 1.2); as a result, hedgehogs were assigned Vulnerable status on an IUCN-compliant Red List by the British Mammal Society in 2020 (Mathews and Harrower, 2020).

Table 1.2. Summary of UK hedgehog population trends interpreted from data collected in national wildlife surveys.

Survey	Years active	Urban or rural?	Description	Results
National Gamebag Census	1961-present	Rural	Established by the Game and Wildlife Conservation Trust (GWCT), this voluntary census comprises records from shooting and gamekeeping activities of the numbers of each species (including birds and mammals) shot annually. Annual kill counts can be used to index trends.	Between 1961 and 2009, data revealed a 52% decline in the quantity of hedgehogs captured/killed. The rate of decline appeared to worsen post-1980, with the largest decline occurring in the Eastern lowlands (-77%, 1984-2009). However, the decline in hedgehogs reported might not reflect the true number of hedgehogs captured; hedgehogs became legally protected from certain methods of killing in 1981, and current guidelines for gamekeepers highlight methods should be taken to avoid catching and killing hedgehogs. These data do indicate that hedgehog populations are likely to have become more patchily distributed and reduced over time.
Waterways Breeding Bird Survey (BTO)	1998-present	Rural	The Waterways Breeding Bird Survey is organised by the British Trust for Ornithology (BTO) and follows methods akin to that of the Breeding Bird Survey (see below), but focuses only on transects along waterways.	Results suggest an overall 78.4% drop in the proportional index of hedgehog sightings between 1998-2009. However, this may be an overestimate since the data could not be fitted to a linear trend and therefore extreme between-year fluctuations are not considered (Roos *et al.*, 2012).
Mammals on Roads (PTES)	2001-present	Rural	The Mammals on Roads survey is a nationwide, annual survey of mammal sightings alongside single-carriage roads. This survey has been organised by the	Linear trends suggested a decline of -14.8% (averaging -1.8% a year) until 2009 (Roos *et al.*, 2012). Counts of hedgehogs/100km rose

			People's Trust for Endangered Species (PTES) since 2001 and collects data from volunteers recording sightings on dedicated car journeys. Routes travelled are decided by volunteers themselves.	between 2015-2017, before dropping again in 2017. Males may be more likely to be observed on roads than females as they are significantly more likely to cross roads (Dowding *et al*., 2010a), and hedgehog road fatalities are disproportionately male (Huijser and Bergers, 2000).
Breeding Bird Survey (BTO)	2002-present	Rural	The Breeding Bird Survey was launched by the BTO with the primary objective of obtaining avian population data. Volunteers are assigned 1km^2 grid sites and asked to record any birds identified by sight or sound during two site visits. Since 1995, the Breeding Bird Survey has included mammal counts, with statistically viable hedgehog data available from 2002.	Between 2002-2009, the proportion of hedgehogs sighted declined by 52.2%, averaging -8.8% a year (linear trend estimated by Roos *et al*., 2012).
Living with Mammals (PTES)	2003-present	Urban	Also run by the PTES is the Living with Mammals survey. This annual survey started in 2003 and collects data on urban mammal sightings in green spaces (including gardens) from members of the public throughout set weeks in spring. All survey sites must be within 200m of buildings. Participation is voluntary.	Roos *et al*. (2012) explains that the Living with Mammals results show a non-significant decline in hedgehog presence between 2003-2010. From 2014, it appears that the proportion of hedgehog-occupied sites has risen if using the measure of mean number of hedgehogs sighted rather than total sites occupied (Wilson and Wembridge, 2018).
HogWatch (BHPS and PTES)	2005-2007	Urban	HogWatch was run by the British Hedgehog Preservation Society (BHPS) and PTES to gather data on hedgehogs in	The results indicated a significant increase in hedgehog numbers, with up to 89% of sites reporting hedgehog presence in one year. However, it is likely that this is due to a lack of

			gardens, requiring volunteers to submit ad hoc sightings.	negative reporting, a bias in site-retention between years (e.g., response rates from previously positive sites remained high whilst overall sample size decreased between years) and surveyor recruitment via advertisements from hedgehog-focussed organisations. When the data from the 1st year of HogWatch were combined with a public dataset of UK hedgehog records submitted online (by anyone, at any time: https://www.gbif.org/), Hof and Bright (2016) calculated that the number of 10x10km grid cells in England where hedgehogs were seen had dropped by approximately 5.0-7.4% between 1960–1975 and 2000–2015.
Garden BirdWatch (BTO)	2007-present	Urban	Garden BirdWatch was launched in 1995 by the BTO and has collected data on hedgehogs since 2007. Garden BirdWatch charges a fee to members of the public to take part in garden surveys in return for feedback on the results. Participants record the maximum number of individuals of a species seen in their garden at one time.	The percentage of participants who recorded mammals and had observed at least one hedgehog declined from 36.3% in 2007 to 30.6% in 2010 (Roos *et al*., 2012). A slight upward trend can be observed from 2010-present, with a generally greater proportion of gardens reported to be hedgehog-positive year-on-year (BTO, 2021).
Make Your Nature Count (RSPB)	2009-2012?	Urban	This survey was launched by the Royal Society of the Protection of Birds (RSPB) in 2009 and required volunteers to record birds, mammals and other taxa on one day at the beginning of June. There are no data records available beyond	The proportion of sites in which hedgehogs were sighted increased from 76.9% to 78.1% between 2009 and 2010 (Roos *et al*., 2012). As with HogWatch, there is a chance that this apparent increase in occupancy may reflect a bias of participants not submitting hedgehog-negative data.

			2010, but online campaigns indicate that the survey continued until 2012.	
National Hedgehog Survey (BHPS and PTES)	2014-2015	Rural	The National Hedgehog Survey was conducted by the University of Reading, Nottingham Trent University, the BHPS and the PTES in 2014-2015. The survey quantified the presence/absence of hedgehogs in rural areas in England and Wales using footprint tunnels and ultimately provided a baseline measure of occupancy.	261 sites were surveyed, of which 21% were occupied by hedgehogs and 62% by badgers. Only 10% of sites were occupied by both hedgehogs and badgers (Williams *et al.*, 2018b). Accounting for each land class in England and Wales, the results give an overall occupancy of 22% nationally. The researchers suggest that a large proportion of the rural landscape is unsuitable for both badgers and hedgehogs.
Big Garden Birdwatch (RSPB)	2014-present	Urban	The Big Garden Birdwatch is a public survey in which householders are asked to record birds observed in their garden over the course of one hour. The RSPB have operated the Big Garden Birdwatch for almost 50 years, yet in 2014 the survey began also collecting data on whether participants had seen hedgehogs in their gardens.	Hedgehogs are one of the most commonly reported mammals reported in the Big Garden Birdwatch, and a small increase in the number of sightings reported was observed for Scotland in 2018 (RSPB, 2019). No further results are publicly available.
Hedgehog Watch Project (Mammal Society)	2016-2018?	Urban	The Mammal Society launched an online Hedgehog Watch survey during October 2016. Participants were asked when and where they saw hedgehogs that year. No evidence could be found of this survey running post-2018.	In all years, the Mammal Society reported that most respondents who observed hedgehogs had seen them in gardens (>80%). Most respondents also provided food for hedgehogs (≥70%), suggesting a marked bias in recruitment and therefore a potential lack of negative reporting. No annual trends or indices have been reported (The Mammal Society, 2018).

Traditionally associated with rural habitats such as farmland or woodland (Yarnell and Pettett, 2020), much of the data described in Table 1.2 suggest that hedgehogs in the UK are nowadays more likely to be found in urban areas. In fact, hedgehog populations are now considered to potentially be stable or even recovering in urban settings, despite an estimated decline during the first decade of the 2000s (Figure 1.3).

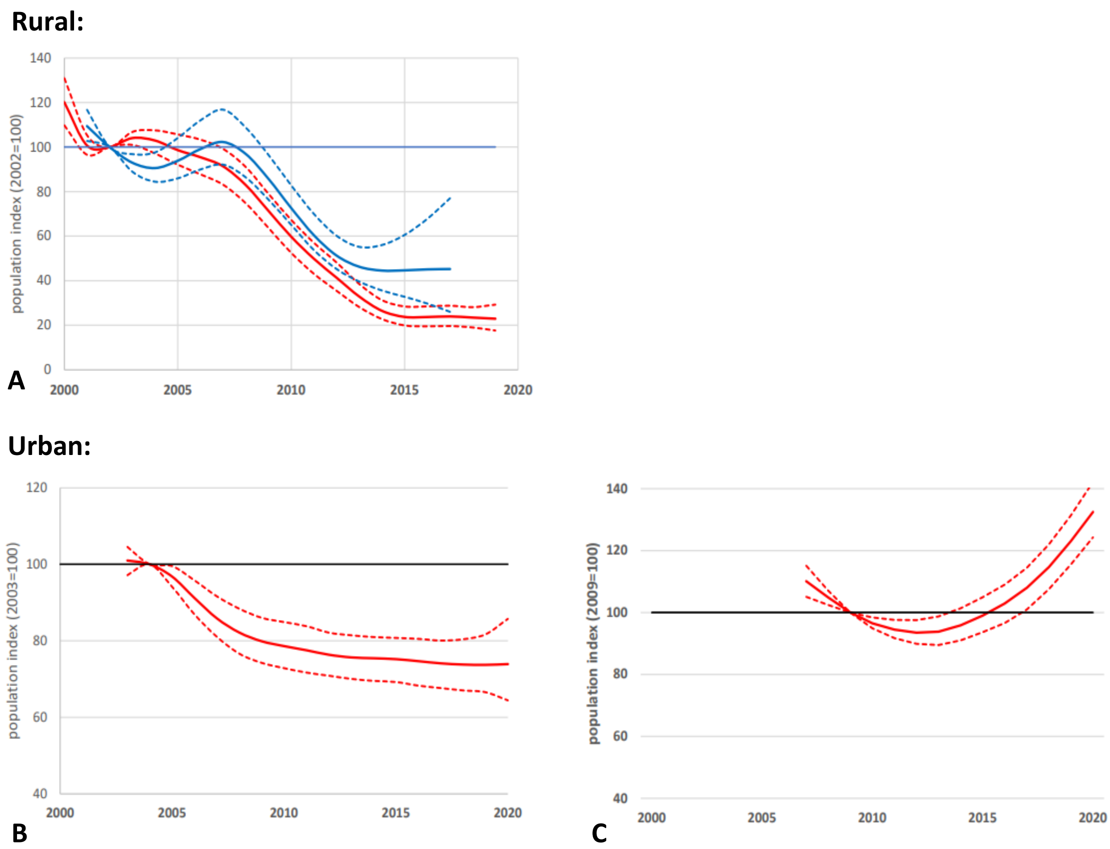

Figure 1.3. Population trends of hedgehogs in rural (A) and urban (B, C) landscapes in Britain. Data were obtained from the *Breeding Bird Survey* (A: red), and *Mammals on Roads* (A: blue), *Living with Mammals* (B) and *Garden BirdWatch* (C) monitoring schemes. Solid lines show trend estimates, dashed lines indicate 95% confidence limits. The population index is expressed relative to the baseline year. From Wembridge *et al.* (2022).

Similarly, higher hedgehog densities have been recorded in urban landscapes in both France (36.5 hedgehogs km^{-2} in urban areas versus 4.4 hedgehogs km^{-2} in rural landscapes: Hubert *et al.*, 2011) and the UK (32.3 versus 4.3 hedgehogs km^{-2}, respectively; Schaus *et al.*, 2020). Additionally, habitat suitability modelling of a UK dataset of road-killed animals indicated that the probability of the occurrence of hedgehog carcasses was strongly linked to urban land cover (Wright *et al.*, 2020), and high roadkill counts are likely to be indicative of increased abundance (Bright *et al.*, 2014).

An apparent preference for urban areas over rural has also been demonstrated in behavioural and movement studies. For example, in an Oxfordshire-based study, a significant proportion of hedgehogs released into agricultural land ultimately moved to and remained closer to urban habitats (Doncaster *et al*., 2001); hedgehogs in this study also moved further and faster in agricultural areas than those in urban locations (Doncaster *et al*., 2001). Similarly, in arable areas in Norfolk and Yorkshire, radio tracked hedgehogs selected villages rather than the surrounding farmland and, of all habitats available, preferentially used areas with gardens and buildings the most relative to their aerial availability (Pettett *et al*., 2017). A study by Williams *et al.* (2018a) further identified a positive relationship between hedgehog occupancy and the proportion of built habitat throughout the UK, which aligns with research undertaken in the Netherlands where hedgehog distribution was found to be largely determined by extent of urban land coverage (van de Poel *et al*., 2015).

The causes of the overall population decline nationally yet persistence or even increase within urban areas (Wembridge *et al*., 2022) are unclear, but are thought to involve a number of factors. Agricultural intensification has resulted in larger field sizes and the widespread loss and degradation of hedgerows, which in turn has limited foraging habitat and green corridors for wildlife (Krebs *et al*., 1999; Robinson *et al*., 2002) – hedgehogs rely heavily on edge habitats in arable landscapes such as field margins and hedgerows (Hof and Bright, 2010). Inhabiting rural spaces can also be energetically costly as hedgehogs may need to travel further across areas interspersed with large fields to find food, nest sites and mates (Doncaster *et al.*, 2001; Pettett *et al*., 2017). Alongside habitat change, a widespread reduction in the abundance and distribution of invertebrate prey in rural areas associated with the use of agricultural pesticides, pollution and/or climate mediated change is likely to have negatively impacted hedgehog populations, although this has not been corroborated (Bale *et al*., 2002; Yarnell and Pettett, 2020).

The decline of hedgehogs in rural areas has, however, been closely associated with a growth in the numbers of badgers following their increased legislative protection (Judge *et al*., 2015). Several studies have reported negative associations between the presence (Williams *et al*., 2018b) or abundance (Micol *et al*., 1994; Young *et al*., 2006) of hedgehogs relative to measures of badger density; similarly, it has been suggested that proximity to rural badger setts might have a negative effect on hedgehog reproductive success (Hubert *et al*., 2011). Likewise, on sites where badgers have been culled to manage the transmission of bovine tuberculosis from badgers to cattle, hedgehog numbers have increased (Trewby *et al*., 2014). The underlying mechanism(s) by which badgers affect hedgehog populations are, however, not clear but, as intra-guild predators, these could involve direct predation, creating a landscape of fear (e.g., hedgehogs are known to avoid foraging in areas with badger scent (Ward *et al*., 1996) and will remain significantly closer to edge cover habitat where badgers are present (Hof *et al*., 2012), and/or outcompeting hedgehogs for food resources (Young *et al*., 2006; Yarnell and Pettett, 2020).

In contrast, badgers are relatively rare in urban areas in the UK, but may be locally abundant (Davison *et al*., 2008). Consequently, it has been suggested that a general absence of badgers is a major factor contributing to the high density of hedgehogs in UK towns and cities (Hof and Bright, 2009). Similarly, Hubert *et al*. (2011) suggested that the reduced abundance of badgers in combination with the increased availability of earthworms and anthropogenic pet food is significantly correlated with hedgehog abundance in the Ardennes region of France. It is plausible that the abundance and predictability of artificial foods supplied by householders in urban areas may facilitate the coexistence of hedgehogs and badgers (Yarnell and Pettett, 2020), but does not entirely remove the risk of predation (Morris, 2018). Indeed, an increase in the number and distribution of badgers in Zurich city, Switzerland, has been associated with a marked decline in local hedgehog numbers in recent decades (Taucher *et al.,* 2020). Additionally, urban foxes will predate hedgehogs (Morris 2018; Rasmussen *et al*. 2019a) but also compete with them for a range of different foods, including those put out by householders (Pettett *et al*., 2018). Foxes are widespread in the UK (Scott *et al*. 2014) and typically occur in higher densities in towns and cities than in rural locations (Bateman and Flemming 2012). Thus, foxes may also pose a threat to hedgehog populations; one study has negatively linked hedgehog distribution to fox abundance in the UK (Pettett *et al*., 2018), though the extent of their impact is not fully understood.

Roads are a major risk to hedgehogs with an estimated 167,000-335,000 casualties occurring in the UK annually (Wembridge *et al.*, 2016). Hedgehogs appear to avoid crossing large roads (Rondinini and Doncaster, 2002) and foraging near even minor roads (Dowding *et al*., 2010a), and there is growing concern that roads fragment and isolate local populations (Becher and Griffiths, 1998; Barthel *et al*., 2020; Moore *et al*., 2020). However, results of genetic studies are equivocal: research conducted recently in Berlin, Germany (Barthel *et al*., 2020) and Helsinki, Finland (Osaka *et al*., 2022), using > 100 hedgehog carcasses, found no genetic differentiation between samples collected from hedgehogs across each city respectively, whereas a study undertaken in Zurich, Switzerland, identified distinct genetic clusters that coincided with the locations of major highways (Braaker *et al*., 2017). It is possible, however, that a lack of genetic differentiation, as observed in Berlin and Helsinki, could be in part due to the release of rehabilitated hedgehogs in areas spread across cities and where they did not necessarily originate.

Hedgehogs may also be vulnerable to the many pollutants released on roads (Rautio *et al*., 2010). Vehicular emissions increase the levels of heavy metals found in roadside soils (Wawer *et al*., 2015) which, in turn, increases the levels of these compounds in invertebrates in proximity to roads (Wade *et al*., 1980). Heavy metals such as lead and mercury can therefore bioaccumulate in mammals (Al Sayegh Petkovšek *et al.*, 2014) potentially leading to organ damage, immune system suppression and foetal abnormalities (Jamal *et al*., 2013), although impacts in hedgehogs specifically have not been quantified. Similarly, the effects of rodenticides and other poisons on hedgehogs are difficult to study, yet it is thought that the former could be obtained via the consumption of target animals that have died above ground, through the ingestion of invertebrate prey that have consumed or become coated in rodenticides after entering bait boxes (Alomar *et al.*, 2018) or through direct consumption of bait (juvenile hedgehogs are small enough to enter rodent bait boxes). Indeed, a study of hedgehog exposure to first- and second-generation anticoagulant rodenticides found that such chemicals were detected in over two thirds of specimens (N = 120; Dowding *et al*., 2010b).

Although formal evidence is lacking, it is likely that the decline in hedgehog numbers in recent decades can be attributed to habitat change, predation by or intraguild competition with badgers, and anthropogenic-associated factors such as the increased road network and volume of vehicular traffic. It is also possible that climate change may have also been a contributory factor as this may have affected the availability of invertebrate prey prior to hibernation, as well as the frequency with which hedgehogs rouse from hibernation. Hedgehogs nonetheless appear to have adapted well to urban environments, potentially due to their generalist nature of habitat use and breadth of diet (Reeve, 1994). Notwithstanding the benefits of residing in urban areas, hedgehogs in towns and cities are exposed to numerous risks and little is known about what specific conservation actions can be implemented to best aid urban hedgehog populations.

Conserving hedgehogs in urban areas

As outlined above, general risks to hedgehogs residing in towns and cities include vehicular traffic (Huisjer and Bergers, 2000; Moore *et al*., 2020; Wright *et al*., 2020), exposure to rodenticides and other toxic chemicals (Dowding *et al*., 2010b), but also artificial lighting (Finch *et al*., 2020), noise (Berger *et al*., 2020), artificial food sources

(Gimmel *et al*., 2021), injury by or disturbance from humans and domestic animals (Rasmussen *et al*., 2019a; Berger *et al*., 2020), and barriers to movement (Hof and Bright, 2009). Importantly, urban habitat connectivity for hedgehogs appears to be limited not only by major roads but also by impenetrable barriers such as fences and walls delineating property boundaries (Hof and Bright, 2009). This has been recognised by the Hedgehog Street campaign which is run in the UK jointly by two charitable organisations: the People's Trust for Endangered Species (PTES) and the British Hedgehog Preservation Society (BHPS).

Hedgehog Street has been operating since 2011 with the principal goal of improving connectivity between residential gardens for hedgehogs. The campaign encourages garden owners to create 'hedgehog highways' (gaps approximately 13cm by 13cm) either through or underneath their garden boundaries (Figure 1.4). In theory, increased connectivity between gardens for hedgehogs should increase the carrying capacity of the environment (if previously inaccessible gardens supply resources that hedgehogs need) whilst reducing the need for hedgehogs to travel across roads between blocks of houses. The population-level impacts of, and engagement rates with, this campaign have thus far not been systematically assessed, even though the campaign has successfully recruited >100,000 people online (members of the public can sign up to log their Hedgehog Highways, to report sightings of hedgehogs and/or to receive newsletters and access additional content). However, such rates of engagement must be considered with regards to the magnitude of the problem at hand; there are approximately 22.7 million households with a garden in the UK (Davies *et al*., 2009), and hedgehog highways would most likely have the greatest impact when installed in dense networks to connect multiple gardens on neighbourhood or local levels.

Figure 1.4. Examples of hedgehog highways created in garden boundaries. Photos by R. Evans (Reading).

The Hedgehog Street website also provides advice for householders on how to make their gardens more 'hedgehog-friendly'. Gardens are considered key habitat for urban-dwelling hedgehogs (Dowding *et al*., 2010a), although little quantified data exist on how hedgehogs actually use them nor which factors might encourage or discourage garden use (see Williams *et al*., 2018a; Schaus Calderón, 2021). For instance, gardens may be of greater value to individual hedgehogs and, in turn, local populations, when they provide nesting opportunities, habitats which supply natural prey, and other food and water sources. Analyses of hedgehog occupancy/sightings have suggested that hedgehog presence in urban green spaces may be influenced by predator distribution (Williams *et al*., 2018b), the presence of artificial nest boxes and anthropogenic food, extent of grass coverage (Hof and Bright, 2009), and the number of microhabitats including food-bearing plants (Baker and Harris, 2007). However, 'preferences' for different site features have been difficult to identify, in part because of the limitations associated with the methods used. Understanding the relative importance of such within-garden factors, as well as factors outside the garden, would be beneficial for informing homeowners on how to best manage their gardens for hedgehogs.

Hedgehog nest boxes (Figure 1.5), for example, are readily available in UK retail settings and are promoted as key features to include in hedgehog-friendly gardens whether they are homemade or purchased commercially (Hedgehog Street, 2021a). Yet, little is known about the significance of varying design features (e.g., external tunnel, base, waterproof lining), dimensions or positioning of boxes. Studies of artificial refugia use by other small mammals have suggested that the provision of nest boxes could help to mitigate the loss of natural nest sites (de Raad *et al*., 2021) by supporting breeding populations (Goldingay *et al*., 2015) and, with respect to hedgehogs, nest boxes could be especially beneficial during hibernation periods by providing effective insulation and protection from predators when in torpor. Conversely, however, poorly designed boxes could result in predators easily gaining access, and inadequate insulative or weather-resistant properties could encourage the rapid decay of nesting material (Morris, 1972) and/or the accelerated heat loss of hibernating animals (Sovio *et al*., 1968). The successive use of boxes by different individuals, as well as internal microclimatic properties, could also exacerbate the transmission of parasitic infections (see Heeb *et al.*, 2000).

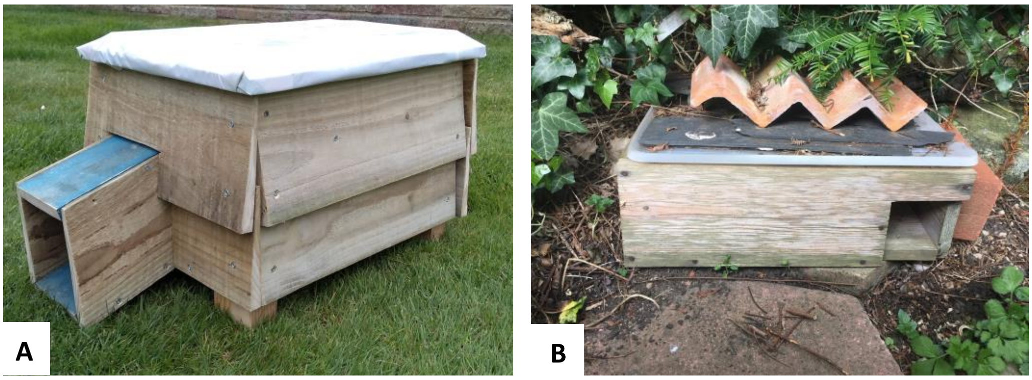

Figure 1.5. Examples of homemade hedgehog nest boxes (see Chapter 4 for further examples). Photos: (A) R. Brenton and (B) C. Gazzard.

Hedgehogs are host to a range of endoparasites and ectoparasites including ticks, fleas and helminths, with severe infections causing weight loss, respiratory difficulties (Gaglio *et al*., 2010), and, in some cases, having lethal consequences (Garcês *et al*., 2020). It has been suggested that parasites and disease may spread more rapidly in high-density hedgehog populations in urban areas (Rasmussen *et al*., 2019b), particularly where individuals frequent the same food sources (Taucher *et al*., 2020). Occupying urban areas further exposes hedgehogs to common hazards such as mowers, strimmers, uncovered ponds, netting, bonfires and pesticides, as well as disturbance by humans and domestic pets (Morris, 2018). Consequently, it is not unusual to encounter sick or injured hedgehogs in urban settings and, as a result, the UK contains an extensive network of hedgehog rehabilitators (see the directory at https://helpwildlife.co.uk). Hedgehogs are the species most commonly admitted to wildlife rescues in the country (Molony *et al*., 2006) with admissions increasing annually (Dowler Burroughes *et al*., 2021). The necessary lengths of admission (Rasmussen *et al*., 2021) as well as timings of release of rehabilitated hedgehogs (Yarnell *et al*., 2019) are often points of contention given that, in the UK, hedgehog rehabilitation is largely an unregulated process. Moreover, the population-level impacts of hedgehog rehabilitation are unknown, despite many thousands of hedgehogs being treated annually (Bearman-Brown, 2020; Dowler Burroughes *et al*., 2021). Regardless, rehabilitators likely play a substantial role in conservation by fostering greater awareness in hedgehog health and preservation.

Coinciding with the high levels of public interest in hedgehogs (Morris, 1987; Bjerke *et al*., 2003; Bjerke and Østdahl, 2004; Baker and Harris, 2007; Borgi and Cirulli, 2015), many householders in the UK enjoy providing food for hedgehogs, often in 'feeding stations' (i.e., food provided under cover – typically in a plastic or wooden box – to protect hedgehogs from predators, or prevent other wildlife from accessing said resource; e.g., Finch *et al*., 2020; Figure 1.6). Hedgehog abundance has been linked to the availability of artificial food (Cassini and Krebs, 1994; Hubert *et al*., 2011) with such resources seemingly utilised extensively in residential gardens (Morris, 2018), although the scale at which food is provided has not been quantified. Artificial food may be particularly beneficial to hedgehogs over winter when natural food supplies become diminished (Reeve, 1994) or during reproduction. For example, a review of food supplementation for terrestrial vertebrates reported that, for mammals, additional food sources could possibly be linked to larger litter sizes or increased growth rates (Boutin, 1990). However, the consequences of supplementary feeding for the survival and persistence of hedgehog populations are unclear. Supplementary feeding may in fact negatively affect natural hedgehog behaviours (University of Brighton, 2017) or diet quality as some commercially available dry hedgehog foods are notably low in crude protein and high in cereal content relative to natural resources (Gimmel *et al*., 2021); foraging at communal food sources may also promote disease transmission (Rasmussen *et al*., 2019a). Householders are nonetheless often encouraged by wildlife groups to leave out food for hedgehogs (e.g., Martin, 2019; BHPS, 2020; Tiggywinkles Wildlife Hospital, 2020), which underlines the need for greater understanding of the significance and potential hazards of anthropogenic food sources.

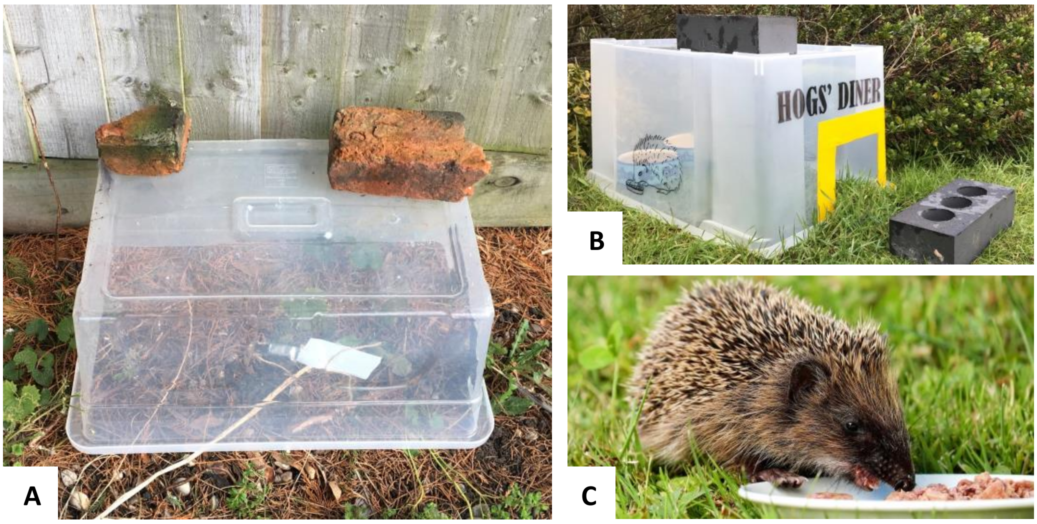

Figure 1.6. Wet and/or dry foods such as pet foods are commonly provided for hedgehogs in gardens in feeding stations (A, B) or in the open (C). Photos: (A) A. Gazzard, (B) BHPS (2022a), and (C) Pixabay (2022).

Thesis rationale and structure

The UK hedgehog population has declined markedly over recent decades (Roos *et al*., 2012; Croft *et al*., 2017; Mathews *et al*., 2018). Although living in towns and cities is not without its challenges, urban habitats may provide key refuge for hedgehogs.

Consequently, there is an urgent need to increase our knowledge of urban hedgehog ecology such that existing and future conservation strategies can be appropriately formulated based on scientific evidence. It is evident that gardens, as well as factors such as garden accessibility, supplementary feeding and artificial refugia, are likely to be important to individual hedgehogs in urban areas. However, our understanding of the relevance of these factors within the context of the conservation of populations is limited. To that end, and considering the current knowledge gaps that exist in the field of urban hedgehog ecology, the work presented here aimed to:

(1) Quantify habitat selection and, on a finer scale, garden use and factors affecting garden use by hedgehogs in an urban residential area;

(2) Document over-winter activity patterns of hedgehogs in gardens and investigate whether they might be influenced by 'urban-associated' factors such as supplementary feeding;

(3) Explore the significance of artificial refugia (nest boxes) to hedgehog conservation by assessing factors affecting nest box use, and

(4) Quantify motivations for and barriers to engagement in creating hedgehog highways as promoted by the Hedgehog Street campaign, and to review the potential ecological consequences of the initiative.

Each corresponding study has been submitted to a peer-reviewed journal and is presented here in its manuscript form; formatting and referencing styles have been made consistent throughout the thesis. Further details of each chapter are given below.

Chapter 2: Fine-scale habitat selection of a small mammalian urban adapter; the West European hedgehog (*Erinaceus europaeus*)

Previous studies of habitat use by urban hedgehogs have provided insight into populations occupying suburbs containing houses built primarily in the 1930s (Dowding *et al*., 2010a), or merged results from multiple locations varying in housing structure and density (Schaus Calderón, 2021). Further studies have identified factors affecting the presence/absence of hedgehogs in gardens (Baker and Harris, 2007; Hof and Bright, 2009; Williams *et al*., 2015; Williams *et al*., 2018a), but these have not been able to determine the extent to which gardens were used by hedgehogs as the data collection protocols were intrinsically unable to discriminate between hedgehogs that were just travelling through gardens versus those spending greater amounts of time in gardens for e.g., foraging. Therefore, in this study, I tracked 28 hedgehogs in an area of modern high-density housing using radio and GPS tags to investigate patterns of habitat use and to identify factors within and outside gardens that affected the proportion of each night spent in individual gardens. The conservation implications of these results, as well as considerations relating to GPS fix acquisition rates <100% when tracking urban hedgehogs in particular and urban animals in general, are discussed.

This study was published in the journal *Mammalian Biology*.

Chapter 3: Patterns of feeding by householders affect activity of hedgehogs (*Erinaceus europaeus*) during the hibernation period

Many wildlife organisations encourage householders to leave out food for hedgehogs in their gardens during winter to aid the accumulation of fat prior to hibernation and also to provide sustenance for individuals during their periodic arousals (BHPS 2020; Tiggywinkles Wildlife Hospital, 2020). However, it is possible that continuing to feed hedgehogs throughout this period may influence natural hibernation behaviours (Morris, 2018).

To investigate levels of hedgehog activity in urban gardens over winter and the potential impacts of supplementary feeding and other within-garden and off-site factors, I recorded weekly hedgehog occupancy in 63 gardens using footprint tunnels during November 2017-April 2018. Data were also gathered on garden features, patterns of supplementary feeding before and during the study, proximity to other habitat types, and environmental parameters. The effects of these variables on hedgehog presence/absence in gardens during the hibernation period were investigated using occupancy analysis.

This study was published in the Applied Hedgehog Conservation Research special issue of the journal *Animals*.

Chapter 4: What makes a house a home? Nest box use by West European hedgehogs (*Erinaceus europaeus*) is influenced by nest box placement, resource provisioning and site-based factors.

In the UK, householders are commonly urged by wildlife organisations to install ground-level nest boxes in their gardens for hedgehogs (BBC, 2014; Hedgehog Street, 2021a; The Wildlife Trusts, 2021b). However, little has been documented with regard to the use of hedgehog nest boxes and whether certain design, placement or site-based features might influence how they are used, yet an absence of knowledge of what constitutes effective artificial refugia can set back conservation efforts (Cowan *et al*., 2020). Therefore, for this study, a questionnaire survey of UK residents owning hedgehog nest boxes was conducted. The questionnaire gathered information that included the types of nest boxes owned, their positioning, other features within the garden as well as resources provided directly by the householder. The results were analysed to investigate factors influencing nest box use, including use for summer day or winter day resting, breeding or hibernation.

This study was published in the journal *PeerJ*.

Chapter 5: An assessment of a conservation strategy to increase garden connectivity for hedgehogs that requires cooperation between immediate neighbours: a barrier too far?

The Hedgehog Street campaign is a UK initiative that has been operating for over a decade with the primary aim of encouraging householders to ensure that their gardens are accessible to hedgehogs. Connecting gardens with hedgehog-accessible points through garden boundaries – termed hedgehog highways – is widely recognised as a potentially valuable conservation action for hedgehogs and is also promoted by other organisations such as The Wildlife Trusts, the RSPB and, more recently, some housing developers. However, the effects of highways on hedgehog movement patterns, and ultimately hedgehog populations, have not been studied to date.

The initial goal of this chapter was, therefore, to conduct a field experiment to quantify hedgehog movements and space-use before and after hedgehog highways had been installed in a residential area of modern high-density housing in Reading, Berkshire. However, volunteer recruitment proved to be very difficult, even after the use of a 'prize draw' to try to incentivise householders (see Appendix E for further details); similar problems were encountered when the experiment was re-located to Oxford. Consequently, the study evolved into a project exploring how successful Hedgehog Street had been and identifying motivations/barriers to creating hedgehog highways in UK gardens.

This chapter presents the analysis of three online questionnaire surveys open to residents across the UK between 2018-2020, one of which specifically targeted volunteers who had signed up to the Hedgehog Street campaign ('Hedgehog Champions'). The specific objectives of this study were to: (i) measure the proportions of Hedgehog Champions and non-Champions who had created a hedgehog highway; (ii) identify the factors associated with the creation of highways; (iii) examine the reasons given for not having created a highway; (iv) discuss the potential effect of the creation of these highways on hedgehog movement patterns; and (v) outline recommendations for the future growth of the Hedgehog Street campaign.

This study was published in the journal *PLoS ONE*.

Chapter 6: Discussion

The final chapter unifies and summarises the results of the four manuscripts included in this thesis. The implications of this research for future hedgehog conservation strategies, as well as future research needs, are also discussed.

Appendices A-D:

Supporting information for each study presented in Chapters 2-5.

Appendix E:

Details of volunteer recruitment rates of an intended field experiment quantifying patterns of hedgehog movements before and after the creation of hedgehog highways in gardens. Appendix E includes a description of methodology, notes on public engagement activities and results of door-to-door questionnaire surveys undertaken to examine why householders within the study site(s) did not wish to take part, despite initially high levels of interest.

Appendix F:

A short report of the results of four seasons (2016-2019 inclusive) of hedgehog capture-mark-recapture surveys that were primarily undertaken to aid Chapters 2 and (the initial aims of) 5. The information presented includes sex ratio, average body mass, marker detachment rates and estimates of apparent survival and encounter probability of an urban hedgehog population. However, it should be noted that intra- and inter-annual recapture rates were relatively low, possibly due to sampling effort or limited access to private gardens.

Appendix G:

Descriptive statistical results of nest box temperature and humidity measurements, relative to varying box designs and placement (in the open or under shrub cover).

Appendix H:

The results of static tests of GPS tags undertaken to explore variations in fix success rate associated with different garden locations believed to be commonly used by hedgehogs (e.g., under sheds; under decking).

Chapter 2

Fine-scale habitat selection of a small mammalian urban adapter; the West European hedgehog (*Erinaceus europaeus*)

Gazzard, A., Yarnell, R.W. & Baker, P.J. (2022) Fine-scale habitat selection of a small mammalian urban adapter; the West European hedgehog (*Erinaceus europaeus*). *Mammalian Biology* 102, 87-403.

Abstract

Understanding patterns of habitat selection and factors affecting space use is fundamental in animal conservation. In urban landscapes, such knowledge can be used to advise householders on how best to manage their gardens for wildlife. In this study, we tracked 28 West European hedgehogs (*Erinaceus europaeus*), a species of conservation concern in the UK, in an area of high-density housing using radio and GPS tags to quantify patterns of habitat use and identify factors associated with the proportion of time spent in individual gardens. Both males and females exhibited a preference for residential gardens, but there were subtle differences between the sexes in relation to house type and front versus back gardens. Hedgehogs spent significantly more time in gardens where artificial food was provided, where a compost heap was present, if foxes (*Vulpes vulpes*) were infrequent visitors, if it rained overnight and as daylength increased (i.e., shorter nights); garden use was not significantly associated with variables potentially likely to reflect invertebrate prey abundance. These data suggest that the primary positive action that householders can undertake for urban hedgehogs is providing supplementary food. However, householders often feed hedgehogs after they know they are already visiting their garden. Consequently, the presence of artificial food may make it difficult to identify other important influences affecting garden use. Finally, we report that a GPS fix acquisition rate <60% likely had no major effect on the results of our analyses but should be a consideration in future studies using this technique on this species and in this habitat.

Introduction

Urbanisation poses significant threats to biodiversity worldwide (Seto *et al.,* 2012; Concepción *et al.,* 2015), causing habitat loss, degradation and fragmentation (Theodorou *et al.,* 2020), human-wildlife conflicts (Soulsbury and White, 2015; Adams, 2016), the introduction of non-native species (McKinney, 2006; Gaertner *et al.,* 2017), exposure to pollutants (Ditchkoff *et al.,* 2006; Grimm *et al.,* 2008) and wildlife-vehicle collisions (Wright *et al.,* 2020). Urban landscapes can, nonetheless, provide key habitats for animals (Goddard *et al.,* 2013; Löki *et al.,* 2019; Soanes and Lentini, 2019; Spotswood *et al.,* 2021) as well as refuge from predators (Møller, 2012) and access to abundant resources (Oro *et al.,* 2013). As a result, some species are now found only in urban areas (Oliveira Hagen *et al.,* 2017; Soanes and Lentini, 2019), whereas other species, including some of conservation concern (e.g., Coleman and Barclay, 2012; Orros and Fellowes, 2015), can be found at substantially higher densities in towns and cities compared to rural landscapes (Blair, 1996; Tryjanowski *et al.,* 2007; Alexandre *et al.,* 2010; Bateman and Fleming, 2012; Kettel *et al.,* 2019). Understanding how animals utilise urban spaces has therefore become increasingly important as urbanisation rates continue to rise (Ritchie, 2018; Gonçalves-Souza *et al.,* 2020).

One way to gain insight into how animals use urban spaces is through habitat selection analyses to assess habitat preferences and/or avoidances within the context of landscape-scale distribution or home range utilisation (Saunders *et al.,* 1997; Dowding *et al.,* 2010a; Thomas *et al.,* 2014; Roberts *et al.,* 2017; Mueller *et al.,* 2018). However, understanding habitat use on a finer scale can yield greater benefits in conservation planning (Gilioli *et al.,* 2018), particularly for species that perceive the environment at small spatial scales (Ritchie and Olff, 1999), have limited dispersal ability (Gilioli *et al.,* 2018) and/or which may be associated with specific habitats or microhabitats (Banks and Skilleter, 2007). The way in which such individuals move within and between habitats will be dependent on intra- and inter-specific interactions, environmental conditions, and site-based variables such as resource availability and quality (Morris, 2003; Roberts *et al.,* 2017; Bista *et al.,* 2019).

Residential gardens within urban areas are favoured by a range of fauna (Saunders *et al.,* 1997; Newman *et al.,* 2003b; Murgui, 2009; Dowding *et al.,* 2010a) and can collectively cover a substantial area. For example, private domestic gardens constitute 35–47% of greenspace in some UK cities (Loram *et al.,* 2007), and cover > 430,000 ha in the UK as a whole (Davies *et al.,* 2009). On a finer scale, the structure of and features within individual gardens can vary markedly as the result of differences in garden size, householders' gardening preferences and their management decisions (Gaston *et al.,* 2005; Smith *et al.,* 2006a; Goddard *et al.,* 2013). Consequently, there is likely to be fine-scale variation in the functional value of different individual gardens both within and between species.

Assessing how animals use individual gardens, and identifying underlying causal factors, can however be challenging. First, it requires gaining access to privately owned land, or recruiting homeowners to provide data; homeowners' willingness to engage in such projects can be affected by pre-existing environmental interests (Dyson *et al.,* 2019) and differences between project types, places and cultures (Sakurai *et al.,* 2015). Second, within-garden characteristics are likely to fluctuate over time, sometimes over very short timescales. For example, invertebrate prey abundance has been shown to vary with weeding practices (Jaganmohan *et al.,* 2013) and temporal and microclimatic parameters (Martay and Pearce-Higgins, 2018), whilst anthropogenic food availability depends on the regularity of householders' wildlife feeding habits and the volume of food supplied (Davies *et al.,* 2012). Last, quantifying how animals use gardens necessitates the use of specialist equipment such as GPS or radio tracking devices, camera traps or microchip readers to monitor fine scale movements (Galbraith *et al.,* 2017; Van Helden *et al.,* 2020b). Each of these are, however, associated with their own advantages and disadvantages including cost, reliability, accuracy and welfare concerns (Coulombe *et al.,* 2010; Wearn and Glover-Kapfer, 2019). In light of these challenges, preliminary studies would be useful in identifying suitable methodologies for use in such investigations.

One species that is commonly associated with gardens, yet is challenging to study in urban landscapes, is the West European hedgehog (*Erinaceous europaeus*; hereafter 'hedgehog'), a small (<1.5kg), nocturnal insectivore (Morris, 2018). It is thought that rural hedgehog populations in Britain have declined markedly in recent decades (Harris *et al.,* 1995; Mathews *et al.,* 2018) probably due to habitat loss and fragmentation (Bearman-Brown *et al.,* 2020), intensive agricultural practices and predation by or intraguild competition with the European badger (*Meles meles*) (Young *et al.,* 2006; Trewby *et al.,* 2014; Williams *et al.,* 2018b). Hedgehogs nowadays occur in higher densities in urban settings (Hubert *et al.,* 2011; van de Poel *et al.,* 2015; Schaus *et al.,* 2020) where the risk of predation by badgers appears to be comparatively low (Hubert *et al.,* 2011; Pettett *et al*., 2017) whilst the abundance of anthropogenic foods and nesting opportunities is likely high (Hubert *et al.,* 2011; Pettett *et al*., 2017; Gimmel *et al.,* 2021). Nonetheless, urban areas are associated with a range of additional mortality risks not typically evident in rural landscapes, including disturbance by humans or domestic animals (Rasmussen *et al*. 2019a; Rast *et al*. 2019), exposure to urban-associated pollutants and pesticides (Dowding *et al*. 2010b;

Taucher *et al*. 2020), barriers to movement created by built structures including roads (Rondinini and Doncaster 2002) and fences (Gazzard *et al*. 2021), and road traffic accidents (Wright *et al*. 2020).

In addition to sex, season and environmental conditions, hedgehog movement behaviour also varies between urban landscapes (Dowding *et al.,* 2010a; Rasmussen *et al.,* 2019a; Schaus Calderón 2021) potentially due to differences in building density (Schaus Calderón 2021), road type (Rondinini and Doncaster, 2002) and disturbance levels (Berger *et al.,* 2020a). Irrespective of this, hedgehogs consistently favour back gardens (Baker and Harris 2007; Hof and Bright 2009; Dowding *et al.,* 2010a; Williams *et al.,* 2015; Williams *et al.,* 2018a; Rasmussen *et al.,* 2019a; Gazzard and Baker, 2020; Schaus Calderón 2021) and are thought to require access to around 13-14 back gardens per night (Rasmussen *et al.,* 2019a; Schaus Calderón, 2021). However, only a minority of gardens available within a given area appear to be utilised (Williams *et al.,* 2018a; Schaus Calderón, 2021). Consequently, multiple studies have attempted to identify those factors affecting garden use (Baker and Harris, 2007; Hof and Bright, 2009; Williams *et al.,* 2015; Williams *et al.,* 2018a; Gazzard and Baker, 2020) but these have relied on hedgehog presence/absence data such that they have not been able to identify whether animals were using gardens for e.g., foraging versus simply passing through, nor differentiate between gardens based on intensity of use. Overall, therefore, our understanding of the extent to which different factors influence patterns of garden use is limited (Williams *et al.,* 2018a; Schaus Calderón, 2021).

Understanding which factors affect hedgehogs' patterns of garden use would have clear conservation implications as members of the public could be advised on how to manage their gardens in a 'hedgehog-friendly' way. This is particularly relevant in the UK where urban gardens may be increasingly important as the national hedgehog population declines. Within the UK at the current time, there is particular emphasis on the construction of high-density housing in urban locations, including on greenfield and brownfield sites (Department for Communities and Local Government, 2017); this type of housing is, by definition, associated with smaller gardens than those evident in earlier periods of rapid housing development (Loram *et al.,* 2007). Therefore, the aim of this study was to investigate patterns of habitat use and garden selection by hedgehogs in an area of high-density housing as these are likely to be the dominant form of new housing in the UK for the foreseeable future. In particular, we: (i) used global positioning system (GPS) and radio tracking data in compositional analyses (Aebischer *et al.,* 1993) to identify key habitats and garden types; and (ii) used GIS data and householder questionnaire surveys to investigate the effects of outside- and within-garden factors on the time hedgehogs spent in individual gardens. Last, GPS fix acquisition rates in mammal tracking studies are commonly <100% (Hofman *et al.,* 2019), including in previous studies of hedgehogs (Rodriguez Recio *et al.,* 2013; Braaker *et al.,* 2014), because tags with limited 'sky-view' (e.g., tags under dense canopy cover) can fail to connect to sufficient satellites (Ironside *et al.,* 2017); such 'missing data' have the potential to confound the sorts of analyses outlined above if they are, for example, associated with particular habitat types and/or movement characteristics. Therefore, we (iii) conducted a series of assessments of these missing fixes to identify whether they were likely to have impacted our results or not.

Methods

The study was conducted in a 5.8 km^2 area of Earley, Reading, UK (51°25'N, 0°55'W; population > 33,000), bordered by a University of Reading campus, major A-roads and the River Loddon. Earley is a residential area that falls within the urban sprawl of Reading Town, having undergone rapid urbanisation in the late 20th century (Earley Town Council, 2017). Earley is now characterised by a series of medium- and high-density housing developments (approximately 20.5 houses ha^{-1} across the entire survey area, but with some estates reaching 38.1 houses ha^{-1}: Schaus Calderón, 2021) constructed predominantly during the 1970s–1990s and which consist of streets and cul-de-sacs of detached, semi-detached and terraced houses with their associated gardens (Ward, 2004; Wokingham Borough Council, 2012; Earley Town Council, 2017). Median garden size is 167m^2, below the national average of 188m^2 (Office for National Statistics, 2022).

Tracking data

Hedgehogs were captured by hand during nocturnal transect surveys undertaken between June-October 2016-2018 inclusive. Trained surveyors walked along public footpaths using torches to systematically search for hedgehogs. On occasion, local householders contacted the surveyors to notify us of active hedgehogs in gardens, in which case surveyors would be granted access to the garden to record and tag hedgehogs as appropriate. Captured individuals were weighed, sexed and uniquely marked by securing short sections of numbered heat shrink tubing over approximately five spines posterior to the head (Reeve *et al.,* 2019a). Suitable healthy adults weighing >600g were fitted with either very high frequency radio (VHF; TW-3, Lotek UK, 10.8g) or GPS (PinPoint 250 VHF Swift, Lotek UK, 10g) tags (hereafter, 'tags'), ensuring tag weight was <5% of the animal's body mass (Sikes and Gannon, 2011). Tags were attached to a clipped area (~2cm^2) of spines below the hedgehog's rump in a central position using epoxy resin. Hedgehogs were released at the point of capture typically within 5-10 minutes and monitored until they moved away to ensure individuals were not impeded by the tags.

Hedgehogs were tracked during June-October of 2016-2018 inclusive for 1-9 full nights (excluding nights on which the tags were attached or detached); one individual was tracked in more than 1 year (in 2017 and 2018), with the tag removed between years. Location fixes were recorded every 5 minutes from 22:00-04:00 British Summer Time (BST), yielding up to 73 fixes per night. VHF tagged animals were tracked on foot by triangulation with a VHF Sika receiver and hand-held three-element Yagi antenna (Lotek UK). Both tag types were retrieved by tracing their radio signal either when they became detached (e.g., when the hedgehog moved through small gaps under garden fences) or by recapturing the animal at the end of the study. All handling, tagging, and tracking procedures were performed under ethical approval by the University of Reading and under licence by Natural England (refs: 20130866-0-0-0-5 and 2017-29687-SCI-SCI).

Outlying data points within the GPS dataset were identified and removed by examining consecutive fixes for implausible locations and speed of travel. In line with Braaker *et al.* (2014), fixes were excluded where they indicated speed of movement was >1m per second; none of the VHF fixes indicated speeds greater than this. The remaining fixes from each full tracking session were used to construct 100% minimum convex polygons in QGIS 3.4.4, representing nightly areas ranged (NAR) by each hedgehog. Differences in mean NAR between the sexes and between tag types were tested using independent t-tests: if a hedgehog was tracked for >1 night, then their nightly MCPs were first averaged before analyses; if the variances of the two samples were unequal, a Welch-Satterthwaite type correction was applied (Ruxton, 2006). For each full night of tracking, the total number of front and back gardens used (defined as a garden where ≥1 fixes were recorded) was also counted in QGIS with the aid of satellite imagery and an OS Mastermap® Topography Layer (© 2020 Ordnance Survey) to define garden boundaries.

Each hedgehog location was assigned to one of eight habitat categories: front gardens of (1) detached, (2) semi-detached, (3) terraced houses; back gardens of (4) detached, (5) semi-detached, (6) terraced houses; (7) amenity grassland; and (8) other habitats (roads and other areas of hardstanding, scrub, woodland and freshwater). Habitats within the study area were digitised in QGIS based upon satellite imagery, the OS Mastermap® Topography Layer (© 2020 Ordnance Survey) and land class datasets available through the UK Centre for Ecology & Hydrology (Morton *et al.,* 2020a).

Missing GPS fixes

Due to changes in tag availability and budget, hedgehogs were fitted with VHF tags in 2017 and GPS tags in 2016 and 2018. These tag types produce movement data of comparable accuracies that generate similar home range estimates (Coulombe *et al.,* 2006; Glasby and Yarnell, 2013), and thus data from both tag types were used in our analyses. However, since GPS tags can sometimes fail to connect to sufficient satellites to generate a location fix (Ironside *et al.,* 2017), we assessed the patterns of missing GPS fixes to determine whether they were associated with abnormal movements or atypical habitats in five ways.

First, we collated the frequency with which different numbers of consecutive fixes were or were not recorded to identify whether missing fixes tended to occur in large groups. Second, we quantified the proportion of programmed fixes that were recorded versus not recorded, and how these varied throughout the 6h tracking regimen. This would help identify whether missing fixes tended to occur at specific times of the night. Third, the size of nightly range areas (see below) was compared between those animals tracked using VHF tags, where all fixes were recorded every night, versus those tracked using GPS tags to see whether missing fixes in the latter resulted in significantly smaller nightly range estimates. Fourth, the minimum straight-line distances moved between different blocks of consecutive fixes where the intervening locations were fully or partially recorded versus those where all intervening locations had been missed were quantified (see Appendix A, Figure A1); these comparisons enabled us to determine whether hedgehogs had tended to move significantly further across blocks of missing data or not. Finally, the possible effect of hedgehogs moving into different habitats where fixes may be particularly prone to be missed was investigated by comparing the habitat composition of pooled home range areas (see below) against the habitat composition of pooled home ranges after a 100m buffer zone had been added to the points immediately preceding and following a block (of any size) of missing fixes.

All of the above analyses indicated that there was little evidence that missing GPS locations were associated with unusual movements or atypical habitats (see Appendix A). Instead, the pattern of missing fixes appeared to be consistent with the assumption that GPS-tagged hedgehogs were moving normally within habitats but were periodically in proximity to structures that could potentially block their GPS signal, such as fences or buildings, but also perhaps underneath structures such as decking and sheds where they may be resting. Overall, therefore, we do not believe that there are likely to be any significant biases in the habitat types nor individual gardens where the positions of GPS tagged hedgehogs were and were not recorded. Consequently, the analyses outlined below are based on the assumption that the locations of GPS tagged animals are a random sub-sample of those of the hedgehogs tracked. The implications of this assumption are considered in the Discussion.

Compositional analysis of habitat use

Compositional analysis was implemented using the adehabitatHS package in R 4.0.3 with 1000 iterations of the randomisation test (Aebischer *et al.,* 1993; Calenge, 2006); this compares the log ratios of each individual's 'used' versus 'available' habitats to indicate whether a habitat was used more (or less) than others based on their aerial availability (Aebischer *et al.,* 1993; Calenge, 2006). A ranking matrix was then constructed to display the differences in log ratios of all possible pairs of habitat categories. Wilks' lambda (Λ) was used to test whether the difference between the proportion of habitat selected/used versus available differed significantly from zero (i.e., habitat use is 'non-random'). Since there are known to be marked spatial differences in the areas ranged by male and female hedgehogs both on a nightly basis but also over the course of several nights (Kristiansson, 1984; Reeve, 1982; Rondini and Doncaster, 2002; Dowding *et al.,* 2010a; Morris, 2018), and to identify any contrasts in habitat preference between the sexes, habitat use was analysed separately for males and females.

Habitat selection was evaluated at two levels (Johnson, 1980). First, the selection of habitats in the context of the positioning of ranges within the wider landscape was quantified by comparing the habitat composition of individual ranges with that of the study site. Individual's overall ranges were calculated as the MCP encompassing all of their known tracking locations (hereafter 'pooled range area': PRA). The study area was defined by a 500m buffer surrounding all PRAs (Sparks *et al.,* 2005; Dickson *et al.,* 2012; Pettett *et al*., 2017); this buffer was based upon existing hedgehog movement data (Kristiansson, 1984; Reeve, 1982; Rondini and Doncaster, 2002; Dowding *et al.,* 2010a; Morris, 2018) and research that identified habitat within 500m was of relevance to hedgehog occupancy in gardens (Gazzard and Baker, 2020). Second, habitat use by each hedgehog within their PRA was assessed by comparing the proportion of fixes recorded in each habitat to the proportion of total habitat available within the range. For both analyses, values of zero of 'used' habitats were substituted with 0.01, as recommended by Aebischer *et al.* (1993). Buildings were considered inaccessible to hedgehogs and were excluded from all analyses.

Factors affecting proportionate garden use

Factors affecting the use of back gardens were further investigated using generalised linear mixed models (GLMMs) with binomial distributions (Warton and Hui, 2011). The response variable comprised the proportion of a tracking night known to have been spent in an individual garden (hereafter 'proportionate garden use': PGU). PGU was calculated by dividing the number of location fixes recorded in a single garden by 73 (the maximum number of fixes that could have been recorded each night).

Measures of PGU could be obtained from the same hedgehog but for different gardens in a single night and/or the same garden over different nights. To account for any parallels between data collected from the same individual, therefore, hedgehog ID was included as a random effect. Similarly, it was possible for an individual garden to appear more than once in the dataset if, for example, they were used by different hedgehogs on the same night or the same hedgehog on different nights. However, we elected to not treat garden ID as a grouping/random effect since we were interested in quantifying the effects of garden differences, rather than controlling for this.

Explanatory variables included factors specific to (a) tagged hedgehogs, (b) gardens, (c) environmental conditions at the time of garden use, and (d) alternative habitats present within 500m of the garden (Table 2.1). Continuous variables were z-transformed so that their effects could be easily compared (Schielzeth, 2010). Habitat data were digitised and measured using Natural Environment Research Council land class datasets (Morton *et al.,* 2020a). Environmental data (temperature and rainfall) were obtained from the University of Reading's Whiteknights campus weather station (Met Office, 2012), which borders the study site; daylength data were taken from the Benson weather station, 18km north (Thorsen, 2020). Therefore, these variables represent general climatic conditions at the time of tracking rather than specific microclimatic parameters within individual gardens. For the variables describing individual garden characteristics, data were collected during door-to-door householder questionnaire surveys undertaken on site during 2016. In some instances, householders were not contactable, or did not wish to take part, and tagged hedgehogs inevitably utilised areas outside of the surveyed households. Therefore, the data that were available for this analysis represent a subsample of gardens (N = 49) that were known to be used by hedgehogs. Although red foxes (*Vulpes vulpes*) were present on the study site, badgers were not.

Table 2.1. Summary of variables considered in GLMM analysis of factors affecting proportionate nightly garden use by hedgehogs. Column headed 'Themes' indicates

variables specific to: (*a*) individuals; (*b*) used gardens; (*c*) environmental conditions; and (*d*) alternative habitats present within 500m of the garden. Data were derived from: VHF and GPS tracking surveys (T); questionnaire surveys of householders (Q); or from an external source described in the main text (E).

Theme	**Name**	**Description**	**Source**
Dependent variable	GARDENUSE	Proportion of time spent in a back garden by an individual hedgehog during a tracking night, measured as the number of fixes recorded there divided by 73 (the total number of nightly fixes)	T
a	SEX	Sex of the tracked hedgehog	T
a	MASS	Body mass (g) of the hedgehog immediately prior to tagging	T
b	AREA	Area (m^2) of the back garden	E
b	HOUSETYPE	Binary measure of whether the house associated with the garden was detached or semi-detached (NB: no other house types were utilised in this sample)	Q
b	ACCESS	Number of adjoining back gardens that were accessible to hedgehogs from the respondent's own back garden (values ranged from 0-3)	Q
b	FRONTTOBACK	Binary measure of whether hedgehogs could access the respondent's back garden via their own front garden	Q
b	GREENHABITAT	Proportion of habitat within the back garden which consisted of 'green' habitat (lawn, plantings such as shrubs)	Q
b	FOX	Frequency at which the respondent observed foxes in their garden. 4 levels: 0 = never, 1 = <monthly, 2 = monthly, 3 = at least weekly	Q
b	PEST	Binary measure of whether molluscicides, insecticides and/or rodenticides were ever applied in the garden	Q
b	FOOD	Binary measure of whether food was ever supplied intentionally for hedgehogs and/or birds in the garden	Q
b	LOGPILE	Binary measure of whether a log pile was present in the garden	Q
b	COMPOST	Binary measure of whether a compost heap was present in the garden	Q
b	POND	Binary measure of whether a pond was present in the garden	Q
b	SHED	Binary measure of whether the garden contained a shed	Q

b	LIGHTING	Binary measure of whether the garden was ever illuminated at night via artificial lighting (motion-activated or timed)	Q
c	TEMPERATURE	Minimum air temperature (°C) logged between 21:00-09:00 on the tracking night	E
c	RAINFALL	Binary measure of whether it rained on the tracking night	E
c	DAYLENGTH	Length of day (time between sunrise & sunset) prior to the nocturnal tracking session	E
d	GARDENS500m	Area (m^2) of all gardens (front, back & communal) within 500m of the 'used' garden	E
d	BACKGARDENS500m	Area (m^2) of all back gardens within 500m of the 'used' garden	E
d	WOODLAND500m	Area (m^2) of woodland within 500m of the 'used' garden	E
d	AMENITY500m	Area (m^2) of amenity grassland within 500m of the 'used' garden	E
d	BUILDINGS500m	Area (m^2) of buildings within 500m of the 'used' garden	E

Multicollinearity checks were performed by examining the correlation structure of the explanatory variables, and further checking variance inflation factors (Fox and Monette, 1992). The variance inflation factor threshold was chosen to be <2 (see Zuur *et al.*, 2010). The modelling process entailed successively adding variables and comparing Akaike's Information Criterion (AIC) values between models, with the lowest AIC value indicating the greatest level of parsimony (Burnham and Anderson, 1998; Richards 2005). However, in some cases, where a variable marginally worsened or did not affect model fit, but which was considered meaningful to interpretation, the variable was retained even if non-significant. Models were constructed with a log link function and fitted by Laplace approximation, using the lme4 package in R; global and final models were checked for overdispersion. Odds ratio values (Rita and Komonen, 2008) and marginal and conditional R^2 values (Nakagawa *et al.,* 2017) are provided for the final model: marginal R^2 represents the proportion of variance explained by fixed effects; conditional R^2 represents the proportion of variance explained by both fixed and random effects.

Results

Including all GPS and VHF tagged hedgehogs, 28 individuals (13 males and 15 females) were tracked over 98 complete nights, generating 2920 fixes via VHF tags (73 fixes collected for all hedgehogs on all nights) and 2254 via GPS tags (nightly mean ± SD: 40 ± 10). Mean (± SD) NAR areas of males (3.54 ± 3.06ha) were significantly larger than those of females (0.71 ± 0.31ha: Table 2.2; $t_{12} = 3.33$, $p < 0.01$); however, mean NAR areas did not differ significantly between tag types for either males (GPS: 5.37 ± 4.66ha; VHF: 3.00 ± 3.24ha; $t_{11} = -1.21$, $p = 0.25$) or females (GPS: 0.87 ± 0.31ha; VHF: 0.61 ± 0.29ha; $t_{13} = 1.69$, $p = 0.11$). The mean number of back gardens used per night was 8.1 ± 5.3 (range: 0-27). Furthermore, on only two occasions did hedgehogs fail to use gardens completely; in both instances, the animals roamed relatively small areas (≤0.25ha) and spent most of the night foraging in hedgerows adjacent to houses. The mean number of front and back gardens used nightly by an individual did not significantly differ between males and females (back gardens: $t_{27} = 1.10$, $p = 0.28$; front gardens: $t_{27} = 0.24$, $p = 0.82$). However, back gardens were visited more frequently by both sexes; males used a mean of 3.4 (± 3.3) front and 8.7 (± 6.8) back gardens compared to 4.5 (± 2.7) and 6.8 (± 3.5) for females, respectively.

Table 2.2. Summary of hedgehogs tracked in Reading, UK, their mean nightly area ranged (100% MCPs), maximum speeds of movements and mean number of back gardens used. If animals were tracked >1 night, the range of nightly MCPs and gardens used are given in parentheses. Body mass indicates mass at the time of tagging. Data are based on complete nights of tracking undertaken between 22:00-04:00 British Summer Time inclusive.

ID	Sex	Year	Mass (g)	Tag type	Nights tracked	Total fixes	Max. speed (m/s)	Mean nightly MCP (ha)	Mean no. gardens used
1	M	2017	977	VHF	1	73	0.73	5.12	4
2	M	2017	987	VHF	1	73	0.63	1.01	5
3	M	2017	875	VHF	1	73	0.56	4.16	9
4	M	2017	782	VHF	1	73	0.35	0.93	3
5	M	2017	944	VHF	1	73	0.24	0.46	3
6	M	2017	962	VHF	1	73	0.49	5.38	5
7	M	2017	1016	VHF	1	73	0.20	0.83	7
8	M	2017	1078	VHF	2	146	0.24	0.68 (0.25-1.11)	3.00 (0-6)
9	M	2017	1062	VHF	3	219	0.80	7.27 (3.94-11.00)	10.33 (8-13)
10	M	2017	993	VHF	4	292	0.93	4.10 (0.20-10.24)	5.75 (5-8)
11	M	2018	1202	GPS	5	245	0.69	10.37 (6.75-14.46)	22.00 (13-27)
12	M	2018	952	GPS	6	244	0.39	4.56 (1.38-7.91)	14.67 (11-22)
13	M	2018	1148	GPS	7	300	0.55	1.20 (0.71-2.23)	11.17 (9-14)
14	F	2016	655	GPS	8	280	0.43	1.23 (0.05-3.04)	10.38 (6-15)
15	F	2016	720	GPS	8	257	0.33	0.97 (0.38-1.47)	5.00 (3-9)
16	F	2017	1081	VHF	1	73	0.31	0.65	8
17	F	2017	871	VHF	1	73	0.21	0.44	11
18	F	2017	926	VHF	1	73	0.19	0.80	8
19	F	2017	1157	VHF	1	73	0.22	1.22	2

20	F	2017	810	VHF	2	146	0.23	0.91 (0.89-0.93)	3.50 (3-4)
21	F	2017	822	VHF	3	219	0.24	0.39 (0.32-0.43)	3.00 (2-4)
22	F	2017	702	VHF	3	219	0.27	0.47 (0.20-0.63)	5.00 (2-7)
23	F	2017	935	VHF	4	292	0.19	0.37 (0.12-0.80)	4.50 (3-6)
24	F	2017	817	VHF	4	292	0.27	0.35 (0.05-0.74)	5.50 (3-9)
25	F	2017	647	VHF	4	292	0.31	0.50 (0.18-1.07)	2.50 (2.00-5.00)
25	F	2018	1102	GPS	5	208	0.30	0.70 (0.25-0.98)	7.83 (4.00-16.00)
26	F	2018	700	GPS	5	243	0.20	0.55 (0.23-0.68)	6.00 (2.00-10.00)
27	F	2018	830	GPS	6	249	0.32	0.59 (0.21-0.78)	8.83 (3.00-15.00)
28	F	2018	1189	GPS	6	226	0.15	1.23 (0.89-1.65)	7.83 (6.00-11.00)

Habitat selection

Front and back gardens comprised 10.1% and 20.7% of the study area, respectively, with 13.6% of land occupied by buildings, 10.8% by roads, 16.3% by amenity grassland and the remaining 28.5% by other habitat types (see Appendix A, Table A2 for a full breakdown). The selection of habitats within each hedgehog's PRA relative to their availability across the study site was non-random for males ($\Lambda = 0.07$, $p < 0.01$) and females ($\Lambda = 0.19$, $p = 0.02$). At this scale, front and back gardens of terraced houses ranked first and second most favoured habitats for both sexes (Table 2.3 overleaf). Amenity grassland occurred the least in PRAs relative to its overall availability.

Within their ranges, males exhibited a preference for the back gardens of detached houses, followed by the back gardens of semi-detached houses ($\Lambda = 0.07$, $p = 0.02$; Table 2.4). Conversely, for females, the front gardens of detached houses and the back gardens of detached and semi-detached houses were equally top-ranking, although, overall, habitats within their ranges did not appear to be used in a statistically non-random manner ($\Lambda = 0.15$, $p = 0.14$).

Table 2.3. Habitat rankings for **(a)** male (N= 13) and **(b)** female (N = 15) hedgehogs estimated using compositional analysis to compare the proportion of habitats present in each individual's overall range relative to the proportion of habitats available in the study area. Habitat abbreviations: gardens associated with D = detached, SD = semi-detached and T = terraced houses; A = amenity grassland; O = other habitats (roads and other areas of hardstanding, scrub, woodland, freshwater). Tables indicate mean differences in log-ratios between 'selected' and 'available' habitats (shown in rows and columns, respectively). Positive values indicate a preference; negative values indicate avoidance. Values in bold represent significantly non-random habitat selection ($p < 0.05$). Habitat categories are ranked from most (8) to least preferred (1).

(a) Males

Habitat		*Front gardens*			*Back gardens*			*Other*		*Rank*
		D	SD	T	D	SD	T	A	O	
Front gardens	D		0.15	-0.84	**0.32**	0.20	-0.71	**1.32**	0.05	*6*
	SD	-0.15		-0.99	0.16	0.05	-0.87	**1.17**	-0.10	*4*
	T	0.84	0.99		**1.16**	1.04	0.12	**2.16**	**0.89**	*8*
Back gardens	D	**-0.32**	-0.16	**-1.16**		-0.12	-1.03	**1.01**	-0.26	*2*
	SD	-0.20	-0.05	-1.04	0.12		-0.91	**1.12**	-0.15	*3*
	T	0.71	0.87	-0.12	1.03	0.91		**2.04**	0.77	*7*
Other	A	**-1.32**	**-1.17**	**-2.16**	**-1.01**	**-1.12**	**-2.04**		**-1.27**	*1*
	O	-0.05	0.10	**-0.89**	0.26	0.15	-0.77	**1.27**		*5*

(b) Females

Habitat		*Front gardens*			*Back gardens*			*Other*		*Rank*
		D	SD	T	D	SD	T	A	O	
Front gardens	D		-0.03	**-1.38**	0.11	0.57	**-1.14**	0.63	-0.01	*4*
	SD	0.03		**-1.35**	0.14	**0.60**	-1.11	0.66	0.02	*6*
	T	**1.38**	**1.35**		**1.48**	**1.95**	0.24	**2.01**	**1.37**	*8*
Back gardens	D	-0.11	-0.14	**-1.48**		0.47	**-1.25**	0.53	-0.12	*3*
	SD	-0.57	**-0.60**	**-1.95**	-0.47		**-1.71**	0.06	-0.58	*2*
	T	**1.14**	1.11	-0.24	**1.25**	**1.71**		**1.77**	**1.13**	*7*
Other	A	-0.63	-0.66	**-2.01**	-0.53	-0.06	**-1.77**		-0.64	*1*
	O	0.01	-0.02	**-1.37**	0.12	0.58	**-1.13**	0.64		*5*

Table 2.4. Habitat rankings for **(a)** male (N = 13) and **(b)** female (N = 15) hedgehogs estimated using compositional analysis to compare the proportion of VHF and GPS fixes recorded in each habitat type to the proportion of habitats available within each hedgehog's total range. Habitat abbreviations: gardens associated with D = detached, SD = semi-detached and T = terraced houses; A = amenity grassland; O = other habitats (roads and other areas of hardstanding, scrub, woodland, freshwater). Tables show mean differences in log-ratios between the 'used' and 'available' habitats (shown in rows and columns, respectively). Positive values indicate a preference; negative values indicate avoidance. Values in bold represent significantly non-random habitat use at $p < 0.05$. Habitat categories are ranked from most preferred (8) to least preferred (1).

(a) Males

Habitat		*Front gardens*			*Back gardens*			*Other*		*Rank*
		D	SD	T	D	SD	T	A	O	
Front gardens	D		0.37	0.77	**-0.81**	0.06	-0.08	0.52	**1.18**	*6*
	SD	-0.37		0.57	**-1.07**	-0.16	-0.29	**0.77**	**0.94**	*4*
	T	-0.77	-0.57		**-1.27**	-0.56	-0.89	-0.27	0.17	*2*
Back gardens	D	**0.81**	**1.07**	**1.27**		**1.06**	0.76	1.20	**2.00**	*8*
	SD	-0.06	0.16	0.56	**-1.06**		-0.40	0.64	**1.11**	*5*
	T	0.08	0.29	0.89	-0.76	0.41		0.30	**1.03**	*7*
Other	A	-0.52	**-0.77**	0.27	-1.20	-0.64	-0.30		0.41	*3*
	O	**-1.18**	**-0.94**	-0.17	**-2.00**	**-1.11**	**-1.03**	-0.41		*1*

(b) Females

Habitat		*Front gardens*			*Back gardens*			*Other*		*Rank*
		D	SD	T	D	SD	T	A	O	
Front gardens	D		0.09	0.23	0.07	-0.12	0.11	0.82	**1.43**	*8*
	SD	-0.09		0.13	-0.26	-0.44	0.07	1.09	**1.15**	*5*
	T	-0.23	-0.13		-0.12	-0.51	-0.13	0.61	**1.14**	*3*
Back gardens	D	-0.07	0.26	0.12		0.05	0.01	0.82	**1.57**	*8*
	SD	0.12	0.44	0.51	-0.05		0.45	**2.30**	**1.37**	*8*
	T	-0.11	-0.07	0.13	-0.01	-0.45		0.69	**1.47**	*4*
Other	A	-0.82	-1.09	-0.61	-0.82	**-2.30**	-0.69		0.13	*2*
	O	**-1.43**	**-1.15**	**-1.14**	**-1.57**	**-1.37**	**-1.47**	-0.13		*1*

Factors affecting proportionate garden use

Data from 118 occasions of garden use were used in the GLMM analysis; these included data from a total of 49 gardens and 7 hedgehogs (4 males, 3 females) tracked in June-September 2017 or September 2018. The variables AMENITY500m and BACKGARDENS500m were excluded from the analysis as they were strongly correlated with garden AREA; similarly, BUILDINGS500m was excluded as it was correlated with WOODLAND500m.

When random effects (individual hedgehogs) were accounted for, proportionate garden use was significantly negatively linked to: the presence of front-to-back access into the garden; fox sightings; the presence of a pond; whether it had rained on the tracking night; and the quantity of garden habitat present within 500m of the used garden (Table 2.5). Conversely, hedgehogs appeared to spend significantly more time in gardens where food was provided, where a compost heap was present and when daylength was longer (i.e., in the summer).

Table 2.5. The final GLMM of factors affecting proportionate nightly garden use by hedgehogs (N = 118). For categorical variables, reference terms are given in parentheses. Coefficients and odds ratios represent population average estimates (non-specific to individual hedgehogs). Schielzeth and Nakagawa's R^2: marginal $R^2 = 0.162$; conditional $R^2 = 0.659$. * = $p < 0.05$, ** = $p < 0.01$., *** = $p < 0.001$.

	Estimate	Std. Error	z	p	OR	95% CI	
(Intercept)	-1.988	0.961	2.069	0.039	0.137	0.021-0.901	
AREA	0.100	0.090	1.120	0.263	1.106	0.927-1.318	
FRONTTOBACK (Inaccessible)	-	-	-	-	-	-	
Front to back accessible	-0.549	0.139	3.952	<0.001	0.578	0.440-0.758	***
GREENHAB	0.003	0.004	0.590	0.555	1.003	0.994-1.011	
FOX (Absent from garden)	-	-	-	-	-	-	
Observed <monthly	0.357	0.180	1.978	0.048	1.429	1.003-2.035	*
Observed monthly	-0.049	0.199	0.245	0.806	0.952	0.645-1.406	
Observed weekly	-0.755	0.294	2.566	0.010	0.470	0.264-0.837	*
FOOD (Food not provided)	-	-	-	-	-	-	
Food provided	0.325	0.157	2.064	0.039	1.384	1.017-1.883	*
POND (Absent)	-	-	-	-	-	-	
Pond present	-0.650	0.191	3.399	0.001	0.522	0.359-0.759	**

COMPOST (Absent)	-	-	-	-	-	-	
Compost heap present	0.331	0.148	2.240	0.025	1.392	1.042-1.860	*
SHED (Absent)	-	-	-	-	-	-	
Shed present	-0.322	0.200	1.614	0.107	0.724	0.490-1.072	
LIGHTING (No artificial lighting)	-	-	-	-	-	-	
Artificial lighting	0.012	0.144	0.085	0.932	1.012	0.763-1.343	
TEMPERATURE	0.145	0.098	1.472	0.141	1.156	0.953-1.401	
RAIN (Did not rain)	-	-	-	-	-	-	
Rained on tracking night	-0.716	0.259	2.769	0.006	0.488	0.294-0.811	**
DAYLENGTH	0.953	0.237	4.029	<0.001	2.593	1.631-4.123	***
GARDENS500	-0.163	0.081	2.004	0.045	0.850	0.725-0.996	*
WOODLAND500	0.123	0.090	1.373	0.170	1.131	0.949-1.349	

Discussion

The use of GPS tags to record animal movements has become increasingly popular in ecological research (Nielson *et al.,* 2009) as they can produce large quantities of continuous data periods whilst reducing surveyor effort and minimising disturbance (Adams *et al.,* 2013; Glasby and Yarnell, 2013). However, GPS tags are often associated with constraints relating to cost, battery life, location error and fix success rate (Adams *et al.,* 2013; Glasby and Yarnell, 2013; Hofman *et al.,* 2019). Missing or erroneous location fixes resulting from restricted 'sky-view' (Ironside *et al.,* 2017) are not unusual when GPS tracking animals in urban areas (e.g., van Heezik *et al.,* 2010; Hanmer *et al.,* 2017), including hedgehogs: for 18 hedgehogs tracked in Zurich, <50% of all possible GPS fixes were obtained (Braaker *et al.,* 2014). Similarly, following data cleaning, a minimum of 46% of fixes were retained for hedgehogs tracked in Berlin (Berger *et al.,* 2020b) and, in a GPS hedgehog tracking project in Regents Park, London, average fix success rate was 41% (Reeve *et al.,* 2019b). In the current study, only 57% of all possible GPS locations were recorded (see Appendix A).

Failure to record GPS locations could be attributed to several factors. Hedgehogs often navigate landscapes by travelling parallel to linear structures (Hof *et al.,* 2012) such as hedgerows, fences or walls (Yarnell *et al.,* 2014) which might block or reflect satellite signals (Adams *et al.,* 2013). Buildings in particular are thought to create difficulties for GPS tracking in urban locations (Rose *et al.,* 2005), yet their effect on fix success rate is likely to be more pronounced where building height is greater, i.e., in highly urbanised centres (Adams *et al.,* 2013); in our study, houses were typically two stories high. Alternatively, the use of artificial features such as garden decking, cavities beneath garden sheds, hedgehog nesting/hibernation boxes and other refugia for shelter during the night (Morris, 2018) could impede satellite connection by GPS tags. Hedgehogs also use 'feeding stations' (typically wooden, brick or plastic boxes) installed by householders in gardens so that they can supply artificial foods for hedgehogs whilst simultaneously preventing non-target species such as domestic cats or foxes from accessing the food, and/or to protect hedgehogs from predators such as badgers (e.g., Rasmussen *et al.,* 2019a; Finch *et al.,* 2020). Consequently, loss of satellite connection could be linked to movements alongside built structures as well as periods of sheltering or feeding under cover, all of which are normal behaviours for hedgehogs in gardens (Morris, 2018).

Overall, it is considered unlikely that the missing fixes reported in this study were linked to atypical movements or habitat use. This is because: (i) the duration of missing fixes primarily comprised short bouts of 1-5 consecutive misses and mirrored the pattern of non-missing fixes; (ii) the distance moved during blocks of missing fixes was broadly similar, or lower, to that observed for straight-line distances moved between known locations; (iii) there was no significant difference in mean nightly area ranged for hedgehogs equipped with VHF versus those fitted with GPS tags, and (iv) the addition of a 100m buffer around all fixes preceding or following a block of missing fixes did not significantly affect the habitat composition of individual pooled ranges. We have therefore assumed that the unrecorded (and recorded) fixes were a random sample of the locations of each hedgehog's movement trajectory over the course of the night, and such random missing data should not have any substantive effect on the results of our habitat use analyses (see Nielson *et al.,* 2009).

Habitat selection

Hedgehogs exhibited a preference for residential gardens: gardens of terraced houses were present disproportionately more in hedgehog ranges relative to their availability in the study site and gardens of detached and semi-detached houses were selected over other habitat types within ranges. This is consistent with previous studies (Dowding *et al.,* 2010a; Schaus Calderón, 2021) and underlines the potential importance of gardens in future conservation efforts for this species.

In contrast, areas of amenity grassland, which were typically present as private or public sports fields, were the least preferred habitat. These are typically highly managed and are often also used for exercising dogs (*Canis lupus familiaris*) throughout the day and early night. Consequently, they are associated with high levels of disturbance and little natural prey (Martay and Pearce-Higgins, 2018), although earthworms may be relatively abundant on warm wet nights. However, foxes are also attracted to sports fields on such nights (Saunders *et al.,* 1997) and hedgehogs may seek to avoid these (see below). Furthermore, such greenfield sites are increasingly being developed to meet housing demands in UK towns and cities. Paradoxically, therefore, although such developments may be controversial, their conversion to housing and associated gardens could represent a net gain in resources for urban hedgehog populations.

Factors affecting use of back gardens

The proportional use of residential back gardens was significantly affected by a range of biotic and abiotic factors as well as within- and outside-garden factors, the former being under the control of individual householders whereas the latter are not. In the context of within-garden variables, garden use was positively associated with the provisioning of artificial food and the presence of a compost heap, and negatively associated with front garden to back garden access, the presence of a pond; four non-significant variables were also retained to improve model fit: the presence of either a garden shed and/or artificial lighting, the proportion of the garden covered by lawn and other plantings, and garden area.

Although definitive data are lacking, the supplemental feeding of hedgehogs does appear to have become increasingly common amongst UK householders (Morris, 1985; Morris, 2018; Gimmel *et al.,* 2021). However, it appears that, in many cases, householders only start to put food out once they know that hedgehogs are already visiting their garden. As such, artificial food cannot be a factor that originally attracted hedgehogs to the garden but, once present, it may become a major influence. In the context of the objectives of our study, this may therefore represent a significant confounding effect (i.e., the presence of anthropogenic food may reduce the ability to identify other factors that initially attracted hedgehogs to those gardens). Disentangling these factors would require some form of experimental manipulation (e.g., temporally withdrawing supplementary food) but this is likely to be logistically difficult given the perceived importance of artificial food by those householders that do feed hedgehogs.

However, it is worth noting that the odds ratio associated with the presence of food (OR = 1.384; Table 2.5) was not that large in comparison with other factors that also positively affected garden use. As outlined above, it is plausible that we may have underestimated the amount of time spent in gardens where artificial food was available if GPS fixes were missed when hedgehogs were inside feeding shelters, but it is also possible that there are limitations associated with using 'time spent in the garden' as the metric by which to judge garden quality. For example, in contrast with natural prey, anthropogenic foods are typically predictable and abundant. Therefore, they require little foraging effort and hedgehogs may be able to obtain their entire daily energy requirement in one location in a relatively short space of time. This negative relationship between anthropogenic food intake and foraging time could also potentially indicate that our approach to measuring garden use would under-estimate the relative importance of gardens where these foods are available.

In addition, supplementary feeding could be associated with a range of negative impacts including changes in hibernation behaviour (Gazzard and Baker, 2020), increased disease transmission risk (Rasmussen *et al.,* 2019a) and/or a reduction in dietary quality (Gimmel *et al.,* 2021). For example, commercially available hedgehog foods in Switzerland contained high quantities of cereals that would otherwise not be part of the hedgehog's natural diet (Gimmel *et al.,* 2021). Additionally, the consumption of soft foods (e.g., canned pet or hedgehog foods) has been linked to tartar formation in hedgehogs (Sainsbury *et al*. 1996; Bexton and Couper 2019) which may have harmful consequences for oral health (Gimmel *et al*. 2021), though this has not been corroborated. Nonetheless, anthropogenic food is likely to be a key driver of hedgehog abundance in urban areas (Hubert *et al.,* 2011) and could provide critical sustenance for vulnerable individuals (Reeve, 1994). Further studies are needed, therefore, to examine the quality and quantity of food supplied by householders and to determine how this benefits and/or impacts local hedgehog populations such that appropriate advice can be given to householders.

Hedgehogs also spent more time in gardens where compost heaps were present; these are thought to be attractive to hedgehogs (Williams *et al.,* 2015; Taucher *et al.,* 2020) either by providing nest sites/material (Molony *et al.,* 2006; Pettett *et al*., 2017), or as a source of invertebrate prey (Curds, 1985). Conversely, the proportion of the garden covered by lawn and other plantings was unimportant, whereas garden ponds were significantly negatively correlated with proportionate garden use. This is perhaps surprising as both can support a diversity of invertebrate prey species (Smith *et al.,* 2006b; Ancillotto *et al.,* 2019) and the creation of ponds is recommended by hedgehog conservation groups. One possible explanation for this negative relationship is that householders who feed hedgehogs also typically put out water for them to drink. Consequently, it may be that hedgehogs attracted to gardens where householders are putting out food are also able to access sufficient water, implying that they then do not necessarily need to visit other gardens with ponds. Furthermore, the metrics used here do not necessarily give any indication of the quality or management practices of ponds or green habitats (such as mowing regimes) within gardens, which may influence the use of gardens by hedgehogs via, e.g., driving invertebrate abundance (Smith *et al.,* 2006b).

Access into and between gardens has been highlighted as a potentially major form of habitat fragmentation for urban hedgehog populations and is the focus of the Hedgehog Street campaign (run by the People's Trust for Endangered Species and British Hedgehog Preservation Society) which aims to persuade householders to create holes in or under their fences to improve inter-garden connectivity (Gazzard *et al.,* 2021). Although access into neighbouring back gardens (ACCESS) did not affect proportionate garden use, hedgehogs spent less time in gardens where access from the back garden to the front garden (FRONTTOBACK) was possible. The underlying reason for this is not immediately obvious. At one level, this could indicate a fragmentation effect (i.e., they are spending more time in gardens where they are not able to leave via the front garden), but this seems unlikely given that they were able to access, and presumably leave, that garden via other routes. Similarly, spending less time in back gardens where access to the front garden was available may reflect the absence of a fragmentation effect, but could conversely indicate a preference for front gardens. In fact, both sexes used the front gardens of detached houses to a much greater extent than their aerial availability and females also exhibited a stronger preference for the front gardens of other types of housing than males. It is possible, therefore, that females may be using front gardens to avoid competition with and/or harassment from males, or simply competition with other conspecifics. Identifying whether this is the case would necessitate detailed observations of the behaviour of animals within both front and back gardens; this could be achieved using trail cameras, CCTV cameras or even security cameras installed by householders as a deterrent to criminal activity. These sorts of recording devices would be unlikely to affect hedgehog behaviour, especially as artificial lighting did not affect garden use in this study and has also been shown not to affect foraging behaviour at artificial feeding stations (Finch *et al.,* 2020).

Further variables retained in the final model were related to factors beyond the control of individual householders: the total area of gardens (GARDENS500) and woodland (WOODLAND500) within a 500m radius of the focal garden, and focal garden area (AREA). Of these, only the former was significant, indicating that hedgehogs spent less time in individual gardens when the area of gardens in the surrounding landscape increased. This possibly reflects the fact that, as garden availability increases, then the reliance on individual gardens decreases. Conversely, the absence of a significant effect of garden size is surprising, given that previous studies have highlighted differences in engagement with wildlife-friendly gardening activities with garden size (Gaston *et al.,* 2007; Loram *et al.,* 2008; Goddard *et al.,* 2013), and that both male and female hedgehogs exhibited a preference for the back gardens of detached houses within their ranges, which typically tend to comprise larger gardens. The latter is marginally different to the results of Dowding *et al.* (2010a) who suggested that female hedgehogs in Bristol potentially avoided the back gardens of detached houses because of the potential presence of badgers. In our study, however, badgers were not reported by any of the householders surveyed indicating that these were unimportant in this district of Reading; in other districts, the presence of badgers does appear to significantly reduce the use of gardens by hedgehogs (Williams *et al.,* 2018a).

Although badgers were absent on the study site, many participants had observed foxes using their back gardens. Urban foxes are widespread in the UK (Scott *et al.,* 2014) and typically occur in higher densities in towns and cities than in rural locations (Bateman and Flemming 2012). Foxes will predate hedgehogs (Morris, 2018; Rasmussen *et al.,* 2019a) but also compete with them for a range of different foods, including that put out by householders (Pettett *et al*., 2018). Consequently, hedgehog distribution has been negatively linked to fox abundance in the UK (Pettett *et al*., 2018). In contrast to other studies where no significant association between hedgehog occupancy and the presence of foxes was observed (Hof and Bright, 2009; Williams *et al.,* 2018b), we found that hedgehogs were likely to spend more time in gardens where foxes were less frequent visitors (<monthly) and less time where foxes visited at least weekly. This suggests that whilst hedgehogs are not completely deterred by foxes, they may seek to reduce their risk of predation and competition by spending less time in gardens which foxes also utilise frequently. Hedgehogs might also exhibit similar behavioural responses to domestic dogs (Williams *et al.,* 2018a; Rasmussen *et al.,* 2019a), although many pet dogs are secured inside their owner's home for much of the night during which hedgehogs are active. We were not able to investigate this in this study as too few householders owned pet dogs.

Abiotic parameters such as temperature and rainfall can also influence the spatial behaviour of mammals (van Beest *et al.,* 2012; Maestri and Marinho, 2014). In hedgehogs, nightly ranges and activity levels have been recorded to increase with higher temperatures, although only after midnight when vehicular and pedestrian traffic is reduced (Dowding *et al.,* 2010a). In our study, minimum nightly temperature did not impact garden use possibly because it was not reflective of temperature change throughout the night or specific temperatures within gardens, implying that future studies need to record microclimatic conditions within individual gardens more intensively. Conversely, hedgehogs did spend significantly less time in gardens during nights when it had rained. As outlined above, studies of urban foxes (Saunders *et al.,* 1997) have noted an increased tendency to utilise playing fields under these conditions because of increased earthworm availability, but they will also do the same in residential gardens (P. Baker, pers. obs.). Therefore, it might be expected that rainfall would increase hedgehog activity within gardens contrary to what we observed. However, the relative abundance of earthworms in gardens versus playing fields is not well known. One alternative possibility is that the reduced use of gardens on rainy nights was associated with hedgehogs seeking shelter (and potentially impacting the satellite connection with GPS tags).

Conclusion

Studying urban wildlife poses its own particular set of problems, not least because much of the landscape is privately-owned and difficult to observe directly from publicly-accessible space. Consequently, there is the need to develop novel approaches to address key questions. In this study, we used radio and GPS tracking in combination with *a priori* questionnaire surveys of householders to identify factors that affected patterns of habitat and individual garden use by West European hedgehogs. Two major limitations were encountered: first, only 57% of planned GPS locations were recorded; second, we were only able to quantify the characteristics of 49 gardens subsequently visited by tracked hedgehogs. Consequently, we were not able to perfectly map the movement trajectory of tracked animals. As such, our results should be regarded as preliminary, with future studies required to validate or refute them.

We therefore recommend that authors should routinely publish the percentage of scheduled GPS fixes which are missed and consider the implications of these missing data on the research questions being considered. In this study, there was no evidence that missing GPS fixes affected estimates of the nightly area ranged by hedgehogs or patterns of habitat use. We postulate that most missing fixes were associated with hedgehogs' tendency to skirt linear features such as fences when travelling, but also to be inside feeding stations or sheltering in refugia under e.g., sheds and decking. This may mean, therefore, that we have under-estimated the relative time spent in gardens where artificial food was supplied by householders.

Residential gardens were preferred habitats although there were differences in the relative rankings of front and back gardens of different house types between male and female hedgehogs. This suggests possible differential uses of resources, and/or patterns of selection and avoidance. The proportion of time spent in back gardens was associated with a range of biotic and abiotic factors both within and outside those gardens. In particular, hedgehogs were more likely to have spent a greater proportion of their time in back gardens where artificial food was available, where compost heaps were present and where householders perceived foxes were uncommon visitors, but spent less time in these gardens on nights when it rained, where access to the front garden was possible and where foxes were perceived as frequent visitors. It was not possible to consider any effects of badgers as these were absent from the study site.

Surprisingly, time spent in gardens was significantly negatively associated with the presence of a pond and not significantly affected by the proportion of garden covered by microhabitats that might support invertebrate prey, factors which are highlighted by conservation NGOs as being of benefit to hedgehogs. It is possible, however, that the absence of any positive benefits from these factors may be obscured by the presence of artificial food and water but also by limited knowledge of how invertebrate prey abundance varies between gardens and within gardens over time. Therefore, we have three further recommendations for future studies. First, the relative contribution of food provided by householders to the total food intake of urban hedgehogs needs to be determined. This is of importance as hedgehogs may potentially be especially dependent on the behaviour of a relatively small number of householders, but also because they may have higher rates of contact with conspecifics at feeding stations: this could increase competition and the risk of disease transfer. In addition, if hedgehogs are obtaining most of their food from householders, this is likely to make it difficult to identify the relative importance of other within-garden factors on patterns of garden use without some form of experimental manipulation. Second, video recordings of hedgehog activity within gardens would enable a much more detailed analysis of how the within-garden factors considered in this study influence their behaviour. In addition, such recordings would also enable us to consider patterns of interactions between individual hedgehogs, but also between hedgehogs and other species including domestic cats and dogs, foxes and badgers. Third, invertebrate surveys are required to determine how the availability of key prey groups varies spatially and temporally within urban gardens.

Chapter 3

Patterns of feeding by householders affect activity of hedgehogs (*Erinaceus europaeus*) during the hibernation period

Gazzard, A. & Baker, P.J. (2020) Patterns of feeding by householders affect activity of hedgehogs (*Erinaceus europaeus*) during the hibernation period. *Animals* 10, 1344.

Abstract

West European hedgehogs (*Erinaceus europaeus*) are likely to encounter unusual ecological features in urban habitats, such as anthropogenic food sources and artificial refugia. Quantifying how these affect hedgehog behaviour is vital for informing conservation guidelines for householders. We monitored hedgehog presence/absence in gardens in the town of Reading, UK, over the winter of 2017-2018 using a volunteer-based footprint tunnel survey, and collected data on garden characteristics, supplementary feeding (SF) habits and local environmental conditions. Over a 20-week survey period, hedgehog presence was lowest between January-March. Occupancy analysis indicated that SF significantly affected hedgehog presence/absence before, during and after hibernation. The number of nesting opportunities available in gardens, average temperatures and daylength were also supported as important factors at different stages. In particular, our results suggest that SF might act to increase levels of activity during the winter when hedgehogs should be hibernating: stimulating increased activity at this sensitive time could push hedgehogs into a net energy deficit or, conversely, help some individuals survive which might not otherwise do so. Further research is therefore necessary to determine whether patterns of feeding by householders have a positive or negative effect on hedgehog populations during the hibernation period.

Introduction

Hibernation is critical for the over-winter survival of a range of vertebrate and invertebrate species (Leather *et al*., 1993; Cáceres, 1997; Wells, 2007; Ruf and Geiser, 2014). A reduced core body temperature and lowered metabolic rate allows individuals to conserve energy during periods of harsh environmental conditions and low food supply at the cost of becoming physically inactive for periods lasting days, weeks or months (Martin and Yoder, 2014). To ensure success, mammalian hibernators must increase food intake prior to entering hibernation to accumulate sufficient fat reserves which will later provide energy for day-to-day body maintenance and inducing arousal (Reeve, 1994; Martin and Yoder, 2014). If too little fat is accumulated, individuals are in danger of depleting their reserves before the hibernation season is over (Kristiansson, 1990; Jensen, 2004; Morris, 2018). In addition, survival during hibernation is also likely to be linked to nest quality (Morris, 1973) and local environmental conditions (Rasmussen *et al*., 2019a).

The West European hedgehog (*Erinaceus europaeus*) is a small (<1.5kg) winter-hibernating mammal that is thought to be in decline in the UK (Roos *et al*., 2012; Mathews *et al*., 2018). The specific drivers of this decline are unclear, although a wide range of threats can be recognized, including: habitat loss, fragmentation and degradation (Becher and Griffiths, 1998; Rondini and Doncaster, 2002; Hof and Bright, 2009; Hof and Bright, 2010; Moorhouse *et al*., 2014); road traffic accidents (Huijser and Bergers, 2000; Wembridge *et al*., 2016; Wright *et al.*, 2020); the application of chemical herbicides, pesticides and molluscicides, as well as the use of anticoagulant rodenticides (Reeve, 1994; Dowding *et al*., 2010b; Morris, 2018); competition with and predation by badgers (*Meles meles*) (Young *et al*., 2006; Trewby *et al*., 2014; Pettett *et al*., 2018; Williams *et al*., 2018a), and climate–driven changes in invertebrate prey availability and hibernation success (Morris, 2018).

Although timings differ in relation to climate, sex, body size and condition, hedgehogs typically hibernate between November and April in the UK (Reeve, 1994; Morris, 2018). It is not unusual for hedgehogs to temporarily rouse during the hibernation period and active individuals may relocate to alternative nests (Morris, 1973; Reeve, 1994; Yarnell *et al*., 2019). These partial arousals can last anywhere from several hours to several days (Walhovd, 1979; Webb and Ellison, 1998; Morris, 2018). Since hedgehog hibernation timings are variable, it is difficult to pinpoint which factors trigger the process of entering and arousing from hibernation, although it is likely to involve environmental and hormonal cues related to lower ambient temperatures, shorter days and reduced invertebrate prey availability (Morris, 2018).

Evidence suggests that hedgehogs are increasingly associated with areas of human habitation (Doncaster, 1994; Williams *et al*., 2018b) with substantially higher densities observed in towns and cities than in rural habitats (Hubert *et al*., 2011; van de Poel *et al*., 2015; Schaus *et al*., 2020). Despite a relative plethora of studies on the winter activity of captive, rehabilitated or rural-dwelling hedgehogs (Soivio *et al*., 1968; Morris, 1973; Parkes, 1975; Tähti and Soivio, 1977; Walhovd, 1979; Dmi'el and Schwarz, 1984; Fowler and Racey, 1990; Webb and Ellison, 1998; Jensen, 2004; Yarnell *et al*., 2019), our understanding of the behaviour of urban-dwelling hedgehogs during this period is limited (Rasmussen *et al*., 2019a).

Urban areas are associated with a range of factors that could potentially positively or negatively affect patterns of hibernation. For example, in addition to potential nesting sites in patches of remnant natural or semi-natural vegetation, hedgehogs can access cavities beneath buildings, gardens sheds or decking within residential gardens; urban residents may also supply artificial refugia in the form of homemade or commercially available 'hedgehog houses' (Hubert *et al*., 2011; Morris, 2018). However, within each of these habitats/locations, hedgehogs will be exposed to different levels of disturbance from: humans and/or companion animals (Stocker, 1987; Rast *et al*., 2019); road traffic (Huijser and Bergers, 2000); and artificial light (Finch *et al*., 2020) and sound. Similarly, temperatures within different microhabitats are likely to vary in relation to e.g., the density and composition of surrounding buildings and associated structures (Hubert *et al*., 2011; Perini and Magliocco, 2014). It is possible that such 'urban-associated' factors could have direct impacts upon the onset of and patterns of arousal during hibernation. For example, warmer temperatures in urban areas (Chapman *et al*., 2017) may stimulate early arousal from hibernation which, in turn, could increase fat consumption, thereby posing a risk to over-winter survival (Morris, 2018; Rasmussen *et al*., 2019a).

It has been suggested that supplementary feeding may, in particular, negatively affect natural patterns of hibernation behaviour in hedgehogs (University of Brighton, 2017). In the UK, many wildlife organisations actively encourage householders to leave out food for hedgehogs in gardens during the colder months in an effort to aid the accumulation of fat prior to hibernation but also to provide sustenance during periodic arousals when natural food availability is low (e.g., Hedgehog Street, 2019; British Hedgehog Preservation Society, 2020; Tiggywinkles Wildlife Hospital, 2020). The effects of anthropogenic feeding on some aspects of the ecology of urban wildlife (e.g., density, health, reproductive output) have been investigated extensively (e.g., Robb *et al*., 2008; Ewen *et al*., 2014; Murray *et al*., 2016), but data on the impacts on hibernating species are limited: key observations are that over-winter supplementary feeding is linked to the increased probability of sighting animals (Bojarska *et al.*, 2019), interruptions to denning behaviour (Krofel *et al.*, 2017) and accelerated telomere attrition (Kirby *et al.*, 2019). Conversely, artificial food sources could provide invaluable additional sustenance for individuals in need (Reeve, 1994).

Overall, urban areas act as significant strongholds for the UK hedgehog population and expanding our knowledge of over-winter activity and the parameters affecting it is fundamental to developing robust conservation management strategies. Studies are therefore needed which investigate (a) activity patterns of urban hedgehogs throughout the hibernation season, and (b) how these are affected by external factors. In this study, we quantified patterns of hedgehog occupancy within residential gardens before, during and after the winter season (see Methods for our definition of the winter season) in relation to within-garden and surrounding habitat characteristics, environmental conditions (e.g., daylength and temperature) and patterns of anthropogenic feeding.

Methods

Footprint tunnel survey

Hedgehog presence/absence surveys were carried out in the back gardens of private households in the town of Reading, UK (51°, 27' N: 0°, 58' W; population: > 230,000; area: > 60 km^2) and its outskirts from 18th November 2017-7th April 2018. Badgers and foxes (*Vulpes vulpes*) – both potential predators of hedgehogs and competitors for hedgehog food – are present in Reading, although records of the former indicate that they are limited to the northern section of the town (Williams *et al.,* 2018a). Domestic dogs (*Canis familiaris*) were present in some gardens surveyed, but these are typically confined to the owner's garden from approximately 11pm whereas hedgehogs can be active throughout the night; consequently, dogs have been shown not to affect patterns of hedgehog occupancy (Williams *et al.,* 2018a). Similarly, there is no evidence to suggest that domestic cats (*Felis catus*) are likely to affect hedgehog occupancy either: cats pose little direct threat to hedgehogs and there is an abundance of anecdotal evidence of both species using the same garden at the same time.

Volunteers (citizen scientists) were recruited through an advert on social media in October 2017: interested participants were asked to provide information on their garden location, current hedgehog-feeding habits and, to the best of their knowledge, the frequency with which hedgehogs used their garden (ranging from 'never' to 'every night'). This information was used to categorise volunteers as those who were feeding hedgehogs prior to the start of the study itself (and, by default, who had hedgehogs in their garden), those who were not feeding hedgehogs at this time but who had them visiting their garden, and those who were not feeding hedgehogs at this time and who did not think they visited their garden. As we were interested in investigating the patterns of behaviour of hedgehogs in relation to the existing pattern of feeding by householders (i.e., this was an observational study), and because we were reliant on members of the public agreeing to participate, the distribution of households relative to one another and garden size were dependent on the volunteers themselves; these issues are considered further below.

Prior to the start of the study, householders that had been feeding hedgehogs were asked to either continue feeding them for the duration of the study (November-April) or to stop feeding completely; asking them to maintain a consistent pattern of feeding throughout the study simplified the analyses, especially as we had to assign the start and end of the hibernation period, retrospectively. Consequently, the sample of householders consisted of four groups: (i) people that had been feeding hedgehogs previously and who continued to feed throughout the study; (ii) people that had been feeding hedgehogs previously but who stopped feeding for the duration of the study; and householders that did not feed hedgehogs before and during the study but who (iii) did or (iv) did not think they had hedgehogs in their garden. For those people that elected to continue feeding hedgehogs throughout the project, we asked that they carried on feeding at the same frequency, giving the same volume of food each time and not altering the type of food: this approach was adopted to avoid unduly affecting patterns of hedgehog behaviour in relation to changes in the amount of food available.

Gardens were surveyed using footprint tunnels, which have been used previously to survey hedgehogs in both rural and urban environments (e.g., Huijser and Bergers, 2000; Yarnell *et al*., 2014; Williams *et al*., 2015; Williams *et al*., 2018a; Williams *et al*., 2018b). Each householder was given one footprint tunnel and instructed to place the tunnel in their rear garden in a position where they thought hedgehogs would be likely to encounter it (e.g., parallel to fences at points where animals could enter the garden). Tunnels consisted of folded corrugated plastic in the form of a triangular tunnel (1200mm x 210mm x 180mm) (Yarnell *et al*., 2014). Ink (carbon powder mixed with vegetable oil) was applied to two strips of masking tape either side of a food bait (~30g of commercially available dry hedgehog food) in the centre of a removable plastic insert inside the tunnel; two sheets of A4 paper were fastened at either end of the insert to 'capture' footprints of any hedgehogs that traversed through. In order to attract animals without significantly influencing their behaviour, the pot containing the food was sealed but pierced with small holes to allow the scent of the bait to escape; this would prevent hedgehogs (and foxes or domestic cats) from depleting the food bait within a given survey period. Volunteers were given sufficient supplies for the footprint tunnel (e.g., food bait, ink, paper) to last the duration of the study as well as an instruction booklet and animal tracks identification guide.

Volunteers checked their tunnels every Saturday and submitted weekly presence/absence results of all tracks recorded through an online survey form (SurveyMonkey.com). Any suspected hedgehog footprints were photographed and sent digitally to one of the authors (AG) for verification. The study was terminated after 20 weeks when volunteer interest had started to decline (weekly reminders to prompt the submission of results needed to be increased markedly in the latter stages).

Dividing the data into seasons

Whilst it is understood that hibernation timings will vary between individuals, we opted to subdivide the data into 'seasons' that broadly reflected stages before, during and after the principal hibernation period (henceforth denoted as autumn, winter and spring). The purpose of this approach was to allow us to analyse the influence of different factors across the contrasting phases of the hibernation season when hedgehogs may be expected to place different emphasis on those factors. For example, the availability of anthropogenic food sources may be more important in the autumn season than the winter season, whereas the reverse may be true when considering access to a secure long-term nest site. Additionally, one assumption of occupancy analysis which we have used to analyse these data is that sites remain closed to changes in occupancy between sampling visits (MacKenzie and Royle, 2005). This assumption would have been violated had the data been analysed as one continuous season as, for example, hedgehogs may have consistently used gardens during autumn and spring but not during winter.

The cut-off dates encompassing each season were informed by the pattern in occupancy observed during the 20-week survey. When ≤ 15% sites were occupied each week, the majority of hedgehogs were considered to be inactive and any data collected during that time were allocated to the winter category. Thus, the three time periods were identified as Weeks 1-7 (18/11/17-05/01/2018), Weeks 8-16 (06/01/2018-09/03/2018), and Weeks 17-20 (10/03/2018-06/04/2018), respectively. Although we concede that this is an a posteriori approach to defining the hibernation period, the timing of low occupancy is in line with that reported elsewhere for hibernation in Britain at this latitude (Morris, 1973; Morris, 2018; Wright *et al.*, 2020). Analyses were, however, also conducted with an alternative cut-off threshold (≤ 20% sites occupied: Weeks 6-16) to investigate the consistency of the occupancy models; no marked differences in the results were evident (see Table B1 in Appendix B).

Data analysis

Pearson Chi-squared tests were used initially to assess whether hedgehogs tended to be consistently present or absent in the same gardens between seasons. The effects of the variables listed in Table 3.1 on hedgehog presence/absence within each season were investigated using occupancy analysis, a technique which has been used successfully in previous studies of hedgehogs (Yarnell *et al*., 2014; Williams *et al*., 2018a; Williams *et al*., 2018b). In occupancy modelling, an optimisation process is used to find the maximum likelihood of an event occurring. Data from each season were initially analysed independently of any covariates to identify whether the best-fitting baseline models were ones where weekly detection rates (p) were considered constant (detection probability did not vary between weeks within that season) or survey-specific (detection probability did vary between weeks within that season). These initial analyses are also used to compare naïve occupancy (the proportion of sites where hedgehogs were detected) and true occupancy (Ψ: an estimate of the proportion of sites where hedgehogs were present, accounting for false absences). Analyses were conducted using Presence 12.24.

Variables were quantified using an online questionnaire at the end of the study, from the data itself or from external sources (Table 3.1). The questionnaire survey requested information about features within the participant's back garden, the proportion of neighbouring gardens that were accessible to hedgehogs from their own garden, patterns of feeding during the study and the number of potential nesting sites.

Table 3.1. Summary of the variables used in analysis, collected from questionnaire surveys and external data sources. Q indicates that the data were derived from a questionnaire survey of the householder; D indicates that the variable was extracted from the occupancy data itself; E indicates data from an external source (see text)

Covariate	**Source**	**Description**
FEEDHOG	Q	An ordinal measure of whether food was left out for hedgehogs during the study: 1 = never, 2 = less frequently (monthly or less), 3 = more frequently (nightly or weekly)
FEDBEFORE	Q	A binary measure of whether the participant usually left out food for hedgehogs prior to the commencement of the study
FEEDOTHERS	Q	A binary measure of whether food was left out by the participant for birds or other animals at some point during the study
NESTSITES	Q	The number of potential types of nest sites available in the participant's garden as assessed by the participant. Tick-box options of possible nesting sites were listed on the questionnaire as "hedgehog house", "under a shed or decking", "under bushes or shrubs", "under a compost heap" or "other (please provide more information)". The total number of potential nest sites were converted to z-scores
CONNECTIVITY	Q	The proportion of front and back gardens neighbouring the participant's household that are accessible for hedgehogs from the participant's own gardens
FRONT2BACK	Q	A binary measure of whether a hedgehog could access the participant's back garden from their front garden
GOODHABITAT	Q	The proportion of habitat in the participant's back garden only that is considered 'good' for wildlife, including lawn, shrubs, flowerbeds and ponds
HOUSETYPE	Q	A binary measure of whether houses were: (i) semi-detached, link-detached or detached; or (ii) other (e.g., terraced)
GARDENSIZE	E	The area of each garden (m^2) converted to z-scores
NEARESTOTHER	D	Distance from each site to the next nearest site (m) converted to z-scores
NEAREST+VE	D	Distance from each site to the next nearest hedgehog-positive site (m) per season (autumn, winter or spring) converted to z-scores
ARABLEDIST	E	Distance from each site to the nearest area of arable land (m) converted to z-scores
ARABLE500m	E	The area of arable land (m^2) within a 500m radius of each site converted to z-scores (NB. as only 4 sites fell within 250m of arable land, the potential variable ARABLE250m was not considered for analyses)

WOODDIST	E	Distance from each site to the nearest area of woodland (m) converted to z-scores
WOOD250m and WOOD500m	E	The area of woodland (m^2) within 250m and 500m radii of each site converted to z-scores
GRASSDIST	E	Distance from each site to the nearest area of grassland (m) converted to z-scores
GRASS250m and GRASS500m	E	The area of grassland (m^2) within 250m and 500m radii of each site converted to z-scores
URBAN250m and URBAN500m	E	The area of urban and suburban habitat (m^2) within 250m and 500m radii of each site converted to z-scores (NB: as all sites fell within the urban habitat classification, the straight-line distance from each site to urban habitat was not considered for analysis)
DAYTIME	E	Mean daylength (time between sunrise and sunset) per week, converted to z-scores
RAINFALL	E	Weekly rainfall volume (mm) converted to z-scores
AIRTEMP	E	Minimum air temperature (°c) averaged per survey week based on hourly recordings taken between 21:00 and 09:00, converted to z-scores
GRASSTEMP	E	Minimum grass temperature (°c) averaged per survey week based on daily recordings taken at 09:00, converted to z-scores

Three variables were used to investigate the potential effects of garden size and proximity to other survey gardens on patterns of detection and occupancy (Table 3.1). For example, garden size (mean ± SD = 238.5 ± 244.8m^2) could have potentially affected detection rates as we only used one footprint tunnel in each garden, although the majority of gardens (93.7%) covered <550m^2, three (4.8%) covered 786-870m^2, and one (1.6%) was 1520m^2 in area. Within each season, the straight-line distance to the nearest other house and the straight-line distance to the nearest other house where hedgehogs were detected were incorporated to determine whether hedgehogs were more likely to be detected in houses close to one another, which would potentially indicate that patterns of detection were not independent.

Habitat characteristics in the area around each house were quantified using the straight-line distances to the nearest arable, grassland and woodland habitats, and the total area of habitats within 250m and 500m radii of each garden: these measures were quantified from Natural Environment Research Council land class datasets (Rowland *et al.*, 2017) with QGIS 3.4.4 (Table 3.1). Radii of 250m and 500m were selected based upon existing data of hedgehog nightly ranges outside the hibernation season (Rondini and Doncaster, 2002; Dowding *et al.*, 2010a). Minimum grass-level and air temperatures, and weekly rainfall volume, were taken from a weather station on the University of Reading's

Whiteknights campus (Met Office, 2012). Mean weekly daylength was quantified from sunset and sunrise measurements from Benson weather station, approximately 18km north of Reading (Thorsen, 2020). As these data were taken from sites in proximity to the survey gardens, but not in the gardens themselves, they reflect general environmental conditions and not the specific microhabitat characteristics of each garden.

Following checks for multicollinearity, single-species, single-season models were fitted; all variables were first considered in single-covariate models. Multi-covariate models were then constructed based upon the known ecology of hedgehogs as well as the hypothesised importance of different variables on occupancy during each season: supplementary feeding before and during the study, as well as feeding intended for other species, was considered important in all seasons; for autumn, models included the availability of and proximity to potential winter nesting sites; for winter and spring, models included environmental conditions that were likely to affect the timing of hibernation, i.e., daylength, ground temperature and air temperature. A maximum of three covariates were considered in each model because of relatively small sample sizes. This approach was favoured to produce a realistic set of candidate models, avoiding the shortcomings of algorithm-based model selection (Burnham and Anderson 1998; Whittingham *et al*., 2006).

The goodness-of-fit of the most global model for each season was tested using the bootstrap method with 1000 replicates. Bootstrapping simulates detection histories for each site and produces a test statistic (Pearson Chi-squared) for each of the 1000 runs (MacKenzie and Bailey, 2004). A measure of 'lack of fit' – defined as a variance inflation factor $\hat{c}$ – is calculated by dividing the observed test statistic by the average bootstrap statistic (Cooch and White, 2019). When $\hat{c} > 1$, there is evidence of poor fit and it is recommended that (a) Akaike's Information Criterion (AIC) values should be converted into quasi-likelihood adjusted AIC (QAIC) and (b) standard errors of beta estimates should be inflated by a factor of $\sqrt{\hat{c}}$ (Burnham and Anderson 1998; MacKenzie and Bailey, 2004; Cooch and White, 2019). Models that did not converge were excluded. Those with ΔQAIC values <2 were considered top-ranking models (Burnham and Anderson, 1998), and covariates were regarded as significant when their associated 95% confidence intervals did not cross 0 (Donovan and Hines, 2007).

Results

General trends

Overall, 63 householders completed the study (Figure 3.1). During Week 1, results were obtained for 26 (41.2%) sites compared to 100% in subsequent weeks; this was associated with the challenges of getting volunteers started but is not likely to have affected the results since occupancy analysis is robust to missing data (MacKenzie *et al.*, 2005). In autumn, or 'pre-hibernation', hedgehogs were and were not being fed in 25 (39.7%) and 38 (60.3%) gardens, respectively (Figure 3.1).

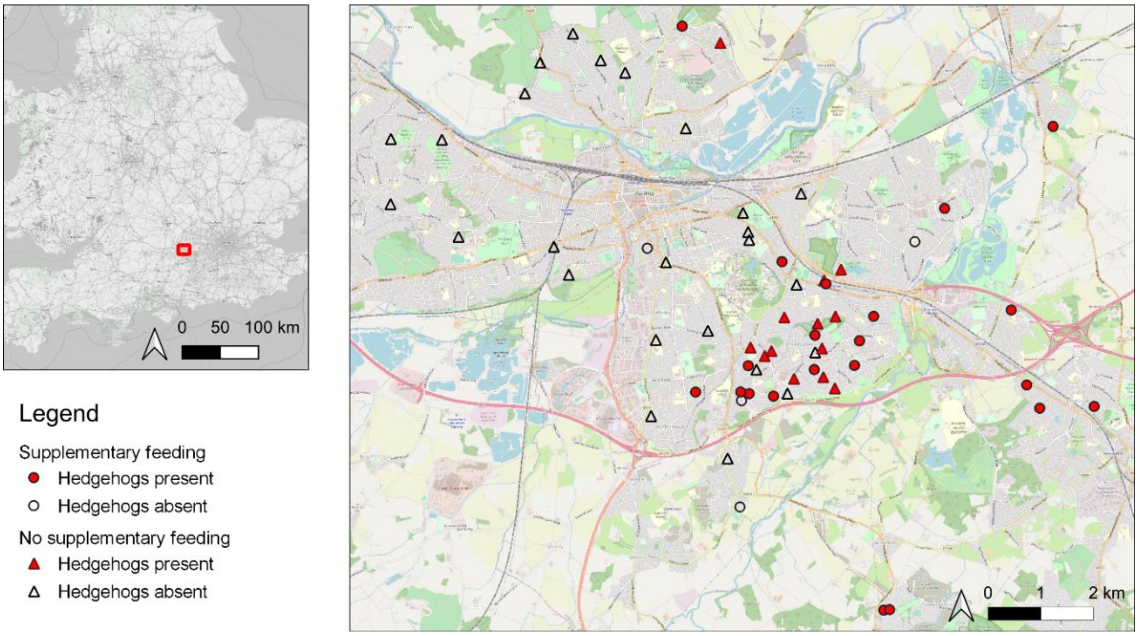

Figure 3.1. The locations of gardens (N = 63) in Reading and surrounding areas surveyed for hedgehogs between November 2017-April 2018 inclusive. Circles denote gardens where hedgehogs were fed by householders prior to the study; diamonds denote gardens where hedgehogs were not fed prior to the study. Filled and open symbols denote gardens where hedgehogs were and were not detected at any point during the current study, respectively.

Hedgehogs were active throughout all survey periods (Figure 3.2) and were recorded on 247 occasions (19.6% of the 1260 surveyor-weeks). In autumn, hedgehogs were detected in 34 (54.0%) gardens: 21 of 25 (84.0%) gardens where they had been fed previously and 13 of 38 (34.2%) gardens where they had not been fed previously (Figure 3.1). Cumulatively, 97.1% of hedgehog-positive sites were detected by the third week of surveying. Occupancy (Ψ) and detection probability (p) were lowest between January-March (autumn true Ψ = 0.54; winter true Ψ = 0.32; spring true Ψ = 0.39); full occupancy estimates from the baseline models are given in Table 3.2. False-absence error rates were very low (autumn: 0.1%; winter: 2.1%; spring: 0.6%).

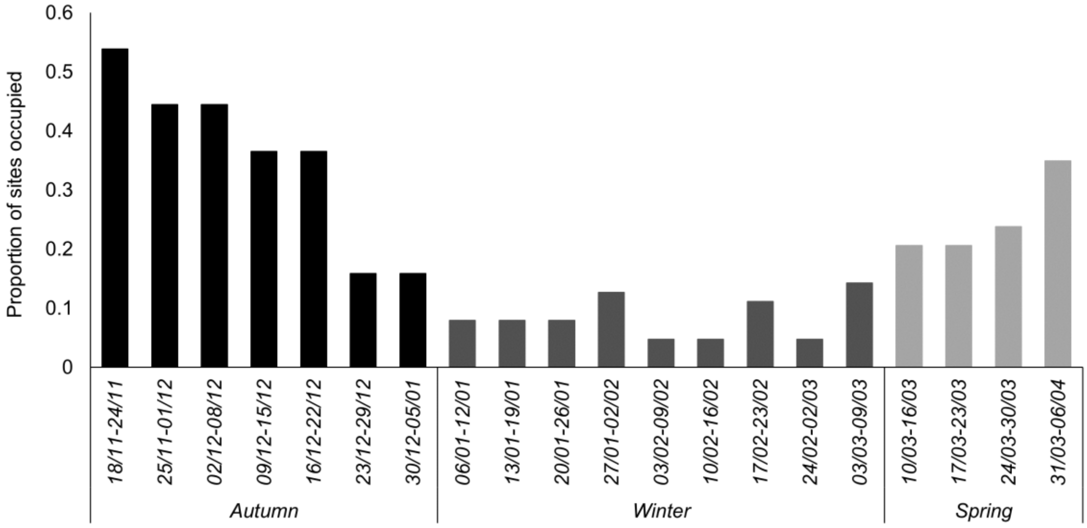

Figure 3.2. The proportion of all gardens surveyed (n = 26 in Week 1; n = 63 for Weeks 2-20) where hedgehogs were recorded each week. Weekly survey dates are given in the format dd/mm, running from November 2017-April 2018 inclusive.

Of the 34 hedgehog-positive gardens, 18 (52.9%) were used every season: 9 (26.5%) were used during the autumn period only; none were used exclusively during winter or spring. Consequently, there was a strong association in the pattern of presence/absence of hedgehogs in individual gardens between successive seasons: autumn-winter (Chi-squared test: $\chi^2_1 = 23.204$, $p < 0.001$) and winter-spring ($\chi^2_1 = 37.010$, $p < 0.001$).

Table 3.2. Summary of baseline hedgehog occupancy models where detection rate was modelled as constant (did not vary between weeks within each season) versus survey-specific (did vary between weeks within each season). Seasons are illustrated in Figure 3.2.

Season	Model	QAIC	ΔQAIC	AIC weight	Model likelihood	*K*	Detection rate	Naïve Ψ	True Ψ
Autumn	Ψ(.), p(survey-specific)	270.59	0.00	1	1.0000	8	0.8234 0.8225 0.8225 0.6756 0.6756 0.2938 0.2938	0.5397	0.5403
	Ψ(.), p(.)	294.26	23.67	0.0000	0.0000	2	0.6138	0.5397	0.5411
Winter	Ψ(.), p(.)	213.63	0.00	0.9852	1.0000	2	0.2626	0.3016	0.3224
	Ψ(.), p(survey-specific)	222.02	8.39	0.0148	0.0151	10	0.2481 0.2481 0.2481 0.397 0.1489 0.1489 0.3474 0.1489 0.4467	0.3016	0.3198
Spring	Ψ(.), p(.)	64.13	0.00	0.8006	1.0000	2	0.6459	0.3810	0.3870
	Ψ(.), p(survey-specific)	66.91	2.78	0.1994	0.2491	5	0.5377 0.5377 0.6204 0.9100	0.3810	0.3838

Ψ = occupancy, p = detection probability, K = number of parameters. ΔQAIC is the change in quasi-likelihood adjusted Akaike's Information Criterion. For each season, the variance inflation factor ĉ was adjusted based on goodness-of-fit tests of the most parameterised models (1.3226, 1.3385 and 3.5534 for autumn, winter and spring, respectively). Naïve occupancy is the number of gardens where hedgehogs were detected; true occupancy is the number of gardens estimated to be occupied by hedgehogs after accounting for the false-absence error rate.

Factors affecting hedgehog occupancy

For analyses incorporating covariates (Table 3.1), all top-ranking models included a feeding variable (Table 3.3): occupancy in autumn and winter was associated with supplementary feeding prior to the hibernation period (FEDBEFORE), whereas in spring it was most associated with feeding in that season (FEEDHOG). There was also some support for detection probability being positively influenced by DAYTIME and FEEDOTHER during spring, but the effect was not significant. All other covariates reported in the best-fitting models in each season had statistically significant positive effects on occupancy and/or detection probability. Full model results can be found in Appendix B, Tables B2-B4: garden size, proximity to other gardens per se and proximity to the nearest other garden where hedgehogs were detected in that season were not included in the top-ranked models in any season.

Table 3.3. A summary of the top-ranking models (ΔQAIC <2) produced in single-season occupancy analyses. Seasons are illustrated in Figure 3.2.

Season	Model	QAIC	ΔQAIC	AIC weight	Model likelihood	*K*
Autumn	Ψ(FEDBEFORE + WOOD500m),p(survey + NESTSITES)	283.85	0.00	0.8966	1.0000	11
Winter	Ψ(FEDBEFORE),p(FEEDHOG + FEEDOTHERS)	214.42	0.00	0.4561	1.0000	5
	Ψ(FEDBEFORE),p(FEEDHOG + GRASSTEMP)	215.41	0.99	0.2780	0.6096	5
	Ψ(FEDBEFORE),p(FEEDHOG + AIRTEMP)	215.51	1.09	0.2645	0.5798	5
Spring	Ψ(FEEDHOG),p(DAYTIME + FEEDOTHERS)	71.83	0.00	0.2413	1.0000	5
	Ψ(FEDBEFORE),p(.)	71.97	0.14	0.2250	0.9324	3
	Ψ(FEEDHOG),p(.)	72.82	0.99	0.1471	0.6096	3

Ψ = occupancy, p = detection probability, K = number of parameters. ΔQAIC is the change in quasi-likelihood adjusted Akaike's Information Criterion. For each season, the variance inflation factor $\hat{c}$ was adjusted based on goodness-of-fit tests of the most parameterised models (1.1309, 1.1531 and 2.8138 for autumn, winter and spring, respectively).

In winter, hedgehogs were recorded in 16 of 25 (64.0%) gardens where the householder had been feeding them in autumn compared to 3 of 38 (7.9%) gardens where they had not been fed. Overall, of the hedgehog-positive sites within each season, gardens where householders had previously put out food were visited, on average, for 4.4 weeks in autumn (N = 21 gardens: 62.9% of weeks in the 7-week season), 2.6 weeks in winter (N = 16 gardens: 28.9% of the 9-week season) and 2.7 weeks in spring (N = 18 gardens: 67.5% of the 4-week season). Comparable figures for gardens where they were not fed were: 3.3 weeks (N = 13 gardens: 47.1%), 2.0 weeks (N = 3 gardens: 22.2%) and 2.5 weeks (N = 6 gardens: 62.5%), respectively. Consequently, hedgehogs were much more likely to be present in gardens where food was supplied by householders (Figure 3.3).

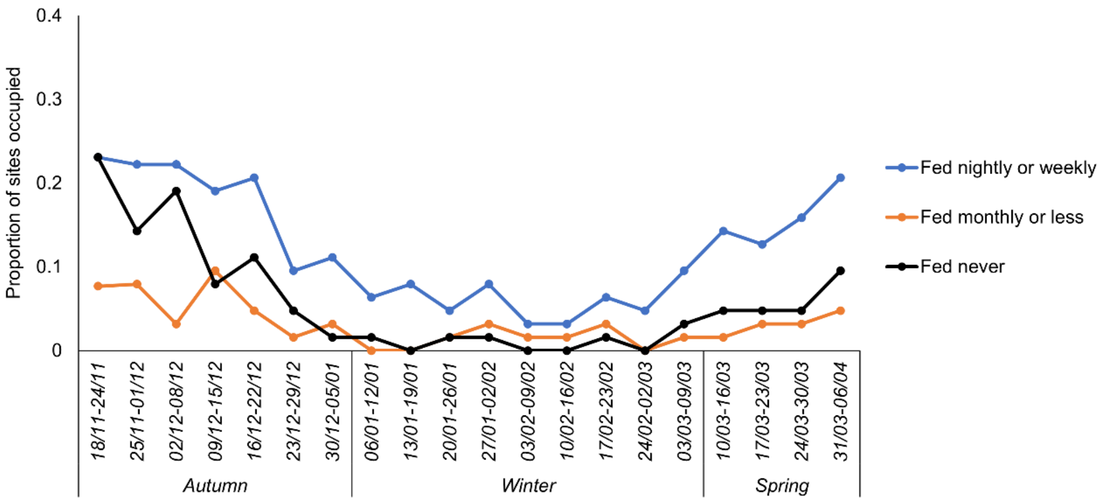

Figure 3.3. The proportion of gardens (N = 26 in Week 1; N = 63 for Weeks 2-20) where hedgehogs were detected in relation to the frequency with which householders provided food at the outset of the study. Weekly survey dates are given in the format dd/mm, running from November 2017-April 2018 inclusive.

Discussion

Hibernation is an adaptive physiological response to reduce energetic requirements during periods of low food availability. Hedgehogs therefore need to accumulate sufficient fat reserves prior to hibernation, and then minimize expenditure of energy during this period. In behavioural terms, this essentially means that hedgehogs need to avoid rousing unnecessarily from hibernation. However, they do need to retain the ability to be able to respond if environmental conditions become unfavourable or if e.g., they are detected by predators or disturbed. Consequently, individuals need to find locations that afford them protection, but which are also in proximity to alternative locations, with appropriate building materials, if they need to move.

In this study, hedgehog occupancy and detection in autumn were significantly linked to the area of woodland habitat within 500m (WOOD500m) of focal gardens and the number of potential nest sites available within gardens (NESTSITES), respectively. Previous studies have reported that a significant proportion of winter nests are constructed in wooded areas (Morris, 1973; Jensen, 2004) and the nearby woodland measured in this study area may have provided valuable pockets of semi-natural nesting habitat within an otherwise built-up area. However, the relative qualities of woodland and within-garden nesting sites are unknown. For example, wooded areas may be associated with a higher abundance of favoured building materials (the leaves of broadleaved trees: (Morris, 2018)) but urban woodlands are often open to the public and are likely to be associated with high levels of disturbance by walkers and especially their dogs. Alternatively, gardens offer potentially advantageous nesting sites such as beneath sheds and decking, but where natural nesting materials may be scarce. Future studies of urban hedgehog populations, therefore, need to focus on quantifying where hibernacula are located and whether this is linked to over-winter survival rates.

Urban areas also pose one additional challenge. Research to date indicates that hedgehogs tend to enter hibernation in response to the combination of a reduction in temperatures and a decline in food availability (Morris, 2018). This was also evident in this study, with hedgehog detection during winter reduced as grass and air temperatures declined. In urban areas, however, food supplied by householders is not directly linked to prevailing temperatures. As a result, hedgehogs might be getting ‘mixed messages’; that food availability is still high even though temperatures are low. Ultimately, this could result in maladaptive responses leading to reduced over-winter survival rates and longevity.

In autumn, hedgehog occupancy was correlated with whether they had been fed in the previous season: hedgehogs were detected in 54.0% of gardens overall, with a marked difference between those houses where they had (84.0%) and had not (34.2%) been fed. Similarly, occupancy in winter (30.2% of gardens overall) was also correlated with the pattern of feeding at the outset of the study, with an increase in the disparity between gardens where they had (64.0%) and had not been fed (7.9%). This is consistent with the radio-tracking data reported by Rasmussen *et al.* (2019a) which indicated that urban-dwelling hedgehogs tended to stay in the vicinity of local feeding stations during both active and inactive seasons, but also potentially suggests that patterns of feeding prior to hibernation may increase the likelihood that hedgehogs visit gardens during the hibernation period. In contrast, in spring, hedgehog occupancy tended to be associated with the frequency with which animals were being fed in that season, with occupancy higher where they were being fed more frequently.

Winter activity is, however, not unusual, and hedgehogs typically relocate nests at least once during the hibernation period (Morris, 1973; Reeve, 1994; Yarnell *et al*., 2019). As we used footprint tunnels to record hedgehog activity on a weekly basis, it is not possible to determine whether detections during the winter season reflected individual animals in the normal process of relocating nests, nor whether they reflect the behaviour of several animals in the same garden. For example, the continued use of a single garden by individual hedgehogs over winter has been recorded previously (Jensen, 2004; Rasmussen *et al*., 2019a). That being said, hedgehogs were detected for an average of 2.6 weeks in winter in gardens where they had been fed previously (N = 16), compared to 2.0 weeks in other gardens (N = 3). Again, this is suggestive of the fact that householder feeding patterns might be influencing over-winter activity.

However, although anthropogenic feeding could negatively affect hedgehogs during hibernation (Baldwin and Bender, 2010; Krofel *et al*., 2017), it is possible that it could be beneficial (Walhovd, 1979; Jensen, 2004). For example, it may enable animals that have not accumulated sufficient body fat to delay the point at which they enter hibernation (Reeve, 1994), especially juveniles born in late summer (Morris, 2018). Similarly, it could also help animals that have roused from hibernation replenish some of their reserves. This might be important for animals that experience an increasing number of arousal events in relation to changing climatic conditions and anthropogenic influences.

Conversely, as hedgehogs are capable of surviving losses of up to 44% of their pre-hibernation weight (Jensen, 2004; Haigh *et al*., 2012; Rasmussen *et al*., 2019a; Yarnell *et al*., 2019), it is not clear whether access to food during winter is beneficial. For example, it has been suggested that hedgehogs may only enter into a ‘partial hibernation’ where food is available (Morris, 2018): since a single rousing even may consume the same amount of energy required to survive 3-4 days of hibernation (Tähti and Soivio, 1977), animals may experience proportionately larger losses in mass over winter if they cannot access sufficient food (Morris, 2018). Furthermore, animals that are active during the winter will also face the additional risks associated with e.g., road traffic, companion animals and domestic gardens (Stocker, 1987; Rasmussen *et al*., 2019a; Wright *et al*., 2020); ‘shortenings’ of the hibernation period - caused by increased arousals or a delay in hibernation commencement - have also been linked to accelerated cellular aging in mammals (Turbill *et al*., 2012; Turbill *et al*., 2013; Hoelzl *et al*., 2016; Kirby *et al*., 2019), thereby potentially having implications for longevity (Lyman *et al*., 1981; Blanco *et al*., 2015; Wu *et al*., 2016). In addition, there is the need to consider the nutritional value of foods being provided by householders. For example, should animals come to rely on non-natural foods as a principal source of energy, it is possible that these might not fulfill their nutritional requirements and could compromise their condition (Murray *et al*., 2016). Additional information is therefore required on the types of food used by householders and its nutritional content relative to the needs of hedgehogs at this time.

Despite the absence of any definitive data that feeding hedgehogs over winter is beneficial, it is encouraged by several NGOs in Britain (Hedgehog Street, 2019; British Hedgehog Preservation Society, 2020; Tiggywinkles Wildlife Hospital, 2020). Given that arguments can be made that over-winter feeding might negatively impact hedgehogs, there is an urgent need to study its effects in more detail so that accurate advice can be given to householders. Such investigations will require the study of the activity and movement patterns, body mass changes, reproductive success and longevity of individual hedgehogs before, during and after the hibernation period in an experimental framework (i.e., controlling the frequency and volume of food supplied by randomly selected householders). These studies are, however, likely to be associated with significant challenges since they will require the cooperation of large numbers of householders for extended periods of time.

Conclusion

This study has indicated that residential gardens may be used frequently by hedgehogs throughout all stages of hibernation. Supplementary feeding in preceding seasons was found to be a key factor associated with hedgehog presence/absence during the hibernation period. This potentially indicates that supplementary feeding might affect key components of the hibernation behaviour of urban-dwelling hedgehogs, which could be detrimental or beneficial to over-winter survival and reproduction. Further intensive studies of known individuals before, during and after the hibernation period are therefore required.

Chapter 4

What makes a house a home? Nest box use by West European hedgehogs (*Erinaceus europaeus*) is influenced by nest box placement, resource provisioning and site-based factors.

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Abstract

Artificial refuges provided by householders and/or conservation practitioners potentially represent one mechanism for mitigating declines in the availability of natural nest sites used for resting, breeding and hibernating in urban areas. The effectiveness of such refuges for different species is, however, not always known. In this study, we conducted a questionnaire survey of UK householders to identify factors associated with the use of ground-level nest boxes for West European hedgehogs (*Erinaceus europaeus*), a species of conservation concern. Overall, the percentage of boxes used at least once varied with season and type of use: summer day nesting (35.5-81.3%), breeding (7.2-28.2%), winter day nesting (20.1-66.5%) and hibernation (21.7-58.6%). The length of time the box had been deployed, the availability of artificial food and front garden to back garden access significantly increased the likelihood that a nest box had been used for all four nesting types, whereas other factors related to placement within the garden (e.g., in a sheltered location, on hardstanding such as paving, distance from the house) and resource provisioning (bedding) affected only some nesting behaviours. The factors most strongly associated with nest box use were the provisioning of food and bedding. These data suggest, therefore, that householders can adopt simple practices to increase the likelihood of their nest box being used. However, one significant limitation evident within these data is that, for welfare reasons, householders do not routinely monitor whether their box has been used. Consequently, future studies need to adopt strategies which enable householders to monitor their boxes continuously. Ultimately, such studies should compare the survival rates and reproductive success of hedgehogs within artificial refuges versus more natural nest sites, and whether these are affected by, for example, the impact of nest box design and placement on predation risk and internal microclimate.

Introduction

The construction of urban areas is typically associated with the loss, fragmentation and degradation of natural habitats (Fischer & Lindenmayer, 2007; Angel *et al*., 2011). Such changes frequently result in a reduction of the availability and quality of fundamental resources for wildlife including suitable sites for breeding, resting or hibernating (Berthier *et al*., 2012; Shanahan *et al*., 2014; Reynolds *et al*., 2019). Within urban areas, these sites can be lost because of changes at different spatial scales and for different underlying reasons. For example, areas of woodland and scrub may be cleared for building developments, native vegetation may be replaced with non-native species for aesthetic reasons, and individual trees may be removed where they affect built structures or pose a threat to human safety (Reynolds *et al*., 2019; Wu *et al*., 2019). The loss or degradation of these sites can have significant impacts on populations if associated directly with reproductive output (Franco *et al*., 2005; Chace & Walsh, 2006; Martin & Martin, 2007; Shanahan *et al*., 2014), but can also disrupt resting (Aulsebrook *et al*., 2018; Grunst *et al*., 2021) and hibernation patterns (Grol *et al.*, 2011). One approach to help mitigate the loss of natural breeding and resting sites in urbanised areas is the use of artificial refuges.

Artificial refuges have been used as conservation tools in towns and cities (Cowan *et al*., 2021) to improve habitat connectivity, facilitate species introductions or translocations, and/or monitor species abundance and distributions (Beyer & Goldingay, 2006; Williams *et al*., 2013; Goldingay *et al.*, 2020). In addition to conservation organisations, individual householders may also provide a range of different types of refuges (e.g., bird nest boxes, bat boxes, insect hotels, toad houses, etc.) in their own gardens on an *ad hoc* basis (Gaston *et al*., 2005; Davies *et al*., 2009). Clearly, the physical structure of any refuge must meet the requirements of the focal species (e.g., Latham & Knowles, 2008; Kaneko *et al*., 2010; Hodges & Seabrook, 2016; Rueegger, 2017; Larson *et al*., 2018; Shaw *et al*., 2021), but householders can potentially purchase a wide range of commercial designs that vary in size and construction materials. Similarly, designs posted online by conservation or gardening organisations can be equally varied, and householders may also create their own designs based on the materials that are available to them and their own perceptions of species' requirements.

Well-designed artificial refuges can help to maintain local populations on a long-term basis (Goldingay *et al*., 2015) and potentially improve breeding success relative to conspecifics using natural nesting sites (Bolton *et al*., 2004; Libois *et al*., 2012; Brazill-Boast *et al.*, 2013). The provision of nest boxes for the common dormouse (*Muscardinus avellanarius*), for instance, has been associated with a more than doubling in adult abundance (Juškaitis, 2005), and, for urban birds, has been known to aid the recovery of populations to approximately 50% of original levels within five years of the loss of original sites (Dulisz *et al*., 2022). However, a use of inappropriate designs, materials and/or positioning could result in negative outcomes for wildlife (Larson *et al*., 2018). For example, nest boxes with poor insulative properties can result in high temperature variability within the nesting chamber (Larson *et al*., 2015; Larson *et al*., 2018) which has been associated with declines in clutch size, nestling growth and fledging success of birds (Larson *et al*., 2015; Bleu *et al.*, 2017). For lactating mammals, warmer nest boxes could reduce nest attendance (van der Vinne *et al*., 2014) or occupancy (Guillemette *et al*., 2008) during breeding periods, but, for hibernators, could help to limit heat loss, and therefore energy expenditure, during torpor (Nedergaard & Cannon, 1990; Madikiza *et al*., 2010) and aid passive rewarming when rousing (Hoeh *et al*., 2018). Alternatively, if hibernacula experience unusually high temperatures, the resulting higher body temperatures could lead to substantial increases in energetic expenditure (Humphries *et al.*, 2002) as well as more frequent arousals from torpor (Pretzlaf & Dausmann, 2012). Different designs may also influence the risk of predation, conspecific parasitism and other forms of disturbance (Davison & Bollinger, 2000). For example, animals using artificial refuges which are more conspicuous than natural nest sites (Evans *et al*., 2002), or those which lack anti-predator devices (Bailey & Bonter, 2017), might experience increased rates of predation. Furthermore, given that variability in refuge design may ultimately affect survival and/or reproductive rates, species might then be expected to exhibit preferences for those design elements that positively affect these outcomes such as material (Rueegger *et al*., 2013), entrance type (Goldingay *et al*., 2015) or orientation (Ardia *et al*., 2006). Ultimately, knowledge of these factors would enable conservation practitioners to optimise refuge design.

In addition to their physical design, the use of artificial refuges can be affected by factors relating to positioning (Madikiza *et al*., 2010) and local- and landscape-level features (Nakamura-Kojo *et al*., 2014; Le Roux *et al*., 2016), such as the quality of nearby foraging habitat (Catry *et al*., 2013) and availability of natural nest sites (Madikiza *et al*., 2010). Even where good quality habitats are available, however, animals may display a preference for poor quality nest sites that inadvertently induces maladaptive breeding and fitness responses (Battin, 2004; Hale & Swearer, 2016). This concept is termed an 'ecological trap' and occurs when there is a mismatch between external cues of nest site selection (e.g., food availability and suitable nest box design) and the actual quality of the site. For example, great tits (*Parus major*) in urban areas preferentially select nest boxes with larger cavities, yet these are associated with lower fledging success (Demeyrier *et al*., 2016). Ultimately, the provision of artificial refuges may facilitate breeding within sub-optimal habitats (Mänd *et al*., 2005), and such ecological traps might drive reductions in species abundance (Battin, 2004; Hale & Swearer, 2016).

An absence of knowledge of what constitutes effective design, appropriate placement and whether artificial refuges are used successfully can limit conservation efforts (Cowan *et al*., 2020). Artificial refuges have been most widely studied (Brady *et al.*, 2000; Cowan *et al*., 2021) and applied (Gryz *et al.*, 2021) for birds both during and outside of breeding seasons (e.g., Mainwaring, 2011); data relating to ground-dwelling terrestrial small mammals are comparatively limited (Cowan *et al*., 2021) despite declines within urban areas (e.g., Baker *et al*., 2003; Gortat *et al*., 2014; Łopucki & Kitowski, 2017). For example, in the UK, householders are commonly urged by wildlife organisations to install nest boxes in their gardens for the West European hedgehog (*Erinaceus europaeus,* hereafter 'hedgehog') (BBC, 2014; Hedgehog Street, 2021; The Wildlife Trusts, 2021), a small (<1.5 kg), solitary, nocturnal hibernator of conservation concern (Mathews *et al*., 2018; Mathews & Harrower, 2020).

Hedgehog numbers have declined substantially in rural areas in the UK over the last few decades (Roos *et al*., 2012), which is likely attributable to agricultural intensification (Hof & Bright, 2010; Yarnell & Pettett, 2020), vehicle collisions (Wright *et al*., 2020), direct predation by or intraguild competition with the European badger (*Meles meles*) (Young *et al*., 2006; Trewby *et al*., 2014; Williams *et al*., 2018b) and habitat loss and fragmentation (Rondinini & Doncaster, 2002; Moorhouse *et al.*, 2014): the latter is most commonly discussed in the context of the loss of hedgerows, a habitat feature that is thought to be particularly important for hedgehogs for nesting, foraging or providing cover from predators (Hof, Snellenberg & Bright, 2012; Pettett *et al*., 2017). Conversely, however, hedgehogs seem to be attracted to (Doncaster *et al*., 2001; Pettett *et al*., 2017) and abundant within (Hubert *et al*., 2011; van de Poel *et al.*, 2015; Schaus *et al*., 2020; Schaus Calderón, 2021) areas of human habitation where residential gardens are a widely-used and favoured habitat (Baker & Harris, 2007; Hof & Bright, 2009; Dowding *et al*., 2010a; Williams *et al*., 2015; Williams *et al*., 2018a; Rasmussen *et al*., 2019; Gazzard & Baker, 2020; Gazzard *et al.*, 2022). Residential gardens (private, typically enclosed, areas adjoining dwellings that may contain lawn(s), ornamental plantings, vegetable plots, ponds, paved areas, decking, sheds and/or other outbuildings) in Britain average 188 m^2 in size (Office for National Statistics, 2020) but collectively can form up to 47% of total green space in some cities (Loram *et al*., 2007). In this habitat, householders commonly leave out food for hedgehogs in the form of soft (e.g., canned pet or hedgehog foods) or solid (e.g., pet kibble) products, though the natural diet of hedgehogs is primarily insectivorous (Haigh *et al.*, 2012). Given that householders have a high affinity for hedgehogs (Morris, 2018), , the implementation of hedgehog-friendly activities within gardens could have a significant positive impact on this species.

Hedgehog nest boxes (also known as hedgehog houses; Figure 4.1) are thought to have grown in popularity over recent years and are now widely commercially available (see Stone, 2020), with numerous guidelines on how to construct homemade versions also available online (e.g., British Hedgehog Preservation Society, 2021; Hedgehog Street, 2021; The Wildlife Trusts, 2021). These are simple boxes or box-like structures within which hedgehogs construct nests out of vegetative material found in the environment or supplied by householders. To date, no studies have been conducted to quantify the frequency with which hedgehogs use nest boxes, whether certain design features or positioning influence their use, and whether influencing factors change between seasons. Such information is fundamental for advising householders and conservation practitioners on how to most effectively provide refuges.

Figure 4.1. Examples of homemade (A-F) and commercially available (G-I) artificial refuges for hedgehogs. Hedgehog nest boxes vary in size and design, but average nest box

dimensions reported in this study (N = 4,509) were 629 x 726 x 423 mm (width x depth x height) for homemade nest boxes, and 499 x 478 x 311 mm for manufactured nest boxes. Image credits: (A) G. Northcott; (B) C. Gazzard; (C) S. Wilkinson; (D) L. Pearse; (E) V. Yates; (F) R. Brenton. Commercially available nest box images: A. Gazzard; produced by (G) Home & Roost, (H) Coopers of Stortford and (I) Tom Chambers.

Throughout the annual cycle, hedgehogs construct nests for four different purposes: daytime nesting outside the hibernation period (hereafter 'summer day nesting' for brevity), breeding, daytime nesting during the hibernation period (hereafter 'winter day nesting') and winter hibernation. In the UK, hedgehogs hibernate between November-April, but typically rouse several times (Reeve, 1994; Morris, 2018). Summer day nesting is therefore defined as day nesting at any time during March-October inclusive. Breeding nests may also be formed at any point during this period: the majority of litters in the UK are produced early in the annual cycle (May-June: Deanesly, 1934; Jackson, 2006; Haigh, 2011), although 'late litters' are not uncommon in August-October (Dowler Burroughes *et al.*, 2021). Breeding nests tend to be occupied by the mother and usually 3-6 young (Morris, 1977; Kristiansson, 1981; Walhovd, 1984), with the litter becoming independent by approximately 6 weeks of age (Morris, 2018).

Rural hedgehogs appear to favour nesting in hedgerows and woodlands (Haigh *et al.*, 2012; Bearman-Brown *et al.*, 2020); knowledge of nest site selection in urban habitats is lacking but hedgehogs have been known to nest in gardens (BHPS, 2022b). Nests are constructed at ground level under shelter, for example, under hedging, scrub or log piles, though are sometimes also formed in rabbit (*Oryctolagus cuniculus*) burrows or cavities beneath garden sheds or decking (Jackson & Green, 2000; Morris, 2018). Day nests are loosely formed (Rautio *et al.*, 2014) compared to the compact hibernacula or larger breeding nests (Reeve, 1994; Morris, 2018). In all cases, a central nesting core is created under a dome of bedding material that typically contains dry broadleaves, grass and other foliage (Reeve & Morris, 1985; Rautio *et al.*, 2014; Pettett *et al.*, 2017). Nest-sharing by adults is very rare (Reeve, 1994), but hedgehogs will readily make use of multiple day and hibernation nests (Haigh *et al.*, 2012; Rautio *et al.*, 2014; Morris, 2018; Yarnell *et al.*, 2019; Bearman-Brown *et al.*, 2020), including those that have been used by other individuals (Riber, 2006; Haigh *et al.*, 2012; Rautio *et al.*, 2014). Distances between successive nest sites have been recorded to range from 2-323m (Jensen, 2004; Yarnell *et al.*, 2019).

Nesting at ground level exposes hedgehogs to numerous risks: they can be disturbed by humans, companion animals or livestock (Bearman-Brown *et al.*, 2020); are potentially accessible to predators including badgers, foxes (*Vulpes vulpes*) and domestic dogs (*Canis* *lupus familiaris*); are vulnerable to damage or destruction caused by activities associated with land management, garden maintenance (e.g., mowing or strimming/weed whacking) and construction works; and flooding (Morris, 2018). Disturbances including noise, light or the accidental uncovering of a nest can prompt hedgehogs to relocate nests more frequently than usual, thereby increasing energetic expenditure (Rast *et al.*, 2019) as well as the risk of mortality from companion animal and road traffic, but can also potentially cause the abandonment or killing of young (Morris, 2018). Furthermore, hedgehogs are likely to be sensitive to changes in the internal microclimate of nests: high levels of humidity have been linked to the advanced decay of broad-leaved nesting material (Morris, 1972), ectoparasite presence (Heeb *et al.*, 2000) and the efficiency of animal evaporative heat loss mechanisms (McComb *et al*., 2021). During hibernation, low temperatures inside nests can accelerate heat loss of individuals in torpor and cause fat stores to rapidly deplete (Soivio *et al.*, 1968; Jensen, 2004; Morris, 2018). Last, if different individuals use or reuse the same box in quick succession, this could potentially increase the risk of parasite transmission (Tomás *et al*., 2007).

Given the lack of quantified information on many aspects relating to the deployment of hedgehog nest boxes by householders, and their use by hedgehogs, we used a questionnaire survey of householders in the UK to identify the factors associated with the use of hedgehog boxes for summer day nesting, breeding, winter day nesting and hibernation. Based on these results, and the associated limitations of these data, we make suggestions for future studies to collect data that would form the basis for recommendations made to householders about how to optimise the deployment of nest boxes (and associated materials such as bedding), as well as identifying the role that artificial refuges may have in the future conservation of this species.

Methods

Data were collected using an online questionnaire survey (15/08/2017-31/10/2017 inclusive) of UK householders who had installed at least one hedgehog nest box in their garden. The questionnaire was promoted as 'The Hedgehog Housing Census' by the Hedgehog Street campaign (run jointly by the People's Trust for Endangered Species and British Hedgehog Preservation Society) and advertised through social media, local radio interviews and newspaper articles. As some of the information requested may have led respondents to be tempted to open their box(es) to see if hedgehogs were using them, a statement was included at the start of the questionnaire that explicitly instructed respondents not to do so as this may have adverse effects on the welfare of nesting animals. Additionally, since this survey was focussed on the use of nest boxes as refuges for sleeping, breeding and/or hibernating, a second statement outlined that respondents were not to complete the survey if they had installed hedgehog nest boxes solely for the purpose of feeding hedgehogs: many householders in the UK use covered feeding stations to protect hedgehogs from other species (e.g., cats (*Felis catus*), foxes and badgers) whilst simultaneously protecting the food from inclement weather and from competition with these other species (see Finch *et al.*, 2020). Householders with >1 nest box were asked to complete one survey for each box. Responses that were incomplete, or those that appeared to describe nest boxes being used in locations other than domestic gardens (e.g., in wildlife rescue centres or for rehabilitated individuals at 'soft release' sites), were removed prior to analyses.

The questionnaire requested information on a wide range of variables including: the respondent's geographical location; characteristics of their garden; whether they owned a dog; the size and design features of the box; the length of time that the box had been installed and how it was positioned in the garden; if and where, relative to the location of the nest box, the respondent put food out for hedgehogs; whether they had put any natural or artificial bedding material in the box; whether they fed garden birds; whether they had seen foxes and/or badgers in their garden; and whether the nest box had ever been used by hedgehogs for day nesting in the summer (March–October) or winter (November–February), breeding or hibernating. Nest box use was defined on the basis of direct or indirect observations (e.g., through the use of motion-activated trail cameras or other monitoring devices) of a hedgehog entering or exiting the box. The aerial coverage of urban, arable, woodland and grassland habitat within a 500m radius around each site (500m was chosen given existing hedgehog movement data: Dowding *et al.*, 2010a; Schaus Calderón, 2021; Gazzard *et al.*, 2022), and the distance to the nearest patch of each of these habitats, were quantified with PostGIS and using a 2017 Land Cover Map of the UK (UK Centre for Ecology & Hydrology; Morton *et al.*, 2020); the aggregate habitat classes in the Land Cover Map are based on Broad Habitat Classifications used in the government's 1994 UK Biodiversity Action Plan (Jackson, 2000). Variables are defined in Table 4.1.

Table 4.1. Variables considered in the analysis of hedgehog nest box use within gardens. Source: Q = the variable was derived from the questionnaire survey; LC = data were quantified using a UK land class dataset (Morton *et al.*, 2020b).

Theme	Variable	Description	Variable type	Source
Nest box use	SUMMERDAY BREEDING WINTERDAY	How long, in months, the respondent believed that the nest box had	Converted to binary variable for analysis:	Q

	HIBERNATION	been used for summer day (March-October), breeding, winter day (November-February) or hibernation nesting	(0) box had not been used (1) box had been used	
Time installed	MONTHSINSTALLED	The number of months the nest box had been installed for in the respondent's garden	Continuous	Q
Nest box design	TYPE	Whether the nest box was homemade or purchased	(0) Purchased (1) Homemade	Q
	MATERIAL	The primary material of the nest box	(0) Timber (1) Plywood/plyboard (2) Brushwood (3) Plastic (4) Other (including wicker, woodcrete and brick)	Q
	HEIGHT	The height (cm) of the nest box	Continuous	Q
	WIDTH	The width (cm) of the nest box	Continuous	Q
	DEPTH	The depth (cm) of the nest box (front to back)	Continuous	Q
	CAPACITY	Maximum capacity (cm^3) of the nest box, as determined by HEIGHT * WIDTH * DEPTH	Continuous	Q
	BASE	Whether the nest box had an integral base	(0) No base (1) Base	Q
	TUNNEL	Whether the nest box had an external tunnel entrance	(0) No tunnel entrance (1) Tunnel entrance	Q
	PARTITION	Whether the nest box had an internal tunnel or partition	(0) No internal partition (1) Internal partition	Q
	VENT	Whether the nest box had ventilation holes	(0) No vent (1) Vent	Q
	LINING	Whether the nest box had a waterproof lining	(0) Nest box is unlined	Q

			(1) Nest box is lined	
Nest box positioning	FRONTORBACK	Whether the nest box was positioned in a front or back garden	(0) Front garden (1) Back garden	Q
	HARDSTANDING	Whether the nest box was located on hardstanding (i.e., patio, paved or decked areas)	(0) Not on hardstanding (1) On hardstanding	Q
	SHELTERED	Whether the nest box was under some sort of shelter (e.g., shrubbery)	(0) Not in sheltered location (1) In a sheltered location	Q
	DISTANCEBUILDING	Whether the nest box was located <5m from a building	(0) ≥5m from a building (1) <5m from a building	Q
	FACING	Whether the nest box entrance was facing into the open or elsewhere	(0) Facing a wall/fence (1) Parallel to a wall/fence (2) Facing shrubs/planting (3) Facing the open (4) Other	Q
	ORIENTATION	The direction that the nest box entrance was facing	(0) North (1) East (2) South (3) West	Q
	RAISED	Whether the nest box was raised off the ground or not	(0) Not raised (1) Raised	Q
Garden characteristics	CONNECTED	The number of neighbouring back gardens which were accessible to hedgehogs from the respondent's back garden	Continuous	Q
	FRONTBACKACCESS	Whether a hedgehog could access the respondent's back garden from their front garden	(0) No front-to-back access (1) Front-to-back access	Q
	OTHERNESTS	Whether the respondent had directly	(0) No alternative	Q

		observed, or found evidence of, hedgehogs nesting outside of a nest box elsewhere in their back garden	nesting sites observed (1) Alternative nesting sites observed	
	POND	Whether the garden contained a pond	(0) No pond (1) Pond	Q
	GOODHAB	The proportion of 'good' habitat present in the garden, including shrubs, a wild area, woodpile, compost heap, shed or decking with cavity beneath, lawn, vegetable patch and/or flowerbeds	Continuous (proportion)	Q
Resources for hedgehogs	BEDDING	Whether the respondent provided artificial (e.g., newspaper) or natural (e.g., leaves, hay) bedding within the nest box, or both	(0) None provided (1) One type of bedding (2) Both types of bedding	Q
	HEDGEHOGFOOD	The location in which food was provided for hedgehogs in the garden	(0) None provided (1) Scattered in varying locations (2) <0.5m from nest box (3) 0.5m-5m from nest box (4) 5.1-10m from nest box (5) >10m from nest box	Q
Other animals	BIRDFOOD	Whether the respondent supplied food for birds in their garden	(0) None provided (1) Food provided	Q
	BADGERFOX	Whether the respondent ever observed badgers or foxes in their garden [NB badger and fox sightings were merged due to the low number of positive sightings]	(0) Not sighted (1) Sighted	Q
	DOGS	Whether the respondent owned any	(0) No dogs	Q

		pet dogs that were allowed access to the garden	(1) Dogs	
Habitats	URBAN500 ARABLE500 WOOD500 GRASS500	The quantity (m^2) of urban/arable/woodland/grassland habitats within 500m of the respondent's location (estimated from the central point of their postcode)	Continuous	LC
	URBANDIST ARABLEDIST WOODDIST GRASSDIST	Distance (m) to the nearest urban/arable/woodland/grassland habitat patches from the respondent's location (estimated from the central point of their postcode)	Continuous	LC

To assess factors affecting whether nest boxes had been used by hedgehogs, we fitted generalised linear models (GLMs) with binomial distributions and logit link functions. Many participants were not aware of whether their nest box had been used for every category of nesting but could indicate whether the nest box had been used for at least one type. Therefore, the data were separated into four groups representing nest boxes that were known to have been or not have been used for: (a) summer day nesting, (b) breeding, (c) winter day nesting or (d) hibernation. In addition, as many nest boxes had only been installed recently, the response variable indicated whether the nest box had been used at any point since it had been deployed rather than the extent of use over time. When the binary responses comprised a greater number of "events" (nest box used) than "non-events" (nest box not used), we opted not to balance (subsample the dataset to obtain an even split of events and non-events) the data in favour of treating each of the four GLM analyses in the same way. Furthermore, the imbalances in proportions of boxes used were not extreme, and biases in maximum likelihood estimates are reduced in larger sample sizes (see Jiménez-Valverde *et al.*, 2009; Salas-Eljatib *et al.*, 2018).

Correlations between explanatory variables were checked prior to analysis, and further examined using generalised variance inflation factors (GVIFs) during the modelling process (Fox & Monette, 1992). For the former, the threshold of 'high' correlation was set at a Pearson coefficient value <-0.5 or >0.5, and for the latter, the GVIF threshold was chosen to be <2 (see Zuur *et al.*, 2010). Models were constructed by sequentially adding variables and examining Akaike's Information Criterion (AIC) values to identify the most parsimonious model (Burnham & Anderson, 1998). In some cases, nonsignificant variables were retained if they improved model fit and/or if it was considered informative to highlight their importance across different nesting types (e.g., BEDDING, BADGERFOX, DOGS). Final model fit was assessed with the Hosmer-Lemeshow test which compares the number of expected events – as deduced from the regression model – to the number of observed events, commonly for 10 divisions of the dataset (Hosmer & Lemesbow, 1980). Additionally, Nagelkerke pseudo-R^2 values are provided for each final model to give an indication of the amount of variance in the dependent variable that was explained by the independent variables (Nagelkerke, 1991). Analyses were performed in R 4.0.3.

Results

In total, 4,309 questionnaire responses were available for analysis: 1,717 (39.8%) and 2,592 (60.2%) responses were associated with homemade and commercially purchased nest boxes, respectively. However, 1,492 respondents did not monitor the use of their nest box and could not provide information on whether it had been used for any type of nesting. Considering only those respondents who stated that they knew whether their nest box had been used or not, 81.3% (N = 1,868), 28.2% (N = 1,104), 66.5% (N = 1,300) and 58.6% (N = 1,592) reported that hedgehogs had used the box at least once for summer day nesting, breeding, winter day nesting or hibernation, respectively.

Of all nest boxes reported, 46.3% had been installed for <1 year, 42.0% for 1-5 years, 8.2% for 5-10 years and 3.6% for >10 years. Overall, 77.9% of homemade boxes and 79.5% of commercial boxes had been installed only after hedgehogs had been sighted in the garden: this is equivalent to 78.9% of all the boxes in the survey. Respondents also collectively directly observed, or observed evidence of, at least 2,546 other nest sites used by hedgehogs within their gardens, which equates to an average of 0.6 per garden. These comprised nests constructed under garden vegetation (46.0%), woodpiles (14.5%), compost heaps (6.3%), decking (5.7%), sheds (21.5%) and buildings (6.1%).

Factors affecting nest box use

The number of survey responses that were available for modelling factors affecting the use of nest boxes varied between nesting types: 1,868 for summer day nesting, 1,104 for breeding, 1,300 for winter day nesting, and 1,592 for hibernation. Multicollinearity checks showed that some of the nest box design variables, as well as habitats variables, were correlated. Consequently, the following variables (Table 4.1) were excluded from the analyses: BASE, TUNNEL, PARTITION, VENT, LINING, ARABLE500, WOOD500, and

GRASS500. In addition, URBANDIST was omitted as most participants lived directly within urban areas; <6% of respondents resided outside of land classified as urban.

For all types of nest box use, the length of time it had been installed, positioning within the garden, the provisioning of resources and site-based factors significantly influenced whether it had been used or not (Tables 4.2, 4.3). Nest boxes were significantly more likely to have been used for all four patterns of use the longer they had been installed, if the back garden could be accessed from the front, if the householder put out food for hedgehogs, and if other nest sites were present in the garden (Table 4.3). Positioning on hardstanding (such as paving, patio or decking), in a sheltered location and the supply of bedding each increased the likelihood that the box was used in three of the four contexts, but these were not consistent. Boxes in close proximity to a building, those that were raised off the ground and were homemade were more likely to have been used in two contexts, but again these patterns were not consistent. Factors that significantly negatively impacted nest box use included whether the entrance to the box faced into the open, the presence of a garden pond, an increase in the extent of potentially valuable habitat (including shrubs, a wild area, woodpile, compost heap, shed or decking with cavity beneath, lawn, vegetable patch and/or flowerbeds) within the garden, and the presence of dogs (Table 4.3).

Table 4.2. Results of generalised linear models examining factors affecting hedgehog nest box use for (a) summer day nesting, (b) breeding, (c) winter day nesting and or (d) hibernation. Reference levels for variables are indicated in parentheses. SE = standard error, OR = odds ratios. Variables that had a significant effect ($p < 0.05$) are highlighted in bold.

(a) Summer day nests (N = 1868). Hosmer and Lemeshow Test: $\chi^2_8 = 10.226$, $p = 0.250$; Nagelkerke $R^2 = 0.235$.

Variable	Estimate	SE	z	p	OR	95% CI
(Intercept)	-1.250	0.524	-2.384	0.017	0.287	0.103-0.810
MONTHSINSTALLED	**0.009**	**0.002**	**3.843**	**<0.001**	**1.009**	**1.005-1.015**
TYPE (Purchased)						
Homemade	0.261	0.140	1.860	0.063	1.298	0.988-1.712
FRONTORBACK (Front garden)						
Back garden	**0.528**	**0.220**	**2.398**	**0.016**	**1.696**	**1.094-2.599**
HARDSTANDING (Not on hardstanding)						
On hardstanding	**0.430**	**0.190**	**2.266**	**0.023**	**1.538**	**1.068-2.251**
SHELTERED (Not in sheltered location)						
In a sheltered location	**0.529**	**0.168**	**3.158**	**0.002**	**1.698**	**1.219-2.354**
DISTANCEBUILDING (≥5m from a building)						
<5m from a building	**0.421**	**0.158**	**2.667**	**0.008**	**1.524**	**1.122-2.085**
FACING (Entrance faces wall/fence)						
Parallel to wall/fence	0.001	0.302	0.003	0.997	1.001	0.541-1.780
Faces shrubs/plantings	-0.043	0.314	-0.138	0.890	0.957	0.507-1.746
Faces the open	**-0.585**	**0.296**	**-1.978**	**0.048**	**0.557**	**0.305-0.976**
Other	-0.267	0.336	-0.794	0.427	0.766	0.390-1.465
RAISED (Not raised)						

Raised	**0.364**	**0.178**	**2.053**	**0.040**	**1.440**	**1.023-2.054**
FRONTBACKACCESS (No front-to-back access for hedgehogs)						
Front-to-back access	**0.470**	**0.143**	**3.277**	**0.001**	**1.599**	**1.206-2.116**
OTHERNESTS (No alternative nesting sites used)						
Alternative nesting sites used	**0.768**	**0.136**	**5.650**	**<0.001**	**2.156**	**1.655-2.821**
POND (No garden pond)						
Pond	**-0.368**	**0.141**	**-2.602**	**0.009**	**0.692**	**0.525-0.914**
GOODHAB	**-0.012**	**0.004**	**-2.982**	**0.003**	**0.988**	**0.980-0.996**
BEDDING (None provided)						
One type	**0.914**	**0.182**	**5.008**	**<0.001**	**2.493**	**1.740-3.560**
Both types	**1.457**	**0.268**	**5.431**	**<0.001**	**4.293**	**2.560-7.347**
HEDGEHOGFOOD (None provided)						
Scattered in varying locations	0.803	0.510	1.574	0.115	2.233	0.865-6.583
<0.5m from nest box	**0.881**	**0.237**	**3.720**	**<0.001**	**2.414**	**1.523-3.857**
0.5m-5m from nest box	**1.463**	**0.185**	**7.903**	**<0.001**	**4.317**	**3.004-6.209**
5.1-10m from nest box	**1.133**	**0.313**	**3.621**	**<0.001**	**3.105**	**1.708-5.849**
>10m from nest box	**1.233**	**0.243**	**5.082**	**<0.001**	**3.433**	**2.145-5.563**
BADGERFOX (Not sighted)						
Sighted	-0.159	0.135	-1.177	0.239	0.853	0.655-1.111
DOGS (Absent)						
Present	-0.224	0.152	-1.471	0.141	0.799	0.594-1.081

(b) Breeding nests (N = 1104). Hosmer and Lemeshow Test: $\chi^2_8 = 8.621$, $p = 0.375$; Nagelkerke $R^2 = 0.230$.

Variable	**Estimate**	**SE**	**z**	**p**	**OR**	**95% CI**
(Intercept)	-3.325	0.422	-7.873	<0.001	0.036	0.015-0.080
MONTHSINSTALLED	**0.017**	**0.002**	**7.908**	**<0.001**	**1.017**	**1.013-1.021**
TYPE (Purchased)						
Homemade	0.267	0.153	1.746	0.081	1.306	0.967-1.762
SHELTERED (Not in sheltered location)						
In a sheltered location	**0.570**	**0.228**	**2.498**	**0.013**	**1.768**	**1.144-2.805**
FRONTBACKACCESS (No front-to-back access for hedgehogs)						
Front-to-back access	**0.462**	**0.177**	**2.606**	**0.009**	**1.587**	**1.127-2.259**
OTHERNESTS (No alternative nesting sites used)						
Alternative nesting sites used	**0.863**	**0.152**	**5.692**	**<0.001**	**2.369**	**1.764-3.196**
POND (No garden pond)						
Pond	**-0.667**	**0.165**	**-4.041**	**<0.001**	**0.513**	**0.370-0.707**
BEDDING (None provided)						
One type	-0.067	0.229	-0.291	0.771	0.936	0.602-1.480
Both types	-0.229	0.286	-0.804	0.422	0.795	0.455-1.395
HEDGEHOGFOOD (None provided)						
Scattered in varying locations	0.992	0.552	1.797	0.072	2.696	0.877-7.810
<0.5m from nest box	-0.054	0.386	-0.140	0.889	0.947	0.440-2.017
0.5m-5m from nest box	**0.976**	**0.280**	**3.485**	**<0.001**	**2.653**	**1.563-4.705**
5.1-10m from nest box	0.719	0.403	1.784	0.074	2.053	0.926-4.531
>10m from nest box	**1.141**	**0.321**	**3.556**	**<0.001**	**3.131**	**1.691-5.978**

BADGERFOX (Not sighted)						
Sighted	-0.096	0.149	-0.645	0.519	0.908	0.678-1.216
DOGS (Absent)						
Present	-0.323	0.182	-1.776	0.076	0.724	0.504-1.029

(c) Winter day nests (N = 1300). Hosmer and Lemeshow Test: $\chi^2_8 = 10.681$, p = 0.220; Nagelkerke $R^2 = 0.240$.

Variable	**Estimate**	**SE**	**z**	**p**	**OR**	**95% CI**
(Intercept)	-1.976	0.516	-3.832	<0.001	0.139	0.050-0.381
MONTHSINSTALLED	**0.014**	**0.003**	**5.442**	**<0.001**	**1.014**	**1.009-1.019**
TYPE (Purchased)						
Homemade	**0.483**	**0.137**	**3.515**	**<0.001**	**1.621**	**1.240-2.125**
HARDSTANDING (Not on hardstanding)						
On hardstanding	**0.468**	**0.184**	**2.547**	**0.011**	**1.597**	**1.119-2.302**
SHELTERED (Not in sheltered location)						
In a sheltered location	**0.495**	**0.175**	**2.821**	**0.005**	**1.640**	**1.163-2.314**
DISTANCEBUILDING (≥5m from a building)						
<5m from a building	0.216	0.148	1.463	0.144	1.241	0.930-1.662
FACING (Entrance faces wall/fence)						
Parallel to wall/fence	-0.077	0.285	-0.270	0.787	0.926	0.523-1.605
Faces shrubs/plantings	0.031	0.297	0.104	0.917	1.031	0.570-1.831
Faces the open	**-0.590**	**0.279**	**-2.112**	**0.035**	**0.555**	**0.317-0.949**
Other	0.188	0.323	0.582	0.561	1.207	0.637-2.266

FRONTBACKACCESS (No front-to-back access for hedgehogs)						
Front-to-back access	**0.366**	**0.150**	**2.445**	**0.014**	**1.441**	**1.074-1.932**
OTHERNESTS (No alternative nesting sites used)						
Alternative nesting sites used	**0.560**	**0.134**	**4.195**	**<0.001**	**1.751**	**1.349-2.278**
POND (No garden pond)						
Pond	-0.232	0.142	-1.626	0.104	0.793	0.600-1.049
GOODHAB	-0.006	0.004	-1.441	0.150	0.994	0.987-1.002
BEDDING (None provided)						
One type	**0.868**	**0.204**	**4.261**	**<0.001**	**2.383**	**1.601-3.564**
Both types	**1.484**	**0.266**	**5.585**	**<0.001**	**4.412**	**2.636-7.482**
HEDGEHOGFOOD (None provided)						
Scattered in varying locations	0.555	0.498	1.116	0.265	1.742	0.665-4.759
<0.5m from nest box	**0.662**	**0.267**	**2.477**	**0.013**	**1.938**	**1.151-3.283**
0.5m-5m from nest box	**1.065**	**0.212**	**5.011**	**<0.001**	**2.900**	**1.916-4.412**
5.1-10m from nest box	**0.633**	**0.306**	**2.071**	**0.038**	**1.883**	**1.038-3.447**
>10m from nest box	**1.251**	**0.270**	**4.635**	**<0.001**	**3.492**	**2.069-5.966**
BIRDFOOD (None provided)						
Provided	0.201	0.134	1.507	0.132	1.223	0.941-1.589
BADGERFOX (Not sighted)						
Sighted	-0.219	0.133	-1.643	0.100	0.803	0.618-1.043
DOGS (Absent)						
Present	-0.224	0.152	-1.471	0.141	0.799	0.594-1.081

(d) Hibernation nests (N = 1592). Hosmer and Lemeshow Test: $\chi^2_8 = 14.175$, $p = 0.077$; Nagelkerke $R^2 = 0.286$.

Variable	Estimate	SE	z	p	OR	95% CI
(Intercept)	-2.731	0.486	-5.622	<0.001	0.065	0.025-0.168
MONTHSINSTALLED	**0.021**	**0.002**	**8.820**	**<0.001**	**1.021**	**1.017-1.026**
TYPE (Purchased)						
Homemade	**0.251**	**0.121**	**2.080**	**0.038**	**1.285**	**1.015-1.630**
FRONTORBACK (Front garden)						
Back garden	0.079	0.221	0.357	0.721	1.082	0.700-1.666
HARDSTANDING (Not on hardstanding)						
On hardstanding	**0.373**	**0.161**	**2.316**	**0.021**	**1.452**	**1.061-1.996**
SHELTERED (Not in sheltered location)						
In a sheltered location	0.299	0.161	1.862	0.063	1.348	0.984-1.848
DISTANCEBUILDING (≥5m from a building)						
<5m from a building	**0.341**	**0.137**	**2.500**	**0.012**	**1.407**	**1.078-1.841**
FACING (Entrance faces wall/fence)						
Parallel to wall/fence	0.001	0.302	0.003	0.997	1.001	0.541-1.780
Faces shrubs/plantings	-0.043	0.314	-0.138	0.890	0.957	0.507-1.746
Faces the open	**-0.585**	**0.296**	**-1.978**	**0.048**	**0.557**	**0.305-0.976**
Other	-0.267	0.336	-0.794	0.427	0.766	0.390-1.465
ORIENTATION (Entrance faces North)						
East	0.305	0.172	1.776	0.076	1.357	0.969-1.902
South	**0.347**	**0.168**	**2.065**	**0.039**	**1.415**	**1.018-1.968**
West	0.189	0.185	1.020	0.308	1.208	0.840-1.737
RAISED (Not raised)						

Raised	**0.364**	**0.178**	**2.053**	**0.040**	**1.440**	**1.023-2.054**
CONNECTED	-0.021	0.045	-0.473	0.636	0.979	0.896-1.070
FRONTBACKACCESS (No front-to-back access for hedgehogs)						
Front-to-back access	**0.496**	**0.134**	**3.697**	**<0.001**	**1.643**	**1.263-2.139**
OTHERNESTS (No alternative nesting sites used)						
Alternative nesting sites used	**0.656**	**0.118**	**5.564**	**<0.001**	**1.926**	**1.530-2.428**
POND (No garden pond)						
Pond	-0.130	0.125	-1.040	0.299	0.878	0.686-1.122
GOODHAB	-0.004	0.003	-1.173	0.241	0.996	0.989-1.003
BEDDING (None provided)						
One type	**0.720**	**0.183**	**3.940**	**<0.001**	**2.055**	**1.440-2.952**
Both types	**1.107**	**0.237**	**4.677**	**<0.001**	**3.024**	**1.909-4.831**
HEDGEHOGFOOD (None provided)						
Scattered in varying locations	0.141	0.477	0.295	0.768	1.151	0.449-2.946
<0.5m from nest box	0.167	0.245	0.684	0.494	1.182	0.732-1.911
0.5m-5m from nest box	**0.933**	**0.188**	**4.957**	**<0.001**	**2.542**	**1.763-3.690**
5.1-10m from nest box	**0.962**	**0.290**	**3.319**	**0.001**	**2.617**	**1.489-4.646**
>10m from nest box	**1.088**	**0.237**	**4.597**	**<0.001**	**2.968**	**1.873-4.739**
BIRDFOOD (None provided)						
Provided	-0.102	0.121	-0.843	0.399	0.903	0.712-1.144
BADGERFOX (Not sighted)						
Sighted	-0.133	0.119	-1.112	0.266	0.876	0.693-1.106
DOGS (Absent)						
Present	**-0.346**	**0.140**	**-2.462**	**0.014**	**0.708**	**0.537-0.932**

Table 3. Summary of explanatory variables considered in GLM analyses that had significant positive (+) or negative (-) influences on the use of nest boxes by hedgehogs for summer day nesting, breeding, winter day nesting and/or hibernation (see Table 2 for detailed breakdown). Single symbol = p <0.05, double symbol = p <0.01, triple symbol = p <0.001.

Variable	SUMMER	BREEDING	WINTER	HIBERNATION
MONTHSINSTALLED	+++	+++	+++	+++
TYPE			+++	+
MATERIAL				
HEIGHT				
WIDTH				
DEPTH				
CAPACITY				
FRONTORBACK	+			
HARDSTANDING	+		+	+
SHELTERED	++	+	++	
DISTANCEBUILDING	++			+
FACING	-		-	-
ORIENTATION				+
RAISED	+			+
CONNECTED				
FRONTBACKACCESS	++	++	+	+++
OTHERNESTS	+++	+++	+++	+++
POND	- -	- - -		
GOODHAB	- -			
BEDDING	+++		+++	+++
HEDGEHOGFOOD	+++	+++	+++	+++
BIRDFOOD				
BADGERFOX				
DOGS				-
URBAN500				
ARABLEDIST				
WOODDIST				
GRASSDIST				

For variables with >2 categories, the effect refers to the following levels: FACING the open; ORIENTATION to the south; BEDDING provided was natural, artificial or both; HEDGEHOGFOOD provided in any of the possible locations listed in the survey including scattered, <0.5m, 0.5-5m, 5.1-10m and/or >10m from the nest box.

Discussion

The percentage of nest boxes reported to have been used at least once varied between nesting types: summer day nesting (81.3%), breeding (28.2%), winter day nesting (66.5%) and hibernation (58.6%). These are, however, maximum figures because of the way in which data were collated for analysis; we were only able to include respondents who had evidence that their box had, or had not, been used for these purposes. If we assume that all additional boxes owned by respondents who did not have such evidence had never been used, then these figures would be markedly reduced: summer day nesting (35.3%), breeding (7.2%), winter day nesting (20.1%) and hibernation (21.7%). This lack of definitive information about patterns of use is, in part, related to the fact that conservation organisations recommend that householders should not look in their box to check if they are being used due to the risks associated with disturbing hedgehogs. Instead, householders are advised to use motion-activated cameras outside the box or other approaches, such as placing a small stick or piece of straw across the entrance, to determine whether an animal (assumed to be a hedgehog) has entered. Although critically important in the context of ensuring the welfare of the animals involved, this does limit the amount of data available for studies such as this one: we were only able to consider whether nest boxes had ever been used during their 'lifetime', rather than the frequency of use.

The majority (88.3%) of hedgehog nest boxes had been installed within the five-year period prior to this survey, implying that there has been a marked increase in recent years in the number of householders providing such refuge structures. In most cases (78.9%), these boxes were deployed after the householder knew that hedgehogs were already visiting their garden implying that personal knowledge of the species' presence is a particularly strong motivational factor influencing whether householders decide to help hedgehogs in this way. Nevertheless, the subsequent use of these boxes will be dependent on the suitability of their design and placement in the householder's garden. Consequently, it is important that the factors influencing nest box use for day nesting, breeding and/or hibernating are identified so that householders and conservation practitioners can be advised appropriately to maximise their use.

Collectively, our analyses indicated that there were subtle differences in the factors associated with the use of nest boxes for day nesting, breeding and hibernating, but, overall, these tended to be factors relating to nest box placement, resource provisioning and site-based features, rather than those relating to box design. For all nesting types, the length of time the box had been deployed, the availability of artificial food and the presence of access points for hedgehogs into back gardens from the front significantly increased the likelihood that a nest box had been used. However, both deployment time and artificial food could be associated with a form of reporting bias. For example, householders may have been increasingly more likely to have noticed, by chance, that their box had been used simply because the box had been in their garden for longer, and those householders who fed hedgehogs may have been more likely to monitor hedgehog activity in their garden; the latter may also explain the positive association between nest box use and the identification of other nesting sites in the garden. Alternatively, it is known that a range of mammal species exhibit neophobic responses to novel objects in the environment (Stryjek *et al*., 2019), such that hedgehogs may need to become habituated to a nest box before using it (*sensu* Madikiza *et al*., 2010).

Conversely, artificial food may represent an attractive resource for hedgehogs in the context of selecting the position of nest sites. Food abundance has been known to influence nest box occupancy by arboreal mammals (Nakamura-Kojo *et al*., 2014) and, for birds, can facilitate greater occupancy of closely spaced refuges when compared to sites where food is less abundant (Hussell, 2012). Supplementary food can simultaneously act to increase energy intake and reduce foraging time, such that animals would have more time for nest building (Smith *et al*., 2013). However, patterns of hibernation may be disrupted where anthropogenic food is regularly available (Gazzard & Baker, 2020), and the nutritional quality of such food may also be inadequate (Gimmel, Eulenberger & Liesegang, 2021). In addition, artificial food often attracts several individuals to the same location, which may increase intra-specific aggression; although this is known to happen at feeding stations, it is not known whether this also extends to artificial refuges. Nonetheless, proximity to a food source may be desirable in those instances where hedgehogs may be reluctant to move far from a nest site, for example, during breeding when vulnerable young are present, and during hibernation when natural food availability is low. Similarly, staying close to a nest site would potentially be important where nest boxes themselves are a limiting resource. Whether this is an issue is, however, equivocal: for example, the householders in this study collectively reported an average of 0.6 other nest sites within their gardens, in locations that are likely to be present in a broad range of other gardens (e.g., in vegetation and compost heaps, as well as underneath woodpiles, sheds and decking). Furthermore, the quantity of urban habitat within 500m of the garden, and the distance to the nearest area of arable land, woodland or grassland, had no effect on nest box use suggesting that these other habitats are not critically important as potential nesting locations.

One of the major factors thought to affect urban hedgehog populations is patterns of connectivity between neighbouring back gardens but also from an individual householder's front garden to their back garden (Gazzard *et al*., 2021; App *et al*., 2022; Gazzard *et al*., 2022). In this study, nest box use was not significantly affected by the number of neighbouring back gardens which were accessible to hedgehogs from the respondent's own garden, but front-to-back access was significantly positively correlated with all four patterns of nest box use. Both results could potentially be explained by the fact that most householders put out boxes once they knew hedgehogs were already visiting; consequently, access into the respondent's garden was already possible. Alternatively, front-to-back access could simply be a proxy for houses with larger gardens: in the UK, detached and semi-detached houses are typically associated with larger gardens which permit access down both or one the sides of the house, respectively; terraced houses typically have the smallest sized gardens, and access from the front to the back is not always possible. However, it has been noted that front-to-back access also significantly decreases the proportion of time hedgehogs spend in back gardens (Gazzard *et al.*, 2022). Although the underlying reason for this is not known, it could suggest that front gardens contain important resources not present in back gardens or that this facilitates movement through the landscape (particularly between blocks of houses separated by roads) and perhaps even helps animals avoid one another when foraging. More detailed information is therefore required on how key resources are distributed throughout the urban landscape, but also the patterns of behaviour exhibited by hedgehogs in different types of gardens.

Given the potential vulnerability of animals that are sleeping, hibernating or which have dependent young, hedgehogs would be expected to select locations which reduce the risk of detection by predators (Evans *et al.* 2002), accidental disturbance and which also offer protection from inclement weather conditions; refuges located in sheltered locations are likely to experience reduced exposure to rain, wind and direct sunshine, and may more closely mimic natural nesting locations (Morris, 2018). Accordingly, nest boxes in the current study were more likely to have been used by hedgehogs when they were positioned in sheltered locations, such as under shrub cover, and less likely to have been used when entrances faced into the open (i.e., facing towards the middle of the garden); these relationships were generally consistent for all nesting types with the exception of sheltered locations during hibernation and the orientation of the box's entrance during breeding. It may be the case that during breeding and hibernation, the influence of other factors are of greater relative importance, aligning with the specific needs and/or vulnerabilities of hedgehogs at these times.

During the hibernation period, there is a risk that exceptionally low temperatures within nests could trigger thermogenesis (Malan, 2010) leading to the utilisation of brown fat stores (Nedergaard & Cannon, 1990) which are critical for rapid metabolism during arousals from torpor (Morris, 2018). Indeed, in hedgehogs, hibernacula temperatures <0 °C have been associated with increased oxygen consumption and shorter periods of torpor, compared to individuals in nests maintained at temperatures >0 °C (Soivio *et al.*, 1968). In this study, nest boxes located on hardstanding, within close proximity (<5m) to buildings and those with entrances oriented to the south were more likely to have been used for hibernation (although summer day nesting was also positively influenced by the former variables). Temperatures of hardstanding and building surfaces tend to be higher than those measured on soil, grass or other green areas due to their greater ability to absorb and retain solar radiation (see Bowler *et al*., 2010; Loughner *et al*., 2012). Additionally, when entrances are oriented east or south, internal nest temperatures can be warmer than in nest boxes facing other orientations (Ardia *et al.*, 2006; Butler *et al.*, 2009). As such, it is possible that the thermal properties of surrounding substrates and ambient sunshine could positively influence temperature profiles within nest boxes during the hibernation period, although this requires verification as well as investigation of how thermal profiles may be affected by the design of the next box itself.

Hedgehogs were also significantly less likely to have used a nest box for hibernating on sites where the respondent owned a dog. Hibernating animals are presumably less responsive to predation attempts or disturbances (Boyles *et al*., 2020) since it takes typically >5 hours for hedgehogs to fully arouse from torpor (Morris, 2018). They may therefore seek to hibernate in locations where predators are less likely to occur. The presence of badgers and/or foxes did not, however, have a marked effect on nest box use during hibernation, although it must be noted that badgers do not often leave their setts over winter (Fowler & Racey, 1988), and we were not able to investigate the effect of foxes alone as only a low number of respondents reported having sighted them in their garden. However, it is reasonable to assume that hedgehog boxes are often likely to be sited in gardens where foxes are present, given their agility and widespread distribution in urban areas in the UK (Scott *et al*., 2014). Similarly, both foxes and badgers are likely to be attracted to gardens where food is put out for hedgehogs by the householder. At the present time, however, there are few data available on the frequency with which hedgehogs, foxes and badgers interact with one another in residential gardens, the manner of these interactions nor the effectiveness of anti-predation features of hedgehog nest boxes such as integral bases, external tunnels or internal partitions (see Bailey & Bonter, 2017).

In this study, we were not able to investigate in detail how the design of nest boxes influenced their use by hedgehogs since many design-related variables had to be excluded due to issues arising from multicollinearity. Of the variables that were included in the analyses, the external dimensions, internal volume and primary construction materials of boxes were not important factors affecting nest box use, whereas the type of nest box and whether it was raised off the ground had significant impacts. First, homemade nest boxes were more likely to have been used than commercially available nest boxes for winter day nesting and hibernation. This could possibly be associated with parameters that were not measured in this study, such as the age, condition, thickness or colour of the materials used to construct homemade boxes. For example, it has been demonstrated that dark-green wooden nest boxes experience greater average daily temperatures when compared to boxes painted with lighter colours (Griffiths *et al*., 2017); it could be possible that homemade nest boxes are more likely to have been painted in such a way that influenced nest box selection during colder periods. Second, boxes that were raised off the ground were significantly more likely to have been used for summer day nesting and hibernation. However, it is not clear whether the latter was representative of a specific design feature (i.e., legs attached to the base), placement decision (e.g., nest box was elevated on bricks), or even a proxy of such boxes possessing bases (by default, a box raised off the ground would have a solid base). Further investigation is needed to determine any preferences for, and the effects of, various nest box design features.

Resources provided by householders strongly influenced nest box use, with the provisioning of bedding and food associated with the largest odds ratios across all models. The provision of bedding materials (e.g., leaves, hay and/or shredded newspaper) within nest boxes significantly positively influenced their use for day and hibernation nesting, but had a (nonsignificant) negative effect in the context of breeding. During reproduction, females with dependent young are particularly sensitive, and mothers may abandon breeding nests and/or kill their young if their nests are disturbed (Morris, 2018). Typically, such disturbance is associated with human activities (e.g., garden maintenance, dog walkers) but could potentially arise because of intra-specific interactions, although there is no definitive evidence of this. Consequently, it may be that pregnant females consider the presence of bedding material to be an indication of the presence of other hedgehogs, particularly if the box retains the scent of individuals who have visited previously.

In studies of naturally constructed nests, the leaves of broadleaved trees appeared to be preferred, especially as these can be “woven” to create a layered structure which is thought to help maintain the temperature within the nest whilst allowing gaseous transfer (Morris, 2018). Unfortunately, broadleaved trees can often be removed from urban areas in the UK because of, e.g., human safety concerns and the risk posed to buildings (Pauleit *et al*., 2005; Andrew & Slater, 2015). In addition, fallen leaves in gardens are often removed by householders for aesthetic reasons. This might consequently be linked to the positive association between nest box use (for summer and winter day nesting, and hibernation) and the active provision of bedding material by humans. However, different nesting materials are likely to vary with respect to their thermal properties (Corrales-Moya *et al*., 2021), longevity (Hebda *et al*., 2017) and/or influence on ectoparasite presence (Reynolds *et al*., 2019). In addition, some man-made materials may contain toxic compounds that could affect survival (Mukai *et al*., 2014). Additional research is therefore required to examine which materials are being used by hedgehogs within nest boxes, how this relates to material availability in the wider environment and how nest structure ultimately affects their behaviour and success. Such research would help to identify the most suitable materials which householders should provide, if this was deemed necessary (*sensu* Slobodník *et al*., 2017), but also help to determine suitable box cleaning regimes (e.g., Tomás *et al*., 2007).

Conclusions

The use of an online questionnaire survey of householders enabled the rapid collection of a large quantity of information relating to factors affecting nest box use by hedgehogs, but was associated with limitations. First, we were only able to investigate factors associated with whether a box had ever been used, rather than their frequency of use. Second, several variables that were significantly associated with the increased use of boxes could have represented a form of reporting bias whereby respondents who were especially ‘hedgehog-friendly’ may have been more likely to monitor their boxes for hedgehog activity. Whilst acknowledging the limitations of these data, the results indicate moderate to high uptake rates of hedgehog boxes for nesting. Subtle differences in the factors associated with the four patterns of nesting were identified relating to nest box placement, resource provisioning and site-based features; in general terms, householders might be able to improve the likelihood that their nest boxes are used by hedgehogs by placing them under shelter, ensuring that their gardens are sufficiently accessible from the front garden to the back, and providing additional resources such as food and bedding. In some seasons, including over winter, positioning the nest box on hardstanding and/or closer (<5m) to a building, and ensuring that the box entrance does not face the open, may increase the chances of it being used. The drivers behind such placement 'preferences' are, however, unclear, and further research is needed to investigate these factors in more detail.

Future research recommendations

Although questionnaire surveys represent a mechanism for rapidly collecting large volumes of data, they are susceptible to reporting biases that may exaggerate the importance of hedgehog boxes as nesting sites. Future studies, therefore, need to adopt experimental or quasi-experimental approaches whereby householders are recruited in a more randomised manner. Such studies need to ensure that all householders monitor their boxes continuously so that definitive data on patterns of use can be obtained; this could involve existing technologies, such as commercially available motion-activated cameras, or the development of new approaches such as cameras or other devices mounted inside nest boxes. Furthermore, additional monitoring techniques and/or novel experimental approaches are required to quantify how the internal conditions of boxes are affected by their design and placement, and the relative vulnerability of boxes to other species; preference experiments within gardens would help to identify whether hedgehogs select particular box designs or types of bedding. Finally, the pattern of use of nest boxes must be considered in the context of natural nest site availability, i.e., are nest boxes used more frequently where natural nest sites are limited? Consequently, field studies are required to quantify the frequency of use of artificial refuges relative to other sites, but which also compare the success of hedgehogs in nest boxes versus other nesting sites in the context of, for example, over-winter survival rates and reproductive success; ideally, such studies should consider both urban and rural landscapes.

Chapter 5

An assessment of a conservation strategy to increase garden connectivity for hedgehogs that requires cooperation between immediate neighbours: a barrier too far?

Gazzard, A., Boushall, A., Brand, E. & Baker, P.J. (2021) An assessment of a conservation strategy to increase garden connectivity for hedgehogs that requires cooperation between immediate neighbours: a barrier too far? *PLoS ONE* 16, e0259537.

Abstract

Urban areas are associated with high levels of habitat fragmentation. For some terrestrial species with limited climbing abilities, property boundaries can pose a significant problem by limiting access to residential gardens. The West European hedgehog (*Erinaceus europaeus*) has declined markedly in the UK but is commonly found in areas of human habitation, including residential gardens. 'Hedgehog Street' is a public engagement campaign aimed at recruiting volunteers ('Hedgehog Champions') to create access points ('hedgehog highways') across garden boundaries to improve habitat connectivity. In this study, we used a series of questionnaire surveys to explore motivations for and obstacles to the creation of highways. Householders were more likely to have created a highway if they were already aware of the Hedgehog Street campaign, if their garden contained a high number of wildlife-friendly features and if they considered watching wildlife to be important. Hedgehog Champions created, on average, 1.69 highways each with 52.0% creating none; this would equate to an estimated >120,000 across all registered Champions. In comparison, 6.1-29.8% of non-Champions stated that they had made a highway. However, most highways had been created in boundaries that could already be traversed via naturally occurring holes: only 11.4% of garden boundaries could be traversed, and 3.2% of gardens accessed, just via a hedgehog highway. In addition, only 5.0% of gardens were considered totally inaccessible to hedgehogs. The most common reasons cited for not having made a highway were that householders' gardens were already accessible to hedgehogs followed by concerns relating to boundary ownership and/or communicating with neighbours. Future studies need to identify strategies for overcoming these obstacles to maximize citizen engagement, particularly with those householders who are not innately 'wildlife-friendly', and to quantify the degree to which networks of highways affect patterns of individual movement and, ultimately, populations.

Introduction

Urbanisation is a major form of anthropogenic land-use change and is typically associated with a decline in biological diversity (Burton *et al*., 2005; Mangialajo *et al*., 2008; Saito and Koike, 2013; Sol *et al*., 2014). Such declines are effects of the destruction, degradation and fragmentation of natural/semi-natural habitats but also the presence of a range of characteristics associated with urban areas that many species cannot tolerate (Sol *et al*., 2013; Sol *et al*., 2014). Consequently, ecological communities in urban areas are often dominated by generalist species (Ducatez *et al*., 2018; Callaghan *et al*., 2019), with some occurring at higher densities in towns and cities than in natural habitats (Blair, 1996; Prange *et al*., 2003; Chace and Walsh, 2004; Hubert *et al*., 2011; Bateman and Fleming, 2012). Urban areas can, nonetheless, support species-rich assemblages (Angold *et al*., 2006; Goddard *et al*., 2010; Borysiak *et al*., 2017; van Helden *et al*., 2020), including species of conservation concern (Meffert and Dziock, 2012; Matthies *et al*., 2015; Threlfall *et al*., 2015). As such, urban areas could function as a conservation tool for wildlife if managed sympathetically (van Helden *et al*., 2020; Doody *et al*., 2009; Goldingay, 2008; Pierret and Jiguet, 2018).

The physical structure of urban areas varies markedly between countries (Besussi *et al*., 2010). In the UK, they contain a wide range of natural and semi-natural green- and blue-spaces but are dominated by private residential gardens (Loram *et al*., 2007). Individually, gardens tend to be small but collectively cover a substantial area. For example, Davies *et al.* (2009) estimated a mean garden size of 190m^2 which, multiplied across the estimated 22.7 million UK households with access to a garden, equates to a combined area of >4,000 km^2. Residential gardens therefore offer potentially substantive conservation benefits, yet present considerable challenges such as the possible need to engage large numbers of householders for these benefits to be realised (Gaston *et al.*, 2005; Goddard *et al*., 2010).

Many UK householders are interested in wildlife as demonstrated by the millions of ponds and nest boxes installed in residential gardens, and the fact that approximately 51% of residents supply food for birds at least some of the time (Davies *et al.*, 2009). However, wildlife gardening activities are often directed at species which are very mobile or not of conservation concern. For example, bird feeders are often utilised by species that are common and widespread or non-native (Le Louarn *et al.*, 2016; Galbraith *et al*., 2017). One corollary of high mobility is that neighbouring householders do not necessarily need to coordinate their wildlife-gardening efforts as fauna can fly between gardens or climb over/dig under garden boundaries. For less agile species, however, coordination between neighbours becomes more critical.

The West European hedgehog (*Erinaceus europaeus*; hereafter 'hedgehog') is a small (<1.5kg), cursorial, nocturnal mammal which has declined markedly in Britain and Europe in recent decades (Mathews *et al*., 2018; Morris, 2018; Williams *et al*., 2018b; Rasmussen *et al*., 2019a). In rural landscapes, primary threats include habitat loss, fragmentation and degradation (Hof and Bright, 2010; Hof *et al*., 2012; Moorhouse *et al*., 2014) and an increase in the number of badgers (*Meles meles*) (Judge *et al*., 2014), an intraguild predator (Trewby *et al*., 2014). As a result, hedgehogs are now increasingly found within or near human settlements (Hubert *et al*., 2011; Parrott *et al*., 2014; van de Poel *et al*., 2015; Pettett *et al*., 2017), with residential gardens (especially rear gardens) a favoured habitat (Pettett *et al*., 2017; Dowding *et al*., 2010a). However, urban-dwelling hedgehogs face a range of challenges including accidental exposure to pesticides (Dowding *et al*., 2010b), human disturbance (Rast *et al*., 2019), injury by domestic animals (Rasmussen *et al*., 2019a), and barriers to movement including roads (Rondini and Doncaster, 2002; Braaker *et al*., 2014) and garden fences (Morris, 2018). The latter is considered of increasing importance because of perceived changes in the numbers of rear gardens fully or partially enclosed by wooden fences, particularly those with gravel boards (horizontal wooden or concrete boards at ground level designed to protect fence panels from ground-level moisture; these have the effect of reducing the number of holes in fences caused by the natural deterioration of the fence material). To this end, two UK charities, the People's Trust for Endangered Species (PTES) and the British Hedgehog Preservation Society (BHPS), launched the citizen engagement programme 'Hedgehog Street' in 2011 to aid the conservation of urban hedgehog populations.

Hedgehog Street, Hedgehog Highways and Hedgehog Champions

Hedgehog Street (HS) is administered via a website (www.hedgehogstreet.org) that summarises information on hedgehog ecology and behaviour, trends in hedgehog numbers and how people can make their gardens more hedgehog-friendly. The website also acts as a forum for people to share information, observations and photographs. Individuals are encouraged to engage with the programme by signing up to become a 'Hedgehog Champion' (hereafter 'Champion').

One major focus of HS is to persuade members of the public (Champions and non-Champions) to create holes (130*130mm) through or under their garden boundaries ('hedgehog highways'; hereafter 'highways') to increase connectivity between gardens. These could potentially help hedgehogs in three ways: (i) enabling entry to previously inaccessible gardens, thereby increasing the carrying capacity of the environment; (ii) reducing travel distances between gardens, thereby reducing the energetic burden of foraging; and/or (iii) reducing the number of road crossings between blocks of houses, thereby reducing the mortality risk from traffic. These putative benefits are, however, predicated on several key assumptions e.g., that currently inaccessible gardens contain resources that hedgehogs require, and that highways do not simply allow animals to traverse boundaries where crossing points already exist. Although comprehensive evidence on the effectiveness of improving inter-garden connectivity is lacking, local field studies have demonstrated that hedgehog detection and occupancy rates are influenced to varying degrees by garden accessibility (Williams *et al.*, 2018a; Gloucestershire Wildlife Trust, 2020).

Given that urban hedgehog populations need up to 90ha of suitable habitat for numbers to be sustainable (Morris, 2018), and that individuals may visit up to 20 gardens nightly (Rasmussen *et al.*, 2019a), relatively large numbers of highways would need to be constructed in a single neighbourhood to generate an effect of significant magnitude to positively influence hedgehog density, survival rates and/or reproductive output. Accordingly, Champions are given access to additional support materials to help them enlist other householders with the goal of creating a high-density network of highways in their neighbourhood. Champions and non-Champions are also asked to upload geo-referenced sightings of hedgehogs (dead or alive) and the position of any highways that they have created to an interactive map (The Big Hedgehog Map: www.bighedgehogmap.org). At the time of writing (October 2021), >100,000 people have signed up as Champions, and >100,000 and >18,000 sightings of live and dead hedgehogs have been reported, respectively, as well as the creation of >15,000 highways.

Despite the apparently high levels of engagement with this campaign, and the public's generally positive attitude towards hedgehogs (Morris, 1987; Bjerke *et al.*, 2003; Bjerke and Østdahl, 2004; Baker and Harris, 2007; Borgi and Cirulli, 2015), UK urban hedgehog populations are still declining (Wilson and Wembridge, 2018). The reasons for this are likely to be multi-faceted, but could be partly associated with the ability of citizens to engage with hedgehog conservation strategies, even if they are willing. For example, HS requires immediate neighbours to create a highway through or under a shared garden boundary, and this is subtly different from most other wildlife-friendly gardening practices since: it requires communication and agreement between neighbouring householders to avoid disputes (householders typically own the rights to just one of the boundaries running down the side of their property); it involves the alteration of a boundary structure which may have been erected to maintain privacy or to keep pets within the owner's garden; and it might be considered aesthetically unpleasing. In addition, residents may not own the property they are living in; approximately 34% of UK households are privately or socially rented houses (Office for National Statistics, 2019) and tenants may not be permitted to modify any boundaries.

It is also reasonable to expect that not all householders are concerned about the plight of hedgehogs, whereas others may have their own perceptual biases about the need to create highways. For example, residents that have already seen hedgehogs in their garden may consider that creating further access points is unnecessary, whilst not appreciating that these could offer additional advantages in terms of movement through the wider landscape. Furthermore, householders that never see hedgehogs in their garden/neighbourhood may conclude that hedgehogs are simply not present, even though this may not be the case. Consequently, the HS campaign could be associated with a number of significant challenges and, as with other conservation campaigns, should ideally be managed adaptively (Keith *et al*., 2011; Rist *et al*., 2012; Jordan *et al*., 2016; Williams and Brown, 2016). This means that progress needs to be assessed periodically with a view to amending, or even abandoning, strategies if deficiencies are evident (Rist *et al*., 2012; Mackenzie and Keith, 2009; Serrouyaa *et al.* 2019). Therefore, in this study we used a series of questionnaire surveys to: (1) quantify the proportions of Champions and non-Champions who have created a highway; (2) identify the factors associated with the creation of highways; (3) examine the relative importance of reasons given for not having created a highway; (4) estimate the potential effect of the creation of these highways on hedgehog movement patterns; and (5) outline recommendations for the future growth of this campaign.

Methods

Data were collected through a series of online questionnaires in September-October 2018, October 2019 and December 2019-April 2020; these are referred to as the 2018, 2019 and 2020 surveys, respectively (see Appendix D). The first two surveys were conducted in collaboration with University of Reading students as part of their undergraduate studies; online links to each questionnaire were advertised via postings on relevant social media groups (e.g., those related to gardening and wildlife, as well as local community groups) and released to family members of all students within the School of Biological Sciences with instructions for them to disseminate it to further friends and family.

The 2020 survey was conducted in collaboration with the PTES and BHPS and released to all Hedgehog Champions registered to receive email communications at that time (N = 43,650), as well as social media followers of PTES and BHPS. Since it was possible for non-

Champions to take part in this survey via the links provided on social media, respondents were asked to clarify whether they were registered as Champions or not. Given the slight differences between surveys, we have selected and/or merged responses from individual surveys where necessary.

Surveys were granted approval by the ethical review panel of the School of Biological Sciences at the University of Reading. At the start of each survey, respondents were informed of the goals of the survey, how the data would be stored and used, that the data would not be shared with any third party and that the data would be anonymous (i.e., it would not be possible to identify any individual from the information supplied). Respondents provided written informed consent and were also asked to confirm that they were aged 18 or over before being granted access to the questionnaire itself.

Proportion of respondents creating hedgehog highways

Survey data were used to derive three estimates of the proportion of Champions (P_C) and non-Champions (P_N) who had made a highway. As respondents in the 2020 survey were asked whether they had registered as a Hedgehog Champion, estimates for P_C and P_N were derived from those respondents that stated that they were and were not registered Champions, respectively.

In the 2018 and 2019 surveys, respondents were asked whether they had heard of the HS campaign, but not whether they had registered as a Champion. Consequently, each data set could have consisted of a combination of Champions and non-Champions. Therefore, data from respondents that had not heard of the HS campaign were used to estimate P_N (by inference these respondents could not have signed up to become a Champion), whereas data from respondents that had heard of HS were used to estimate P_C (this assumes that these respondents may have signed up to become Champions). Estimates for both parameters were derived from the 2018 and 2019 surveys separately. Differences in P_C and P_N between surveys were compared using chi-squared tests; post hoc groups were identified using the procedure outlined by Siegel and Castellan (1988).

To investigate possible biases in the households surveyed, we used a series of chi-squared tests to compare the proportion of respondents that fed birds, had a bird box and/or pond in their garden with the corresponding proportions cited by Davies *et al.* (2009) for the UK (51%, 21% and 16%, respectively). These analyses compared: (i) all individuals in each of the three surveys; (ii) those respondents who had/had not made a hedgehog highway; and (iii) those respondents who had/had not heard of the Hedgehog Street campaign. A Bonferroni correction was applied to adjust for multiple testing.

In addition, all respondents were asked whether they fed hedgehogs or had a hedgehog house in their garden. Champions were further asked whether they had created their highway before or after they knew hedgehogs were present in their garden and whether they thought hedgehog activity in their garden had increased after having created a highway.

Hedgehog accessibility into neighbouring gardens

Patterns of accessibility into back gardens and across individual boundaries between neighbouring gardens were quantified using data from 2019 and 2020. In both surveys, householders were asked to state: (1) the number of neighbouring gardens bordering their own back garden; (2) the number of these gardens that were accessible to hedgehogs via (i) a natural hole only (e.g., a hole that had been dug under the fence by an animal or a hole in the fence caused by natural deterioration), (ii) a highway only, and (iii) via a combination of both natural holes and highways; and (3) whether their back garden could be accessed by a hedgehog from their front garden. These data were used to identify how many gardens were totally inaccessible to hedgehogs, how many gardens were accessible via highways only, and how many boundaries could be traversed via highways only.

Hedgehog Champions who had made a highway were also asked to provide information on the number of additional householders that they had successfully recruited into making highways in their immediate neighbourhood (defined as a contiguous set of houses on the householder's street where the back gardens were linked) and further afield.

Factors affecting the decision to have made a hedgehog highway

The questionnaires requested information on whether householders had created ≥1 highways in their garden (HIGHWAY) as well as variables considered to potentially influence this decision: the respondent's physical location (geographical REGION and HOUSESETTING); the number of people living at the house (RESIDENTS); the length of time that they had been living at the house (YEARSRESIDED); the type of house they lived in (HOUSETYPE); the respondent's level of employment (EMPLOYMENT); whether they had a front garden, back garden, communal garden or a combination of these (GARDENTYPE); whether their garden contained wild flowers (FLOWERS), water that could be accessed by wildlife (excluding a pond: WATER) and/or a flowering LAWN, wild PATCH, hedgerow (HEDGE), LOGPILE, POND, BIRDBOX, BATBOX, HEDGEHOGHOUSE, insect HOTEL and COMPOST heap; whether they had sighted badgers (BADGER), foxes

(*Vulpes vulpes*; FOX), rodents (RODENT) and/or hedgehogs (HEDGEHOG) in their garden in the previous 12 months; whether they left food out for hedgehogs (FEEDHEDGEHOG); whether they had heard of Hedgehog Street prior to the survey (HEDGEHOGSTREET); and whether they belonged to any wildlife or environmental groups (ENVIGROUPS). Because of the small number of cases in some categories, the variables BADGER and FOX were merged to indicate whether the respondent had sighted badgers or foxes in their garden in the previous 12 months (BADGERFOX), and the 12 variables FLOWERS-COMPOST outlined above were tallied to create a binary variable indicating low (≤6 features) or high (>6) numbers of wildlife-friendly GARDENFEATURES in the respondent's garden.

To consider differences in how people may value wildlife in their gardens versus using their garden for other activities, respondents were asked to rank how important they considered each of the following ten activities: watching birds, watching other wildlife, gardening, growing their own food, socialising, relaxing, use by pets, use by children, for drying laundry and for storage. All variables were measured using a four-point Likert scale: less important, somewhat important, important and very important, with data coded as 1-4 respectively. Values were then averaged across subsets of these ten activities to create three variables: WATCHWILDLIFE (mean of watching birds and other wildlife); GARDENING (mean of gardening and growing own food); and RECREATION (mean of socialising, relaxing, use by pets and children, drying laundry and storage). Scores >2 and ≤2 indicated that the activity was or was not important to the respondent, respectively. All variables are summarised in Table 5.1.

Table 5.1. Summary of variables requested in the 2018, 2019 and 2020 surveys that were used to investigate the factors affecting a householder's decision to create a hedgehog highway.

Name	**Description**	**Levels**
HIGHWAY	Dependent variable; a binary measure of whether the respondent had made a hedgehog highway or not	(0) No (1) Yes
RESIDENTS	Number of residents occupying the address at the time of the survey	Continuous
YEARSRESIDED	The length of time that the address had been occupied by the respondent	(1) 0-5 years (2) 6-20 years (3) >21 years
REGION	The region of the UK where the respondent lived	(1) East (2) Southeast (3) Southwest

		(4) Northwest (5) London (6) East Midlands (7) Northeast (8) Yorkshire and the Humber (9) West Midlands (10) Wales (11) Scotland (12) Northern Ireland
SETTING	Type of location where house is situated	(0) In a village or smaller (1) In a town or city
HOUSETYPE	Type of house	(1) Detached (2) Semi-detached (3) Terraced (4) Flat
GARDENTYPE	Extent/type of gardens associated with property	(1) One private front garden OR one private back garden OR communal garden (2) Both a private front AND back garden
GARDENFEATURES	Extent of wildlife-friendly features present within respondent's garden, selected from multiple-choice options (flowering lawn; wildflowers; wild patch; hedgerow; log pile; pond; bird box; bat box; hedgehog house; insect hotel; compost heap; water for wildlife)	(0) Six or less features (1) Seven or more features
BADGERFOX	Whether the respondent had sighted a badger or fox in their garden in 12 months prior to the survey (NB badger and fox sightings were merged due to the low number of positive sightings)	(0) Not sighted in last 12 months (1) Sighted in last 12 months
HEDGEHOG	Whether the respondent had sighted a hedgehog in their garden in 12 months prior to the survey	(0) Not sighted in last 12 months (1) Sighted in last 12 months
RODENT	Whether the respondent had sighted a rodent in their garden in 12 months prior to the survey	(0) Not sighted in last 12 months (1) Sighted in last 12 months
HEDGEHOGSTREET	Whether the respondent was aware of or had engaged with Hedgehog Street prior to the survey	(0) Not aware (1) Aware

FEEDHEDGEHOG	Whether the respondent ever leaves food out for hedgehogs in their garden	(0) Does not leave food out (1) Leaves food out
ENVIGROUPS	Whether the respondent was a member of any environmental or wildlife groups	(0) Not a member (1) Is a member
EMPLOYMENT	Respondent's level of employment	(1) Part-time (2) Full-time (3) Unemployed or homemaker (4) Student (5) Retired (6) Prefer not to say/other
WATCHWILDLIFE	A ranking of how important the respondent considered garden wildlife-watching activities to be (averaged from the variables 'watching birds' and 'watching other wildlife')	(0) Less important or not important (1) Important or very important
GARDENING	A ranking of how important the respondent considered gardening to be (averaged from the variables 'gardening' and 'growing food')	(0) Less important or not important (1) Important or very important
RECREATION	A ranking of how important the respondent considered recreational uses of the garden to be (averaged from the variables 'socialising', 'relaxing', 'use by pets', 'use by children', 'laundry' and 'storage')	(0) Less important or not important (1) Important or very important

Generalised linear models (GLM) with binomial distributions were used to examine factors affecting people's decisions to have made a highway in R (version 4.0.3). Although the choice to make a highway may have been a household decision, we included individual-level variables in the analyses because of the impracticalities surrounding questioning all household members. The interaction term HOUSETYPE*HOUSESETTING was included as it was theorised that any effect of house type might be dependent on whether the house was in an urban (town or city) or rural (village or smaller) setting.

Candidate models were constructed through an iterative process of variable selection whereby covariates were added successively and the Akaike's Information Criterion (AIC) of each model compared. The data were examined for multicollinearity using Generalized Variance Inflation Factors (GVIF) in the form $GVIF^{(1/(2*Df))}$ (Fox and Monette, 1992) with GVIF values <2 considered acceptable (see Zuur *et al.*, 2010). Variables that were not significant, but which improved model fit, were retained. Optimal models were selected by comparing AIC values and model fit using Hosmer and Lemeshow and pseudo-R^2 values (Smith and McKenna, 2013).

Three of the variables listed in Table 5.1 (RODENT, HEDGEHOG, FEEDHEDGEHOG) could potentially complicate interpretation of the results of this analysis as they may have influenced a householder's decision to create a hedgehog highway in the first instance, or they may have changed as a result of the creation of a highway. Therefore, we present two final models: one including these three variables and one where they have been excluded.

Reasons cited for not having made a hedgehog highway

Respondents in all three surveys who had not made a highway were asked to indicate why they had not done so from a list of 11 possible reasons: I am not interested; I don't want to damage the boundary structure; I don't want to speak to my neighbour or carry out works to their boundary structure; it would be unsightly; it might encourage rats; there are no hedgehogs where I live; small pets might escape; I rent my property; I don't have enough time; my garden is already accessible to hedgehogs; I don't have the correct tools and/or don't know how to make a highway. Respondents were able to select multiple reasons and outline any "other" possible underlying reason(s) as well.

Results

Responses were received from 5986 individuals (2018: N = 506; 2019: N = 402; 2020: N = 5078; S4). Overall, 4759 respondents in the 2020 survey (93.7%) confirmed that they were registered as Champions, giving a response rate for Champions of 6.7% (N = 71,166 Champions registered at the time of surveying in December 2019). Of those, 2285 (P_C = 48.0%) had created at least one highway in their own garden. This figure was significantly different to the corresponding proportions of respondents who had made a highway: (i) in both the 2018 (P_N = 19.1%, N = 241) and 2019 (P_N = 6.1%, N = 230) surveys but stated that they had not heard of the HS campaign (χ^2_2 = 223.66, $p < 0.001$; overall P_N = 12.7%, N = 471); (ii) who stated that they had heard of HS in the 2018 (P_C = 56.2%, N = 265) and 2019 (P_C = 20.3%, N = 172) surveys (χ^2_2 = 59.44, $p < 0.001$; overall P_C = 42.1%, N = 437); and (iii) those who were not Champions in the 2020 survey (P_N = 29.8%, N = 319) (χ^2_1= 39.92, $p < 0.001$).

In general, a significantly greater proportion of respondents within each of the three surveys fed birds frequently (except in 2019), had a bird box and/or a pond in their garden compared to the national figures reported by Davies *et al.* (2009) (Table 5.2). This was also the case when the data were partitioned into those respondents who had and who had not made a highway, and those who had heard of HS; however, there was no significant difference with regards feeding birds and having a pond for that subset of respondents who had not heard of HS (Table 5.2). Many respondents also reported that they fed hedgehogs frequently (2018: 19.4%; 2019: 9.2%; 2020: 66.2%) and/or had a hedgehog box in their garden (2018: 25.1%; 2019: 12.4%; 2020: 68.0%).

Table 5.2. Comparisons of the number of respondents (N = 5986) who (a) fed birds frequently, (b) had a bird box or (c) pond in their garden, relative to the estimates reported for the UK population by Davies *et al.* (2009). Chi-squared test results are provided for all survey years (2018, 2019, 2020), for those respondents who had or had not made a hedgehog highway at the time of surveying, and those who had or had not heard of the Hedgehog Street campaign. Figures in parentheses in the observed and expected columns are the proportion of respondents. * indicates difference is significant ($p < 0.05$) after applying Bonferroni correction (0.05/21 = 0.002) for multiple testing.

Grouping	Garden wildlife factor	Observed	Expected	χ^2_1	*p*	SIG
2018 (N = 506)	Fed birds	307 (0.61)	258.06 (0.51)	9.28	0.002	*
	Bird box	286 (0.57)	106.26 (0.21)	304.03	<0.001	*
	Pond	145 (0.29)	80.96 (0.16)	50.66	<0.001	*
2019 (N = 402)	Fed birds	224 (0.56)	205.02 (0.51)	1.76	0.185	
	Bird box	170 (0.42)	84.42 (0.21)	86.76	<0.001	*
	Pond	93 (0.23)	64.32 (0.16)	12.79	<0.001	*
2020 (N = 5078)	Fed birds	4336 (0.85)	2589.78 (0.51)	1177.43	<0.001	*
	Bird box	3611 (0.71)	1066.38 (0.21)	6072.03	<0.001	*
	Pond	2151 (0.42)	812.48 (0.16)	2151.75	<0.001	*
Made highway (N = 2624)	Fed birds	2328 (0.89)	1338.24 (0.51)	732.02	<0.001	*
	Bird box	2009 (0.76)	551.04 (0.21)	3857.52	<0.001	*
	Pond	1212 (0.46)	420 (0.16)	1493.49	<0.001	*
Not made highway (N = 3362)	Fed birds	2539 (0.76)	1714.62 (0.51)	396.36	<0.001	*
	Bird box	2058 (0.61)	706.02 (0.21)	2588.95	<0.001	*
	Pond	1177 (0.35)	537.92 (0.16)	759.26	<0.001	*
Heard of HS (N = 5515)	Fed birds	4638 (0.84)	2812.65 (0.51)	1184.61	<0.001	*
	Bird box	3958 (0.72)	1158.15 (0.21)	6768.69	<0.001	*
	Pond	2299 (0.42)	882.4 (0.16)	2274.20	<0.001	*
Not heard of HS (N = 471)	Fed birds	229 (0.49)	240.21 (0.51)	0.52	0.470	
	Bird box	193 (0.41)	98.91 (0.21)	89.50	<0.001	*
	Pond	90 (0.19)	75.36 (0.16)	2.84	0.092	

Of the 2285 Champions that had created a highway, 1681 (73.8%) had done so after they knew that hedgehogs were visiting their garden, with 1226 (53.7%) stating that they had subsequently observed an increase in hedgehog activity in their garden.

Hedgehog accessibility into neighbouring gardens

Overall, 3978 respondents bordered by ≥1 back garden(s) provided information about accessibility into their own back garden; 118 respondents had no neighbouring back gardens. Of the former, 2969 (74.6%) were (Figure 5.1a) and 1009 (25.4%) were not (Figure 5.1b) accessible via the respondent's front garden. Collectively, 543 respondents (13.7%) indicated that they thought hedgehogs could not access their back garden from neighbouring back gardens. However, 345 of these gardens were accessible from the respondent's own front garden (Figure 5.1a). Consequently, only 198 (5.0%) gardens were considered completely inaccessible to hedgehogs (Figure 5.1b).

The back gardens of 1574 respondents (40.0% of bordered gardens) were accessible from neighbouring back gardens only via natural holes, 1469 (36.9%) were accessible via a combination of natural holes and hedgehog highways, and 392 (9.9%) were accessible only via highways. Of the latter, however, 264 could also be accessed via a front garden (Figure 5.1a), indicating that highways only granted access to 128 (3.2%) previously inaccessible back gardens.

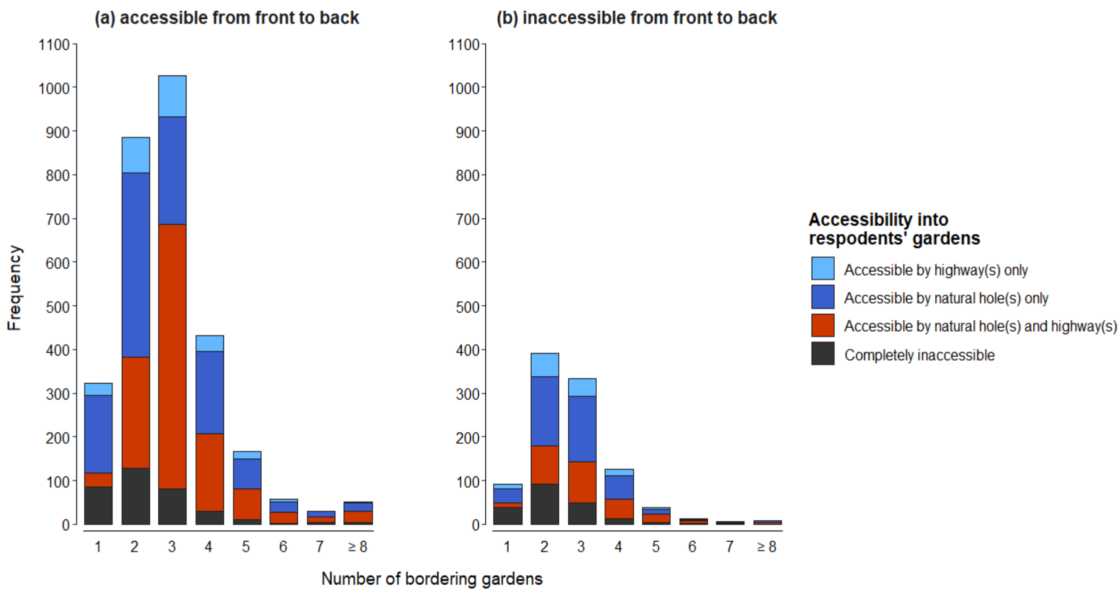

Figure 5.1. The number of respondents' back gardens that were accessible to hedgehogs via hedgehog highways and/or naturally occurring holes in relation to the number of bordering gardens. Data are split into those back gardens which were **(a)** accessible (N = 2969) and **(b)** not accessible (N = 1009) from the respondent's own front garden.

Collectively, the 3978 houses illustrated in Figure 5.1 were bordered by 11,449 boundaries (Figure 5.2). Of these boundaries, 3522 (30.8%) could not be traversed by hedgehogs at all; 4688 (40.9%), 1940 (16.9%) and 1308 (11.4%) were traversable via natural holes only, a combination of natural holes and hedgehog highways, and hedgehog highways only, respectively.

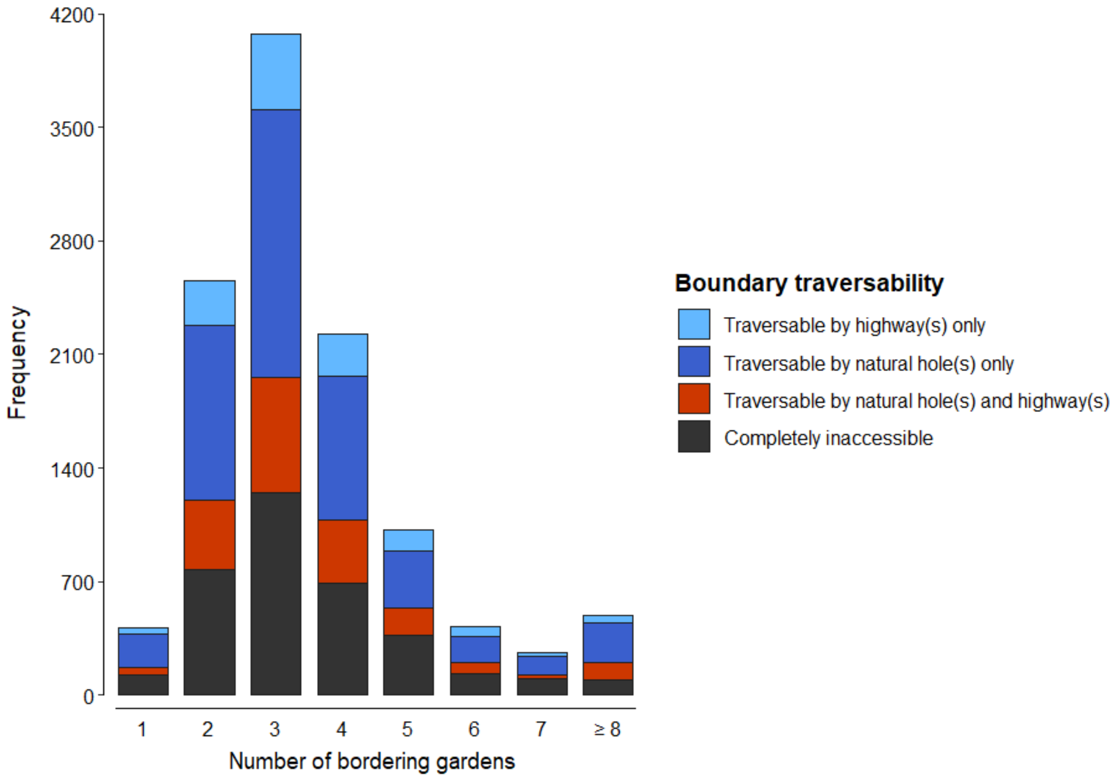

Figure 5.2. The number of back garden boundaries (N = 11,449) that could be traversed via hedgehog highways and/or naturally occurring holes in relation to the number of bordering gardens.

The 2285 Champions in the 2020 survey who had successfully created at least one highway constructed a total of 4516 highways in their own gardens (1.98 per individual). Of these individuals, 1087 (47.6%) failed to recruit any further households into making a highway in their local neighbourhood, 511 (22.4%) recruited one additional household, 324 (14.2%) recruited 2-4 households, 35 (1.5%) recruited ≥5 households, and 328 (14.4%) attempted to recruit further households but were unaware of whether they had been successful (Figure 5.3). Comparable figures for areas beyond the local neighbourhood were 1055 (46.2%), 318 (13.9%), 327 (14.3%), 81 (3.5%) and 504 (22.1%), respectively. Assuming median values of 1, 3 and 6.5 for these three size classes, and assuming that respondents with unknown success had failed to generate any highways, these figures translate to a minimum of 1711 (0.75 per individual) additional hedgehog highways in the respondents' immediate neighbourhood and 1826 (0.80 per individual) further afield. This would indicate that each successful Champion generated, on average, 3.53 highways.

However, 52.0% of Champions who responded to the 2020 survey had failed to create any highways at all. Incorporating these additional respondents, each Champion would have, on average, generated 1.69 highways each (0.95 in their own garden + 0.36 in their local neighbourhood + 0.38 further afield).

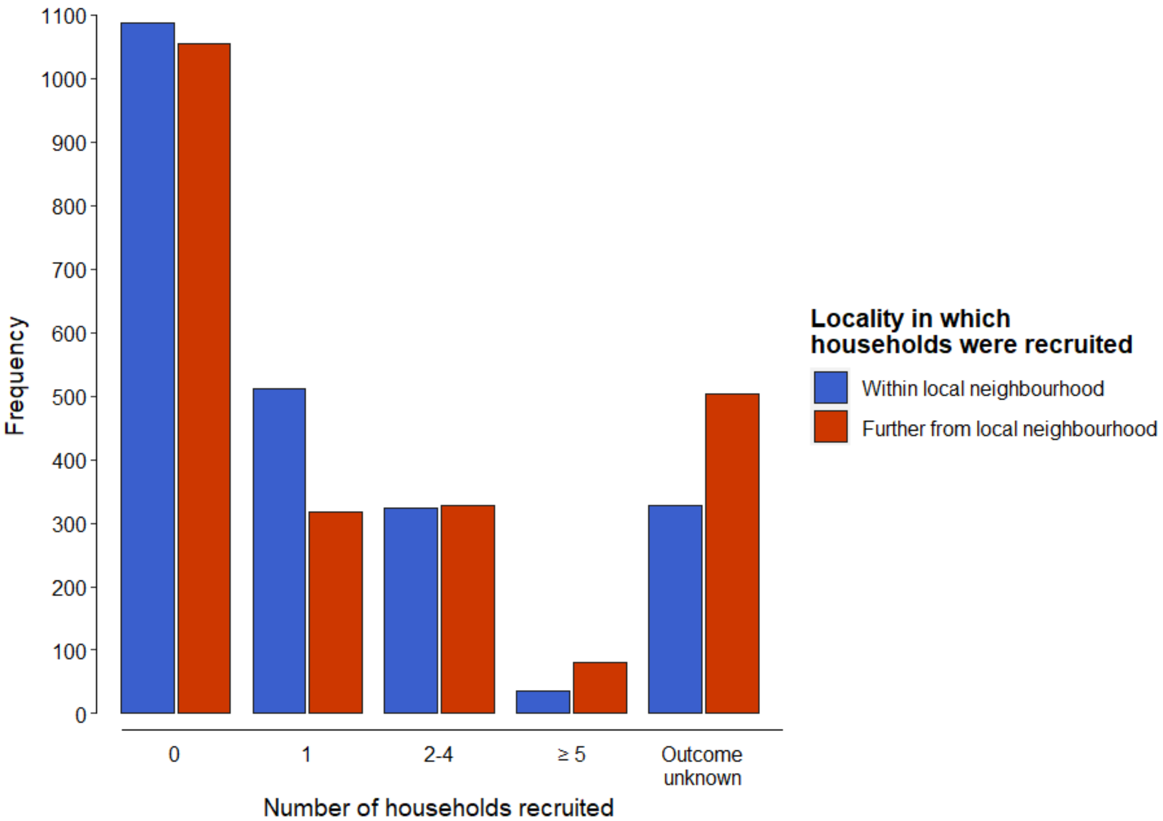

Figure 5.3. The number of additional households recruited to make hedgehog highways by Champions who had already made highways themselves (N = 2285) within their own neighbourhood and/or further afield.

Factors affecting the decision to have made a hedgehog highway

The inclusion (Table 5.3) and exclusion (Table 5.4) of the variables RODENT, FEEDHEDGEHOG and HEDGEHOG did not markedly affect coefficient values or model fit, although there were subtle differences. In both models, the decision to have made a hedgehog highway was significantly affected by YEARSRESIDED, HOUSETYPE, HOUSESETTING, GARDENFEATURES, BADGERFOX, HEDGEHOGSTREET, WATCHWILDLIFE and HOUSTETYPE*SETTING. In the model including RODENT, FEEDHEDGEHOG and HEDGEHOG, all three variables also had a significant effect (Table

5.3); the variable ENVIGROUPS was also retained to improve model fit. In the second model, the variables ENVIGROUPS, GARDENING and EMPLOYMENT were retained to improve model fit (Table 5.4).

Table 5.3. Summary of the binary logistic regression analysis examining the effects of garden- and householder-related variables on the respondent's decision to make a hedgehog highway (HIGHWAY) (N = 5986). This analysis included the variables RODENT, FEEDHEDGEHOG and HEDGEHOG (see Methods). Reference levels for variables are indicated in parentheses. AIC = 7407.2; Hosmer and Lemeshow Test: χ^2_8 = 7.83, $p = 0.45$; Nagelkerke $R^2 = 0.18$. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Estimate	**Std. error**	**z**	**p**	**Odds**	**95% CI**	
(Intercept)	-3.6143	0.1768	-20.4404	<0.0001	0.0269	0.019-0.0379	
YEARSRESIDED (0-5 years)							
6-20 years	0.1949	0.0722	2.7008	0.0069	1.2152	1.055-1.3999	***
>21 years	0.1164	0.0772	1.5081	0.1315	1.1234	0.9658-1.3069	
HOUSETYPE (Detached)							
Semi-detached	0.3722	0.1034	3.5981	<0.0001	1.4509	1.1847-1.7772	***
Terraced	0.4830	0.1543	3.1309	0.0017	1.6210	1.1975-2.1935	**
Flat	0.7692	0.4460	1.7246	0.0846	2.1581	0.8898-5.2085	
HOUSESETTING (In a village or smaller)							
In a town or city	0.6362	0.0861	7.3865	<0.0001	1.8894	1.5964-2.2377	***
HOUSETYPE * HOUSESETTING (Detached house in village or smaller)							
Semi-detached house in a town or city	-0.4543	0.1312	-3.4626	0.0005	0.6349	0.4909-0.8211	***
Terraced house in a town or city	-0.4699	0.1808	-2.5991	0.0093	0.6251	0.4386-0.8912	**
Flat in a town or city	-1.0269	0.4998	-2.0545	0.0399	0.3581	0.1337-0.9612	*
GARDENFEATURES (Six or less)							
Seven or more	0.5047	0.0631	8.0037	<0.0001	1.6564	1.4641-1.8746	***

BADGERFOX (Not sighted)							
Sighted	-0.1239	0.0582	-2.1263	0.0335	0.8835	0.7881-0.9903	*
HEDGEHOG (Not sighted)							
Sighted	0.5621	0.1125	4.9977	<0.0001	1.7544	1.4091-2.1905	***
HEDGEHOGSTREET (Not aware)							
Aware	0.6738	0.1025	6.5718	<0.0001	1.9617	1.6076-2.4035	***
WATCHWILDLIFE (Less important or not important)							
Important or very important	0.5691	0.1018	5.5907	<0.0001	1.7666	1.4495-2.1607	***
ENVIGROUPS (Not a member)							
Is a member	-0.0790	0.0581	-1.3589	0.1742	0.9241	0.8245-1.0355	
FEEDHEDGEHOG (Not fed)							
Fed	0.9158	0.0879	10.4159	<0.0001	2.4988	2.1056-2.9724	***
RODENT (Not sighted)							
Sighted	0.2906	0.0878	3.3109	0.0009	1.3372	1.1265-1.5892	***

Table 5.4. Summary of the binary logistic regression analysis examining the effects of garden and householder-related variables on the respondent's decision to make a hedgehog highway (HIGHWAY) (N = 5986). This analysis excluded the variables RODENT, FEEDHEDGEHOG and HEDGEHOG (see Methods). Reference levels for variables are indicated in parentheses. AIC = 7675.6; Hosmer and Lemeshow Test: χ^2_8 = 10.52, p = 0.23; Nagelkerke R^2 = 0.12. * = $p < 0.05$, ** = $p < 0.01$., *** = $p < 0.001$.

	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	**Odds**	**95% CI**	
(Intercept)	-2.6388	0.1606	-16.4319	<0.0001	0.0714	0.052-0.0976	
YEARSRESIDED (0-5 years)							
6-20 years	0.3083	0.0700	4.4056	<0.0001	1.3611	1.1869-1.5615	***
>21 years	0.2529	0.0769	3.2862	0.0010	1.2877	1.1075-1.4975	**
HOUSETYPE (Detached)							
Semi-detached	0.4149	0.1026	4.0436	0.0001	1.5143	1.2384-1.8518	***
Terraced	0.4517	0.1505	3.0013	0.0027	1.5710	1.1688-2.1094	**
Flat	0.7781	0.4382	1.7757	0.0758	2.1773	0.9099-5.1672	
HOUSESETTING (In a village or smaller)							
In a town or city	0.6478	0.0848	7.6349	<0.0001	1.9112	1.619-2.2579	***
HOUSETYPE * HOUSESETTING (Detached house in village or smaller)							
Semi-detached house in a town or city	-0.5395	0.1291	-4.1784	<0.0001	0.5830	0.4526-0.7509	***
Terraced house in a town or city	-0.5371	0.1758	-3.0556	0.0022	0.5844	0.4142-0.8253	**
Flat in a town or city	-1.1986	0.4891	-2.4507	0.0143	0.3016	0.1151-0.7938	*
GARDENFEATURES (Six or less)							
Seven or more	0.6632	0.0620	10.6909	<0.0001	1.9410	1.7192-2.1926	***

BADGERFOX (Not sighted)							
Sighted	-0.1346	0.0567	-2.3748	0.0176	0.8741	0.7821-0.9767	*
HEDGEHOGSTREET (Not aware)							
Aware	0.9134	0.0994	9.1856	<0.0001	2.4928	2.0560-3.0368	***
WATCHWILDLIFE (Less important or not important)							
Important or very important	0.7295	0.0996	7.3261	<0.0001	2.0740	1.7095-2.5262	***
ENVIGROUPS (Not a member)							
Is a member	-0.0350	0.0570	-0.6144	0.5390	0.9656	0.8636-1.0797	
GARDENING (Less important or not important)							
Important or very important	-0.1061	0.0565	-1.8790	0.0602	0.8993	0.8050-1.0045	
EMPLOYMENT (Employed part-time)							
Employed full-time	0.0249	0.0799	0.3121	0.7550	1.0253	0.8767-1.1993	
Unemployed or homemaker	-0.0329	0.1270	-0.2594	0.7953	0.9676	0.7539-1.2404	
Student	-0.7055	0.2272	-3.1050	0.0019	0.4938	0.3112-0.7606	**
Retired	0.0283	0.0794	0.3562	0.7217	1.0287	0.8805-1.2019	
Prefer not to say/other	0.0790	0.1307	0.6040	0.5458	1.0822	0.8372-1.3980	

Focusing on the model outlined in Table 5.3, respondents were more likely to have created a highway if: they had lived in their home for 6-20 years; their garden contained ≥6 wildlife friendly features; they had sighted rodents or a hedgehog in their garden in the previous 12 months, but not a fox or badger; they were aware of the Hedgehog Street campaign; they ranked watching wildlife as important/very important; and they did feed hedgehogs. In general terms, respondents were significantly more likely to have created a highway if they lived in a semi-detached or terraced property, or lived within a town or city; however, respondents living in flats in a village or smaller hamlet were significantly more likely to have created a highway (Figure 5.4).

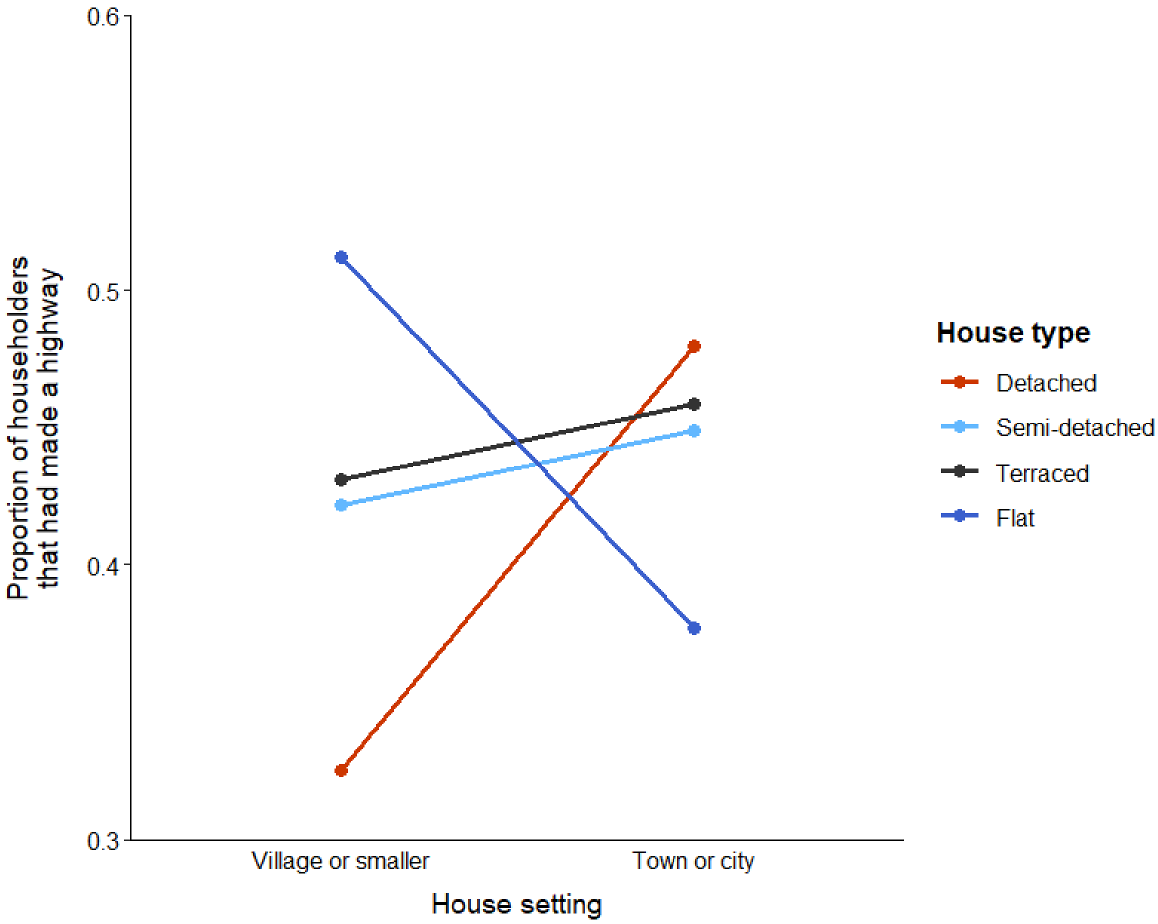

Figure 5.4. Probability that householders (N = 5986) had created a hedgehog highway in relation to house type and house location.

Reasons cited for not having made a hedgehog highway

Across all three surveys, 3362 respondents had not made a hedgehog highway; 3141 (93.4%) of these indicated why they had not done so, with a total of 4779 reasons given. The most common reason cited was that their garden was already accessible to hedgehogs

(51.1%), followed by concerns relating to boundary ownership and/or talking to neighbours (12.6%; Figure 5.5).

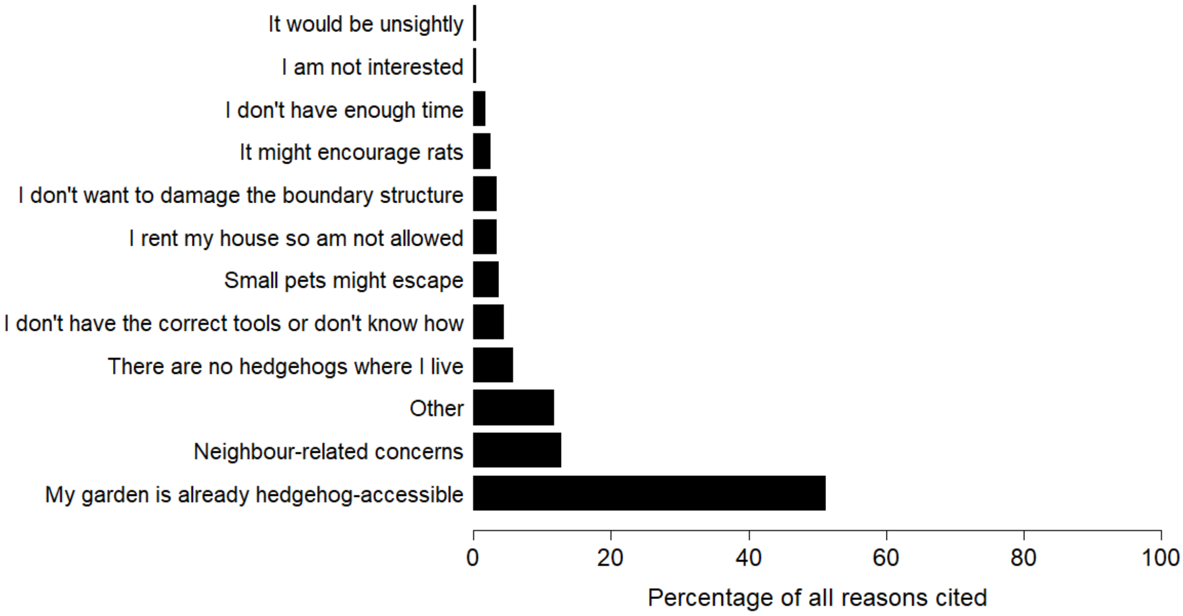

Figure 5.5. Reasons given by householders for not having created a hedgehog highway at the time of surveying. Figures are the percentage of all 4779 reasons cited by 3141 respondents.

Discussion

Judging the success of the Hedgehog Street campaign is difficult because, as a public engagement exercise, there are few specific targets other than attempting to engage as many householders as possible, nor are there any quantified data on how frequently hedgehogs use these highways, although numerous photographs and videos online indicate that they are utilised readily once they are available. One potentially useful metric, however, is to estimate the proportion of Champions versus non-Champions that had created highways, and the number of highways created.

On average, the Hedgehog Champions that responded to the 2020 questionnaire survey generated a minimum of 1.69 highways each: 0.95 in their own garden, 0.36 in their immediate neighbourhood and 0.38 further afield. Extrapolating these figures to the total number of Champions enrolled at the time of surveying (N = 71,166), this would equate to the creation of >120,000 highways connecting >240,000 gardens, equivalent to approximately 1.1% of UK households with access to a garden (Davies *et al.*, 2009). These mean figures were, however, markedly reduced by the 52.0% of Champions who failed to create any highways; of the 48.0% of Champions that were successful, they led to the creation, on average, of 3.53 highways.

In comparison, significantly fewer respondents (6.1-29.8%) who stated that they had not heard of HS had created highways. Any estimate of the number of highways created nationally by these non-Champions is, however, dependent on the assumption that the householders in our study were a random sample of the UK population. Unfortunately, this does not appear to be the case: considering all respondents, significantly larger proportions of householders stated that they fed birds (81%), had created a pond (40%) and/or put up a bird box (68%) compared to the nationwide figures (51%, 16% and 21%, respectively) reported by Davies *et al.* (2009); respondents were also significantly more likely to have created a highway if they stated that watching wildlife was important to them. Moreover, a higher number of wildlife-friendly garden features within their garden increased the likelihood that respondents had made a highway by a factor of 1.66-1.94 (Tables 5.3-5.4). This would suggest that our sample is dominated by householders who are innately more 'wildlife-friendly' such that the 6.1-29.8% figures listed above are likely to be over-estimates. Nonetheless, since most UK householders are not registered as Champions, even a very low uptake rate (>0.4%) by non-Champions would result in the creation of a number of highways comparable to that which we have estimated for Champions.

The relatively low number of householders that have managed to successfully create highways compared to the numbers known to engage in other forms of wildlife-friendly activities (Davies *et al.*, 2009) would suggest that: (i) there are significant obstacles to persuading householders and/or their neighbours to construct highways; and (ii) the benefits arising from their creation may be limited. The latter is associated with the impacts of highways on hedgehog movement trajectories and the increase in resources that are available in previously inaccessible gardens, which may, in turn, reduce the number of times roads need to be crossed. It is important, therefore, to consider how such changes might affect existing patterns of movement.

Approximately 83% of UK citizens live in urban areas (Department for Environment, Food & Rural Affairs, 2021), such that hedgehog highways are potentially most beneficial for urban hedgehog populations. In UK towns and cities, houses are frequently arranged in blocks consisting of two rows with rear gardens backing onto one another. To access the rear gardens of these houses, the preferred foraging habitat (Dowding *et al.* 2010a), hedgehogs can move from back garden to back garden and/or access the rear garden from the front via the side of the house where possible. Although there are numerous permutations of how adding even one highway could influence distances travelled, highways between neighbouring houses that are side-by-side could be associated with a reduction in the order of tens of metres, as a hedgehog would no longer need to leave one back garden to enter the other via the front of the second house. Conversely, a highway between two gardens that are back-to-back could result in a reduction in the order of a hundred metres or more, as the animal might not need to travel around the periphery of the block of houses to enter the second garden. Although these distances are small, Dowding *et al.* (2010a) recorded mean distances travelled of just 861m and 514m per night for male and female hedgehogs, respectively, in Bristol, UK, and Schaus Calderón (2021) recorded comparable figures of 656m and 404m for hedgehogs in four urban sites across England. In this context, even the minor improvements in connectivity outlined above could be associated with reductions in nightly distances travelled of >10%; whether this would have a significant effect on the survival and/or reproductive output of hedgehogs is, however, unclear.

The biggest impact of highways would most likely be realised by enabling access to previously inaccessible gardens, as this would increase connectivity and potentially increase resource availability. Unfortunately, most highways in this study did not seem to increase connectivity in this way: 73.8% of Champions who had created a highway had done so after knowing that hedgehogs were visiting their garden, and 16.9% of boundaries between gardens were traversable by both a highway and a natural hole. In comparison, only 11.4% of garden boundaries and 3.2% of gardens could be traversed and accessed, respectively, via a highway alone. Furthermore, the fact that hedgehogs were already visiting their garden was the most cited reason for respondents not having created a highway. Overall, only 5% of respondents thought their back garden was completely inaccessible to hedgehogs, although this may be an over-estimate as Williams *et al.* (2015) reported a 20-30% discrepancy in the number of gardens considered inaccessible based on householder perceptions versus surveys performed by the researchers themselves. Nonetheless, these data do suggest that the fragmentation effect of garden boundaries in preventing access to gardens in the UK may not be as big a problem as has previously been supposed.

Factors affecting the creation of hedgehog highways and future recommendations

In addition to increasing numbers of wildlife-friendly features and the importance that householders placed on watching wildlife, the decision to create a highway was: positively correlated with the householder’s length of occupation, house type, house location and whether the householder was aware of the Hedgehog Street campaign or not; but negatively associated with sightings of badgers and foxes. In addition, where they were included in the analyses, householders were more likely to have made a highway if they had seen hedgehogs and rodents in their garden, and if they fed hedgehogs. In many respects, these patterns reflect the reasons given by householders for not creating highways. For example, short periods of tenure are likely to be associated with people living in rental properties where landlords may prevent them changing the property's boundaries. Similarly, although the creation of hedgehog highways could lead to hedgehogs being able to enter previously inaccessible gardens, 73.8% of respondents in the 2020 survey stated that they had created a highway after they knew hedgehogs were already visiting. As such, the positive relationship between highway construction and hedgehog presence in these analyses is most likely to be correlational rather than causal. This may also be the case for feeding hedgehogs (i.e., householders are likely to have started providing food once they knew hedgehogs were visiting their garden).

Likewise, the reduced likelihood that highways had been created in gardens where foxes and/or badgers had been sighted in the previous 12 months could reflect different underlying processes e.g., a conscious decision by householders to minimise the risk of predation, especially by badgers (Williams *et al*., 2018b; Trewby *et al*., 2014; Young *et al*., 2006; Hof *et al*., 2019), or hedgehogs are avoiding those gardens where foxes and badgers are present (Williams *et al.*, 2018a; Ward *et al.*, 1997). However, it is important to note that, even in gardens where badgers are present, highways might allow hedgehogs to evade them more effectively and to access gardens that badgers cannot. Foxes, on the other hand, would likely be able to access all the same gardens as hedgehogs because of their greater agility, although the importance of foxes as a predator of hedgehogs is equivocal (Harris and Baker, 2001; Pettett *et al*., 2018). In addition, there are numerous reports of hedgehogs visiting gardens in the presence of foxes and/or badgers with limited apparent conflict, although this is often associated with the provision of supplementary food; this food might, therefore, help to reduce predation risk but it is an extra level of involvement that not all members of the public would be willing to undertake. Consequently, on the balance of (albeit anecdotal) evidence, householders should not be discouraged from creating highways, even if they have sighted badgers or foxes in their garden.

Knowledge of the Hedgehog Street campaign was associated with the largest odds ratio values from the binary logistic regression analyses (Table 5.3), indicating that it was a particularly important factor associated with householders' decisions to create a highway.

Therefore, continuing to increase householders' awareness of the potential benefits of creating highways is critical for the future expansion of this programme. Further, based on the analyses of the results above, we make the following recommendations:

(1) Additional effort needs to be focused on finding mechanisms to appeal to householders who are not inherently 'wildlife-friendly', as these comprise approximately half of all UK householders (Davies *et al.* 2009). As such, these will often be the immediate neighbours of those householders who want to create highways and whose cooperation is therefore pivotal. The fact that 12.7% of householders stated that they had created a hedgehog highway but had not heard of Hedgehog Street does suggest that they had heard of the programme's underlying premise from some other source; these, and other, sources therefore need to be identified and expanded.

(2) In parallel with the above, additional studies are required to help identify householders' reservations concerning the creation of highways and to devise approaches for alleviating these concerns (*sensu* Crowley *et al.* 2020). This will necessitate collaborations with social scientists (Martin 2020) to devise multi-faceted approaches to help persuade householders with varying reasons for opposing the construction of hedgehog highways in their garden.

(3) Greater emphasis needs to be placed on explaining how multiple highways from individual gardens would benefit hedgehogs. Householders should be advised that, even if hedgehogs are already accessing their garden, additional entry and exit points will help them move more efficiently through the wider landscape but these must be built into boundaries which hedgehogs cannot currently cross.

(4) Additional data are required on the potential impact of predation by badgers and foxes on hedgehog populations in urban areas, and the patterns of interactions of these species in individual gardens.

(5) Local planning authorities should commit to improving habitat connectivity for hedgehogs. The government's National Planning Policy Framework for England (Ministry of Housing, Communities & Local Government, 2021) requires local plans to promote the conservation of priority species that are most threatened, which includes hedgehogs (Joint Nature Conservation Committee, 2021). Developers therefore should be encouraged to incorporate hedgehog highways in property boundaries as standard, as has already been adopted by some companies (e.g., Bovis Homes, 2020; Somerset County Gazette, 2021). In addition, it is important to engage with owners of rental properties to facilitate the creation of highways in the one-third of UK homes that are rented (Office for National Statistics, 2019).

(6) Finally, field studies are required to quantify patterns of movement, energetic expenditure and hedgehog density in neighbourhoods before and after networks of highways have been constructed to identify the degree to which these affect individual animals and, ultimately, populations.

Conclusion

Hedgehog Street has had significant success in recruiting participants and encouraging the creation of >120,000 highways by Hedgehog Champions. However, the fact that 52.0% of Champions surveyed had not been able to create a highway suggests that this initiative is impacted by challenges not normally evident in other public conservation campaigns; these include the need to interact with, and obtain permission from, immediate neighbours, the presence of hedgehogs in gardens leading to a perception that there is no need to create additional access points, and the creation of highways in boundaries that can already be traversed. Future studies therefore need to find mechanisms by which to address these limitations. Particular effort needs to be focused on identifying why householders are reluctant to create hedgehog highways so that strategies can be developed which address these concerns; such strategies must also target landlords and housing developers given the importance of rental properties in the UK and the current growth in housing construction. Finally, studies of hedgehog movement patterns are required so that the benefits of the creation of networks of hedgehog highways can be quantified.

Chapter 6

Discussion

Successful conservation practice is a process characterised by multiple stages including planning, implementation, monitoring and review (Rodríguez-Izquierdo *et al*., 2010). Public participation in the implementation of conservation can be invaluable in achieving positive outcomes for wildlife (Guiney, 2009; Crockford and Buchanan, 2017; Sterrett *et al*., 2018) particularly for programmes that do not incorporate 'traditionally' protected areas (Horwich and Lyon, 2007) such as private residential gardens. Also vital to the conservation process is the gathering of scientific evidence for informing decision-making and evaluating potential actions and results (Gaston *et al*., 2005; Sutherland and Wordley, 2017).

In Britain, hedgehogs are classified as Vulnerable (Mathews and Harrower, 2020) as populations have declined markedly since the 1900s (Burton, 1969; Roos *et al*., 2012; Croft *et al*., 2017; Mathews *et al*., 2018; Mathews and Harrower, 2020). Whilst researchers have started to examine approaches for aiding rural populations (e.g., Williams, 2018; Yarnell and Pettett, 2020), there remains an urgent need to gather and apply evidence to formulate conservation actions for hedgehogs in urban settings. Crucially, the high human population density and extensive garden coverage that characterises urban areas in this country provide key opportunities for householder- and garden-based strategies.

Existing ecological studies of hedgehogs in urban areas have focused on abundance (Switzerland: Taucher *et al*., 2020), density (UK: Schaus *et al*., 2020), monitoring techniques (UK: Williams *et al*., 2018a; Schaus *et al*., 2020), impacts of noise (Germany: Berger *et al*., 2020a) and artificial lighting (Germany: Berger *et al*., 2020b; UK: Finch *et al*., 2020), juvenile survival (Denmark: Rasmussen *et al*., 2019a), nesting patterns (Finland: Rautio *et al*., 2014), genetic fragmentation (Germany: Barthel *et al*., 2020; Finland: Osaka *et al*., 2022; Switerzland: Braaker *et al*., 2017), release of rehabilitated animals (UK: Molony *et al*., 2006; Yarnell *et al*., 2019) and habitat selection in city suburbs (UK: Dowding *et al*., 2010a). Conversely, studies of hedgehogs in gardens, and how householders can aid conservation efforts in gardens, are lacking, and little is understood about how management actions could help sustain urban populations. This thesis has expanded our knowledge of urban hedgehog ecology and behaviour in four areas: hedgehog garden use during the active season; patterns of garden activity during the hibernation period; factors affecting the use of artificial refugia; and householder engagement with a campaign to improve garden connectivity for hedgehogs. In the sections below, a brief summary of each study's major findings are outlined, followed by a discussion of the implications of these results within the context of urban hedgehog conservation. Finally, an outline of future research approaches and needs is provided.

Summary of main research findings

In Chapter 2, areas ranged nightly, habitat selection and garden use by 28 radio and GPS tracked hedgehogs in a residential area of Reading were quantified. The results of compositional analyses indicated a preference for gardens over other habitat types. Using mixed models to assess factors affecting back garden use by hedgehogs, it was found that proportionately less time was spent in gardens on nights when it rained, where access to the front garden was possible and where foxes were perceived to be frequent visitors by the householder. In contrast, time spent in back gardens was significantly positively linked to the supply of artificial food, the presence of compost heaps, increased day length (i.e., shorter nights) and where foxes were perceived to be less frequent visitors. As part of this chapter, the impacts of GPS fix acquisition rates <100% on these results were also considered.

In Chapter 3, hedgehog activity in urban gardens was then examined over a single hibernation period (November-April). Using footprint tunnels monitored by 63 householders, hedgehog occupancy was found to be lowest between January and March, although hedgehogs were detected during every week of the survey. Activity during winter is not unusual as hedgehogs may periodically rouse from hibernation to switch nests and/or if the temperature increases. However, hedgehog activity appeared to be linked to the presence of supplemental food sources. This aligns with the findings of Chapter 2 and suggests that anthropogenic feeding is important to hedgehogs – and a key driver of garden use – throughout the year, affecting their behaviour during seasons where they are both typically active (spring-autumn) and when they are hibernating (winter).

Having established the importance of residential gardens for urban-dwelling hedgehogs, therefore highlighting the capacity for householders to influence hedgehog presence and/or activity on their property, Chapter 4 explored the value of artificial refugia as nesting sites for hedgehogs in gardens. The results of a nationwide questionnaire survey indicated that nest boxes were used at least moderately frequently for all types of nesting (summer day, breeding, winter day and hibernation nesting) but the likelihood of a nest box being used may be influenced by time since installation, placement, site-based variables and the provision of bedding material and food.

Finally, to build upon our understanding of how urban residents could improve their gardens for the benefit of hedgehogs, in Chapter 5 an extensive assessment was made of factors encouraging, or discouraging, householders from improving inter-garden connectivity via hedgehog highways. The results indicated that people who had made hedgehog highways appeared to be those who were already highly interested in wildlife. Yet, despite above average levels of engagement in other wildlife-friendly gardening activities, less than half (48.0%) of Hedgehog Champions who responded had created a hedgehog highway, and a low proportion (3.2%) of the highways reported provided access into previously inaccessible gardens. Willingness to construct hedgehog highways was diminished when respondents believed that there was an existing access point for hedgehogs into their garden, if they were concerned about boundary ownership and interacting with neighbours, and/or if they perceived hedgehogs to be absent from the local area. Subsequently, at the current scale of highway-creation, the ecological benefits of making hedgehog highways could potentially be limited.

Conservation implications

Hedgehog highways

Knowledge of how garden boundaries impact wildlife in terms of space use or populations is generally lacking, but for ground-dwelling animals with limited climbing abilities, impenetrable boundaries are very likely to fragment networks of interconnected habitat and prevent access to potentially valuable resources. The presence and/or permeability of such boundaries, compared to other barriers such as roads, are generally unmapped or undocumented (Jakes *et al*., 2018). For hedgehogs, the scale of this issue was examined in Chapter 5 using a nationwide questionnaire survey aimed at people who had access to a garden. It was found that 40.0%, 36.9% and 9.9% of 3978 reported back gardens were accessible to hedgehogs through at least one location via natural hole(s) only, both natural hole(s) and hedgehog highway(s), and hedgehog highway(s) only, respectively. Nonetheless, 31% of all 11,449 garden boundaries reported could not be traversed by hedgehogs at all, implying that gardens tended not to be completely connected to all bordering plots.

Hedgehog Street was launched in 2010 to tackle this issue by actively encouraging householders to create hedgehog highways, and with >100,000 Champions currently registered online, it provides a substantial platform through which conservation information can be disseminated. However, as outlined in Chapter 5, the ability of householders to successfully construct hedgehog highways can be constrained by several factors, including the level of pre-existing interest in wildlife. Therefore, the continued growth of this campaign, as well as other similar projects concerning garden accessibility for wildlife, needs to find mechanisms to enlist the support of 'unengaged' individuals and groups (i.e., those with little interest in wildlife and conservation). For example, effort to engage with people who are not innately wildlife-friendly has been investigated by Shaw and Miller (2016) who examined motivations of participation in eight wildlife gardening programmes in Australia. Their results suggested that the recruitment of people who had previously had no intention of improving their gardens for wildlife was comparatively low, but positively linked to money-saving incentives (i.e., the provision of plants or vouchers) and site-based assessments provided by experts. Furthermore, Woolley *et al*. (2021) suggest that people who have a limited interest in nature may be more willing to participate in garden conservation when the benefits are obvious and observable; the latter may indicate particular problems for species that are elusive and nocturnal. Additionally, many householders who took part in the hedgehog highways study appeared to be discouraged from creating highways by concerns surrounding communicating with neighbours and/or interfering with neighbours' garden boundaries. Invoking social interaction in structured formats – for example, by recruiting and training community volunteers, or providing financial support to local groups in implementing hedgehog highways – could generate greater levels of participation, and sociological research would likely benefit the development and assessment of such strategies (e.g., Bennett and Roth, 2015) by providing insight into the links between social interaction and community-level conservation action.

Vitally, promoting hedgehog highways should be supported by ecological evidence of the impacts of improving inter-garden connectivity on hedgehog space use, energetic expenditure, survival and, ultimately, population density. This could be achieved by monitoring hedgehog movements and population demographics before and after highways are created, but this requires coordinated participation from dense networks of householders, as was initially attempted as part of this research, but was ultimately unsuccessful due to insufficient householder participation (see Appendix E). The primary reasons for poor volunteer uptake in the initial project aligned with those reported in Chapter 5 and included the notion that gardens were already sufficiently accessible to hedgehogs (27%), as well as concerns associated with damaging boundaries or boundary ownership (15%) (N = 155; Appendix E). This somewhat creates a 'Catch 22'; namely, strategies need to be devised by which disinterested householders can be persuaded to take part in any field experiment focussed on quantifying the benefits of increased inter-garden connectivity, in order to gain the evidence to persuade future such householders to also create hedgehog highways.

Alternatively, movement data could be collected and compared between areas of similar housing types and densities, but with varying levels of existing garden connectivity without any need to persuade householders to alter their garden boundaries. Relatedly, an interesting opportunity to examine the use of highways would be in monitoring hedgehog colonisation of and, subsequently, movements within areas of new-build housing. Some building developers have already committed to adding hedgehog highways to gardens of new homes (e.g., Bovis Homes, 2020; Somerset County Gazette, 2021). Yet, despite the 'biodiversity enhancements' that highways would provide (such enhancements are often viewed favourably by local planning authorities), hedgehog highways remain uncommon features of new housing developments (see Warwick, 2022). As such, an additional direction for hedgehog conservation is for practitioners to collaborate with local planning authorities and developers to ensure that highways are included in new property boundaries as standard; this continues to be challenging (Warwick, 2022), given that hedgehogs are afforded relatively little legislative consideration within the planning systems of the UK.

However, although increasing inter-garden connectivity is considered to be an important factor likely to positively affect hedgehog populations, metrics of back garden to back garden connectivity did not significantly influence proportionate back garden use (Chapter 2), over-winter occupancy (Chapter 3) nor nest box use (Chapter 4) by hedgehogs in these studies, although connectivity may have had some impact on demographic parameters that were not measured. Nonetheless, access for hedgehogs to the back garden via the householder's front garden was a key variable in two studies presented in this thesis. First, where access between the front and back gardens was possible, radio and GPS tracked hedgehogs spent significantly less time in the associated back garden (Chapter 2). Second, hedgehogs were more likely to have made use of nest boxes in either the front or back garden where movement between the two was possible (Chapter 4). Such access points from front to back gardens may therefore represent crucial entry/exit locations within networks of inter-connected gardens within individual blocks of houses, reducing the need for back gardens to be directly inter-connected with one another. However, the overall relevance of front to back access for hedgehogs is unclear given the different directions of odds ratio reported in Chapters 2 and 4;

hedgehogs were 0.6 times (less) likely to spend time in back gardens (Chapter 2), but between 1.4-1.6 times (more) likely to use nest boxes in gardens (Chapter 4), where front to back garden access existed.

The benefits of improving inter-garden connectivity for hedgehogs are, to some extent, contingent on the overall 'conservation value' of such gardens. Although hedgehogs appear to favour gardens over other available habitat types, preference may vary between individual plots due patterns of intra- and inter-specific interactions and/or differences in the quantity or quality of resources available, such as artificial food.

Artificial food

The research presented in this thesis indicates that artificial food is a significant resource for hedgehogs in gardens: radio and GPS tagged hedgehogs were found to spend greater lengths of time in gardens with an artificial food supply (Chapter 2); hedgehog occupancy over the hibernation period was associated with supplementary feeding (Chapter 3); and nest boxes were more likely to be used in gardens where food was offered (Chapter 4). This aligns with the findings of Hubert *et al*. (2011) who reported that hedgehogs were more abundant on transects where pet food availability was highest, although food availability was estimated through an index of the number of cats and gardens observed rather than direct measurement of supplemental resources. Within this thesis, "supplementary feeding" has also been used as a relatively broad descriptor given that it did not always reflect food type, quantity, rate of provision, nor location (e.g., in a feeding station, bowl or scattered). Nonetheless, given that this research has identified strong links between artificial food sources and hedgehog occupancy and activity, and considering that householders are encouraged by wildlife organisations to leave out food for hedgehogs in their gardens, either in the form of pet foods or products marketed specifically as hedgehog foods (e.g., Martin, 2019; BHPS, 2020; Tiggywinkles Wildlife Hospital, 2020), additional research is urgently needed to identify the scale at which supplementary feeding is performed and to quantify its health and ecological implications.

Commercially available wildlife foods in the UK may be nutritionally inadequate for hedgehogs, as has been discovered for Swiss products: many hedgehog foods have low crude protein content relative to the natural diet of hedgehogs, and dry foods in particular can contain high proportions of cereals which are not normally consumed in the wild (Gimmel *et al*., 2021). Cereals are often incorporated in animal feed as they are inexpensive and readily available (e.g., Yamka *et al*., 2005). However, the high carbohydrate content typically provided by cereal grains has been linked to low digestibility (Pezzali and Aldrich, 2019) and increased blood glucose levels and body mass in dogs (Brännback, 2020). Hedgehogs might not reject unsuitable foods (Reeve, 1994), such that an overabundance of nutritionally-poor foods could lead to health issues such as obesity – preventing hedgehogs from curling up into defensive balls – and dental conditions (see Gimmel *et al*., 2021), although this has not been substantiated.

Continuous anthropogenic feeding could also induce changes in animal behaviour. It has previously been suggested that hedgehogs use mutual avoidance, rather than strict territoriality, to avoid interacting or competing directly with other individuals (Morris, 1969; Reeve, 1994; Rautio, 2014) as studies, albeit conducted only in fields and amenity areas, have historically reported few encounters between conspecifics in the wild (Wroot, 1984; Cassini and Krebs, 1994; Reeve, 1994). In recent years, however, as the popularity of feeding hedgehogs has grown and the use of trail cameras by members of the public has increased simultaneously, aggressive encounters between hedgehogs have been recorded frequently within residential gardens and around food sources (see Jones and Chapman, 2020; Hedgehog Street, 2020b). This is likely because reliable food sources (and those which have relatively large volumes of food) can alter the spatial behaviour of hedgehogs, as demonstrated by Cassini and Krebs (1994); this is then potentially likely to lead to smaller nightly range areas *per se* (e.g., Pettett *et al*., 2017) but also increased overlap between the ranges of different individuals at sites where artificial food is located (e.g., Rasmussen *et al*., 2019a). Whilst there is no evidence to suggest that aggressive encounters between hedgehogs are fatal (Gómez *et al*., 2016), food-induced competition may have implications for stress (i.e., the secretion of glucocorticoids: Creel *et al*., 2012) and, in turn, animal health (Rasmussen *et al*., 2021). Indeed, there is increasing discussion on social media accounts of hedgehog rehabilitators that injuries related to fighting between hedgehogs appear to be on the rise (P. Baker, pers. obs.).

Supplementary feeding could also trigger changes in hibernation behaviour. In natural situations, it is thought that hedgehogs would not normally feed during periodic arousals (Reeve, 1994) owing to a lack of invertebrate prey and other natural food sources during winter, and that during most arousal events, they would not normally leave the nest before re-entering torpor (Morris, 2018). However, as reported in Chapter 3, supplementary feeding could stimulate increased winter activity, possibly by preventing or delaying the onset of hibernation, stimulating periodic arousals and/or attracting individuals to predictable feeding sites during periodic arousals. Existing data detailing the timings of hibernation and periodic arousals are largely restricted to research undertaken in captivity where food is continually available (e.g., Walhovd, 1979; Webb and Ellison, 1998; South *et al*., 2020), such that the effects of supplemental food resources on hibernation behaviours are difficult to predict. Regardless, becoming and/or remaining active over winter could be energetically costly for hedgehogs and exposes them to common risks such as road traffic, gardening activities and domestic animals, during a period when inactivity is otherwise thought to correspond with greater survival rates (Appendix F; Yarnell *et al*., 2019; Bearman-Brown *et al*., 2020).

Conversely, the high carbohydrate content associated with e.g., cereal-based pet foods could provide an invaluable source of energy to vulnerable individuals over winter, such as juveniles from litters born late in the year; admissions of underweight juveniles to wildlife rehabilitation centres peak towards winter when natural food availability dwindles (Dowler Burroughes *et al*., 2021). At other times of the year, the provision of artificial food may have benefits for reproduction. For mammals, reproduction is energetically costly, particularly throughout lactation (Speakman, 2007), but access to artificial food could help to satisfy high energetic demands (Heldstab *et al*., 2017) or even alter reproductive outputs. Food availability, for instance, has been linked to the litter size of the edible dormouse (*Glis glis*) (Kager and Fietz, 2009) and reproductive success in red squirrels (*Tamiasciurus hudsonicus*) (Descamps *et al*., 2007). However, the impacts of artificial foods may vary with their nutritional profiles; breeding females might be expected to select food items that are higher in animal fats and proteins, as has been demonstrated by pregnant bank voles (*Myodes glareolus*; Eccard and Ylönen, 2006), but commercially-available wildlife food is often low in such compounds relative to natural sources (Gimmel *et al*., 2021).

Alternatively, supplementary feeding could be a useful tool in negating the effects of competition between hedgehogs and their intraguild predators, badgers and foxes (the abundance of which have both been negatively linked to hedgehog numbers and/or distribution: Pettett *et al*., 2018; Williams *et al*., 2018b), as the increased availability of food subsidies used by predators can be associated with diminished predation pressure (Rodewald *et al*., 2011; Newsome *et al*., 2015). In urban settings, badgers will consume anthropogenic foods in all seasons given its constant availability, whilst appearing to remain more dependent on natural food sources (Gomes *et al*., 2020). In contrast, scavenged anthropogenic foods, including foods left out in gardens for wildlife, can occur disproportionately more in urban fox diets relative to natural prey items (Saunders *et al*., 1993). This ties in with the findings of Chapter 2; although badgers were not recorded within the study area, foxes were, and it was found that hedgehogs were likely to have spent greater lengths of time in gardens where foxes were less frequent visitors

(<monthly) and less time where foxes visited at least weekly. However, since hedgehogs did not appear to wholly avoid using spaces visited by foxes, it could be the case that a high artificial food supply alleviated some level of predation risk for hedgehogs. In fact, some suggest that householders should supply a 'diversionary' source of food for e.g., badgers in their gardens away from where hedgehogs are being fed as a means to reduce possible negative interactions (e.g., McLeish, 2020); this will, however, not stop predation entirely.

In light of the poorly understood positive and negative ramifications of supplementary feeding, reviews of current advice to householders (e.g., Hedgehog Street, 2019; BHPS, 2020; Tiggywinkles Wildlife Hospital, 2020) must be guided by further research input on these subjects. Specifically, studies are needed to bridge knowledge gaps concerning: the scale at which householders provide food for hedgehogs and the scale at which hedgehogs consume it (e.g., dietary analyses, stable isotope analyses, video recording); nutritional values of artificial food for hedgehogs; impacts of supplementary feeding on health, behaviour, reproduction, torpor and survival; and the relationship between food subsidies and predation pressure on hedgehogs. In addition, further research should also consider interactions at feeding sites as possible sources of increased intra-specific aggression, but also as possible sites associated with the transmission of diseases and parasitic infections between hedgehogs as well as between species. Such studies might require manipulations of food provisioning to permit robust comparisons between individuals/populations that heavily utilise supplemental food sources versus those who do not. Additionally, there is a need to quantify natural food availability within gardens and evaluate its significance relative to artificial sources; preliminary studies undertaken by students at the University of Reading have indicated that invertebrate prey diversity and abundance may have limited impact on hedgehog occupancy in gardens in an area where many householders supply food (Bull, 2017).

Nesting opportunities

As well as food supply, the availability of breeding and hibernation sites can be a limiting factor affecting species' distributions (Brockie, 1975; Sutherland *et al*., 2014; Morris, 2018). In urban landscapes, where public green space can be highly fragmented (Liu *et al*., 2016) or intensively managed (Aronson *et al*., 2017) (see Chapter 1), private residential gardens may act as vital sources of nesting opportunities whilst effectively supporting connectivity between habitats. Indeed, many members of the public appear to be interested in creating nesting opportunities in their gardens; Davies *et al.* (2009) estimated that 21% of all UK gardens possess a bird box, and, in Chapter 5, 68% of respondents of the hedgehog highways surveys stated that they had fitted bird boxes in their gardens. For hedgehogs, however, the use and value of artificial refugia has thus far been overlooked, despite a growing interest amongst householders in installing hedgehog nest boxes (see Stone, 2020). As such, Chapter 4 identified factors influencing the use of nest boxes by hedgehogs for day, breeding or hibernation nesting. Nest box use was linked to variables relating to providing bedding and food, nest box placement (namely, being positioned on hardstanding, in a sheltered location, close to a building, raised off the ground, with the entrance oriented south or with the entrance not facing into the open), site-based factors (the lack of a pond, extent of 'good' habitat, front-to-back garden accessibility or the existence of other nest sites), as well as time since installation.

Whilst this knowledge can be used to provisionally advise householders on how to best position their nest boxes, the impact of such factors on nest box 'suitability' are unknown, and animals may inadvertently select refugia of suboptimal designs or placement, falling victim to ecological traps (Demeyrier *et al*., 2016). For example, certain physical features of artificial refugia could heighten the risk of disturbance or predation (Evans *et al*., 2002), use by non-target and/or pest species (Lindenmayer *et al*., 2009), or unsuitable microclimatic conditions (Ardia *et al*., 2006); thermal properties of nest boxes might have critical implications for breeding (van der Vinne *et al*., 2014) and hibernation (Madikiza *et al*., 2010) processes. Subsequently, data to demonstrate how hedgehog nest box design and placement influence the temperature and relative humidity of nesting chambers have been collected for formal analyses (see Appendix G).

It is also essential to consider the effectiveness of deploying nest boxes as substitutes for natural nesting habitats, since it is not known whether the outcomes arising from the use of hedgehog nest boxes are better or worse than those from natural sites (see Evans *et al*., 2002; Bolton *et al*., 2004). For instance, for birds, natural tree cavities are better thermal insulators (Marziarz *et al*., 2017) with more stable microclimates (Strain *et al*., 2021) than artificial boxes. Aligning with this, there is a need to quantify how hedgehog nest box use might affect disease transmission, breeding, torpor and survival, and how this is affected by nest box design-, site- and placement-based features, relative to the use of natural sites. Time-scale is also important: hedgehog nest boxes are not permanent features of gardens, and little is known about their longevity, whereas the creation and appropriate management of e.g., semi-natural habitat patches could potentially produce more suitable and long-term nesting opportunities, alongside yielding other biodiversity benefits.

However, whilst the exact extent of hedgehog nest box provisioning in gardens is unknown, it likely occurs on a wide scale (considering the response rate of Chapter 4's questionnaire), and householders appear amenable to either making or purchasing nest boxes of their own volition. As such, nest boxes for hedgehogs in gardens across the UK represent a potentially economically viable and substantial conservation resource, but it is imperative that further research is undertaken to tailor relevant advice to practitioners and householders, ensuring that the effectiveness of such refugia is not constrained by inefficient design or placement.

Another key garden feature for hedgehogs advocated by the current research is compost heap(s); in Chapter 2, it was reported that compost heaps were associated with more extensive garden use by radio and GPS tagged individuals. Within this study, it was not known whether the compost heaps were stored in containers. In any case, open-air compost piles or compost heaps that are secured by slatted wood are likely to be most accessible to wildlife. Compost heaps may promote the presence of invertebrate prey, though this has not been thoroughly corroborated (Curds, 1985; Wildlife Gardening Forum 2021b). Perhaps more crucially, compost heaps could provide nest sites and/or materials for hedgehogs (Molony *et al*., 2006; Pettett *et al*., 2018), as supported by the findings of the nest box survey (Chapter 4) in which respondents reported on 160 nests located under compost heaps. Temperatures in compost can fluctuate widely with external conditions yet, overall, tend to be warmer than other nesting sites such as log piles (Löwenborg *et al*., 2010) and likely provide sufficient protection for, at least, temporary day nests. Since they are already a relatively common feature of urban gardens (in a study of five UK cities, 21.1% of gardens were reported to possess composting sites (Gaston *et al*., 2007)), additional observations of compost 'use' by hedgehogs within wider garden-based studies would be beneficial.

Other nesting opportunities within gardens include locations under vegetation or log piles, or cavities beneath sheds, garages or decking; occasionally, hedgehogs will also nest within sheds and garages. Accordingly, in the current research it was found that the quantity of nest sites available can influence hedgehog presence in gardens. In the study of over-winter hedgehog activity (Chapter 3), hedgehogs were more likely to have been detected in the lead up to hibernation in gardens possessing a higher number of potential nesting sites. Similarly, nest boxes were more likely to have been used by hedgehogs where householders had observed hedgehogs nesting elsewhere within the same garden (Chapter 4). This could reflect the general quality or suitability of those gardens for hedgehogs; more nesting opportunities might be indicative of greater structural diversity, or perhaps greater 'hedgehog-friendly awareness' of the householder. Nevertheless, the potential value of gardens as locations for nesting warrants further investigation. In particular, data are required on the patterns of use of nest boxes, artificial cavities and vegetation within gardens as sites for daytime nesting, breeding and hibernation, but also on the relative frequency with which gardens are utilised for these reasons in comparison with other urban habitats.

Other garden variables

Within residential gardens, ponds, water bowls and/or bird baths can also represent valuable sources of water for wildlife. This is likely to be of particular importance during extended hot and dry periods when increased temperatures can drive reductions in the abundance of ground-level invertebrates (Figueroa *et al.*, 2021) as these are thought to provide most of a hedgehog's water intake (Morris, 2018). Thus, water bowls and wildlife ponds are encouraged as elements of hedgehog-friendly gardens (Hedgehog Street 2021b). Surprisingly, however, time spent in gardens by hedgehogs (Chapter 2), and the use of nest boxes for summer day nesting or breeding (Chapter 4), were found to be negatively associated with the presence of ponds. The latter could be the result of effort to reduce exposure of, e.g., young to a common urban hazard. However, it is difficult to untangle the link between hedgehog activity within gardens and the significance of garden elements such as ponds without directly observing the activity patterns of individuals within the garden itself. Unfortunately, this is frequently not possible as most gardens cannot be viewed directly from publicly accessible areas. One way to overcome this problem would be to install video cameras within the garden itself, or to gather footage from members of the public who have installed home-security video systems.

This work has also shown that some garden features are generally unimportant for hedgehogs. For example, garden size was included as a variable in the studies of proportionate garden use (Chapter 2) and over-winter activity (Chapter 3), but had no significant impact on the outcomes. Notwithstanding the fact that householders with smaller gardens tend to engage less with wildlife-gardening activities (Gaston *et al.*, 2007; Loram *et al.*, 2008; Goddard *et al.*, 2013), small-sized plots likely provide sufficient space to, for example, install a nest box or provide supplementary food. Furthermore, the presence of artificial lighting did not appear to affect time spent in gardens by radio or GPS tagged individuals (Chapter 2), which aligns with previous research suggesting that artificial lighting has no impact upon hedgehog presence or foraging activity at feeding stations (Finch *et al.*, 2020).

Summary

The importance of gardens for hedgehogs is emphasised by the fact that few “outside-garden” factors, other than environmental conditions, were found to have any influence on variables measuring hedgehog activity. Non-garden habitats, such as amenity grassland, ranked consistently low in the habitat selection analysis, and where hedgehogs spent proportionately less time in gardens, this tended to be where there was an abundance of additional ‘garden land’ nearby (Chapter 2). It is therefore clear that conservation strategies for urban hedgehogs – and perhaps even rural hedgehogs – may be most effective when focussing on encouraging action in residential gardens, though mechanisms for improving outside-garden habitats should also be explored.

Within gardens, householders have the capacity to influence hedgehog occupancy and possibly behaviours exhibited via the provision of certain resources and/or their management actions. The results discussed here suggest that householders can positively affect hedgehog activity in gardens by: ensuring garden boundaries are permeable to hedgehogs by creating access points (at least) via the front-to-back; providing food; creating compost heaps; providing multiple potential nesting sites (e.g., nest boxes, shrubby vegetation, log piles); and, with regard to nest boxes, siting them in likely ‘preferred’ locations, i.e., on hardstanding, in a sheltered location, close to a building, raised off the ground, with the entrance oriented south or with the entrance not facing into the open (summarised in Figure 6.1).

Such resource provisioning and related actions could translate to benefits that support the growth of urban hedgehog populations. However, impacts on health, breeding, survival or population change have not been systematically tested. The studies discussed here nonetheless provide a foundation for future research into conservation efforts for hedgehogs within the urban landscape and, in particular, the likely consequences of such efforts.

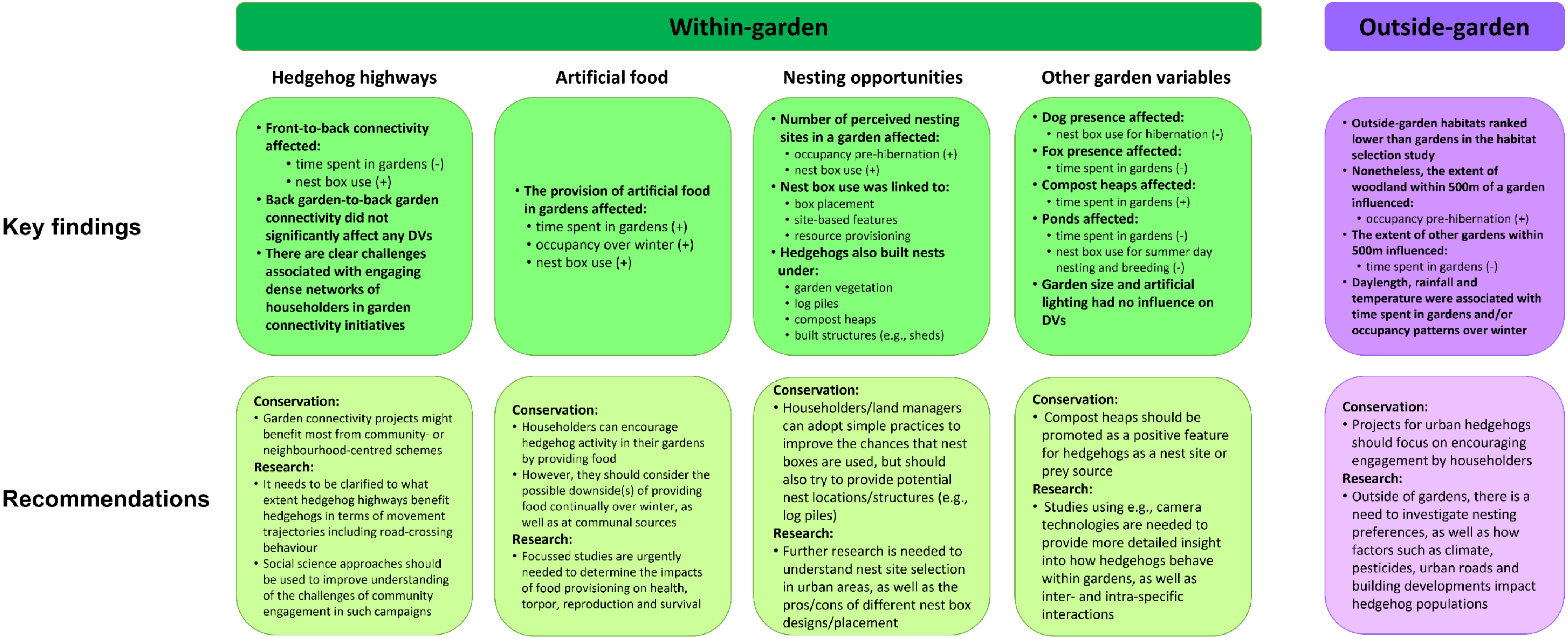

Figure 6.1. Diagram outlining the main findings and recommendations (relating to conservation and research) of this thesis. The findings and recommendations correspond to within-garden (i.e., hedgehog highways; artificial food, nesting opportunities and other features) and outside-garden features of interest. Where appropriate, a significant influence of within-garden or outside-garden factors upon dependent variables (DVs) are denoted by + symbols for a positive effect and - symbols for a negative effect. DVs: time spent in gardens (Chapter 2), occupancy over winter (Chapter 3) and nest box use (Chapter 4) by hedgehogs. The standalone phrase “nest box use” refers to nest box use in all seasons.

Research outlook

Methodological approaches

Hedgehogs can be used as model organisms to investigate the impacts of urbanisation and anthropogenic actions on wild, ground-dwelling mammals (e.g., Barthel *et al*., 2020). In recent years, for example, research has provided insight into the implications of road fragmentation (Braaker *et al*., 2017; Barthel *et al*., 2020), human disturbance (Berger *et al*., 2020a) and wildlife rehabilitation (Yarnell *et al*., 2019; Rasmussen *et al*., 2021) for hedgehogs. Much of the knowledge gained in urban settings can also be applied to rural environments – even within these rural areas, hedgehogs appear to favour gardens over e.g., woodland and pasture (Pettett *et al*., 2017). Whatever the setting, hedgehog-focussed studies have often benefitted from high levels of public interest in hedgehog welfare and conservation (Morris, 1987; Baker and Harris, 2007; Borgi and Cirulli, 2015) leading to significant inputs from 'citizen scientists' in the context of supplying data but also in helping to physically collect data (e.g., Williams *et al*., 2018; Schaus *et al*., 2020; Turner *et al*., 2021).

Within the research presented in this thesis, questionnaire surveys have been a key source of data on garden variables, wildlife sightings and public perceptions: site-based surveys were conducted for Chapters 2 and 3, and nationwide online surveys were conducted for Chapters 4 and 5. In particular, the online questionnaire surveys provided extensive sets of results from >10,000 respondents collectively. However, online surveys can suffer from a high amount of non-response bias relative to face-to-face, postal or telephone surveys (White *et al*., 2005), where only those people interested in the survey topic choose to participate (Duda and Nobile, 2010). Additionally, samples can be constrained by 'self-selection' if the questionnaires are advertised through subject-focussed websites (Duda and Nobile, 2010) – for example, both the nest box (Chapter 4) and hedgehog highway (2020 survey; Chapter 5) surveys were advertised via Hedgehog Street. With regard to the nest box survey, by virtue of the study aims, it was necessary to target householders who had some level of interest in hedgehogs. However, this may have resulted in response bias whereby those respondents who were highly interested in hedgehogs were more likely to feed them as well as monitor the use of their nest box. Additionally, the sample obtained for the hedgehog highways study appeared to comprise people who tended to already be interested in wildlife, as they had, on average, engaged in garden conservation activities relatively more than those respondents in other nationwide studies (Davies *et al*., 2009). Research using online surveys will inevitably continue to be helpful in obtaining large sample sizes for assessing attitudes and actions for hedgehogs (and other wildlife) on privately-owned land such as gardens, but additional survey design and implementation approaches should be explored in future studies in an effort to minimize both response and non-response biases (e.g., Zahl-Thanem *et al*., 2021).

Studying hedgehogs in urban areas also frequently necessitates engaging with members of the public and, sometimes, obtaining permission to access and/or monitor their gardens. As outlined in Chapter 1, this is associated with a range of challenges, some of which are linked to the perceptions and interest levels of householders. Nevertheless, as part of this research, good levels of sustained participation by householders were achieved, with 63 volunteers out of ~70 successfully providing weekly results over a 5-month project (winter footprint tunnel study; Chapter 3). This level of engagement was likely supported by the provision of periodic research updates, verification of results by an expert, a social media page and email account for sharing images, small tokens of thanks at the halfway point (i.e., a hedgehog themed postcard and sticker), possibly alongside the fact that footprint tunnels were temporary additions to the garden rather than permanent. Achieving sufficient levels of engagement with regard to more permanent changes (i.e., making hedgehog highways in garden boundaries), however, was found to be a vastly more challenging task (Appendix E). Overcoming some of the issues surrounding highway-making as well as response bias associated with citizen-based studies could be helped with cross-disciplinary collaborations between social scientists and conservation biologists. For example, comprehensive studies considering attitudes, values, beliefs and satisfactions could be applied to shape methods of volunteer recruitment and communications.

Physically surveying hedgehogs in urban areas is also not without its challenges. In Chapter 2, the drawbacks of using GPS tags are highlighted; the loss of GPS data in studies of urban hedgehogs appears to be substantial, with failures of >50% of scheduled location fixes demonstrated (Braaker *et al*., 2014; Berger *et al*., 2020b; Reeve *et al*., 2019). However, descriptions of missing GPS data and considerations of the impacts of such fix failures are not often evident in hedgehog studies, nor ecological research in general (Nielson *et al*., 2009). It is important to provide this information and attempt to evaluate how missing data might affect any subsequent analyses so that results can be interpreted appropriately (Adams *et al*., 2013). Particularly, data obtained from GPS tracking small, ground-dwelling mammals in urban gardens could be constrained by normal movements close to or under buildings, decking or sheds. For hedgehogs specifically, behaviours associated with the use of nest boxes or feeding stations may also be masked by the failure of GPS tags to connect with satellites when positioned beneath such shelters.

As shown in Appendix H, the results of exploratory static tests of GPS tags conducted in early 2022 support the notion that particular garden features might restrict fix success rate. Namely, when averaged from GPS data collected in two residential gardens, GPS tags achieved 1%, 27%, 62% and 79% of 2880 scheduled fixes when located under a shed, under decking, next to a fence, and in the open (in a central location of the garden on mowed lawn), respectively. Thus, depending on the aims of the study, future projects may benefit from supplementing (or replacing) GPS tracking data with information gathered using other techniques such as the use of radio tags, accelerometer tags (Barthel *et al*., 2019) or video surveillance.

Accelerometers are increasingly used in behavioural studies to log movements that characterise e.g., resting, walking or foraging (Yu and Klaassen, 2021). Accelerometers have been used by researchers in Berlin to differentiate between active and passive behaviours of hedgehogs (Berger *et al*., 2020) as well as to investigate hedgehog locomotion, balling up and inactivity, in an urban park following large-scale human-induced disturbance (Rast *et al*., 2019). Hedgehog foraging behaviours were not classified in these studies, potentially since they were not relevant to the objectives, or because identifying fewer behaviour classes can yield greater model performance (Yu and Klaassen, 2021). Nonetheless, studies within residential locations would benefit from the use of accelerometers ideally to identify foraging patterns across different habitats as well as other behaviours that cannot be continuously physically observed (due to the extent of private land coverage), though this may also require the collection of corresponding location data.

Alternatively, video surveillance – particularly of whole gardens or within nest boxes – would enable researchers to make detailed assessments of garden use, including the quantification of foraging, nesting and movement behaviours, as well as inter- and intra-specific interactions. Yet, motion-activated trail cameras can fail to capture all relevant events; in a study undertaken in France, trail cameras were found to miss 43.6% and 17.0% of small and medium-sized mammal events, respectively (Jumeau *et al*., 2017). An alternative could be the use of permanent recording systems, such as closed-circuit television (CCTV) systems, which offer greater control of recording parameters, including varying triggers of motion detection, improved video quality and improved choice of image settings (Young, 2021). For continuous footage, however, automated methods for identifying species (or relevant frames) has seldom been applied (see Weintstein, 2015).

Furthermore, recording video footage within gardens is associated with financial, logistical and ethical limitations, with the latter relating to the capture of human images (Sharma *et al.*, 2020) or footage of neighbouring private land. Nonetheless, if feasible, the use of camera surveillance, potentially in combination with animal tracking, could provide highly detailed insights into behaviours exhibited by individual hedgehogs in gardens.

Remaining questions

As outlined above, there remains a need to identify ways through which householders can be effectively encouraged to engage, and maintain engagement, in hedgehog conservation activities other than resource provisioning. Although many people are generally positive about hedgehogs in gardens, positive attitude alone do not always directly correlate with conservation behaviours (McCleery *et al*., 2010). This was observed in Chapter 5 in which many survey respondents appeared to be highly interested in wildlife yet did not wish to create hedgehog highways (52% of Champions had not made highways). Numerous social studies have also reported that increases in knowledge or awareness tend to have limited impacts on environmentally conscious behaviours (Kollmuss and Agyeman, 2002; Boyes and Stanisstreet, 2011; Braun and Dierkes, 2019). Thus, the factors influencing participation in garden-based conservation and research should be explored more deeply, ideally through qualitative methods such as interviews which enable highly detailed insights into individual viewpoints that are typically obscured in predesigned questionnaires (Rust *et al*., 2017). Such approaches could shed light on the ways in which participation rates in hedgehog conservation projects are tied to individual factors (e.g., Hurst *et al*., 2019), community-reinforcement (e.g., Moncure and Burbach, 2013), social norms (e.g., Calyton, 2007), conservation psychology (e.g., Saunders, 2003) and/or cultural contexts (e.g., Waylen *et al*., 2010). This information could then be applied to the formulation of robust strategies to recruit and sustain volunteer participation not just within hedgehog projects, but broader garden- and wildlife-based schemes.

Aside from studies of the human behavioural element of hedgehog conservation, additional research is needed to provide evidence of the biological impacts of conservation actions for hedgehogs. In this thesis, three studies identified variables that affected hedgehog activity or presence in gardens, and there is now a further need to quantify outcomes on factors such as behaviour, health, breeding, genetics, survival or population measures. Behavioural studies of hedgehogs would improve our understanding of habitat – and specifically, garden – requirements (e.g., Thibault *et al*., 2006), antipredator behaviours (e.g., Steindler and Letnic, 2021) and foraging preferences (e.g., Reher *et al*., 2016). Fundamentally, comparative measures of reproductive success or over-winter survival are required to determine whether such processes are directly affected by actions such as the provision of artificial nest sites and food sources, as has been observed in avifauna (Brittingham and Temple, 1988; Llambias and Fernandez, 2009). Survival or breeding outcomes could be further dependent on finer details such as nest box design or nutritional quality of supplemental food, necessitating detailed studies focused on these aspects. These sorts of investigations would help to contextualise the importance of existing conservation advice for urban-dwelling hedgehogs, but also guide the development of future strategies. Specific topics for which there are currently few data are summarised in Table 6.1.

Table 6.1. Summary of knowledge gaps that exist within urban hedgehog ecology and conservation.

Theme	Topics
Supplementary feeding	• Scale of provision, and scale of consumption (e.g., to what extent do hedgehogs use/rely on supplemental food sources?) • Foraging behaviour in gardens and elsewhere in urban settings (e.g., how long do hedgehogs spend foraging where artificial food is available?) • Nutritional value of commercially available hedgehog foods in the UK (and elsewhere) • Impacts of supplemental food sources on health (including nutritional intake), behaviour, torpor, reproduction and survival • Comparison with natural food availability • Relationship between food subsidies and predation pressure • Relationship between supplemental feeding sites and disease transmission and/or prevalence • Feeding sites as a focus for intra-specific aggression and/or inter-specific interactions
Nest sites	• Scale of provision of nest boxes • Influence of nest box design and placement on internal microclimate and risk of predation/other disturbances • Influence of box design, nest material, cleaning regime, nest box use, etc., on ectoparasite presence • Longevity of artificial refugia • Nesting behaviours (including patterns of torpor) in urban areas and breeding success when using artificial refugia, in comparison to natural nest sites • Breeding success rates • Nest site selection in urban areas (e.g., are gardens the preferred nesting sites?)

Other urban-associated factors	• Impact of inter-garden connectivity on hedgehog movements (including road crossing behaviours), areas ranged, carrying capacity, etc. • Colonisation of and movements within new-build sites • Influence of within-garden features (including more detailed observations of the impacts of ponds, compost heaps, vegetation structure, etc.) on hedgehog behaviours, nutritional intake and nesting patterns • Interactions with conspecifics, foxes and dogs in urban settings • Impacts of climate (e.g., to what extent do warmer temperatures/other environmental conditions in urban areas affect hibernation timings/natural prey availability?) • Effects and use of safe road-crossings such as culverts or bridges • Relationship between, and large-scale impacts of, hedgehog rehabilitation and genetic differentiation across urban areas • Extent of risk posed by other urban hazards including land development, loss and/or homogenisation of green spaces, and urban-associated chemicals (rodenticides, herbicides, molluscicides, roadside pollutants, etc.)

Conclusion

The research presented in this thesis provides insights into previously unexplored topics associated with hedgehogs in urban gardens, specifically those factors affecting: the proportionate use of residential gardens; over-winter activity in a residential area; use of artificial refugia; and householder engagement in hedgehog conservation activities and their potential value, or shortcomings, as conservation tools. Knowledge of important garden elements can be used to advise householders on how to best encourage and support individuals in their gardens: in the current studies, it was found that supplementary feeding was positively linked to hedgehog activity, as well as nest box use, in gardens during all seasons. The likelihood of a nest box being used could be improved with appropriate placement-based decisions, although additional nesting opportunities (e.g., compost heaps) also appeared to be important drivers of garden use. Of course, hedgehogs can only benefit from these features if gardens are accessible; tracked hedgehogs were found to use an average of eight back gardens per night, although more than 20 were visited on some occasions. Consequently, one key action that householders (and hence neighbourhoods) should undertake is to ensure that gardens are inter-connected; this will have specific benefits for hedgehogs, but is likely to also benefit other wildlife. It is evident, however, that there may be numerous barriers to achieving this goal.

The impacts of garden conservation actions on hedgehogs in terms of health, breeding, survival and/or population change, are largely unknown. Further work is therefore needed to rectify this, as it is clear that gardens and their management by individual householders could collectively play a critical role in reversing hedgehog population declines and, in the face of rapid urban expansion, will become an increasingly important focus for long-term conservation efforts.

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Appendix A

Fine-scale habitat selection of a small mammalian urban adapter; the West European hedgehog (*Erinaceus europaeus*) (Chapter 2)

Missing GPS fixes

Introduction

Analysis of the hedgehog tracking data for those animals fitted with GPS tags indicated that a large proportion of the location fixes were not recorded because of a failure to connect with sufficient satellites. This limited "sky-view" is caused by e.g., dense canopy cover (Ironside *et al*., 2017) and/or, in the case of urban studies, proximity to (or even inside/underneath) buildings. Therefore, we assessed the patterns of missing GPS fixes to examine whether they were associated with abnormal movements or atypical habitats, which would indicate a potential bias in the data itself (i.e., missing fixes were associated with particular habitats).

Data analysis

The potential effect(s) of missing GPS fixes were investigated in five ways. First, we collated the frequency with which different numbers of consecutive fixes were or were not recorded to identify whether missing fixes tended to occur in large blocks or not. Second, we quantified the proportion of programmed fixes that were recorded versus not recorded, and how these varied throughout the tracking regimen (22:00-04.00). This would help identify whether missing fixes tended to occur at specific times of the night or not.

Third, locations from nights where animals were tracked using VHF tags (all 73 fixes were recorded every night for these animals) and the fixes from each full GPS tracking session that were recorded were used to construct 100% minimum convex polygons (nightly MCPs) in QGIS 3.4.4, representing nightly areas ranged by each hedgehog. If a hedgehog was tracked for >1 night, then the mean of their nightly MCPs was calculated. Differences in mean nightly MCP areas between sexes and tag types were tested using independent t-tests.

Fourth, the minimum straight-line distance moved between different blocks of consecutive fixes where the intervening locations were fully or partially recorded versus those where no intervening locations were recorded was quantified (Figure A1). For the latter, for example: the term "1 fix missing" refers to a block of three consecutive fixes where the first and third fixes were recorded but the intervening fix was missing; whereas the terms “2 fix missing” and “3 fix missing” refer to blocks of four and five consecutive fixes where the first and last fixes were recorded but the intervening two or three fixes were not recorded (Figure A1a). Conversely, the term “1 fix not missing” refers to a block of three consecutive fixes where all three locations were recorded, whereas the terms “2 fix not missing” and “3 fix not missing” refer to blocks of four and five consecutive fixes where the first and last fixes were recorded but at least one of the intervening two or three fixes were also recorded (Figure A1b). Differences in the median distance moved between pairs of blocks of the same length where the intervening fixes were not or were at least partially recorded were compared using a series of Mann-Whitney tests.

Last, the possible effect of hedgehogs moving into different habitats which may be particularly prone to fixes not being recorded was investigated by comparing the habitat composition of pooled home range areas (calculated as the minimum convex polygon, ‘MCP’, around all known fixes) against the habitat composition of pooled home ranges after a 100m buffer zone was added to the points immediately preceding and following a block (of any size) of missing fixes. We tested whether the proportions of each habitat type (see the main text) in MCPs based on known locations only versus MCPs based on known locations plus buffered locations were statistically different by calculating Wilks’ lambda.

Figure A1. Schematic illustrating how distance travelled (m) was calculated for blocks of consecutive fixes where **(a)** all intervening fixes were missing (D_M) and (b) where at least some of the intervening fixes were also recoded (D_R). The former are referred to as "1 fix missing", "2 fixes missing", etc. to indicate the number of consecutive fixes where data were not recorded. The latter are referred to as "1 fix not missing", "2 fixes not missing", etc. to indicate that one or all of the intervening consecutive fixes were recorded. Consecutive blocks of cells shaded (a) red or **(b)** orange indicate the locations within the data record used to calculate D_M and D_R, respectively: in all cases, distances were calculated as the straight-line distance between the first and last recorded location in that block of cells.

(a) Instances where all intervening fixes were missing (D_M)

Data record	**1 fix missing**				**2 fixes missing**		**3 fixes missing**		
Fix recorded									
Fix recorded									
Fix missed									
Fix missed									
Fix recorded									
Fix missed									
Fix missed									
Fix missed									
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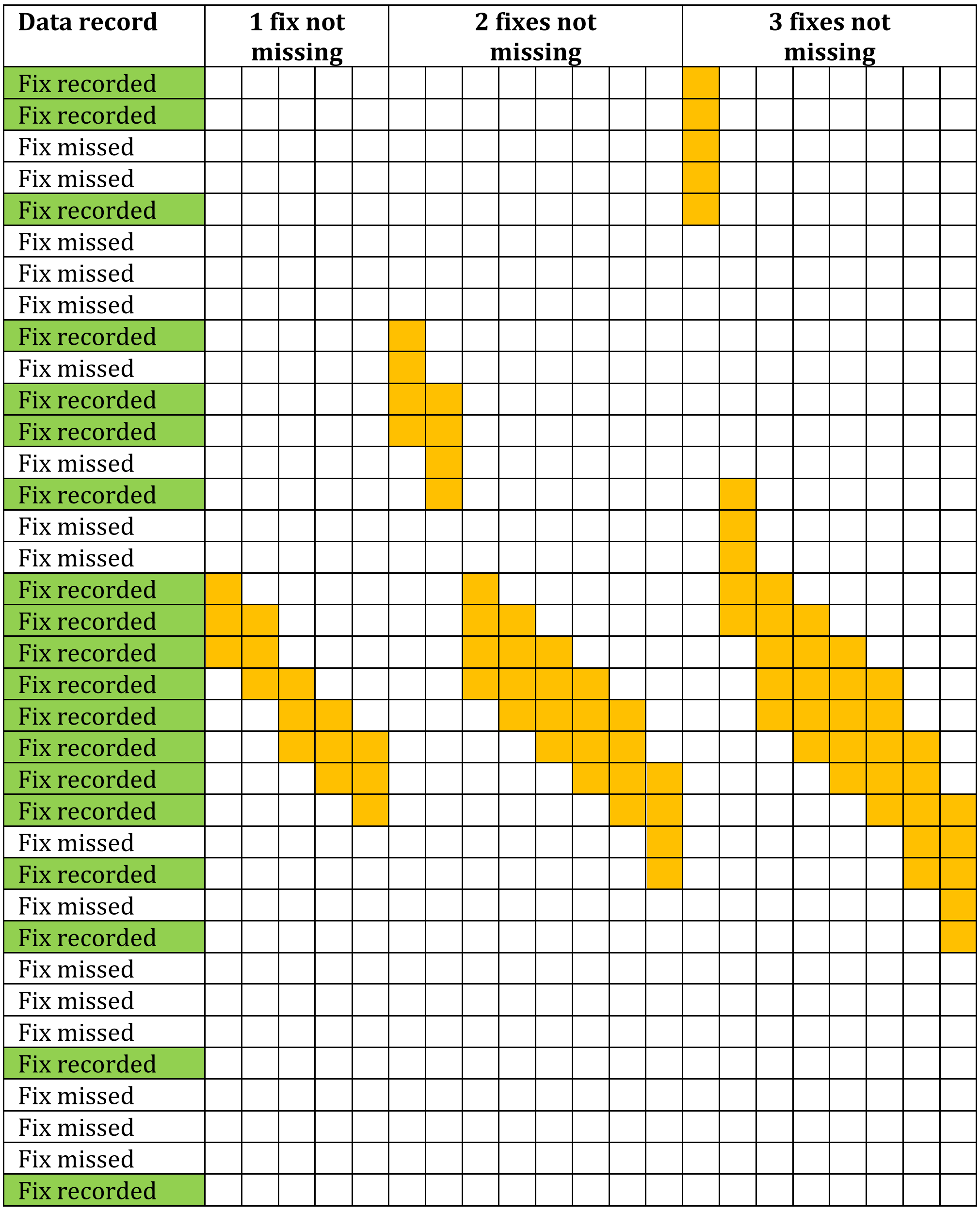
Fix missed									
Fix missed									
Fix recorded									

(b) Instances where one or more intervening fixes were also recorded (D_R)



Results

Overall, nine hedgehogs were GPS tracked for a total of 71 nights (range: 6-10 nights each). Excluding instances where the animal's tag was attached at the start and/or removed at the end of its tracking period (N = 448 fixes), tags were potentially able to record a total of 4,735 locations; of these, a total of 2496 fixes (57.1%) were recorded. The majority of missing fixes (N = 2239) were single locations (N = 488; 21.8%: Figure A2). Cumulatively, 64.4% of missing fixes (N = 1442) occurred in blocks of 1-5 locations, 20.0% occurred in blocks of 6-10 fixes (N = 448) and 11.8% occurred in blocks of 11-20 fixes (N

= 264). However, one block each of 22, 28 and 35 consecutively missed fixes were observed (N = 85, 3.8%: Figure A2).

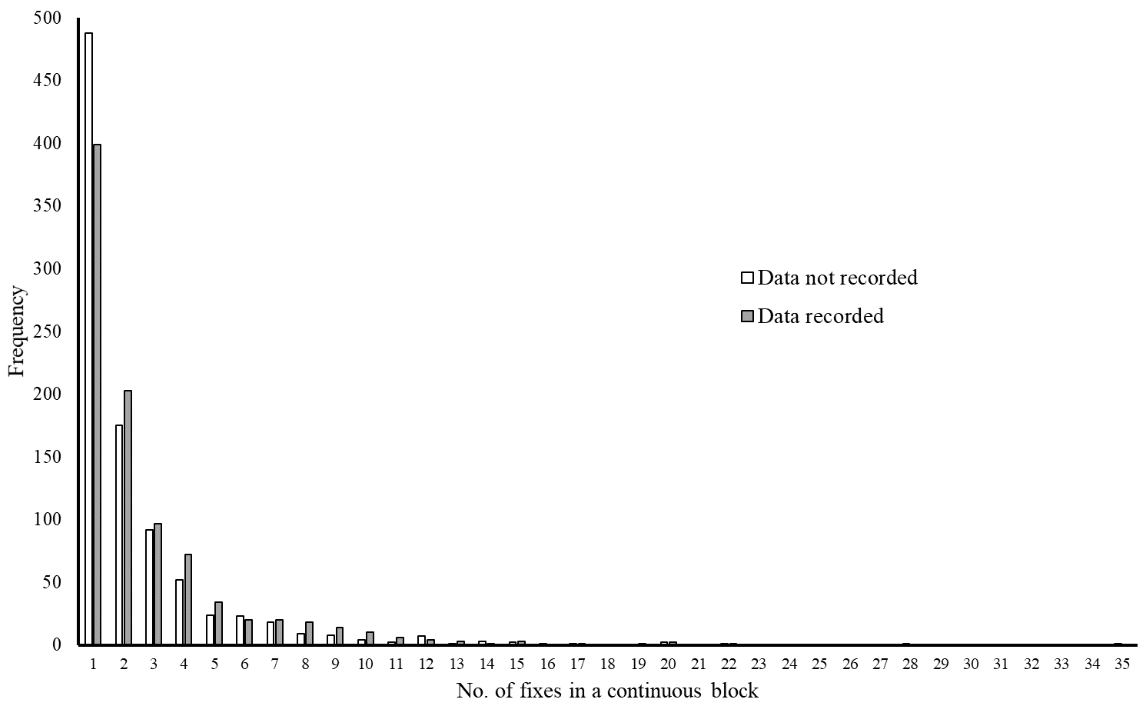


Figure A2. Summary of the number of recorded versus missed locations documented for nine hedgehogs tracked for a total of 71 nights in 2016-2018 inclusive. Data were collated in the context of the length of continuous sequential blocks of recorded or missed fixes (see Figure A1).

Fixes recorded in relation to time of night

In relation to time during the nightly tracking regimen, and excluding instances where tags were not attached, proportionally more fixes were recorded in the latter half of the night, although there was a lot of variation across all parts of the tracking period (Figure A3).

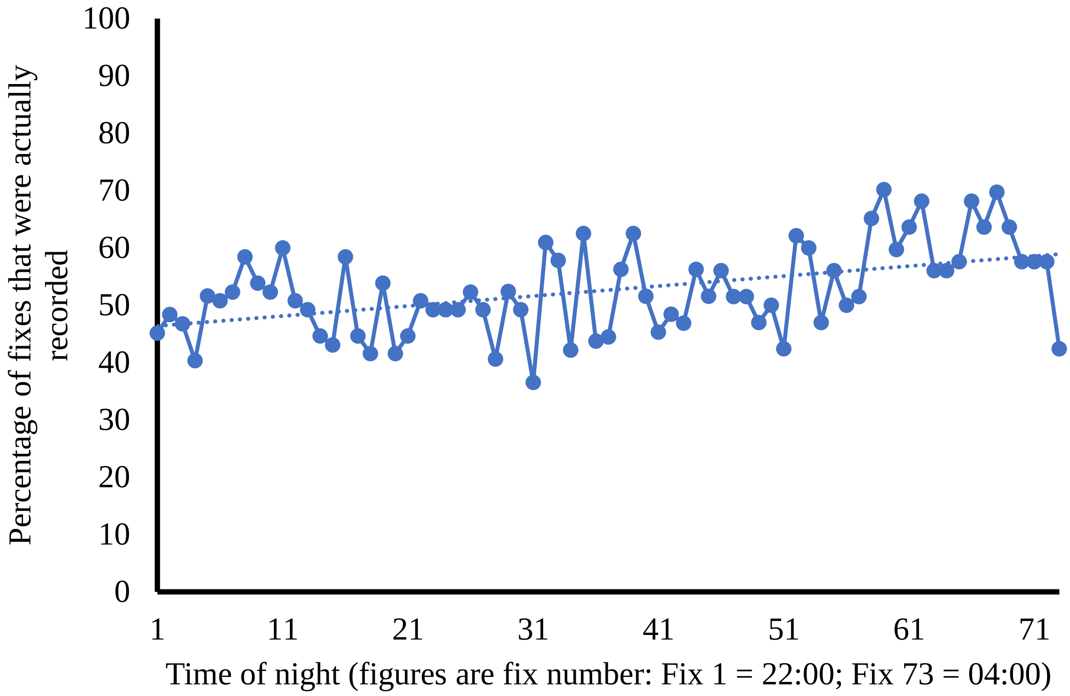


Figure A3. Summary of the percentage of location fixes recorded for GPS-tagged hedgehogs in relation to the time of night. Hedgehogs were tracked for a continuous 6-hour period from 22:00 (10pm) to 04:00 (4am) with fixes recorded every five minutes.

Difference between nightly range area in relation to tag type

Although the mean (± SD) nightly MCP area of males (3.54 ± 3.06ha) was significantly larger than that of females (0.71 ± 0.31ha: $t_{12} = 3.33$, $p < 0.01$), nightly MCP area did not differ significantly between tag types for either sex (males: $t_{11} = -1.21$, $p = 0.25$; females: $t_{13} = 1.69$, $p = 0.11$).

Distance moved between blocks of missing and non-missing fixes

In general terms, the straight-line distances moved between blocks of consecutive fixes of different length were broadly similar for those instances where all intervening fixes were missing versus those instances where at least one intervening fix was recorded (Table A1; Figure A4). Where a significant difference was detected, hedgehogs had tended to move further where intervening data had been recorded versus those instances where intervening data were completely absent (Table A1).

Table A1. Summary of the analyses comparing median distance moved: (i) across blocks of consecutive missing fixes (e.g., "2 fix missing" indicates instances where two consecutive fixes were missing, but the positions before and after these two fixes were known); versus (ii) between any two fixes of a given time span where some of the intervening fixes were also known (e.g., "2 fix not missing" indicates a segment of four fixes where the first and last positions were known but where at least one of the intervening two fixes was also known). Data were analysed using a series of Mann-Whitney tests. Data are illustrated in Figure A4.

Length of block of fixes being considered (B)[1]	Max. no. of missing fixes within block[2]	Median distance (D_M) moved where fixes were missing (N)[3]	Median distance (D_R) moved where fixes were not missing (N)[4]	Mann-Whitney test	Conclusion[5]
3	1	20.5 (448)	23.5 (1076)	W = 322890.0, P = 0.017	Recorded > Missed
4	2	22.6 (159)	27.2 (1301)	W = 105826.0, P = 0.040	Recorded > Missed
5	3	26.7 (85)	31.9 1323)	W = 54336.5, P = 0.127	NS
6	4	24.2 (45)	35.5 (1362)	W = 26046.5, P = 0.036	Recorded > Missed
7	5	27.6 (19)	38.5 (1309)	W = 10810.0, P = 0.274	NS
8	6	28.4 (17)	40.5 (1320)	W = 10144.0, P = 0.437	NS
9	7	25.6 (14)	43.2 (1265)	W = 6172.0, P = 0.043	Recorded > Missed
10	8	30.4 (7)	46.2 (1248)	W = 3249.5, P = 0.231	NS
11	9	18.9 (5)	47.9 (1233)	W = 1771.0, P = 0.097	NS
12	10	21.7 (4)	51.1 (1188)	W = 1326.5, P = 0.123	NS
13	11	- (0)		-	-
14	12	30.2 (4)	54.6 (1136)	W = 1515.0, P = 0.244	NS

[1] B is the total number of consecutive fixes under consideration; the first and last fix within this block must be known, but the number of known fixes between these known locations can vary from 1 to (B-2). These data were used to calculate D_R. [2] This is the maximum number of fixes in a column of length B that can be missing; these data were used to calculate D_M. [3] D_M is the median distance moved between a block of fixes of length B where the first and last fixes were known but all intervening locations were missing. N is total sample size. [4] D_R is the median distance moved between a block of fixes of length B where the first and last fixes were known and at least one intervening fix was also known. N is total sample size. [5] "Recorded > Missed" indicates that the median distance travelled across a set of consecutive fixes of length B where at least one intervening fix was recorded (D_R) was significantly greater than the median distance travelled across a set of consecutive fixes of length B where all intervening fixes were missing (D_M). NS indicates median distances travelled were not significantly different.

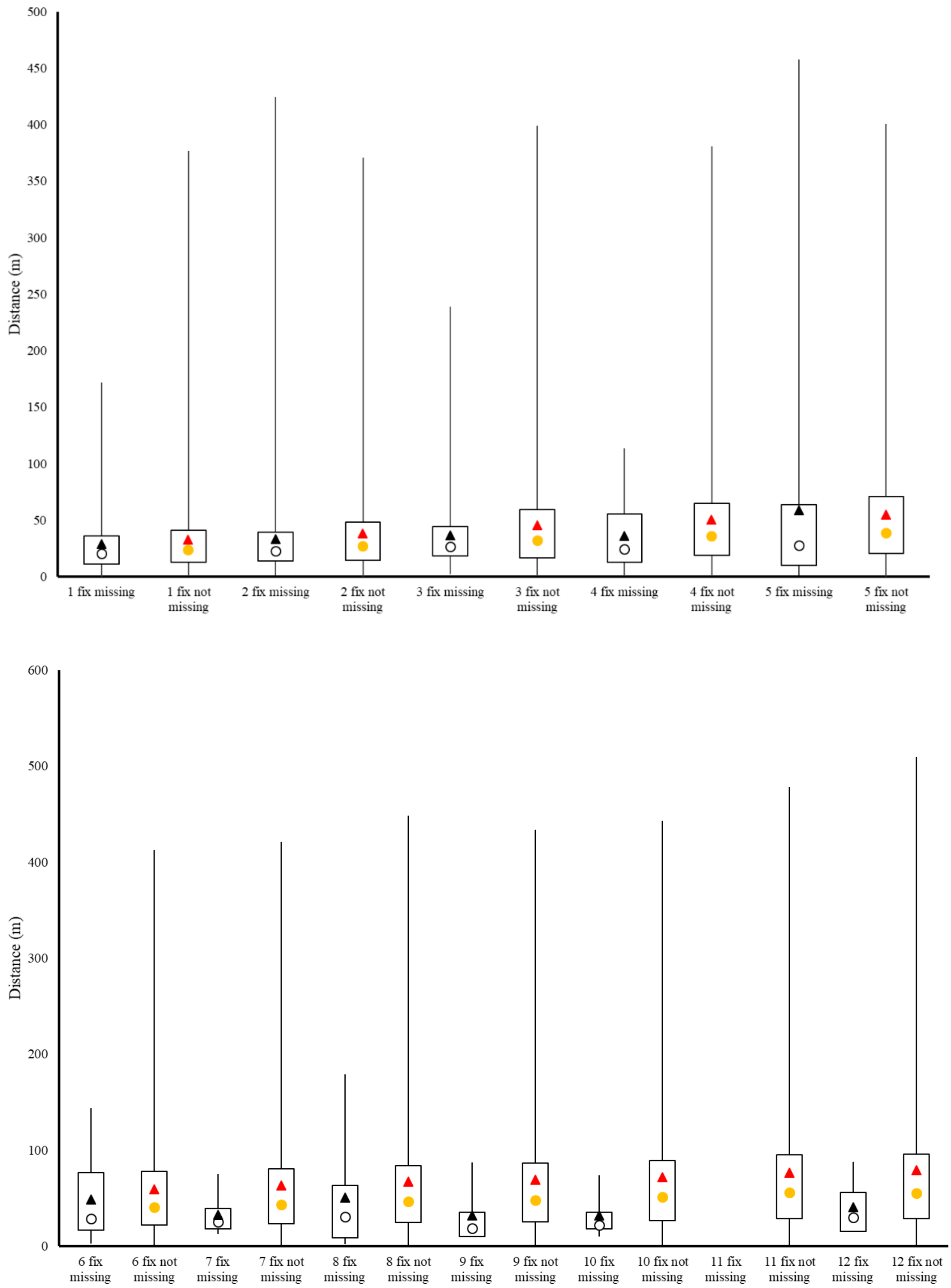


Figure A4. Boxplots indicating distance moved (metres): (i) across blocks of consecutive missing fixes; versus (ii) between any two fixes of a given time span where some of the intervening fixes were also known (see Figure A1). Triangle symbols indicate mean values; circles indicate median values. Vertical error bars indicate maximum and minimum values; boxes indicate inter-quartile ranges. Sample sizes are indicated in Table A1.

Habitat composition

The proportion of habitats present in pooled MCPs of known locations did not significantly differ from the proportion of habitats present in pooled MCPs generated by the buffered GPS locations ($\Lambda = 0.35$, $p = 0.78$). As such, the observed habitat compositions in this study are not considered to have been markedly affected by missing GPS fixes.

Summary and conclusion

There was little evidence that missing GPS locations were associated with unusual movements nor atypical habitats: (i) the duration of blocks of missing fixes closely mirrored the pattern observed for recorded GPS locations; (ii) the distance moved across blocks of missing fixes was broadly similar to that observed for straight-line distances moved between know locations (and where significant pair-wise differences were recorded, the distance moved across missing fixes tended to be smaller); (iii) there was no significant difference in area ranged nightly based on VHF tagged animals (where all location fixes were recorded every night) versus GPS tagged animals; and (iv) the addition of a 100m buffer around all fixes preceding or following a block of missing fixes did not significantly affect the habitat composition of individual pooled ranges. However, the proportion of GPS locations that were recorded tended to be lower at the start of the night and higher at the end of the night, although there was a lot of variation in all time periods.

Although we do not have definitive data, this pattern of missing fixes would be consistent with GPS-tagged hedgehogs moving primarily within and between residential gardens but periodically being in proximity to structures that could potentially block their GPS signal, such as fences or buildings, but also perhaps underneath structures such as decking and sheds where they may be resting. In addition, hedgehogs are often fed by householders in covered feeding stations to protect the food from being stolen by cats and foxes. Given that hedgehogs are likely to be familiar with the location of supplementary feeding stations, and therefore likely competing with one another, it is plausible that they may tend to access this food source early in the night; as such, this pattern of foraging behaviour might also explain the increased tendency to miss fixes early in the night.

Overall, therefore, we do not believe that there are likely to be any significant biases in the habitat types nor individual gardens where the positions of GPS tagged hedgehogs were and were not recorded and that the results presented are valid. However, at the same time, we acknowledge that these assumptions do need to be verified. As a consequence, the results arising from this study should be considered a preliminary investigation of the factors affecting the use of individual gardens by urban hedgehogs in the UK.

Appendix A cont.

Habitats within study site and pooled ranges

Table A2. The quantity (hectares; ha) and proportion of habitats available within **(a)** the study area and **(b)** pooled hedgehog ranges, and **(c)** the quantity and proportion of location fixes recorded in habitats of pooled ranges. NB. In the analyses, *buildings* were excluded, and *scrub*, *woodland*, *roads* and *other* were combined into *other*.

(a) Study area

Measure	Front gardens			Back gardens			Other						Total
	Detached	Semi-detached	Terraced	Detached	Semi-detached	Terraced	Amenity grassland	Scrub	Woodland	Roads	Buildings	Other	
ha	34.53	16.94	7.38	67.55	39.00	13.62	94.59	8.92	57.11	62.67	79.22	99.94	581.47
Proportion	0.06	0.03	0.01	0.12	0.07	0.02	0.16	0.02	0.10	0.11	0.14	0.17	1.00

(b) Habitats in pooled ranges. Habitat measurements are provided first in hectares, and then in proportions

ID	Sex	Measure	Front gardens			Back gardens			Other						Total
			Detached	Semi-detached	Terraced	Detached	Semi-detached	Terraced	Amenity grassland	Scrub	Woodland	Roads	Buildings	Other	
1	M	ha	0.30	0.20	0.11	0.38	0.49	0.32	0.34	0.04	0.03	1.08	1.04	0.69	5.03
2	M		0.01	0.01	0.14	0.00	0.02	0.19	0.11	0.04	0.00	0.21	0.18	0.26	1.16
3	M		0.37	0.02	0.25	0.44	0.07	0.48	0.08	0.02	0.00	0.85	1.15	0.54	4.26
4	M		0.09	0.03	0.00	0.10	0.09	0.00	0.00	0.16	0.00	0.27	0.09	0.24	1.07
5	M		0.04	0.02	0.02	0.04	0.05	0.07	0.03	0.00	0.00	0.01	0.12	0.09	0.49

6	M		0.16	0.21	0.19	0.25	0.45	0.67	0.58	0.02	0.17	0.83	0.99	1.10	5.61
7	M		0.03	0.13	0.00	0.09	0.25	0.00	0.00	0.00	0.00	0.10	0.19	0.05	0.83
8	M		0.27	0.04	0.02	0.48	0.17	0.01	0.23	0.16	0.00	0.47	0.50	0.40	2.76
9	M		0.89	0.17	0.83	1.08	0.26	1.46	0.97	0.02	0.14	2.15	2.77	2.18	12.92
10	M		0.46	0.27	0.86	0.86	0.55	1.60	1.11	0.41	0.06	1.88	2.62	2.10	12.78
11	M		2.68	1.12	0.00	6.57	2.82	0.00	0.00	0.02	0.00	1.93	3.14	2.68	20.98
12	M		2.48	0.37	0.00	5.21	1.26	0.00	2.59	1.22	9.11	1.56	2.15	3.11	29.05
13	M		0.20	0.02	0.67	0.13	0.03	0.95	0.17	0.11	0.00	0.39	1.26	1.48	5.42
14	F		0.29	0.04	0.82	0.28	0.06	1.20	0.17	0.41	0.00	0.89	1.63	2.64	8.43
15	F		0.13	0.25	0.16	0.34	0.33	0.45	2.74	0.12	0.00	0.38	0.69	0.94	6.52
16	F		0.04	0.02	0.11	0.08	0.03	0.08	0.00	0.02	0.00	0.09	0.16	0.05	0.66
17	F		0.00	0.08	0.00	0.01	0.15	0.00	0.00	0.00	0.00	0.05	0.12	0.03	0.44
18	F		0.16	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.12	0.09	0.16	0.18	0.91
19	F		0.00	0.00	0.00	0.05	0.00	0.00	1.14	0.01	0.00	0.00	0.01	0.00	1.21
20	F		0.01	0.00	0.05	0.03	0.00	0.11	0.17	0.02	0.00	0.02	0.14	0.07	0.62
21	F		0.17	0.05	0.00	0.48	0.15	0.00	0.00	0.00	0.64	0.32	0.33	0.24	2.37
22	F		0.21	0.21	0.00	0.50	0.58	0.02	0.00	0.00	0.00	0.30	0.50	0.14	2.46
23	F		0.07	0.04	0.04	0.09	0.07	0.06	0.16	0.00	0.00	0.08	0.24	0.10	0.96
24	F		0.37	0.16	0.05	0.67	0.47	0.12	0.00	0.00	0.00	0.41	0.65	0.35	3.25
25	F		0.46	0.18	0.09	1.06	0.25	0.27	3.53	0.37	0.00	0.39	0.74	2.03	9.35
26	F		0.03	0.01	0.21	0.03	0.00	0.46	0.27	0.02	0.00	0.19	0.53	0.52	2.28
27	F		0.09	0.01	0.51	0.04	0.02	0.73	0.27	0.28	0.00	0.43	0.77	1.70	4.85
28	F		0.12	0.02	0.62	0.11	0.01	0.97	0.60	0.32	0.00	0.43	1.07	1.72	5.98
1	M	Proportion	0.06	0.04	0.02	0.08	0.10	0.06	0.07	0.01	0.01	0.21	0.21	0.14	1.00
2	M		0.01	0.01	0.12	0.00	0.02	0.16	0.09	0.04	0.00	0.18	0.15	0.22	1.00
3	M		0.09	0.00	0.06	0.10	0.02	0.11	0.02	0.00	0.00	0.20	0.27	0.13	1.00

4	M		0.09	0.03	0.00	0.10	0.08	0.00	0.00	0.15	0.00	0.25	0.09	0.22	1.00
5	M		0.08	0.05	0.03	0.09	0.10	0.14	0.05	0.00	0.00	0.02	0.25	0.19	1.00
6	M		0.03	0.04	0.03	0.04	0.08	0.12	0.10	0.00	0.03	0.15	0.18	0.20	1.00
7	M		0.04	0.16	0.00	0.10	0.30	0.00	0.00	0.00	0.00	0.12	0.23	0.06	1.00
8	M		0.10	0.01	0.01	0.17	0.06	0.00	0.08	0.06	0.00	0.17	0.18	0.15	1.00
9	M		0.07	0.01	0.06	0.08	0.02	0.11	0.08	0.00	0.01	0.17	0.21	0.17	1.00
10	M		0.04	0.02	0.07	0.07	0.04	0.13	0.09	0.03	0.00	0.15	0.21	0.16	1.00
11	M		0.13	0.05	0.00	0.31	0.13	0.00	0.00	0.00	0.00	0.09	0.15	0.13	1.00
12	M		0.09	0.01	0.00	0.18	0.04	0.00	0.09	0.04	0.31	0.05	0.07	0.11	1.00
13	M		0.04	0.00	0.12	0.02	0.01	0.18	0.03	0.02	0.00	0.07	0.23	0.27	1.00
14	F		0.03	0.00	0.10	0.03	0.01	0.14	0.02	0.05	0.00	0.11	0.19	0.31	1.00
15	F		0.02	0.04	0.02	0.05	0.05	0.07	0.42	0.02	0.00	0.06	0.11	0.14	1.00
16	F		0.05	0.02	0.17	0.12	0.04	0.12	0.00	0.02	0.00	0.14	0.24	0.07	1.00
17	F		0.00	0.17	0.00	0.03	0.33	0.00	0.00	0.00	0.00	0.12	0.28	0.07	1.00
18	F		0.18	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.13	0.10	0.18	0.19	1.00
19	F		0.00	0.00	0.00	0.04	0.00	0.00	0.94	0.01	0.00	0.00	0.01	0.00	1.00
20	F		0.01	0.00	0.08	0.05	0.00	0.18	0.28	0.03	0.00	0.03	0.23	0.11	1.00
21	F		0.07	0.02	0.00	0.20	0.06	0.00	0.00	0.00	0.27	0.13	0.14	0.10	1.00
22	F		0.08	0.09	0.00	0.20	0.24	0.01	0.00	0.00	0.00	0.12	0.20	0.06	1.00
23	F		0.07	0.04	0.04	0.09	0.08	0.06	0.17	0.00	0.00	0.09	0.25	0.11	1.00
24	F		0.11	0.05	0.01	0.21	0.14	0.04	0.00	0.00	0.00	0.13	0.20	0.11	1.00
25	F		0.05	0.02	0.01	0.11	0.03	0.03	0.38	0.04	0.00	0.04	0.08	0.22	1.00
26	F		0.01	0.01	0.09	0.01	0.00	0.20	0.12	0.01	0.00	0.08	0.23	0.23	1.00
27	F		0.02	0.00	0.10	0.01	0.00	0.15	0.06	0.06	0.00	0.09	0.16	0.35	1.00
28	F		0.02	0.00	0.10	0.02	0.00	0.16	0.10	0.05	0.00	0.07	0.18	0.29	1.00

(c) Location fixes in each habitat within pooled ranges. Measurements are first provided as the raw number of fixes, then proportion of all fixes

ID	Sex	Measure	Front gardens			Back gardens			Other						Total
			Detached	Semi-detached	Terraced	Detached	Semi-detached	Terraced	Amenity grassland	Scrub	Woodland	Roads	Buildings	Other	
1	M	no. fixes	19	0	0	31	1	2	0	4	0	8	0	8	73
2	M		0	0	2	0	5	52	3	1	0	6	0	5	73
3	M		0	0	7	18	0	29	15	0	0	3	0	1	73
4	M		33	3	0	21	0	0	0	0	0	0	15	0	73
5	M		21	6	0	12	8	10	9	6	0	0	0	1	73
6	M		0	8	5	16	4	7	3	0	5	5	8	12	73
7	M		2	18	0	52	60	0	0	0	0	6	8	0	146
8	M		33	2	0	81	24	0	0	33	0	5	24	17	219
9	M		31	4	3	50	9	74	14	0	0	31	58	17	292
10	M		22	3	20	14	32	48	17	11	0	13	46	20	245
11	M		12	5	0	124	62	0	0	0	0	15	15	12	244
12	M		15	3	0	168	22	0	8	4	6	14	42	19	300
13	M		32	0	18	21	3	35	33	18	0	16	54	49	280
14	F		8	1	49	1	12	69	13	8	0	38	42	18	257
15	F		1	9	4	2	11	4	5	1	0	9	13	13	73
16	F		11	0	22	18	0	16	0	0	0	4	1	1	73
17	F		0	9	0	18	45	0	0	0	0	0	0	1	73
18	F		25	0	0	22	6	0	0	10	2	0	6	3	73
19	F		0	0	0	65	0	0	75	4	0	0	2	0	146
20	F		16	0	14	43	0	105	17	0	0	1	22	0	219
21	F		15	2	0	74	0	0	0	0	98	0	9	23	219
22	F		49	29	0	124	87	0	0	0	0	3	0	0	292

23	F		93	6	2	134	20	0	13	0	0	2	6	15	292
24	F		28	1	0	194	47	14	0	0	0	8	0	0	292
25	F		12	18	3	30	19	11	15	44	0	3	24	29	208
26	F		7	0	37	4	0	46	99	5	0	11	26	8	243
27	F		5	5	24	0	6	96	51	3	0	22	17	21	249
28	F		2	0	29	1	0	66	8	4	0	26	58	33	226
1	M	Proportion	0.25	0.00	0.00	0.42	0.01	0.03	0.00	0.06	0.00	0.11	0.00	0.11	1.00
2	M		0.00	0.00	0.03	0.00	0.06	0.71	0.04	0.01	0.00	0.08	0.00	0.06	1.00
3	M		0.00	0.00	0.10	0.25	0.00	0.39	0.20	0.00	0.00	0.04	0.00	0.01	1.00
4	M		0.46	0.04	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	1.00
5	M		0.29	0.08	0.00	0.16	0.11	0.14	0.12	0.08	0.00	0.00	0.00	0.01	1.00
6	M		0.00	0.11	0.06	0.22	0.05	0.09	0.04	0.00	0.07	0.06	0.12	0.17	1.00
7	M		0.01	0.12	0.00	0.36	0.41	0.00	0.00	0.00	0.00	0.04	0.05	0.00	1.00
8	M		0.15	0.01	0.00	0.37	0.11	0.00	0.00	0.15	0.00	0.02	0.11	0.08	1.00
9	M		0.11	0.01	0.01	0.17	0.03	0.25	0.05	0.00	0.00	0.11	0.20	0.06	1.00
10	M		0.09	0.01	0.08	0.06	0.13	0.19	0.07	0.05	0.00	0.05	0.19	0.08	1.00
11	M		0.05	0.02	0.00	0.51	0.25	0.00	0.00	0.00	0.00	0.06	0.06	0.05	1.00
12	M		0.05	0.01	0.00	0.56	0.07	0.00	0.03	0.01	0.02	0.05	0.14	0.06	1.00
13	M		0.11	0.00	0.07	0.08	0.01	0.13	0.12	0.07	0.00	0.06	0.19	0.17	1.00
14	F		0.03	0.00	0.19	0.00	0.05	0.27	0.05	0.03	0.00	0.15	0.16	0.07	1.00
15	F		0.02	0.12	0.06	0.02	0.16	0.06	0.06	0.02	0.00	0.13	0.17	0.18	1.00
16	F		0.15	0.00	0.30	0.25	0.00	0.22	0.00	0.00	0.00	0.05	0.01	0.01	1.00
17	F		0.00	0.12	0.00	0.25	0.62	0.00	0.00	0.00	0.00	0.00	0.00	0.01	1.00
18	F		0.34	0.00	0.00	0.30	0.08	0.00	0.00	0.13	0.03	0.00	0.08	0.04	1.00
19	F		0.00	0.00	0.00	0.44	0.00	0.00	0.51	0.03	0.00	0.00	0.01	0.00	1.00
20	F		0.07	0.00	0.06	0.20	0.00	0.48	0.08	0.00	0.00	0.00	0.10	0.00	1.00
21	F		0.07	0.01	0.00	0.34	0.00	0.00	0.00	0.00	0.45	0.00	0.04	0.10	1.00

22	F		0.17	0.10	0.00	0.42	0.30	0.00	0.00	0.00	0.00	0.01	0.00	0.00	1.00
23	F		0.32	0.02	0.01	0.46	0.07	0.00	0.05	0.00	0.00	0.01	0.02	0.05	1.00
24	F		0.10	0.00	0.00	0.66	0.16	0.05	0.00	0.00	0.00	0.03	0.00	0.00	1.00
25	F		0.06	0.09	0.02	0.14	0.09	0.05	0.07	0.21	0.00	0.02	0.12	0.14	1.00
26	F		0.03	0.00	0.15	0.02	0.00	0.19	0.41	0.02	0.00	0.05	0.11	0.03	1.00
27	F		0.02	0.02	0.10	0.00	0.02	0.39	0.21	0.01	0.00	0.09	0.07	0.08	1.00
28	F		0.01	0.00	0.13	0.00	0.00	0.29	0.04	0.02	0.00	0.11	0.26	0.15	1.00

Appendix B

Patterns of feeding by householders affect activity of hedgehogs (*Erinaceus europaeus*) during the hibernation period (Chapter 3)

<u>Full occupancy models</u>

Table B1. Full occupancy models for winter season based upon alternative cut-off threshold of <20% of gardens occupied per week. Under this scenario, the winter season would have been defined as Weeks 6-16 (23/12/2017–09/03/2018) rather than Weeks 8-16 (06/01/2018-09/03/2018) as presented in the manuscript. Detection probability was modelled as constant. The variance inflation factor ĉ was adjusted based on goodness-of-fit tests of one of the most parameterised models (2.5817). The three top models in this extended timeframe (11 weeks) are the same as those presented in the manuscript (9 weeks).

Model	**QAIC**	**ΔQAIC**	**AIC weight**	**Model likelihood**	***K***	**-2*LogLike**	**Covariates**	**Estimate**	**SE**	**Inflated SE**	**Lower limit**	**Upper limit**
psi(FEDBEFORE),p(FEEDHOG + GRASSTEMP)	136.82	0.00	0.3436	1.0000	5	327.41	psi(FEDBEFORE)	2.408	0.730	1.173	0.109	4.707
							p(FEEDHOG)	1.089	0.275	0.442	0.223	1.955
							p(GRASSTEMP)	0.501	0.177	0.285	-0.057	1.060
psi(FEDBEFORE),p(FEEDHOG + AIRTEMP)	137.08	0.26	0.3017	0.8781	5	328.09	psi(FEDBEFORE)	2.408	0.730	1.173	0.108	4.708
							p(FEEDHOG)	1.087	0.275	0.441	0.222	1.952
							p(AIRTEMP)	0.489	0.181	0.291	-0.081	1.059
psi(FEDBEFORE),p(FEEDHOG + FEEDOTHERS)	138.76	1.94	0.1303	0.3791	5	332.41	psi(FEDBEFORE)	2.628	0.834	1.340	0.002	5.255
							p(FEEDHOG)	0.919	0.279	0.448	0.042	1.796
							p(FEEDOTHERS)	1.398	0.670	1.077	-0.712	3.508
psi(.),p(FEDBEFORE)	140.14	3.32	0.0653	0.1901	3	346.32	p(FEDBEFORE)	2.373	0.445	0.715	0.972	3.773
psi(.),p(FEEDHOG)	141.12	4.30	0.0400	0.1165	3	348.85	p(FEEDHOG)	1.293	0.290	0.465	0.380	2.205

psi(FEDBEFORE),p(.)	142.34	5.52	0.0217	0.0633	3	352.00	psi(FEDBEFORE)	2.300	0.629	1.010	0.320	4.281
psi(FEEDHOG),p(.)	143.95	7.13	0.0097	0.0283	3	356.15	psi(FEEDHOG)	1.187	0.385	0.619	-0.026	2.400
psi(.),p(GARDENSIZE)	144.11	7.29	0.0090	0.0261	3	356.56	p(GARDENSIZE)	-1.007	0.363	0.584	-2.151	0.137
psi(.),p(FEEDOTHERS)	144.71	7.89	0.0066	0.0194	3	358.10	p(FEEDOTHERS)	1.906	0.638	1.026	-0.104	3.917
psi(NEAREST+VE),p(.)	144.90	8.08	0.0060	0.0176	3	358.60	psi(NEAREST+VE)	-1.171	0.499	0.802	-2.742	0.400
psi(.),p(GRASSTEMP)	145.00	8.18	0.0058	0.0167	3	358.86	p(GRASSTEMP)	0.487	0.175	0.281	-0.063	1.038
psi(.),p(AIRTEMP)	145.26	8.44	0.0051	0.0147	3	359.52	p(AIRTEMP)	0.476	0.179	0.287	-0.087	1.038
1 group, Constant P	146.43	9.61	0.0028	0.0082	2	367.70						
psi(.),p(RAINFALL)	146.60	9.78	0.0026	0.0075	3	362.98	p(RAINFALL)	0.322	0.149	0.239	-0.146	0.791
psi(.),p(ARABLE500m)	146.73	9.91	0.0024	0.0070	3	363.32	p(ARABLE500m)	0.249	0.117	0.188	-0.119	0.618
psi(.),p(GOODHABITAT)	146.91	10.09	0.0022	0.0064	3	363.78	p(GOODHABITAT)	-1.741	0.865	1.389	-4.464	0.982
psi(GARDENSIZE),p(.)	147.08	10.26	0.0020	0.0059	3	364.22	psi(GARDENSIZE)	-0.703	0.457	0.734	-2.141	0.736
psi(.),p(URBAN500m)	147.11	10.29	0.0020	0.0058	3	364.30	p(URBAN500m)	-0.318	0.170	0.274	-0.855	0.218
psi(WOODDIST),p(.)	147.14	10.32	0.0020	0.0057	3	364.38	psi(WOODDIST)	-0.543	0.319	0.513	-1.548	0.463
psi(CONNECTIVITY),p(.)	147.32	10.50	0.0018	0.0052	3	364.84	psi(CONNECTIVITY)	1.684	1.034	1.661	-1.572	4.939
psi(GRASS250m),p(.)	147.45	10.63	0.0017	0.0049	3	365.17	psi(GRASS250m)	-0.520	0.375	0.603	-1.701	0.661
psi(WOOD500m),p(.)	147.45	10.63	0.0017	0.0049	3	365.19	psi(WOOD500m)	0.434	0.280	0.451	-0.449	1.317
psi(FEEDOTHERS),p(.)	147.62	10.80	0.0016	0.0045	3	365.63	psi(FEEDOTHERS)	0.976	0.717	1.152	-1.281	3.233
psi(.),p(GRASS250m)	147.66	10.84	0.0015	0.0044	3	365.73	p(GRASS250m)	0.412	0.277	0.445	-0.461	1.286
psi(.),p(HOUSETYPE)	147.67	10.85	0.0015	0.0044	3	365.74	p(HOUSETYPE)	0.604	0.455	0.731	-0.829	2.037
psi(.),p(ARABLEDIST)	147.72	10.90	0.0015	0.0043	3	365.87	p(ARABLEDIST)	-0.222	0.168	0.271	-0.752	0.308
psi(.),p(GRASS500m)	147.73	10.91	0.0015	0.0043	3	365.91	p(GRASS500m)	0.291	0.210	0.337	-0.370	0.951
psi(.),p(NEARESTOTHER)	147.82	11.00	0.0014	0.0041	3	366.13	psi(NEARESTOTHER)	0.144	0.114	0.183	-0.213	0.502
psi(GRASS500m),p(.)	147.91	11.09	0.0013	0.0039	3	366.38	psi(GRASS500m)	-0.339	0.314	0.505	-1.329	0.650
psi(GOODHABITAT),p(.)	147.94	11.12	0.0013	0.0038	3	366.44	psi(GOODHABITAT)	1.849	1.732	2.783	-3.607	7.304
psi(.),p(DAYTIME)	147.94	11.12	0.0013	0.0038	3	366.45	p(DAYTIME)	-0.169	0.152	0.244	-0.648	0.310

psi(.),p(CONNECTIVITY)	148.06	11.24	0.0012	0.0036	3	366.76	p(CONNECTIVITY)	0.565	0.602	0.967	-1.331	2.461
psi(URBAN250m),p(.)	148.13	11.31	0.0012	0.0035	3	366.93	psi(URBAN250m)	0.247	0.292	0.469	-0.672	1.167
psi(.),p(NESTSITES)	148.13	11.31	0.0012	0.0035	3	366.94	p(NESTSITES)	0.126	0.145	0.234	-0.332	0.584
psi(FRONT2BACK),p(.)	148.19	11.37	0.0012	0.0034	3	367.08	psi(FRONT2BACK)	-0.424	0.543	0.873	-2.135	1.288
psi(ARABLE500m),p(.)	148.22	11.40	0.0011	0.0033	3	367.18	psi(ARABLE500m)	0.189	0.263	0.423	-0.640	1.018
psi(.),p(NEAREST+VE)	148.31	11.49	0.0011	0.0032	3	367.40	p(NEAREST+VE)	-0.462	0.434	0.698	-1.830	0.906
psi(WOOD250m),p(.)	148.32	11.50	0.0011	0.0032	3	367.43	psi(WOOD250m)	0.137	0.266	0.428	-0.702	0.975
psi(NESTSITES),p(.)	148.34	11.52	0.0011	0.0032	3	367.48	psi(NESTSITES)	0.125	0.271	0.435	-0.727	0.978
psi(.),p(GRASSDIST)	148.35	11.53	0.0011	0.0031	3	367.51	p(GRASSDIST)	0.066	0.153	0.247	-0.417	0.549
psi(URBAN500m),p(.)	148.36	11.54	0.0011	0.0031	3	367.52	psi(URBAN500m)	0.116	0.279	0.448	-0.761	0.994
psi(.),p(WOODDIST)	148.37	11.55	0.0011	0.0031	3	367.56	p(WOODDIST)	-0.081	0.216	0.347	-0.762	0.599
psi(.),p(URBAN250m)	148.37	11.55	0.0011	0.0031	3	367.55	p(URBAN250m)	-0.069	0.187	0.300	-0.657	0.520
psi(GRASSDIST),p(.)	148.38	11.56	0.0011	0.0031	3	367.59	psi(GRASSDIST)	0.092	0.270	0.434	-0.760	0.943
psi(.),p(FRONT2BACK)	148.38	11.56	0.0011	0.0031	3	367.58	p(FRONT2BACK)	-0.100	0.313	0.503	-1.085	0.885
psi(.),p(WOOD250m)	148.40	11.58	0.0011	0.0031	3	367.63	p(WOOD250m)	-0.042	0.167	0.269	-0.569	0.486
psi(NEARESTOTHER),p(.)	148.41	11.59	0.0010	0.0030	3	367.67	psi(NEARESTOTHER)	0.042	0.267	0.429	-0.799	0.882
psi(ARABLEDIST),p(.)	148.41	11.59	0.0010	0.0030	3	367.65	psi(ARABLEDIST)	-0.057	0.273	0.439	-0.917	0.802
psi(.),p(WOOD500m)	148.42	11.60	0.0010	0.0030	3	367.68	p(WOOD500m)	-0.020	0.165	0.266	-0.541	0.501
psi(HOUSETYPE),p(.)	148.42	11.60	0.0010	0.0030	3	367.68	psi(HOUSETYPE)	0.088	0.690	1.108	-2.084	2.261

Table B2. Full occupancy model results for autumn (Weeks 1-7: 18/11/17-05/01/2018). Detection probability was modelled as survey-specific [p(survey)].

Model	QAIC	ΔQAIC	AIC weight	Model likelihood	*K*	-2*LogLike	Covariates	Estimate	SE	Inflated SE	Lower limit	Upper limit
psi(FEDBEFORE + WOOD500m),p(survey + NESTSITES)	283.85	0.00	0.8966	1.0000	11	296.13	psi(FEDBEFORE)	2.771	0.792	0.843	1.119	4.423
							psi(WOOD500m)	1.308	0.432	0.459	0.407	2.208
							p(NESTSITES)	0.456	0.161	0.171	0.122	0.791
psi(FEDBEFORE + WOOD500m),p(survey)	289.43	5.58	0.0551	0.0614	10	304.70	psi(FEDBEFORE)	2.730	0.769	0.818	1.127	4.334
							psi(WOOD500m)	1.290	0.421	0.447	0.413	2.167
psi(WOOD500m),p(survey + FEEDHOG)	290.47	6.62	0.0327	0.0365	10	305.87	psi(WOOD500m)	1.088	0.365	0.388	0.328	1.848
							p(FEEDHOG)	0.872	0.236	0.251	0.380	1.364
psi(NEAREST+VE),p(survey)	292.12	8.27	0.0143	0.0160	9	310.00	psi(NEAREST+VE)	-2.288	0.693	0.737	-3.732	-0.843
psi(FEDBEFORE),p(survey)	299.15	15.30	0.0004	0.0005	9	317.95	psi(FEDBEFORE)	2.316	0.646	0.687	0.969	3.664
psi(.),p(survey + FEEDHOG)	299.44	15.59	0.0004	0.0004	9	318.28	p(FEEDHOG)	0.873	0.239	0.254	0.374	1.372
psi(FEEDHOG),p(survey)	301.97	18.12	0.0001	0.0001	9	321.14	psi(FEEDHOG)	1.153	0.347	0.369	0.430	1.876
psi(WOOD500m),p(survey)	302.48	18.63	0.0001	0.0001	9	321.72	psi(WOOD500m)	1.038	0.336	0.358	0.338	1.739
psi(.),p(survey + NEARESTOTHER)	303.15	19.30	0.0001	0.0001	9	322.48	p(NEARESTOTHER)	0.633	0.218	0.232	0.179	1.088
psi(.),p(survey + FEDBEFORE)	303.45	19.60	0.0000	0.0001	9	322.81	p(FEDBEFORE)	1.118	0.345	0.367	0.399	1.836
psi(.),p(survey + GRASS250m)	303.93	20.08	0.0000	0.0000	9	323.36	p(GRASS250m)	1.325	0.447	0.476	0.393	2.257
psi(WOODDIST),p(survey)	305.61	21.76	0.0000	0.0000	9	325.26	psi(WOODDIST)	-0.850	0.322	0.342	-1.521	-0.179
psi(.),p(survey + NESTSITES)	305.89	22.04	0.0000	0.0000	9	325.57	p(NESTSITES)	0.456	0.161	0.172	0.120	0.792
psi(.),p(survey + CONNECTIVITY)	308.45	24.60	0.0000	0.0000	9	328.47	p(CONNECTIVITY)	1.277	0.547	0.582	0.136	2.417
psi(.),p(survey + GRASS500M)	308.51	24.66	0.0000	0.0000	9	328.54	p(GRASS500M)	0.526	0.231	0.246	0.044	1.007
psi(.),p(survey + URBAN500m)	308.69	24.84	0.0000	0.0000	9	328.74	p(URBAN500m)	-0.449	0.200	0.213	-0.866	-0.032
psi(GRASS250m),p(survey)	308.85	25.00	0.0000	0.0000	9	328.92	psi(GRASS250m)	-0.656	0.330	0.351	-1.344	0.033

psi(.),p(survey + NEAREST+VE)	309.12	25.27	0.0000	0.0000	9	329.23	p(NEAREST+VE)	0.987	0.475	0.505	-0.003	1.977
psi(CONNECTIVITY),p(survey)	309.18	25.33	0.0000	0.0000	9	329.30	psi(CONNECTIVITY)	2.023	0.958	1.019	0.025	4.020
psi(.),p(survey + FRONT2BACK)	310.09	26.24	0.0000	0.0000	9	330.32	p(FRONT2BACK)	0.614	0.320	0.340	-0.053	1.281
psi(NEARESTOTHER),p(survey)	310.11	26.26	0.0000	0.0000	9	330.35	psi(NEARESTOTHER)	-0.534	0.299	0.318	-1.156	0.089
psi(.),p(survey + URBAN250m)	310.29	26.44	0.0000	0.0000	9	330.55	p(URBAN250m)	-0.349	0.191	0.203	-0.747	0.049
psi(WOOD250m),p(survey)	310.42	26.57	0.0000	0.0000	9	330.70	psi(WOOD250m)	0.549	0.343	0.365	-0.166	1.263
psi(GARDENAREA),p(survey)	310.62	26.77	0.0000	0.0000	9	330.92	psi(GARDENAREA)	-0.520	0.332	0.353	-1.213	0.172
psi(.),p(survey + GOODHABITAT)	311.02	27.17	0.0000	0.0000	9	331.38	p(GOODHABITAT)	1.311	0.802	0.853	-0.361	2.983
1 group, Survey-specific P.	311.41	27.56	0.0000	0.0000	8	334.08						
psi(.),p(survey + GRASSDIST)	311.62	27.77	0.0000	0.0000	9	332.05	p(GRASSDIST)	-0.239	0.168	0.179	-0.590	0.112
psi(.),p(survey + ARABLE500m)	311.84	27.99	0.0000	0.0000	9	332.30	p(ARABLE500m)	0.216	0.166	0.177	-0.130	0.562
psi(.),p(survey + ARABLEDIST)	312.04	28.19	0.0000	0.0000	9	332.53	p(ARABLEDIST)	0.211	0.171	0.182	-0.146	0.567
psi(GRASS500m),p(survey)	312.40	28.55	0.0000	0.0000	9	332.94	psi(GRASS500m)	-0.275	0.264	0.280	-0.825	0.274
psi(.),p(survey + WOODDIST)	312.41	28.56	0.0000	0.0000	9	332.95	p(WOODDIST)	-0.241	0.234	0.248	-0.728	0.246
psi(.),p(survey + HOUSETYPE)	312.69	28.84	0.0000	0.0000	9	333.27	p(HOUSETYPE)	0.370	0.411	0.437	-0.487	1.226
psi(.),p(survey + GARDENAREA)	312.72	28.87	0.0000	0.0000	9	333.30	p(GARDENAREA)	-0.196	0.233	0.248	-0.681	0.290
psi(.),p(survey + FEEDOTHERS)	312.76	28.91	0.0000	0.0000	9	333.34	p(FEEDOTHERS)	0.327	0.381	0.406	-0.468	1.122
psi(NESTSITES),p(survey)	312.93	29.08	0.0000	0.0000	9	333.54	psi(NESTSITES)	0.188	0.258	0.275	-0.350	0.726
psi(FEEDOTHERS),p(survey)	313.03	29.18	0.0000	0.0000	9	333.65	psi(FEEDOTHERS)	0.386	0.594	0.632	-0.853	1.625
psi(ARABLEDIST),p(survey)	313.10	29.25	0.0000	0.0000	9	333.73	psi(ARABLEDIST)	-0.150	0.256	0.272	-0.684	0.384
psi(URBAN250m),p(survey)	313.12	29.27	0.0000	0.0000	9	333.75	psi(URBAN250m)	0.145	0.256	0.272	-0.388	0.678
psi(.),p(survey + WOOD250m)	313.14	29.29	0.0000	0.0000	9	333.77	p(WOOD250m)	0.074	0.134	0.143	-0.206	0.354
psi(GRASSDIST),p(survey)	313.23	29.38	0.0000	0.0000	9	333.87	psi(GRASSDIST)	0.116	0.257	0.273	-0.420	0.651
psi(.),p(survey + WOOD500m)	313.23	29.38	0.0000	0.0000	9	333.88	p(WOOD500m)	0.071	0.158	0.168	-0.259	0.401
psi(HOUSETYPE),p(survey)	313.32	29.47	0.0000	0.0000	9	333.98	psi(HOUSETYPE)	0.197	0.643	0.684	-1.143	1.537
psi(GOODHABITAT),p(survey)	313.37	29.52	0.0000	0.0000	9	334.03	psi(GOODHABITAT)	-0.301	1.444	1.535	-3.310	2.708

psi(FRONT2BACK),p(survey)	313.40	29.55	0.0000	0.0000	9	334.07	psi(FRONT2BACK)	-0.048	0.507	0.539	-1.105	1.008
psi(.),p(survey + RAINFALL)	313.41	29.56	0.0000	0.0000	9	334.08	p(RAINFALL)	-0.627	22.009	23.405	-46.501	45.247
psi(.),p(survey + AIRTEMP)	313.41	29.56	0.0000	0.0000	9	334.08	p(AIRTEMP)	0.143	4.183	4.449	-8.577	8.863
psi(.),p(survey + DAYTIME)	313.41	29.56	0.0000	0.0000	9	334.08	p(DAYTIME)	0.578	69.709	74.132	-144.720	145.876
psi(.),p(survey + GRASSTEMP)	313.41	29.56	0.0000	0.0000	9	334.08	p(GRASSTEMP)	-0.111	30.739	32.689	-64.182	63.960
psi(URBAN500m),p(survey)	313.41	29.56	0.0000	0.0000	9	334.08	psi(URBAN500m)	-0.010	0.255	0.272	-0.542	0.523
psi(ARABLE500m),p(survey)	343.05	59.20	0.0000	0.0000	3	381.17	psi(ARABLE500m)	0.075	0.259	0.275	-0.464	0.614

Table B3. Full occupancy model results for winter (Weeks 8-16: 06/01/2018-09/03/2018). Detection probability was modelled as constant.

Model	QAIC	ΔQAIC	AIC weight	Model likelihood	*K*	-2*LogLike	Covariates	Estimate	SE	Inflated SE	Lower limit	Upper limit
psi(FEDBEFORE),p(FEEDHOG + FEEDOTHERS)	214.42	0.00	0.4561	1.0000	5	235.72	psi(FEDBEFORE)	3.674	1.099	1.180	1.362	5.986
							p(FEEDHOG)	1.168	0.359	0.385	0.413	1.924
							p(FEEDOTHERS)	1.913	0.794	0.853	0.241	3.586
psi(FEDBEFORE),p(FEEDHOG + GRASSTEMP)	215.41	0.99	0.2780	0.6096	5	236.86	psi(FEDBEFORE)	3.196	0.901	0.968	1.299	5.093
							p(FEEDHOG)	1.277	0.368	0.395	0.503	2.052
							p(GRASSTEMP)	0.440	0.201	0.216	0.018	0.863
psi(FEDBEFORE),p(FEEDHOG + AIRTEMP)	215.51	1.09	0.2645	0.5798	5	236.97	psi(FEDBEFORE)	3.196	0.901	0.968	1.299	5.093
							p(FEEDHOG)	1.277	0.368	0.395	0.502	2.051
							p(AIRTEMP)	0.444	0.207	0.222	0.009	0.878
psi(FEDBEFORE),p(.)	226.65	12.23	0.0010	0.0022	3	254.43	psi(FEDBEFORE)	3.157	0.772	0.829	1.533	4.781
psi(.),p(FEEDHOG)	229.40	14.98	0.0003	0.0006	3	257.60	p(FEEDHOG)	1.714	0.372	0.400	0.931	2.497
psi(FEEDHOG),p(.)	232.95	18.53	0.0000	0.0001	3	261.70	psi(FEEDHOG)	1.609	0.477	0.512	0.605	2.614
psi(.),p(FEDBEFORE)	233.80	19.38	0.0000	0.0001	3	262.68	p(FEDBEFORE)	2.540	0.513	0.551	1.460	3.620
psi(.),p(GARDENSIZE)	234.66	20.24	0.0000	0.0000	3	263.67	p(GARDENSIZE)	-1.829	0.565	0.606	-3.017	-0.640
psi(.),p(FEEDOTHERS)	239.51	25.09	0.0000	0.0000	3	269.26	p(FEEDOTHERS)	2.326	0.826	0.887	0.587	4.065
psi(NEAREST+VE),p(.)	240.59	26.17	0.0000	0.0000	3	270.51	psi(NEAREST+VE)	-1.113	0.522	0.560	-2.211	-0.016
psi(GARDENSIZE),p(.)	241.65	27.23	0.0000	0.0000	3	271.73	psi(GARDENSIZE)	-1.245	0.653	0.701	-2.618	0.129
psi(.),p(NEAREST+VE)	242.03	27.61	0.0000	0.0000	3	272.17	p(NEAREST+VE)	-0.997	0.396	0.425	-1.830	-0.163
psi(.),p(GRASSTEMP)	242.56	28.14	0.0000	0.0000	3	272.78	p(GRASSTEMP)	0.430	0.198	0.213	0.013	0.848
psi(.),p(AIRTEMP)	242.66	28.24	0.0000	0.0000	3	272.89	p(AIRTEMP)	0.434	0.204	0.219	0.004	0.863
psi(FEEDOTHERS),p(.)	244.44	30.02	0.0000	0.0000	3	274.95	psi(FEEDOTHERS)	1.299	0.829	0.890	-0.446	3.043

psi(.),p(CONNECTIVITY)	244.88	30.46	0.0000	0.0000	3	275.45	p(CONNECTIVITY)	1.118	0.747	0.802	-0.455	2.690
psi(.),p(GOODHABITAT)	244.97	30.55	0.0000	0.0000	3	275.56	p(GOODHABITAT)	-1.635	1.043	1.120	-3.830	0.560
1 group, Constant P	245.01	30.59	0.0000	0.0000	2	277.91						
psi(.),p(ARABLE500m)	245.27	30.85	0.0000	0.0000	3	275.90	p(ARABLE500m)	0.198	0.137	0.147	-0.091	0.486
psi(.),p(FRONT2BACK)	245.45	31.03	0.0000	0.0000	3	276.11	p(FRONT2BACK)	-0.531	0.403	0.433	-1.379	0.318
psi(GRASS250m),p(.)	245.52	31.10	0.0000	0.0000	3	276.19	psi(GRASS250m)	-0.445	0.381	0.409	-1.246	0.356
psi(WOOD500m),p(.)	245.57	31.15	0.0000	0.0000	3	276.25	psi(WOOD500m)	0.367	0.290	0.311	-0.242	0.977
psi(HOUSETYPE),p(.)	245.80	31.38	0.0000	0.0000	3	276.51	psi(HOUSETYPE)	0.937	0.843	0.905	-0.837	2.712
psi(.),p(WOODDIST)	245.94	31.52	0.0000	0.0000	3	276.67	p(WOODDIST)	-0.335	0.313	0.336	-0.993	0.322
psi(WOODDIST),p(.)	245.94	31.52	0.0000	0.0000	3	276.67	psi(WOODDIST)	-0.287	0.251	0.269	-0.814	0.241
psi(ARABLE500m),p(.)	246.03	31.61	0.0000	0.0000	3	276.78	psi(ARABLE500m)	0.289	0.275	0.295	-0.289	0.867
psi(NESTSITES),p(.)	246.09	31.67	0.0000	0.0000	3	276.85	psi(NESTSITES)	0.293	0.288	0.310	-0.314	0.900
psi(CONNECTIVITY),p(.)	246.14	31.72	0.0000	0.0000	3	276.91	psi(CONNECTIVITY)	1.025	1.044	1.121	-1.172	3.222
psi(.),p(HOUSETYPE)	246.16	31.74	0.0000	0.0000	3	276.93	p(HOUSETYPE)	-0.588	0.564	0.605	-1.775	0.598
psi(NEARESTOTHER),p(.)	246.23	31.81	0.0000	0.0000	3	277.01	psi(NEARESTOTHER)	0.260	0.277	0.298	-0.323	0.844
psi(URBAN250m),p(.)	246.30	31.88	0.0000	0.0000	3	277.09	psi(URBAN250m)	0.273	0.314	0.337	-0.387	0.934
psi(GRASS500m),p(.)	246.47	32.05	0.0000	0.0000	3	277.29	psi(GRASS500m)	-0.239	0.317	0.341	-0.907	0.429
psi(.),p(URBAN250m)	246.55	32.13	0.0000	0.0000	3	277.38	p(URBAN250m)	0.181	0.255	0.274	-0.355	0.717
psi(.),p(DAYTIME)	246.66	32.24	0.0000	0.0000	3	277.50	p(DAYTIME)	0.114	0.178	0.191	-0.261	0.488
psi(ARABLEDIST),p(.)	246.68	32.26	0.0000	0.0000	3	277.53	psi(ARABLEDIST)	-0.179	0.294	0.316	-0.798	0.441
psi(FRONT2BACK),p(.)	246.72	32.30	0.0000	0.0000	3	277.57	psi(FRONT2BACK)	-0.328	0.571	0.613	-1.529	0.873
psi(.),p(NEARESTOTHER)	246.73	32.31	0.0000	0.0000	3	277.59	p(NEARESTOTHER)	-0.086	0.154	0.166	-0.411	0.239
psi(.),p(RAINFALL)	246.75	32.33	0.0000	0.0000	3	277.61	p(RAINFALL)	0.096	0.176	0.188	-0.274	0.465
psi(.),p(WOOD500m)	246.78	32.36	0.0000	0.0000	3	277.64	p(WOOD500m)	-0.097	0.188	0.201	-0.491	0.298
psi(GOODHABITAT),p(.)	246.83	32.41	0.0000	0.0000	3	277.70	psi(GOODHABITAT)	0.744	1.680	1.804	-2.791	4.280
psi(GRASSDIST),p(.)	246.84	32.42	0.0000	0.0000	3	277.71	psi(GRASSDIST)	0.127	0.283	0.304	-0.470	0.723

psi(.),p(GRASSDIST)	246.88	32.46	0.0000	0.0000	3	277.76	p(GRASSDIST)	0.068	0.177	0.190	-0.306	0.441
psi(.),p(URBAN500m)	246.90	32.48	0.0000	0.0000	3	277.78	p(URBAN500m)	-0.078	0.214	0.230	-0.528	0.372
psi(.),p(GRASS500m)	246.91	32.49	0.0000	0.0000	3	277.79	p(GRASS500m)	-0.107	0.317	0.341	-0.775	0.561
psi(.),p(WOOD250m)	246.92	32.50	0.0000	0.0000	3	277.81	p(WOOD250m)	-0.080	0.254	0.273	-0.615	0.454
psi(.),p(ARABLEDIST)	246.96	32.54	0.0000	0.0000	3	277.85	p(ARABLEDIST)	-0.043	0.187	0.201	-0.437	0.350
psi(WOOD250m),p(.)	246.99	32.57	0.0000	0.0000	3	277.89	psi(WOOD250m)	-0.042	0.292	0.313	-0.656	0.572
psi(URBAN500m),p(.)	247.00	32.58	0.0000	0.0000	3	277.90	psi(URBAN500m)	0.016	0.287	0.309	-0.589	0.621
psi(.),p(NESTSITES)	247.00	32.58	0.0000	0.0000	3	277.90	p(NESTSITES)	-0.015	0.182	0.195	-0.397	0.367
psi(.),p(GRASS250m)	247.01	32.59	0.0000	0.0000	3	277.91	p(GRASS250m)	0.020	0.598	0.642	-1.239	1.278

Table B4. Full occupancy model results for spring (Weeks 17-20: 10/03/2018-06/04/2018). Detection probability was modelled as constant.

Model	QAIC	ΔQAIC	AIC weight	Model likelihood	*K*	-2*LogLike	Covariates	Estimate	SE	Inflated SE	Lower limit	Upper limit
psi(FEEDHOG),p(DAYTIME + FEEDOTHER)	71.83	0.00	0.2413	1.0000	5	173.97	psi(FEEDHOG)	1.555	0.422	0.708	0.168	2.943
							p(DAYTIME)	0.758	0.278	0.467	-0.158	1.674
							p(FEEDOTHER)	1.356	0.550	0.923	-0.453	3.166
psi(FEDBEFORE),p(.)	71.97	0.14	0.2250	0.9324	3	185.63	psi(FEDBEFORE)	2.657	0.644	1.081	0.538	4.776
psi(FEEDHOG),p(.)	72.82	0.99	0.1471	0.6096	3	188.02	psi(FEEDHOG)	1.546	0.418	0.701	0.172	2.921
psi(NEAREST+VE),p(.)	76.13	4.30	0.0281	0.1165	3	197.32	psi(NEAREST+VE)	-1.183	0.503	0.844	-2.837	0.470
psi(.),p(FRONT2BACK)	76.35	4.52	0.0252	0.1044	3	197.94	p(FRONT2BACK)	-1.365	0.481	0.806	-2.945	0.216
psi(.),p(NEAREST+VE)	76.41	4.58	0.0244	0.1013	3	198.13	p(NEAREST+VE)	-1.410	0.468	0.786	-2.949	0.130
psi(.),p(DAYTIME)	76.67	4.84	0.0215	0.0889	3	198.85	p(DAYTIME)	0.710	0.267	0.449	-0.169	1.590
psi(.),p(FEEDOTHER)	77.28	5.45	0.0158	0.0655	3	200.58	p(FEEDOTHER)	1.277	0.532	0.892	-0.471	3.026
1 group, Constant P	77.41	5.58	0.0148	0.0614	2	206.57						
psi(WOOD500m),p(.)	77.53	5.70	0.0140	0.0578	3	201.27	psi(WOOD500m)	0.626	0.285	0.478	-0.311	1.563
psi(.),p(AIRTEMP)	78.29	6.46	0.0095	0.0396	3	203.42	p(AIRTEMP)	0.252	0.143	0.239	-0.217	0.721
psi(.),p(GRASSTEMP)	78.46	6.63	0.0088	0.0363	3	203.90	p(GRASSTEMP)	0.257	0.159	0.267	-0.266	0.779
psi(ARABLEDIST),p(.)	78.47	6.64	0.0087	0.0362	3	203.93	psi(ARABLEDIST)	-0.454	0.293	0.492	-1.418	0.509
psi(.),p(FEEDHOG)	78.52	6.69	0.0085	0.0353	3	204.06	p(FEEDHOG)	1.084	0.427	0.716	-0.319	2.487
psi(WOODDIST),p(.)	78.58	6.75	0.0083	0.0342	3	204.22	psi(WOODDIST)	-0.432	0.296	0.496	-1.405	0.541
psi(GRASS250m),p(.)	78.75	6.92	0.0076	0.0314	3	204.70	psi(GRASS250m)	-0.410	0.329	0.552	-1.492	0.671
psi(ARABLE500m),p(.)	78.80	6.97	0.0074	0.0307	3	204.85	psi(ARABLE500m)	0.344	0.271	0.455	-0.547	1.236
psi(URBAN250m),p(.)	78.85	7.02	0.0072	0.0299	3	204.98	psi(URBAN250m)	0.355	0.295	0.495	-0.614	1.324
psi(.),p(GRASS250m)	79.00	7.17	0.0067	0.0277	3	205.42	p(GRASS250m)	0.526	0.492	0.826	-1.093	2.144
psi(GARDENSIZE),p(.)	79.07	7.24	0.0065	0.0268	3	205.60	psi(GARDENSIZE)	0.001	0.004	0.007	-0.014	0.015

psi(.),(GARDENSIZE)	79.07	7.24	0.0065	0.0268	3	205.61	p(GARDENSIZE)	0.001	0.013	0.021	-0.041	0.043
psi(.),p(GRASS500m)	79.08	7.25	0.0064	0.0266	3	205.62	p(GRASS500m)	0.282	0.292	0.489	-0.677	1.241
psi(CONNECTIVITY),p(.)	79.11	7.28	0.0063	0.0263	3	205.72	psi(CONNECTIVITY)	0.869	0.953	1.599	-2.266	4.004
psi(.),p(GRASSDIST)	79.11	7.28	0.0063	0.0263	3	205.73	p(GRASSDIST)	-0.186	0.204	0.341	-0.855	0.483
psi(.),p(URBAN500m)	79.17	7.34	0.0061	0.0255	3	205.89	p(URBAN500m)	-0.204	0.250	0.419	-1.024	0.617
psi(NESTSSITES),p(.)	79.17	7.34	0.0061	0.0255	3	205.89	psi(NESTSITES)	0.217	0.266	0.446	-0.658	1.092
psi(GRASSDIST),p(.)	79.18	7.35	0.0061	0.0253	3	205.91	psi(GRASSDIST)	0.213	0.265	0.445	-0.659	1.085
psi(.),p(RAINFALL)	79.19	7.36	0.0061	0.0252	3	205.93	p(RAINFALL)	0.198	0.251	0.421	-0.626	1.023
psi(.),p(FEDBEFORE)	79.19	7.36	0.0061	0.0252	3	205.94	p(FEDBEFORE)	0.497	0.673	1.130	-1.717	2.711
psi(URBAN500m),p(.)	79.22	7.39	0.0060	0.0248	3	206.04	psi(URBAN500m)	-0.190	0.263	0.442	-1.056	0.675
psi(.),p(ARABLE500m)	79.23	7.40	0.0060	0.0247	3	206.05	p(ARABLE500m)	0.139	0.198	0.333	-0.513	0.792
psi(.),p(WOOD250m)	79.26	7.43	0.0059	0.0244	3	206.13	p(WOOD250m)	-0.234	0.363	0.609	-1.429	0.960
psi(GOODHABITAT),p(.)	79.26	7.43	0.0059	0.0244	3	206.15	psi(GOODHABITAT)	-0.950	1.468	2.463	-5.777	3.876
psi(.),p(ARABLEDIST)	79.27	7.44	0.0058	0.0242	3	206.17	p(ARABLEDIST)	-0.147	0.236	0.396	-0.923	0.629
psi(.),p(HOUSETYPE)	79.28	7.45	0.0058	0.0241	3	206.20	p(HOUSETYPE)	0.329	0.546	0.916	-1.466	2.124
psi(WOOD250m),p(.)	79.30	7.47	0.0058	0.0239	3	206.26	psi(WOOD250m)	-0.152	0.281	0.471	-1.076	0.772
psi(.),p(CONNECTIVITY)	79.33	7.50	0.0057	0.0235	3	206.33	p(CONNECTIVITY)	0.406	0.835	1.400	-2.338	3.150
psi(.),p(WOOD500m)	79.36	7.53	0.0056	0.0232	3	206.41	p(WOOD500m)	-0.086	0.219	0.368	-0.806	0.635
psi(.),p(URBAN250m)	79.37	7.54	0.0056	0.0231	3	206.45	p(URBAN250m)	0.106	0.324	0.543	-0.958	1.171
psi(FRONT2BACK),p(.)	79.38	7.55	0.0055	0.0229	3	206.48	psi(FRONT2BACK)	0.156	0.525	0.880	-1.569	1.881
psi(HOUSETYPE),p(.)	79.38	7.55	0.0055	0.0229	3	206.48	psi(HOUSETYPE)	-0.187	0.660	1.108	-2.358	1.985
psi(.),p(WOODDIST)	79.38	7.55	0.0055	0.0229	3	206.49	p(WOODDIST)	0.101	0.342	0.573	-1.023	1.225
psi(.),p(GOODHABITAT)	79.39	7.56	0.0055	0.0228	3	206.51	p(GOODHABITAT)	0.229	0.973	1.633	-2.971	3.429
psi(.),p(NEARESTOTHER)	79.39	7.56	0.0055	0.0228	3	206.50	p(NEARESTOTHER)	0.048	0.189	0.318	-0.575	0.670
psi(GRASS500m),p(.)	79.40	7.57	0.0055	0.0227	3	206.54	psi(GRASS500m)	-0.039	0.267	0.448	-0.916	0.839
psi(.),p(NESTSITES)	79.40	7.57	0.0055	0.0227	3	206.54	p(NESTSITES)	-0.042	0.229	0.384	-0.795	0.710

psi(FEEDOTHER),p(.)	79.40	7.57	0.0055	0.0227	3	206.53	psi(FEEDOTHER)	-0.106	0.612	1.026	-2.118	1.905
psi(NEARESTOTHER),p(.)	79.41	7.58	0.0055	0.0226	3	206.56	psi(NEARESTOTHER)	-0.018	0.264	0.443	-0.887	0.851

Appendix C

What makes a house a home? Nest box use by West European hedgehogs (E*rinaceous europaeus*) is influenced by nest box placement, resource provisioning and site-based factors (Chapter 4)

Raw data can be found at **doi.org/10.7717/peerj.13662**

Questionnaire survey – text copy

This is the first ever national census of hedgehog houses, brought to you by Hedgehog Street: a national campaign from People's Trust for Endangered Species and the British Hedgehog Preservation Society. This survey is in partnership with the University of Reading and Warwickshire Wildlife Trust.

There is a lot of advice about how best to use hedgehog houses, but we need to do some research to be sure that this advice is well-founded and appropriate. The aim of this survey is to collect evidence that will help to guide people on how best to use hedgehog houses to help hedgehogs, based on the experiences of the thousands of you that already have them. However, please do not infer any guidance or advice on using hedgehog houses from the wording of the questions in the survey; we are just asking about your past experiences, not suggesting any particular course of action. So please do not disturb any hedgehogs or nests in order to complete this survey. We will share the results with you and give guidance once the data have been collected and analysed.

If you would like to provide information about more than one hedgehog house in your garden, and if you have the time fill, please in the survey for each house separately. If this is too much not to worry, please just select those that you know have been definitely used by hedgehogs. But, just make sure that in the final question "Any other comments" please write "2nd house" or "4th house", etc.

Thank you very much!

PART 1:

Q1. First name [short text answer]

Q2. Surname [short text answer]

Q3a. Address [short text answer] (was not mandatory)

Q3b. Postcode [short text answer]

Q4. Email [short text answer]

Q5. Are you registered as a Hedgehog Champion on Hedgehog Street? [Yes/No]

All of the questions in this survey relate to hedgehog houses designed for animals to nest in, not feeding stations designed to shelter hedgehogs whilst they eat supplementary food. We are interested only in the former, which should not provide food.

PART 2:

Q6. Is your hedgehog house commercially available or is it homemade?

[If person responds commercially available, they are directed to **Question 7**]

[If person responds homemade, they are directed to **Question 8**]

Commercially available hedgehog houses

Q7. If your house is commercially available, which design is it? (images were provided)

(a) Chapelwood [Tick response]

(b) Coopers of Stortford [Tick response]

(c) Eco-plate Royal [Tick response]

(d) Gardman Norfolk [Tick response]

(e) Hogilo [Tick response]

(f) Hogitat [Tick response]

(g) Home with inbuilt cameras [Tick response]

(h) Igloo domed [Tick response]

(i) Orkney [Tick response]

(j) RSPB [Tick response]

(k) Schwegler [Tick response]

(l) Tom Chambers [Tick response]

(m) UK garden supplies [Tick response]

(n) Waitrose wicker [Tick response]

(o) Wooden domed [Tick response]

(p) Wudwerx [Tick response]

(q) Other (if other, please specify and add a link to the supplier)

DIY hedgehog houses

Q8. What is the main material the box is made from? Please tick one option.

(a) Timber [Tick response]

(b) Plywood/plyboard [Tick response]

(c) Plastic [Tick response]

(d) Concrete [Tick response]

(e) Brick [Tick response]

(f) Other [Tick response]

Q9. Please provide the approximate dimensions of the box, in centimetres.

(a) Width (side to side) [Number]

(b) Height (top to bottom) [Number]

(c) Depth (front to back) [Number]

Q10. Does your box have any of the following features?

(a) A base or floor [Tick response]

(b) An external tunnel entrance [Tick response]

(c) An internal tunnel or partition [Tick response]

(d) An air vent [Tick response]

(e) A waterproof lining [Tick response]

[Now all to be directed to **Question 11**]

PART 3:

Q11. Is your hedgehog house in the front or back garden?

(a) Front garden [Tick response]

(b) Back garden [Tick response]

Q12. Approximately when did you install your hedgehog house? [Month and Year]

Q13. Did you put your hedgehog house in your garden:

(a) BEFORE you knew whether hedgehogs might be visiting? [Tick response]

(b) AFTER you knew that hedgehogs were visiting? [Tick response]

Questions 14-17 relate to whether hedgehogs have used your hedgehog house for resting, breeding and/or hibernating. For each question, we would also like to know what evidence you may have for substantiating your answers. However, please be aware that this is a survey of historic actions only. ***We request that you avoid checking or disturbing hedgehogs currently residing in your hedgehog house(s) as this may affect their behaviour and lead to abandonment of the nest box, abandonment of hoglets or unnecessary disturbance during hibernation.***

Q14a. Since it was installed, how many years do you think that the hedgehog house has been used for **RESTING DURING THE DAYTIME** between the months of **March and October** (please answer "don't know" if applicable): [short text answer]

Q14b. What evidence do you have for this (please tick all that apply)?

(a) I saw a hedgehog using the entrance [Tick response]

(b) I saw one inside [Tick response]

(c) I recorded activity on a wildlife camera [Tick response]

(d) I placed an object in front of the entrance and it was displaced [Tick response]

(e) I have other evidence: please describe [short text answer]

(f) Not applicable [Tick response]

Q15a. Since it was installed, how many years do you think that the hedgehog house has been used for **RESTING DURING THE DAYTIME** between the months of **November and February** (please answer "don't know" if applicable): [short text answer]

Q15b. What evidence do you have for this (please tick all that apply)?

(a) I saw a hedgehog using the entrance [Tick response]

(b) I saw one inside [Tick response]

(c) I recorded activity on a wildlife camera [Tick response]

(d) I placed an object in front of the entrance and it was displaced [Tick response]

(e) I have other evidence: please describe [short text answer]

(f) Not applicable [Tick response]

Q16a. Since it was installed, how many years do you think that the hedgehog house has been used for **BREEDING** (please answer "don't know" if applicable): [short text answer]

Q16b. What evidence do you have for this (please tick all that apply)?

(a) I saw a mother and babies using the entrance [Tick response]

(b) I saw a mother and babies inside [Tick response]

(c) I recorded a mother and babies on a wildlife camera [Tick response]

(d) I have other evidence: please describe [short text answer]

(e) Not applicable [Tick response]

Q17a. Since it was installed, how many years do you think that the hedgehog house has been used for **HIBERNATING** (please answer "don't know" if applicable): [short text answer]

Q17b. What evidence do you have for this (please tick all that apply)?

(a) I saw a hibernating hedgehog inside [Tick response]

(b) I have other evidence: please describe [short text answer]

(c) Not applicable [Tick response]

Q18. In the past, have you ever provided any of the following inside your hedgehog house (please select all that apply)?

(a) Food [Tick response]

(b) Water [Tick response]

(c) Artificial bedding (e.g., newspaper) [Tick response]

(d) Natural bedding (e.g., leaves, hay) [Tick response]

(e) Other [Tick response]

The following questions relate to bedding material you may have found in your hedgehogs box in two time periods: March-October and November-February. In each case, we would like you to list the range of natural (e.g., leaves, grass) and man-made materials (e.g., newspaper, rubbish) that the animals may have used to construct their nests. When describing the *materials you have found, please be as accurate as possible. For example, it would help if you were able to identify the species of leaves used if possible.*

Q19a. Have you ever found bedding material in your hedgehog box that the animals would have used between the months of **March and October?**

(a) No [Tick response]

(b) Yes – please list the range of materials that the hedgehogs used to construct the nest [short text answer]

Q19b. Have you ever found bedding material in your hedgehog box that the animals would have used between the months of **November and February?**

(a) No [Tick response]

(c) Yes – please list the range of materials that the hedgehogs used to construct the nest [short text answer]

Q20. Where is your hedgehog house positioned? Please select all that apply:

(a) On a natural substrate [Tick response]

(b) On hardstanding [Tick response]

(c) In a sheltered spot (e.g., under vegetation) [Tick response]

(d) In the open [Tick response]

(e) Near my house (<5m away) [Tick response]

(f) Away from my property (>5m away) [Tick response]

(g) It is raised off the floor (e.g., it has its own legs) [Tick response]

Q21. Does the entrance of the hedgehog house:

(a) Face a wall or fence [Tick response]

(b) Lie parallel to a wall or fence [Tick response]

(c) Face into a bush [Tick response]

(d) Face into the open [Tick response]

(e) Other (please specify): [short text answer]

Q22. Does the entrance of the hedgehog house face:

(a) North [Tick response]

(b) South [Tick response]

(c) East [Tick response]

(d) West [Tick response]

Q23. Since your hedgehog house has been installed, are you aware of hedgehogs (a) resting during the daytime, (b) breeding or (c) hibernating in **ANY OTHER LOCATION** in your garden (please put at least one answer in each column)?

	(a) Resting during daytime	(b) Breeding	(c) Hibernating	(d) Not applicable
Yes – under the shed				
Yes – in compost heap				
Yes – in woodpile				
Yes – in bushes				
Yes – under decking				
Yes – inside building				
Yes - other				
No				

Q24. Do you think that your hedgehog house is the only reasonable site in your garden where hedgehogs could rest/breed/hibernate? [Yes/No]

Q25a. How many front gardens does your front garden border? [Number]

Q25b. Of these, how many do you think hedgehogs could access from your front garden? [Number]

Q26. Can hedgehogs access your back garden from your front garden? [Yes/No]

Q27a. How many back gardens does your back garden border? [Number]

Q27b. Of these, how many do you think hedgehogs could access from your back garden? [Number]

Q28. How often do you think these mammal species visit your garden (please tick one option for each of the four species indicated)?

	Daily	Weekly	Monthly	Every 3 months	Every 6 months	Less regularly	Never

Badger							
Fox							
Hedgehog							
Rat							

Q29. Please indicate the approximate percentage area of your BACK GARDEN covered by each of the following features (adding up to 100%). If your back garden does not have any of the features listed, please enter a zero in the appropriate cell.

Feature	% coverage
Lawn	
Paving/gravel	
Flowerbed(s)	
Shrubs	
Decking	
Shed with cavity beneath	
Compost heap	
Woodpile	
Wild area	
Vegetable patch	
Pond	
Other (please describe)	

Q30. Do you ever put out any of the following foods? Please tick all that apply.

(a) Food for hedgehogs in a covered feeding station [Yes/No]

(b) Food for hedgehogs not in a covered feeding station [Yes/No]

(c) Food for other mammals such as foxes or badgers [Yes/No]

(d) Food for birds on the ground [Yes/No]

Q31. If you do put out food for hedgehogs, how far away (metres) **from the hedgehog house** is the site where you put out the food? [Number]

Q32. How many pet dogs do you own which have access to your garden? [Number]

Q33. Space for additional comments.

Appendix D

An assessment of a conservation strategy to increase garden connectivity for hedgehogs that requires cooperation between immediate neighbours: a barrier too far? (Chapter 5)

2020 questionnaire survey – text copy (NB. This questionnaire builds on the 2018 and 2019 surveys. The original 2018 and 2019 surveys, and raw data from all surveys, can be accessed at **doi.org/10.1371/journal.pone.0259537**)

Hedgehog Champions Survey

Thank you for your interest in our survey. We'd like to see how effective the Hedgehog Street campaign has been at making positive impacts for hedgehogs in gardens and local communities. The data you will provide is vital to assess the impact of this important project.

You'll be asked a few details about the garden of your **current** home and how you use it. Then we'd like to know whether you or your neighbours have been able to make any Hedgehog Highways. Finally, we have some questions about you and where you live. The survey will take around 10 minutes.

Even if you don't have hedgehogs or any links into your garden, it would still be fantastic to hear from you so that we can get as full a picture as possible of hedgehogs in the UK.

Please only complete this survey if you live in a property with access to a garden. This survey is for residents of the UK who are at least 18 years old. All information supplied will be treated in the strictest confidence. The data collected will be analysed by a postgraduate student at the University of Reading as part of her PhD studies, and to further develop the Hedgehog Street campaign.

1. Consent: By continuing with this survey, I confirm that I have read the information above and am aware that it will not be possible to identify me personally from any of the information I supply; I am 18 years or older; live in mainland England, Scotland or Wales; live in a property with access to a garden; and that the data will be used by a student at Reading University for her PhD, and may also be submitted subsequently for publication in a scientific journal.

Part 1 – questions about your back garden

We would like to know a bit about your back garden. It will tell us what factors, other than Hedgehog Highways, might affect hedgehog presence in your garden.

2. You have been contacted for this survey because you enrolled as a Hedgehog Champion through the Hedgehog Street campaign, which launched in 2011. When did you sign up to become a Hedgehog Champion?

- In the last month
- In the last year
- In the last 2-3 years
- In the last 4-5 years
- More than 5 years ago
- I don't remember
- I am not a Hedgehog Champion

3. Please indicate how important the following are to you, in terms of activities you carry out in your back garden:

Please select one option from each row.

	Very important	Important	Somewhat important	Not important
Watching birds				
Watching other wildlife				
Socialising				
Gardening				
Growing food				
Relaxing				
Exercising				
Use by children				
Use by pets				
Hanging washing out				
Storage				

4. Please indicate whether you currently own or have previously owned any of the following pets

Please select one option from each row.

	Currently own	Have previously owned	Never owned
Dog(s)			
Cat(s) with access to the outdoors			
Other indoor pet(s)			
Caged pet(s) outdoors (e.g., rabbit, chickens)			
Temporary animal(s) outdoors (e.g., wild hedgehogs that are being overwintered or rehabilitated in association with a hedgehog rescue)			

5. On average, how often have you seen – or have seen/heard signs of – the following animals in your garden over the past year?

Please select one option from each row.

	Daily	A few times a week	A few times a month	Less	Never
Badgers					
Foxes					
Hedgehogs					
Rodents (e.g., rats and mice)					

6. Please indicate whether you think each of the following species has increased or decreased in abundance over the course of the last 5 years in your neighbourhood.

If you believe the species in question has always been absent, please select "stayed the same".

If you have not lived in your house for five years or more, please answer "not lived here long enough".

	Decreased	Stayed the same	Increased	Not lived here long enough	Unsure
Badgers					
Foxes					
Hedgehogs					
Rodents					

7. Do you currently have any of the following wildlife-friendly features in your garden?

Please select one option from each row.

	Yes	No	No – but would consider having
Flowering lawn			
Wildflowers			
Wild patch			
Hedgerow			
Log pile			
Pond			
Bird box			
Bat box			
Hedgehog house			
Insect hotel			
Compost heap			
Drinking water for animals			

8. How often do you leave food out for the following animals in your garden?

Please select one option from each row.

	Daily	A few times a week	A few times a month	Less	Never
Badgers					
Foxes					
Birds (from a feeder)					
Birds (on the ground)					
Hedgehogs					

9. What type of boundaries surround your back garden? (Please tick all that apply)

- Wooden fence
- Concrete or brick wall
- Wire fence
- Hedge
- Other (please specify)

10. Of those, which is the most common type of boundary around your back garden? (Please tick one) NB. Your answer should match one of those selected above.

- Wooden fence
- Concrete or brick wall
- Wire fence
- Hedge
- Other (please specify)

Q11 for those who most commonly have wooden fences:

11. We would like to know what sort of fence you have based upon its structure at ground level.

Please tick all that apply.

- Slats that go right to the ground
- Slats that sit on a wooden gravel board
- Slats that sit on a concrete gravel board
- Other (please specify)

Part 2 – questions about hedgehog highways

We would like to know how easy it is for hedgehogs to move into and out of your garden. We are particularly interested in whether they can enter or leave your garden through (a) **naturally occurring holes** and (b) **Hedgehog Highways**.

Naturally occurring holes refers to "holes through or under you garden boundaries which were not made by humans". These could have arisen in a number of different ways including, for example, as a consequence of an animal digging under your fence or pushing through a hedge, or general wear and tear of your fencing.

Hedgehog Highways are defined as "any hole through or under you garden boundaries which was DELIBERATELY created for the purposes of helping hedgehogs get into or out of your garden". These hedgehog highways may have been created by you personally, or your neighbour.

12. Could a hedgehog access your back garden from the front garden?

- Yes, ONLY through a naturally occurring hole (e.g., under a gate)
- Yes, ONLY through a Hedgehog Highway
- Yes, through both naturally occurring holes *and* Hedgehog Highways
- Yes, my back garden is openly connected to the front (e.g., there is no gate)
- No
- N/A (e.g., I do not have a front garden)

13. How many gardens border your own back garden? *This includes gardens on either side of your garden and/or at the back of your garden. Please remember this number, as it is important for the next question.*

14. Of those, how many neighbouring gardens could a hedgehog hypothetically access from your own? *Please enter your answers as numbers. If the answer is "none", please enter "0" in each box. NB. The total number reported below should not exceed your answer to the question above.*

	Number (type in)
Through ONLY a naturally occurring hole(s):	
Through ONLY a Hedgehog Highway(s):	
Through BOTH a naturally occurring hole(s) and Hedgehog Highway(s):	

15. To the best of your knowledge, how many Hedgehog Highways have been made by someone else (e.g., neighbour) that directly lead into your own back garden?

This excludes Hedgehog Highways made by yourself. Please enter your answer as a number. If the answer is "none", enter "0".

	Number (type in)
# Hedgehog Highways made by neighbour(s):	
# Hedgehog Highways made by previous resident(s):	
# Hedgehog Highways made by developer/builder(s):	

16. Have you or anyone currently living at your address personally made any Hedgehog Highways in your back garden?

- Yes
- No

TWO PATHWAYS DEPENDING ON ANSWER TO Q16

Pathway 1 – respondents who have made highways

17. How many Hedgehog Highways have you or anyone living at your address made in your back garden?

Please enter your answer as a whole number. If the answer is "none", enter "0".

18. In what year did you make your first Hedgehog Highway at your current address?

19. Did you make your first Hedgehog Highway *before* or *after* becoming a Hedgehog Champion?

- Before signing up to become a Hedgehog Champion
- After I signed up to become a Hedgehog Champion
- I am not a Hedgehog Champion

20. What motivated you to create a Hedgehog Highway? Please tick all that apply.

- I saw a hedgehog in my garden
- I had noticed a lack of hedgehogs in my garden
- The decline of hedgehog numbers in the UK
- The decline of wildlife in general in the UK

- Hearing about the Hedgehog Street campaign
- Hearing about hedgehogs on TV/in other media
- A neighbour or friend recommended constructing a Hedgehog Highway
- It was a good activity to carry out with children
- A desire to make my garden more wildlife-friendly
- Other – please specify

21. Did you create your Hedgehog Highway(s) with or without knowing that hedgehogs were visiting the *local area*?

- I created my Hedgehog Highway(s) knowing that hedgehogs were already visiting the **local area**
- I created my Hedgehog Highway(s) ***without*** knowing whether hedgehogs were visiting the **local area**

22. And in particular, did you create your Hedgehog Highway(s) with or without knowing that hedgehogs were visiting *your garden*?

- I created my Hedgehog Highway(s) knowing that hedgehogs were already visiting **my garden**
- I created my Hedgehog Highway(s) ***without*** knowing whether hedgehogs were visiting **my garden**

23. Have you observed a hedgehog(s) using your Hedgehog Highways(s)?

- Yes, I (and/or people living at my address/neighbours) have directly observed a hedgehog walking through my Hedgehog Highway(s)
- Yes, I saw a hedgehog using the Hedgehog Highway on a trail camera
- Yes - I have not seen hedgehogs using the highway directly, but I have seen other evidence that they have (e.g., footprints)
- No

24. Since making your Hedgehog Highway(s), in your opinion, how has hedgehog activity changed in your garden and the local area on the whole?

	Decreased	Stayed the same	Increased	Unsure

Hedgehog activity in **my garden** has…				
Hedgehog activity in **the local area** has…				

We would like to know whether you have been able to encourage any other households in your neighbourhood to create hedgehog highways. We are particularly interested in whether you have been successful in influencing people in (a) **your own block of houses** and/or (b) **elsewhere**.

Your own block of houses consists of the contiguous set of houses on your street - and any connecting streets - where the back gardens are linked. From a hedgehog's perspective, if all the gardens in your block of houses had Hedgehog Highways, then it would be able to access every garden without ever having to cross a road! The images below show several examples of blocks of houses with connecting gardens, highlighted in green.

25. Have you been able to encourage **any other households in your block** into making their own Hedgehog Highways? If so, how many?

- Yes, 1 household
- Yes, 2 households
- Yes, 3 households
- Yes, 4 households
- Yes, 5 or more households
- Yes I tried, but they were not interested

- Yes I tried, but I do not know whether my neighbours followed through with it
- No, my dwelling does not form part of a block of houses
- No, and I am unlikely to try to encourage others in the future
- No, but I am likely to try to encourage others in the future

26. Have you been able to encourage any other households ***further away*** **from your immediate area** into making their own Hedgehog Highways? If so, how many?

(For example, this might include friends or family that do not live on your street nor 'block')

- Yes, 1 household
- Yes, 2 households
- Yes, 3 households
- Yes, 4 households
- Yes, 5 or more households
- Yes I tried, but they were not interested
- Yes I tried, but I do not know whether they followed through with it
- No, and I am unlikely to try to encourage others in the future
- No, but I am likely to try to encourage others in the future

Pathway 2 – people who have not made highways

We would like to know whether you have been able to encourage any other households in your neighbourhood to create hedgehog highways. We are particularly interested in whether you have been successful in influencing people in (a) **your own block of houses** and/or (b) **elsewhere**.

Your own block of houses consists of the contiguous set of houses on your street - and any connecting streets - where the back gardens are linked. From a hedgehog's perspective, if all the gardens in your block of houses had Hedgehog Highways, then it would be able to access every garden without ever having to cross a road! The images below show several examples of blocks of houses with connecting gardens, highlighted in green.

27. Although you have not made a Hedgehog Highway yourself, have you been able to encourage any other households in your block into making their own Hedgehog Highways? If so, how many?

- Yes, 1 household
- Yes, 2 households
- Yes, 3 households
- Yes, 4 households
- Yes, 5 or more households
- Yes I tried, but they were not interested
- Yes I tried, but I do not know whether my neighbours followed through with it
- No, my dwelling does not form part of a block of houses
- No, and I am unlikely to try to encourage others in the future
- No, but I am likely to try to encourage others in the future

28. Have you been able to encourage any other households **further away from your immediate area** into making their own Hedgehog Highways? If so, how many?

(For example, this might include friends or family that do not live on your street nor 'block')

- Yes, 1 household
- Yes, 2 households
- Yes, 3 households
- Yes, 4 households

- Yes, 5 or more households
- Yes I tried, but they were not interested
- Yes I tried, but I do not know whether my neighbours followed through with it
- No, and I am unlikely to try to encourage others in the future
- No, but I am likely to try to encourage others in the future

29. What are the main reasons you have not made a Hedgehog Highway yourself?

Please tick all that apply.

- There are no hedgehogs where I live
- My garden is already accessible
- I am not interested
- I rent my house so am not allowed
- It might encourage rats (despite their ability to climb)
- Small pets could escape
- My neighbour owns the fence
- I don't think my neighbour would like it
- I don't want to damage the boundary structure
- It would be unsightly
- I don't have enough time
- I don't have the right tools
- Other (please specify)

30. Do you plan on making a Hedgehog Highway in the future?

- Yes, likely over this winter
- Yes, likely over next spring
- Yes, likely over next summer
- Yes, but further into the future
- No

- Undecided

Part 3 – questions about you

The following questions relate to information about **you.** Your answers to these questions will help us find out what type of people are becoming Hedgehog Champions and whether our Champions are representative of the wider community. They will also help us to understand what might motivate different people into helping hedgehogs and ultimately help us recruit more Champions to help hedgehogs more widely.

31. Are you a member or involved with any environmental groups or wildlife charities (e.g., RSPB, National Trust, WWF) other than Hedgehog Street?

    - No
    - Yes (please specify)

32. Please enter your postcode below:

33. Approximately how long have you lived at your current address? Please round your answer to the nearest year.

34. How would you classify the position of your current home?

    - Isolated
    - In a small hamlet
    - In a village
    - In a town (suburban areas/fringes)
    - In a town (urban centre)
    - In a city (suburban areas/fringes)
    - In a city (urban centre)

35. What type of house do you live in?

- Detached
- Semi-detached
- Mid-terrace
- End-of-terrace

- Flat
- Other (please specify)

36. Please indicate whether your property has the following:

Please tick all that apply.

- Private front garden
- Private back garden
- Communal garden
- No garden

37. Approximately how old were you when you signed up to become a Hedgehog Champion?

- 18-24
- 25-30
- 31-40
- 41-50
- 51-60
- 61+
- Prefer not to say/ I am not a Hedgehog Champion

38. How many people live in your house?

Please enter your answer as a number. If the answer is "none", please enter "0".

- Number of adults (18+): ____
- Number of children (<18): ____
- Number of temporary residents (e.g., Students home for the holidays): ____

39. What is your employment status?

This information will help us to look into how employment and other social factors might affect people's involvement with hedgehog conservation, if at all. This sort of insight will be useful in informing future hedgehog conservation strategies.

- Work full-time
- Work part-time
- Unemployed
- Homemaker/stay at home parent
- Student
- Retired
- Prefer not to say

Q40 (For those who answered employed to Q39):

40. Please select the option that best represents your occupation. For this question we are using the same divisions as outlined by the Office of National Statistics (ONS).

This information will help us to look into how employment and other social factors might affect people's involvement with hedgehog conservation, if at all. This sort of insight will be useful in informing future hedgehog conservation strategies.

- Managers, directors and senior officials
- Professional occupation
- Associate professional and technical occupations
- Administrative and secretarial occupations
- Skilled trades occupation
- Caring, leisure and other service occupation
- Sales and customer service occupations
- Process, plant and machine operatives
- Elementary occupations
- Prefer not to say

41. What have you enjoyed **most** about being a Hedgehog Champion?

Please select one answer.

- Knowing I'm helping hedgehogs
- Getting involved in my local community
- Learning about local wildlife
- Meeting new people
- Learning new skills
- Sharing ideas with other Champions via the forum/gallery
- Other (please elaborate)
- I am not a Hedgehog Champion

42. Do you have any suggestions on what might encourage people to create Hedgehog Highways?

43. Do you have a photo of a Hedgehog Highway to share with us? Please upload it here!

By uploading a photo here, you are agreeing to making your photos viewable to the public. This will include you agreeing to Hedgehog Street using your imagery for promotional purposes. If you wish for us to remove these images at any time, please email hedgehogs@ptes.org.

44. Please enter additional comments here:

You have reached the end of the survey. If you'd like to tell us about any other Hedgehog Highways belonging to previous addresses, please fill in another survey form with your answers relating to your previous address.

Appendix E

<u>Volunteer recruitment for an attempted study of hedgehog movements before and after hedgehog highways had been installed</u>

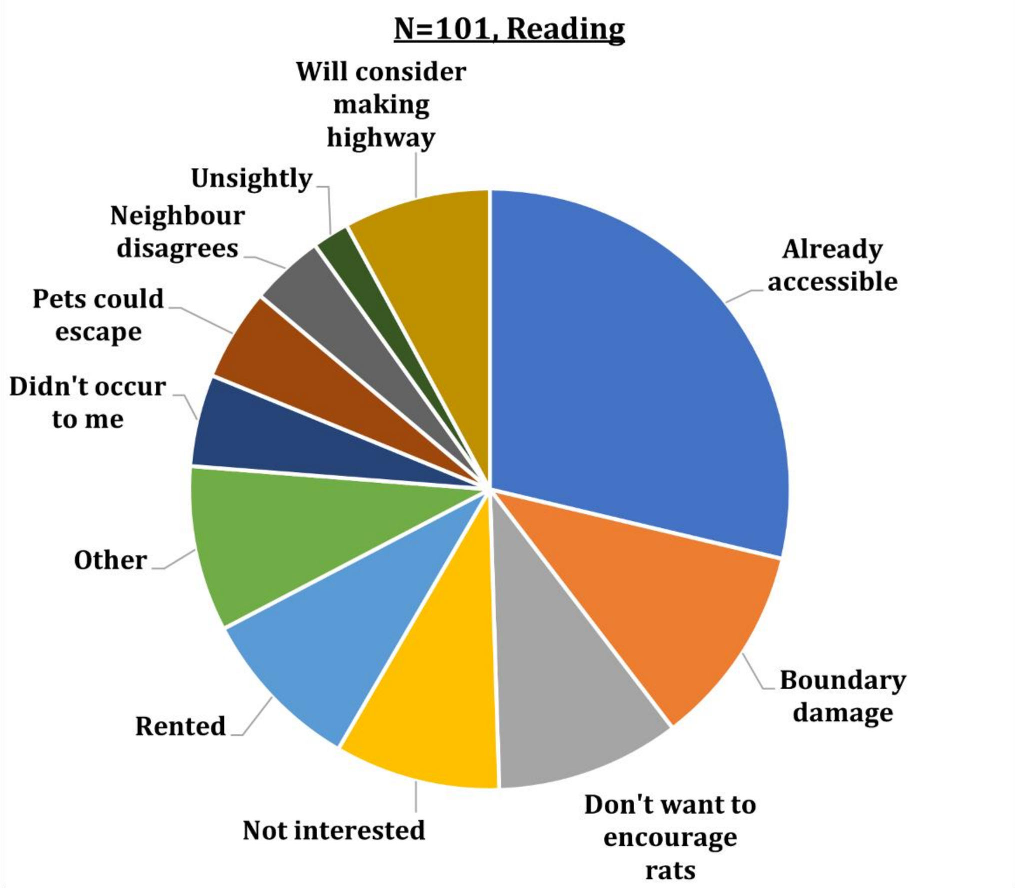
The original objective of Chapter 5 had been to measure the effects of increasing inter-garden connectivity upon hedgehog movement patterns (e.g., rates of road crossing, number of gardens used, ranging behaviour, etc.) by tracking hedgehogs before and after residents created hedgehog highways. Unfortunately, an insufficient number of households in sites in Reading and Oxford (UK) created a highway, regardless of their initial intention to do so.

In Reading, questionnaire surveys undertaken by myself with MSc students in 2016 originally indicated that 408 householders (N = 713) were willing to create highways. However, following on from a period of radio tracking in 2017, only two householders made a highway when prompted to do so by a bout of leafletting, door-knocking, advertisements on social media and at local stalls, and the offer of guaranteed entry into a prize draw. As such, in 2018, I continued tracking hedgehogs but targeted different areas of housing. This time, insufficient households (8 out of 101) initially reported that they would be willing to participate in adding highways to their gardens.

After discussions with the project sponsors (PTES/BHPS), we decided to try this study at a new site in Oxford in 2019, following a different approach by recruiting a "community engagement" volunteer who lived within the site. Here, initial survey work found that at least 87 households were willing to participate (N = 485). As such, GPS tagging and tracking commenced throughout the summer. Following a period of data collection, however, only five householders made highway(s). I also encountered difficulties in capturing hedgehogs (their movements seemed to be mostly confined to private land), and it was later discovered that badgers were present on the site borders.

Overall, uptake by householders was poor in all attempted sites, in spite of a considerable and ongoing public engagement efforts spanning 2016-2018 in Reading, and 2019 in Oxford, all of which involved: door-to-door surveys; leaflet drops; information stalls at local markets; public hedgehog surveys; craft making sessions for children; project newsletters; social-media advertising and private social media groups; advertisements in school newsletters; public talks with guest speakers; and the offer of prizes (including a camera trap, hedgehog house or £100 cash prize), and, in Oxford, the recruitment of a dedicated community engagement volunteer. Householders were also offered to have highways constructed for them, rather than do it themselves.

Following on from the failure to recruit sufficient households, I conducted further face-to-face questionnaire surveys of 54 and 101 households in the Reading and Oxford sites, respectively, to ask for the primary reason householders did not wish to participate (Figure E1). The surveys revealed that many residents in fact felt that their gardens were already accessible to hedgehogs (Reading: 29%; Oxford: 22%). Further, residents expressed concerns regarding highway-making associated with damaging boundaries (Reading: 11%; Oxford: 9%), boundary ownership (Reading: 4%; Oxford: 7%) and pets escaping gardens (Reading: 5%; Oxford: 7%). Thus, although Hedgehog Street had been successful in encouraging householders to create highways across the UK (at the time, >50,000 highways were logged on the Hedgehog Street website), it was unclear whether householders were engaging with the campaign on scales beneficial to hedgehogs (i.e., within dense networks of houses). Further, it appeared likely that many householders were actively deterred from improving garden access for hedgehogs for various reasons including boundary-related issues. As such, whilst the original targets of this study were not achieved, these findings provided impetus for investigating levels of highway-creation amongst UK householders as well as key barriers to engagement (Chapter 5).



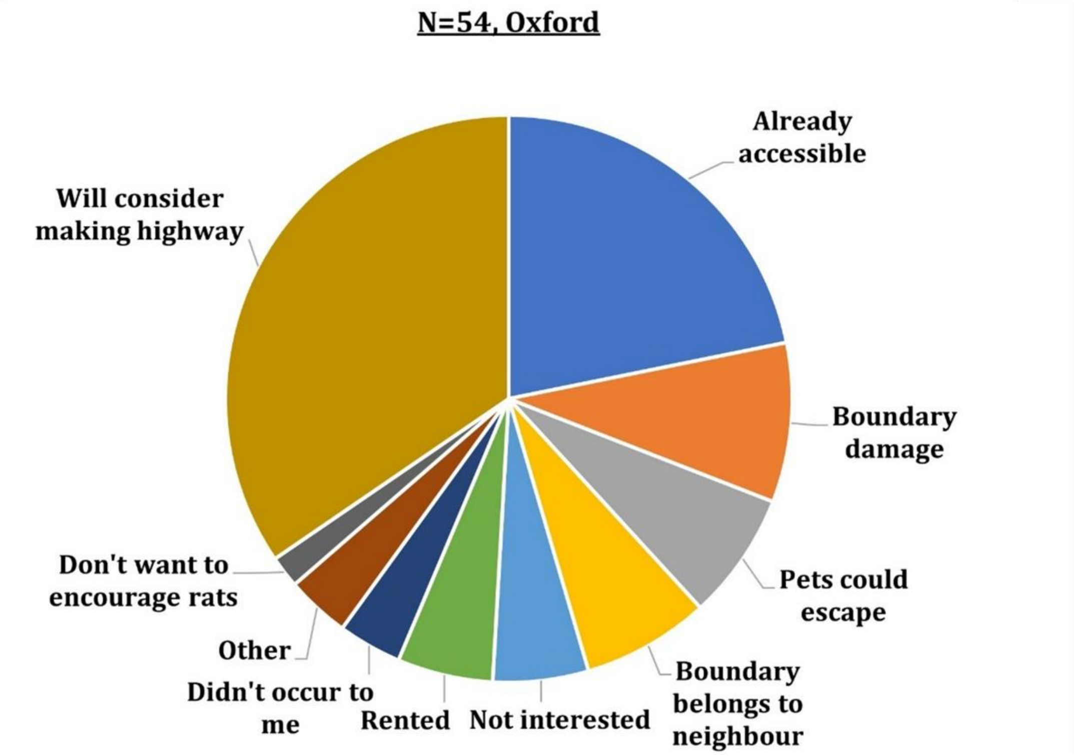


Figure E1. Primary reason for not having made a hedgehog highway, as cited by householders in Reading and Oxford sites. Some householders still reported that they were willing to considering making a highway, but ultimately did not construct one.

Appendix F

The following comprises a short report of the results of 4 seasons (2016-2019 inclusive) of hedgehog capture-mark-recapture surveys.

<u>Demographic variables of the West European hedgehog (*Erinaceus europaeus*) in an urban area</u>

Introduction

Population ecology is central to the formulation of conservation strategies (Simberloff, 1988; Rockwood, 2015) and, in its most basic form, involves the study of population structure, abundance and survival (Begon *et al.*, 2006). Knowledge in the field of mammalian population ecology is growing considerably (Kelt *et al.*, 2019); in recent decades, comprehensive datasets have been applied to modelling mammal population dynamics (Macdonald and Rushton, 2003; Hostetler *et al.*, 2021), monitoring trends in abundance (Whitlock *et al.*, 2003; Taucher *et al.*, 2020), and projecting population change (Banks *et al.*, 2011; Kaschner *et al.*, 2011). However, for some species, the fundamental demographic and ecological data underpinning such analyses are lacking (e.g., Mathews *et al.*, 2018).

One such species is the West European hedgehog (*Erinaceus europaeus*; hereafter 'hedgehog'), a small (<1.5kg), winter-hibernating mammal with a lifespan of typically <3 years in the wild, although data on longevity are sparse (Kristofferson, 1971; Rautio *et al.*, 2010; Haigh *et al.*, 2014; Morris, 2018). Hedgehogs are of conservation concern in the UK (Mathews and Harrower, 2020) yet have been subject to relatively few field studies at the population level.

Existing data on hedgehog population variables such as age structure, sex ratio, reproduction rate and survival are restricted to either populations occupying rural areas, data gathered from short-term (≤2 years) studies, hibernation studies and/or studies undertaken in climates incomparable to that of the UK (see: Brockie, 1957; Morris, 1969; Kristofferson, 1971; Parkes, 1975; Hoeck, 1987; Morris, 1988; Kristiansson, 1990; Micol *et al.*, 1994; Young *et al.*, 2006; Dowding, 2007; Jackson, 2007; Hubert *et al.*, 2011; Parrott *et al.*, 2014; Rautio, 2014; Rasmussen *et al.*, 2019a; Yarnell *et al.*, 2019; Bearman-Brown *et al.*, 2020; Schaus *et al.*, 2020). Bar a study of abundance and distribution undertaken in 1992 and again in 2016-2018 in Zurich, Switzerland (Taucher *et al.*, 2020), there are no published data of urban hedgehog populations that have been monitored for >2 years. This may be because hedgehogs are nocturnal and elusive, and difficult to directly survey in towns and cities where large proportions of land are inaccessible e.g., private residential gardens (Loram *et al*., 2007). Survey methods using technologies such as camera trapping or radio telemetry are costly (Glasby & Yarnell, 2013; Schaus *et al*., 2020) and are associated with numerous ethical and logistical considerations (Jung *et al*., 2020). Nonetheless, results are available from short-term studies that provide some insight into survival and density of urban-dwelling hedgehogs (Dowding, 2007; Hubert *et al*., 2011; Rasmussen *et al*., 2019a; Yarnell *et al*., 2019; Schaus *et al*., 2020).

The current report provides baseline data on body mass, sex ratio, age structure and apparent survival, estimated from four years (2016-2019 inclusive) of capture-mark-recapture surveys undertaken in the town of Reading, UK. Surveys were conducted primarily to aid to the research presented in Chapter 2 as well as the initial aims of Chapter 5 (in search of hedgehogs to be radio or GPS tagged), as well as for the purpose of training volunteers and encouraging community engagement.

Methods

Surveys took place in a residential area of Earley, UK (51°25’N, 0°55’W; population >33,000). The study area was 0.79km^2 comprising a mixture of detached, semi-detached and terraced properties, amenity spaces and a school, and was bound by B- and C-roads.

Capture-mark-recapture (CMR) data were collected during four annual survey periods in 2016-2019 inclusive and conducted at least twice per month (Table F1). In 2016, sampling did not commence until August due to a survey training period and ended in October. Otherwise, in 2017-2019, surveys were undertaken throughout the “active season” of hedgehogs in May-October (in the UK, hedgehogs tend to hibernate at some point between November-April: Reeve, 1994; Morris, 2018).

Table F1. Monthly survey frequency.

Year	Month					
	May	Jun	Jul	Aug	Sept	Oct
2016	-	-	-	2	13	4
2017	2	2	2	2	2	4
2018	2	4	4	5	2	2
2019	2	2	3	2	3	3

Surveys were carried out after dusk for approximately 3 hours. To search for hedgehogs, a minimum of two surveyors jointly walked a 4km route covering the site on public footpaths with the use of torches. Hedgehogs were captured by hand, weighed, and sexed, and underwent a basic health check before being marked and released at their capture location. Hedgehogs were marked with uniquely numbered sections of white heat shrink tubing applied with non-drip superglue over five spines posterior to the head, where the tubing was subject to minimal wear (Reeve *et al*., 2019a). Although hedgehogs naturally shed individual spines, they do not undergo complete moults – with the exception of the gradual loss of juvenile spines at around 1-2 months (Reeve, 1994) – which minimises the risk of total marker loss. Reeve *et al*. (2019a) have reported that it is not uncommon for markers to remain attached for periods ≥1 year and, applying this technique with six markers, found that hedgehogs retained an average of 3.78 markers after eight months. In the present study, using data available from recapture events, I estimated average duration of marker attachment after two and eight months. Markers were replenished in the field as appropriate.

Captured individuals were assigned an age class (juvenile or adult) based upon mass, body condition and size, and time of year. Juveniles typically weigh ≤500g (Morris, 2018) but can exceed this in the lead up to hibernation (Rasmussen *et al*., 2019a; Yarnell *et al*., 2019); adults typically weigh >500g but can weigh less, e.g., 400g-500g post-hibernation (Rasmussen *et al*., 2019a). The sex ratio and differences in body mass per sex were assessed via binomial and two-sample t-tests, respectively.

In between formal surveys but within the primary sampling period, animals that were opportunistically encountered by surveyors during radio-tracking sessions (for Chapter 2) were also captured and marked. All animals were captured using handling methods approved by the University of Reading and under licence from Natural England.

Apparent survival analysis

Since mortalities were rarely observed, apparent survival (φ) and encounter probabilities (p) were estimated using live encounter data in Cormack-Jolly-Seber models. Analyses were conducted in program MARK 6.2. Apparent survival is estimated from one sampling period (defined below) to the next, whilst encounter probabilities are estimated for each sampling event following the first.

The CMR data were used to code encounter histories for each individual where 1 = encountered and 0 = not encountered. Due to small sample sizes and to allow for potential estimation of survival within (May-October) and between hedgehog active seasons (November-April), data were pooled into 2 periods per year following a similar protocol described by Monticelli *et al*. (2013). The resulting sampling periods comprised May-July and August-October. Accordingly, over the four years of surveying, there were 7 survey periods: August-October 2016; May-July 2017; August-October 2017; May-July 2018; August-October 2018; May-July 2019; and August-October 2019. The unequal time intervals between these seasons were specified in MARK. Incidental encounters with hedgehogs recorded within the survey seasons (but outside of formal survey nights) were included in the pooled CMR datasets; the use of auxiliary observations alongside systematically collected observations in CMR models reduces bias in estimating survival (Kendall *et al.*, 2013), and a range of studies have utilised this approach (e.g., Hastings *et al.*, 1999; Arnold *et al.*, 2002; Hastings *et al.*, 2011).

The candidate models were constructed with apparent survival and encounter probabilities (i) held constant, (ii) varying with each sampling period and (iii) as a function of the covariates sex, age class at first capture and body mass at first capture (z-transformed). Since sample size was small, models included a maximum of one covariate for apparent survival and recapture estimation, and interaction terms were not considered.

The most parameterised model was tested for goodness-of-fit using the parametric bootstrapping procedure with 1,000 replicates (Buckland and Garthwaite, 1991). Bootstrapping simulates encounter histories for all individuals marked (in this case, 1,000 times) and the global model is applied to these histories to produce a measure of lack of fit, namely a variance inflation factor $\hat{c}$. A value of $\hat{c} > 1$ indicates that there is some degree of overdispersion, which, if ≤ 3, is generally considered to be acceptable (Lebreton *et al.*, 1992). In that scenario, Akaike's information criterion (AIC) values should be adjusted into quasi-likelihood adjusted AIC (QAIC) values and standard errors of beta estimates multiplied by $\sqrt{\hat{c}}$ (Burnham and Anderson, 1998; Cooch and White, 2004). Models with ΔQAIC values ≤ 2 were identified as top-ranking (Burnham and Anderson, 1998) and parameters were considered to have a significant effect when the corresponding 95% confidence interval of the beta coefficient did not overlap 0 (Arnold, 2010).

Results

Overall, 110 hedgehogs were marked (Table F2; Figure F1) and 37 (33.6%) were recaptured at some point, in a total of 179 capture events across all four survey years. The mean number of markers retained were 3.33 (± SD 1.49; N = 27) after two months, and 2.84 (± 1.42; N = 19) after eight months. Two hedgehogs were recorded having retained some original markers for at least 22 months.

Table F2. The number of new individuals marked per sampling season.

Season	No. capture events	No. of new individuals
Aug-Oct 2016	47	35
May-Jul 2017	40	24
Aug-Oct 2017	10	2
May-Jul 2018	30	23
Aug-Oct 2018	25	11
May-Jul 2019	11	7
Aug-Oct 2019	16	8

Of the recaptured individuals, 22 (20.0%) were re-encountered exclusively within their first season or year of being marked, whereas 15 (13.6%) were re-encountered within subsequent years: 12 individuals were recorded in two survey years, and three individuals were recorded in three survey years. Of the total 179 captures, 39 (21.8%) occurred outside of systematic survey sessions. A total of 10 mortalities were recorded, at least one of which comprised a marked individual, and all of which resulted from road-traffic accidents.

Figure F1. The location of the study site within the UK (left) and hedgehog captures recorded on site between 2016-2019 inclusive (right) (N = 179).

Adult females made up the majority of the surveyed population (adult females: 41.8%, N = 46; adult males: 28.2%, N = 31; juvenile females: 16.4%, N = 18; juvenile males: 13.6%, N = 15). The overall proportion of individual males recorded (42.7%) relative to females (57.3%) was not significantly lower than the expected 50.0% ($p = 0.15$).

For all years pooled, June and October experienced the greatest proportions of adult and juvenile captures, respectively (Figure F2), corresponding with mean body mass which was highest in June (mean ± SD = 885.2g ± 200.8g) and lowest in October (580.5g ± 275.6g) (Figure F3a). Collectively, body mass differed significantly between the sexes of adult hedgehogs (males: mean ± SD = 962.2g ± 153.7g, females: 895.6g ± 206.51g; t = -2.13, df = 130, p = 0.035) but not juveniles (males: 373.0g ± 107.82g, females: 389.18g ± 115.85g; t = -0.46, df = 38, p = 0.645) (Figure F3b).

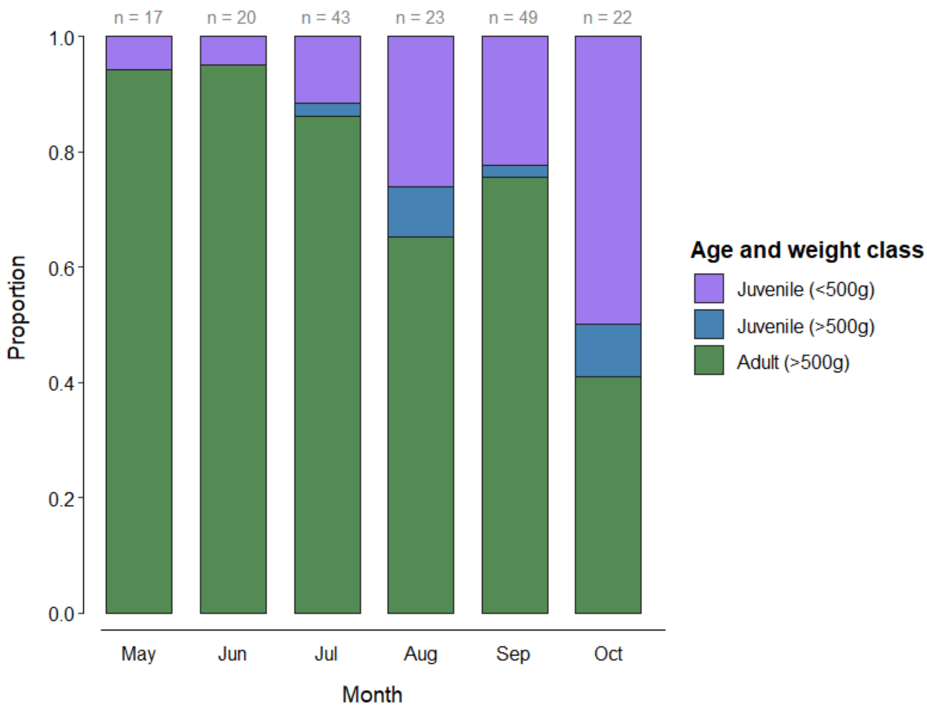


Figure F2. The proportion of juvenile (shown as <500g or >500g) and adult (none <500g) hedgehogs recorded relative to each survey month. Data are pooled over four years: surveys were undertaken in August-October in 2016, and in May-October in 2017-2019 inclusive, in Reading, UK (total captures = 174; five captures were discounted due to equipment error).

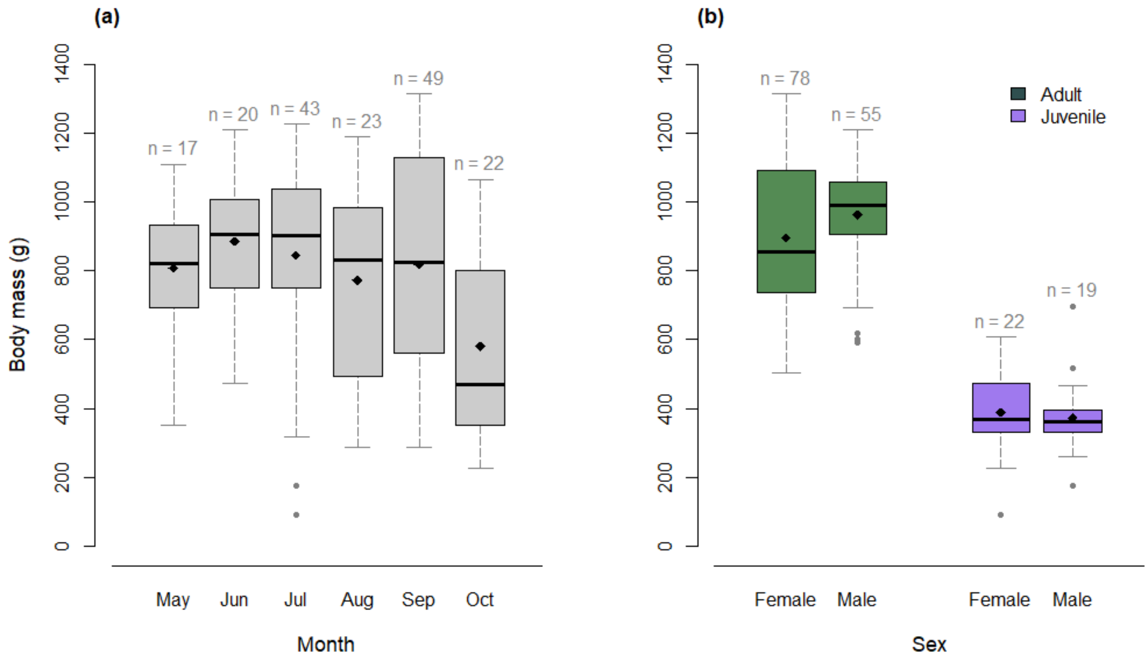


Figure F3. Body mass of captured hedgehogs per (a) month of capture (all hedgehogs), and (b) sex and age class. Mean masses are shown as filled diamonds. Data were collected over four years: surveys were undertaken in August-October in 2016, and in May-October in 2017-2019 inclusive, in Reading, UK (total captures = 174; five captures were discounted due to equipment error).

Apparent survival

The best-fitting CMR model held apparent survival and encounter probability constant across surveys with no covariate effect (Table F3). However, models 2-6 – which incorporated season, sex, age class and mass – were found to be equally parsimonious (ΔQAIC ≤2) with model weights distributed reasonably evenly across said models (i.e., model weight did not differ by >0.03). As such, there is some evidence to support that survival varied with sex, season and body mass; and encounter probability varied with season and age, though the coefficient effects were not significant.

Table F3. Candidate models of apparent survival (φ) and encounter probability (p) of hedgehogs surveyed seasonally in a capture-mark-recapture framework between August 2016–October 2019 in Reading, UK.

Model no.	Model	QAIC	ΔQAIC	AIC weight	*K*	Deviance
1	φ(.), p(.)	129.41	0.00	0.13	2	125.31
2	φ(sex), p(.)	130.46	1.05	0.08	3	124.26

3	φ(season), p(.)	130.65	1.24	0.07	3	124.45
4	φ(mass), p(.)	130.94	1.53	0.06	3	124.75
5	φ(.), p(age)	131.10	1.69	0.06	3	124.90
6	φ(.), p(season)	131.19	1.78	0.05	3	124.99
7	φ(age), p(.)	131.49	2.08	0.05	3	125.30
8	φ(.), p(mass)	131.50	2.09	0.05	3	125.30
9	φ(.), p(sex)	131.51	2.10	0.05	3	125.31
10	φ(mass), p(age)	131.92	2.52	0.04	4	123.60
11	φ(sex), p(sex)	132.06	2.65	0.03	4	123.74
12	φ(sex), p(season)	132.24	2.83	0.03	4	123.91
13	φ(sex), p(age)	132.26	2.85	0.03	4	123.94
14	φ(sex), p(mass)	132.58	3.17	0.03	4	124.25
15	φ(mass), p(mass)	132.61	3.20	0.03	4	124.28
16	φ(season), p(age)	132.62	3.21	0.03	4	124.29
17	φ(mass), p(season)	132.74	3.33	0.02	4	124.41
18	φ(season), p(season)	132.75	3.34	0.02	4	124.42
19	φ(season), p(mass)	132.78	3.37	0.02	4	124.45
20	φ(season), p(sex)	132.78	3.37	0.02	4	124.45
21	φ(mass), p(sex)	133.08	3.67	0.02	4	124.75
22	φ(age), p(age)	133.15	3.74	0.02	4	124.82
23	φ(age), p(season)	133.30	3.89	0.02	4	124.98
24	φ(age), p(mass)	133.62	4.21	0.02	4	125.29
25	φ(age), p(sex)	133.62	4.21	0.02	4	125.30

φ = apparent survival, p = encounter probability, K = number of parameters, ΔQAIC = change in quasi-likelihood adjusted Akaike's information criterion. Model notations are: '.' = constant, 'sex' = male or female, 'age' = juvenile or adult at first capture, 'mass' = body mass at first capture, 'season' = May-July or August-October survey period. Variance inflation factor $\hat{c}$ = 1.49.

Apparent survival, as estimated by the top-ranking models, ranged from 0.65 (± SE = 0.19) to 0.87 (± 0.04) (Table F4). Apparent survival was greater for males (0.87 ± 0.04) than females (0.82 ± 0.05), and greater during the hibernation period (0.86 ± 0.01) than the active season (0.65 ± 0.19). Encounter probability was highest (0.38 ± 0.16) during the August-October survey periods.

Table F4. Estimates of apparent survival and encounter probability of hedgehogs in Reading, UK.

Model no.	Parameter	Estimate ± SE	95% CI
1	Apparent survival held constant	0.84 ± 0.03	0.77 - 0.90
2	Apparent survival of males	0.87 ± 0.04	0.77 - 0.93
2	Apparent survival of females	0.82 ± 0.05	0.71 - 0.89
3	Apparent survival during the active season (May-October)	0.65 ± 0.19	0.27 - 0.90
3	Apparent survival between active seasons (November-April)	0.86 ± 0.01	0.77 - 0.92
4	Apparent survival as a function of body mass	0.84 ± 0.03	0.76 - 0.90
1	Encounter probability held constant	0.29 ± 0.08	0.17 - 0.46
5	Encounter probability of juveniles	0.27 ± 0.08	0.15 - 0.45
5	Encounter probability of adults	0.38 ± 0.16	0.13 - 0.70
6	Encounter probability during May-July	0.28 ± 0.08	0.16 - 0.46
6	Encounter probability during August-October	0.35 ± 0.15	0.14 - 0.67

Estimates were taken from top-ranking models (ΔQAIC ≤2) computed in capture-mark-recapture analysis. Standard errors (SE) and corresponding confidence intervals (CI) have been adjusted by $\sqrt{\hat{c}} = \sqrt{1.49}$.

Discussion

Since very few mortalities were recorded and as the recapture rate between years was not sufficiently high, inferences could not be made regarding hedgehog lifespan, though at least three individuals were recorded in three survey years. The lack of observed mortalities was not wholly unusual given that Kristiansson (1990) recovered an average of 4.25 dead hedgehogs per year and Parkes (1975) recovered six over an 18-month period, though these studies were undertaken in rural areas. Alternatively, Rautio *et al.* (2016) recovered 106 carcasses over a two-year radio telemetry study in a town in Finland, yet the site was approximately nine times greater in size than that of the present study and more intensively surveyed. Hedgehog mortalities in residential areas are commonly attributed to road traffic accidents, infections, dog attacks and injuries inflicted by gardening machinery (Rautio *et al.*, 2016; Morris, 2918; Rasmussen *et al.*, 2019a). In the current study, most mortalities may have remained undetected since researchers did not have access to all privately-owned land (e.g., residential back gardens) and/or survey effort was not intensive. Future CMR surveys should ideally incorporate more frequent monitoring of e.g., private land and road networks; this would also allow robust estimation of population density.

The ranges of hedgehog body mass reported here are in line with that described for rural hedgehogs (Kristiansson, 1990; Jackson, 2006; Haigh, 2011; Mori *et al*., 2015); comparable estimates from urban areas are not available since any such data documented have originated from studies excluding hedgehogs below certain weight thresholds (e.g., Dowding *et al*., 2010a; Rautio, 2014; Barthel, 2019). Data are also limited in relation to population age structure. In the current study, between May-September, captured animals predominantly consisted of adults whilst, in October, captured animals were mostly juveniles. The higher proportion of juveniles captured in October could be indicative of greater breeding activity occurring later in the season (Morris, 2018), though the collective October sample size was small. The production of late or second litters is not unusual (Peters and McEvinney, 2019; Clinton, 2019; Yarnell *et al*., 2019; South *et al*., 2020), yet existing data gathered from rural areas suggest that early season (>June) litters are more common (Deanesly, 1934; Jackson, 2006; Haigh, 2011). Breeding timings might be more variable in urban habitats where warmer conditions and continuous food supplies could influence reproductive timings and success, as observed in other wild mammals (e.g., Bomford and Redhead, 1987; Banks and Dickman, 2000; Robert *et al*., 2015).

Apparent survival was generally high: 0.84 when all parameters were held constant. Similarly, in Denmark (Rasmussen *et al*., 2019a) and the UK (Yarnell *et al*., 2019), researchers have estimated survival probabilities of 0.70 (juveniles; from September-July) and 0.96 (mixed ages in mixed urban and rural habitats; 100 days overwinter) for urban areas, respectively. In the current study, there was some support for survival varying with sex – for females, apparent survival was lower, which could be attributed to high production of late litters, and high energetic demands of rearing young (Jackson, 2006; Morris, 2018) or another, unrelated, mechanism. When modelled as a function of season, apparent survival was greatest overwinter relative to the active season. This is consistent with results of other studies (Kristiansson, 1990; Rasmussen *et al*., 2019a; Yarnell *et al*., 2019) and likely reflects a general reduction in hedgehog activity overwinter and thus decreased exposure to risks including road traffic accidents, encounters with predators and/or people.

Overall, whilst improvements should be made to sampling design by increasing survey intensity and/or coverage of the study area – e.g., by gaining permission to systematically survey private back gardens – the data included here provide a basic insight into hedgehog population demographics in an urban location. Additional systematic long-term (≥ four years) studies of hedgehog populations and their behaviours would enable the quantification of lifespan as well as reliable density estimates. Such data would aid the planning of future field and population modelling studies (Morris, 2018).

Appendix G

Building on Chapter 4, data have been collected to compare the microclimatic conditions of varying nest box designs. Sampling protocol, and basic results, are given below.

Nest box design and microclimatic conditions

To measure microclimatic parameters, eight different designs of commercially available hedgehog nest boxes were selected. The designs were chosen to reflect attributes that are common to artificial hedgehog refugia, and they varied in shape, dimensions, primary material, entrance type, and other features (Table G1). Two of each design (N = 16 boxes in total) were purchased.

Table G1. Summary of the characteristics of 8 commercially available hedgehog houses in the UK.

ID	Shape (material)[1]	Dimensions (cm) (width * depth * height)				Anti-predation measures[6]				Raised	Vents
		External[2]	Nest chamber[3]	Entrance hole[4]	Tunnel[5]	SB	ET	IP	SR		
1	R with F (W)	40*30*32	37*27*30	10*10 (S)	13*30*13 (E)	✓	✓	×	×	✓	×
2	D (M)	52*52*20	50*50*18	15*14 (D)	18*14*14 (E)	×	✓	×	-	×	×
3	C with F (W)	52*39*22	27*35*17	12*13 (D)	13*20*20 (I)	✓	×	✓	✓	✓	✓
4	R with S (W)	46*41*26	29*23*23	13*13 (S)	13*21*13 (I)	✓	×	✓	✓	✓	✓
5	R with P (W)	40*29*20	36*25*20	11*11 (D)	-	×	×	×	✓	×	×
6	R with P (W)	45*36*18	41*32*18	13*13 (D)	14*26*14 (I)	✓	×	✓	✓	✓	✓
7	R with S (R)	49*37*32	47*35*29	11*10 (S)	11*26*26 (I)	✓	×	✓	×	✓	✓
8	F (Wi)	31*29*26	29*32*25	20*14 (D)	25*14*13 (E)	×	✓	×	-	×	×

[1] Shape: C = circular; D = domed; F = flat roof; P = pitched roof; R = rectangular; S = sloping roof. Material:
M = internal wire mesh frame with waterproof lining and brush 'wood' on outside; R = non-wood recycled materials; W = wood; Wi = wicker.
[2] For boxes with pitched or sloping roofs, height measurements are listed as the distance to the midpoint of the slope or pitch, respectively.
[3] Measurements are internal: width * depth * height. Height measurements have been adjusted to account for boxes with pitched or sloping roofs.
[4] Measurements for entrance hole are width * height: D = domed entrance hole (height measurement taken to the apex of the domed hole); S = square/rectangular entrance hole.
[5] E = external tunnel; I = internal tunnel taken as the portion of the box separated from the nest chamber by the internal divider. For internal tunnels, depth taken as the distance from the entrance to the midpoint of the access point to the nest chamber.
[6] ET = external tunnel; IP = internal partition; SB = solid base; SR = secured roof

The nest boxes were deployed in a private residential garden (19m x 7m) associated with a semi-detached house, in a town in Wiltshire, UK (51°19'N, 002°13'W). A pre-calibrated data logger (Gemini Data Loggers UK, Tinytag TGP-4500) was placed in each nest box recording temperature and relative humidity (RH) at ten-minute intervals (day and night). During the sampling period, one of each pair of nest box designs was positioned (i) in the open and (ii) under shrub cover; data loggers were placed approximately in the centre of the nest box chamber and on a top of identical lidded plastic containers 3.5cm in height. Concurrently, two data loggers were set up to measure ambient temperature and humidity externally to the nest boxes (i) in the open and (ii) under shrub cover within the same garden, positioned on top of the 3.5cm high plastic containers and secured to the ground with pegs. Nest boxes and external loggers were checked daily to ensure that they had not been moved nor damaged. The nest box entrances were oriented south and blocked with wire mesh to prevent usage. Boxes that were positioned in the open were placed alongside the same fence line to mimic where householders might be likely install them; common advice is to place hedgehog nest boxes alongside linear features (British Hedgehog Preservation Society, 2021). All boxes were positioned on natural substrate and were located a minimum of 5m from buildings and 2m from any other boxes being monitored in this study.

A total of 10 data loggers were available at any one time, which meant that half of the nest boxes could be sampled at once: eight loggers could be used in four pairs of nest boxes (one of each pair in the open and under shrub cover), plus two loggers for measurements of external temperature and RH. As such, nest boxes were split into two random groups and sampled over three occasions: Group A were measured during the first five full days (and nights) of the session, and Group B were measured in the next five-day-and-night block (Table G2). The groupings were re-randomised in each of the three sampling sessions, and all pairs of nest boxes were deployed for 15 days/nights in total. Data were collected from 06:00 on the first day to 06:00 on the final day, and sampling was undertaken between December 2021-January 2022.

Table G2. Randomly allocated groupings for each sampling session. Groups were sampled for 5 consecutive days and nights within the sampling session, totalling 15 days and nights for each nest box over 3 sessions. Sampling dates are as follows: Session 1: Group A: 13/12/2021-18/12/2021, Group B: 21/12/2021-26/12/2021. Session 2: Group A: 28/12/2021-02/01/2022, Group B: 03/01/2022-08/01/2022. Session 3: Group A: 10/01/2022-15/01/2022, Group B: 16/01/2022-21/01/2022.

Box ID	Sampling session		
	1	**2**	**3**
1	A	B	A
2	B	A	B
3	B	B	A
4	A	A	B
5	B	A	B
6	A	B	B
7	B	B	A
8	A	A	A

Data analysis

For each box design, the minimum, maximum and mean daily temperature and relative humidity are reported for the entire sampling period specific to that box. Paired t-tests were used to assess the difference between mean daily measurements logged in boxes in the open and under shrub cover. Additionally, differences between average daily nest box temperature and average daily external ambient temperature, as well as average daily nest box RH and average daily external RH, are displayed. Here, a daily period is defined as a 24-hour period from the first logger measurement at 06:00 to the final measurement the following morning at 05:50 rather than from midnight, so that full nights are captured within the analyses.

It is intended that this data will be further used to estimate variability in temperature and RH per nest box by calculating daily coefficients of variation (CV); the coefficient of variation corrects for the means of each sampling session (see Korb and Linsenmair, 2000; Chaplin *et al.*, 2002), thereby accounting for some natural variation in weather fluctuations between sampling sessions. Additionally, I will model factors affecting average daily temperature and RH, as well as their variability (CV). Explanatory variables to be considered should include the positioning of the nest box (sheltered or in the open), design features and dimensions (Table G1), length of day, total rainfall, and parameters relating to external temperature and RH measurements to account for the effect of varying ambient conditions, since nest boxes were not all deployed under identical conditions/time periods.

Results

In general, nest boxes tended to experience warmer daily mean temperatures than that recorded externally in the open, though on some occasions, average internal box temperature was lower than the outside (see Boxes 2, 6 and 8; Figure G1). The coldest ambient temperatures were experienced during the third sampling session (10/01/2022-21/01/2022) during which frost occurred on numerous days, as is reflected in Figures G1 and G2. Boxes positioned under shrub cover were generally the warmest (Figures G1 and G2; Table G3), and the average daily difference in temperature between matching box designs located in the open and under shrub cover was -0.86°C ± 0.85 (-3.36-0.33); this difference was significant (paired t-test: $t_{119} = -11.09$, $p < 0.001$).

Other than Box 2, nest boxes tended to experience lower daily mean RH levels than that measured in the open (Figure G3). Nonetheless, it was not unusual for daily mean RH in nest boxes to sometimes exceed that recorded by the external logger located under shrub cover (Figure G4). Nest boxes positioned in the open tended to experience higher levels of RH compared to the corresponding box positioned under shrub cover (Figures G3 and G4; Table G3), and the average daily difference in RH between matching boxes in the open and under shrub cover was 3.23% ± 4.14 (-2.59-16.58); this difference was significant ($t_{119} = -8.54$, $p < 0.001$).

Table G3. Summary of mean daily (24-hour) temperatures and relative humidity (RH) levels recorded within hedgehog nest boxes positioned in the open and under shrub cover, averaged across 15 sampling days. Temperature and relative humidity are provided as °C ± SD and RH ± SD (%), respectively, and the minimum and maximum values recorded are given in parentheses. Dates of sampling are provided in Table G2.

Box ID	Placement	Mean daily temp. ± SD (°C)	Mean daily RH ± SD (%)
1	Open	5.0 ± 4.1 (-3.1-12.0)	94.8 ± 4.6 (77.8-100)
	Shrub cover	5.9 ± 3.4 (-1.4-12.0)	93.6 ± 4.0 (79.1-100)
2	Open	6.5 ± 3.7 (-0.8-13.1)	99.9 ± 0.3 (88.9-100)
	Shrub cover	7.1 ± 3.6 (-1.8-16.8)	98.1 ± 3.1 (50.2-100)
3	Open	3.8 ± 3.2 (-3.9-11.5)	95.9 ± 5.0 (71.5-100)
	Shrub cover	4.8 ± 2.8 (-1.7-18.9)	91.9 ± 5.6 (45.9-100)
4	Open	7.3 ± 4.7 (-5.4-14.4)	94.7 ± 3.5 (81.7-100)
	Shrub cover	8.1 ± 4.1 (-2.7-14.1)	91.4 ± 2.7 (77.6-100)
5	Open	6.2 ± 4.6 (-4.7-13.9)	97.5 ± 2.2 (83.6-100)
	Shrub cover	7.0 ± 4.0 (-3.4-14.0)	97.1 ± 2.8 (65.4-100)
6	Open	4.3 ± 4.2 (-6.6-12.3)	93.4 ± 5.0 (80.4-100)
	Shrub cover	5.4 ± 3.5 (-3.3-11.7)	85.7 ± 5.3 (74.4-100)
7	Open	4.0 ± 3.2 (-3.2-11.8)	93.8 ± 4.5 (71.4-100)
	Shrub cover	5.1 ± 2.3 (-1.0-16.2)	86.9 ± 8.7 (55.7-100)
8	Open	7.6 ± 4.4 (-2.4-13.7)	98.6 ± 2.4 (80.8-100)
	Shrub cover	8.0 ± 3.9 (-1.6-14.2)	98.1 ± 2.5 (83.1-100)

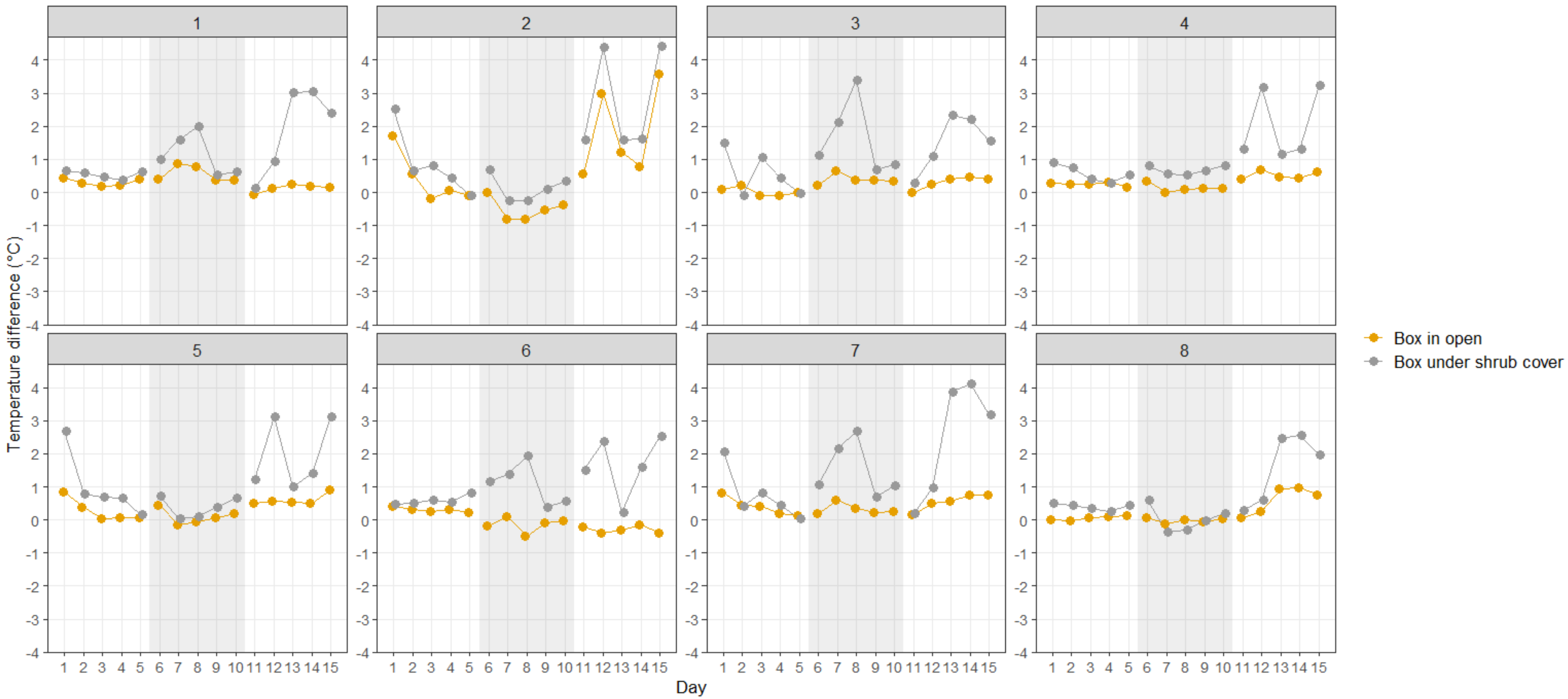


Figure G1. Difference in average daily temperatures recorded in each nest box type (N = 8) positioned in the open and under shrub cover, relative to average daily temperatures recorded by the data logger positioned in the open. NB. start dates of five-day sampling sessions varied between, but not within, pairs of box designs (see Table G2); chart shading separates the sampling sessions.

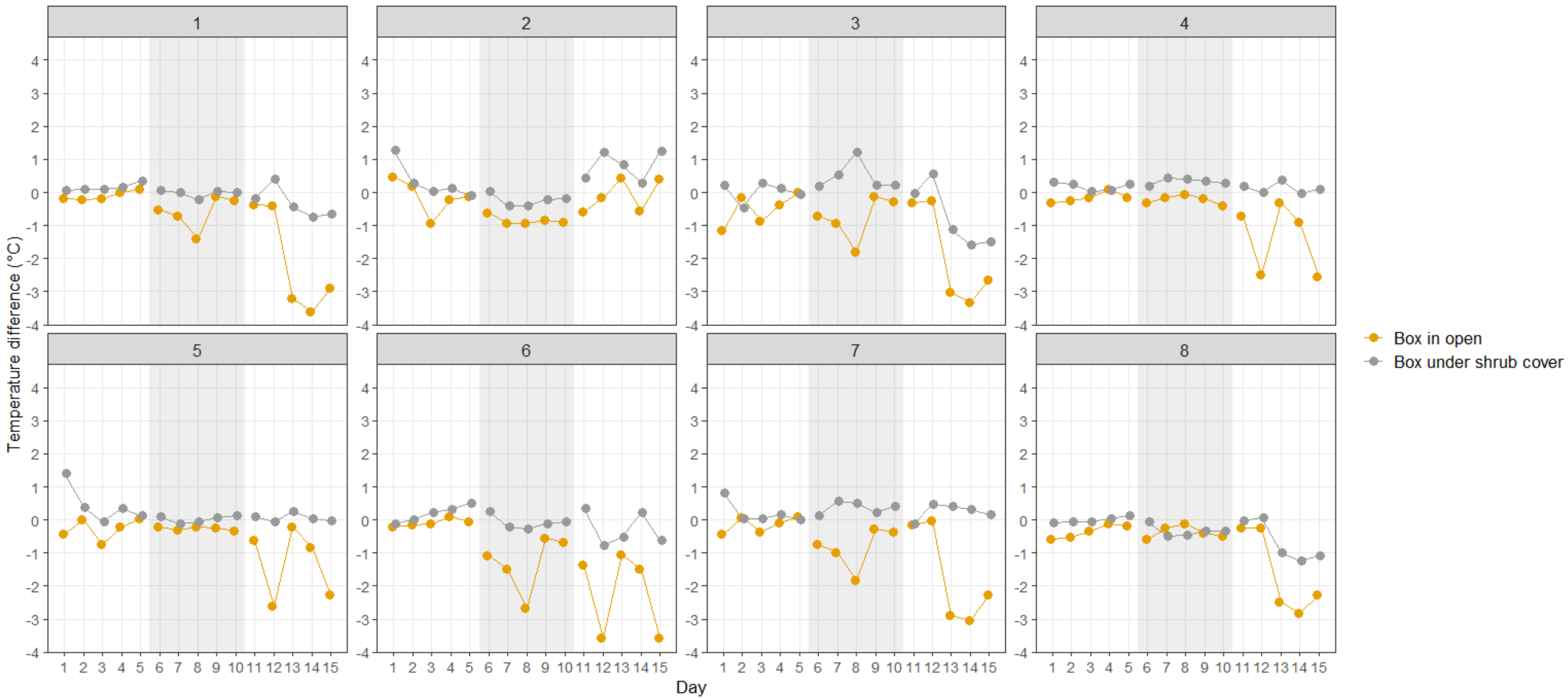


Figure G2. Difference in average daily temperatures recorded in each nest box type (N = 8) positioned in the open and under shrub cover, relative to average daily temperatures recorded by the data logger positioned under shrub cover. NB. start dates of five-day sampling sessions varied between, but not within, pairs of box designs (see Table G2); chart shading separates the sampling sessions.

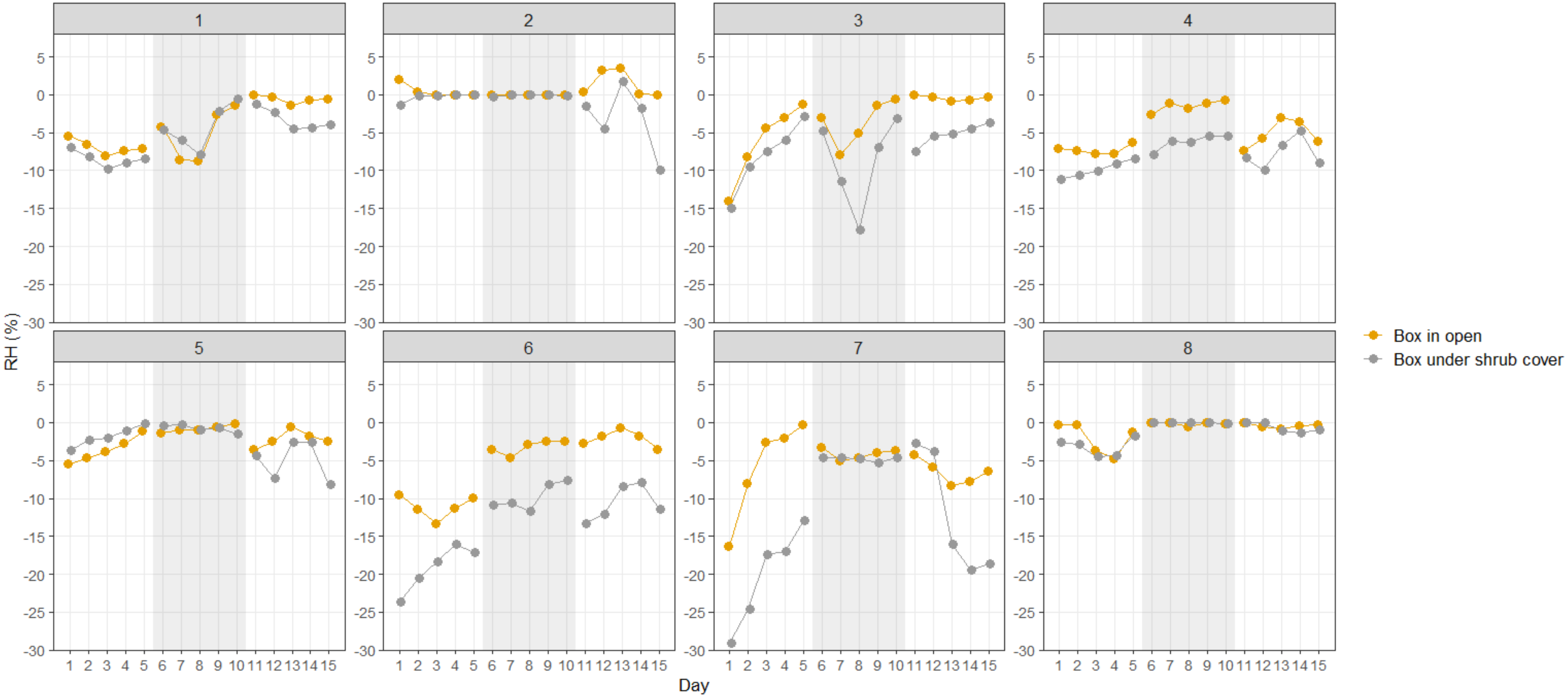


Figure G3. Difference in average daily relative humidity (RH) recorded in each nest box type (N = 8) positioned in the open and under shrub cover, relative to average daily RH recorded by the data logger positioned in the open. NB. start dates of five-day sampling sessions varied between, but not within, pairs of box designs (see Table G2); chart shading separates the sampling sessions.

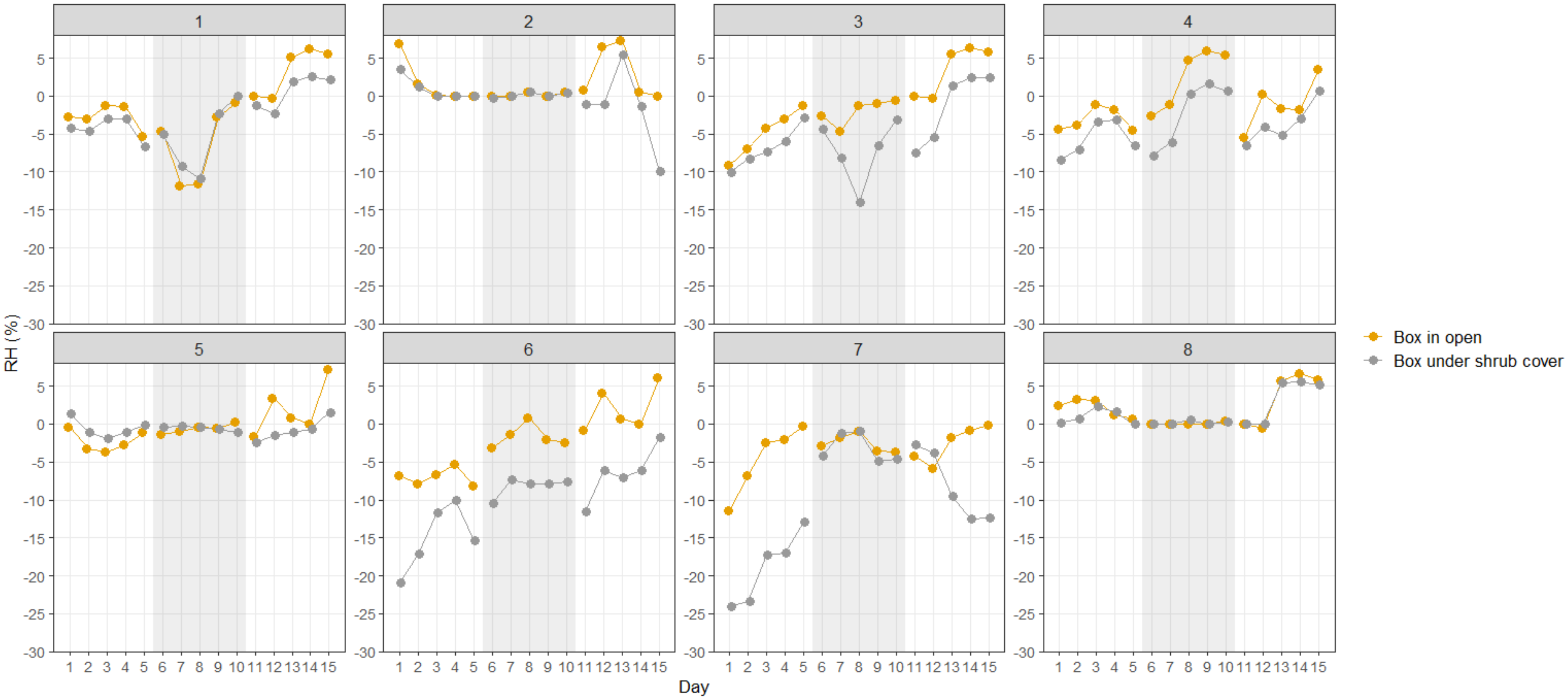


Figure G4. Difference in average daily relative humidity (RH) recorded in each nest box type (N = 8) positioned in the open and under shrub cover, relative to average daily RH recorded by the data logger positioned under shrub cover. NB. start dates of five-day sampling sessions varied between, but not within, pairs of box designs (see Table G2); chart shading separates the sampling sessions.

Appendix H

Building on Chapter 2, GPS tags were deployed for static tests in varying locations within two residential gardens.

GPS static tests – fix success rate in residential gardens

To clarify how using GPS tags on hedgehogs in gardens might be associated with a loss of data when hedgehogs move e.g., under decking, I conducted static tests of GPS tag fix success rate in nine settings within gardens: (1) in the open (on mowed lawn); (2) adjacent (<5cm) to a two-storey semi-detached house; (3) adjacent (<5cm) to a wooden garden fence (approx. 6ft); (4) in a cavity under wooden shed; (5) in a cavity under wooden decking; (6) in a plastic feeding station; (7) in a wooden-roofed nest box; (8) in wooden nest box with a slate roof; (9) and wicker nest box. Tags were placed at ground level (or within nest boxes on the ground) >5m from buildings, unless specified otherwise. All nest boxes and feeding stations were empty and were placed adjacent to a wooden garden fence to mimic where householders are likely to position nest boxes normally; common advice is to place hedgehog nest boxes alongside linear features (BHPS, 2021).

A single tag in each of the nine settings was deployed for five consecutive days and scheduled to record location fixes every five minutes from 00:00 UST. Excluding the tag(s) located under decking, each deployment was repeated in a second garden, yielding 10 days of data collection and 2880 fixes per setting, and 25,920 fixes overall. Tags were deployed twice under decking but within the same garden, as decking was not available in both sites. Both garden sites were located in Wiltshire, UK (51°, 20’ N: 1°, 55’ W) and associated with semi-detached houses. Garden sizes were 133m^2 and 280m^2; the national average outside of London is 188m^2 (Office for National Statistics, 2020).

Due to a limited number of tags available for testing (N = 6), tests of the nine settings within the two gardens could not be run simultaneously. Thus, tags were deployed on an ad-hoc basis throughout January-February 2022, and data of cloud cover were also collected. Future analysis will consider to what extent tag performance was influenced by natural conditions, as well as quantify location error, and ideally incorporate further garden sites. Presently, average fix success rates (taken as the mean from each of the two deployments in each setting and provided as a proportion of total scheduled fixes) are provided in Table H1.

Table H1. Fix success rate (FSR) averaged across two static deployments of GPS tags in varying settings in residential gardens.

Setting	**Average FSR**
Open	79.38
Adj. house	29.72
Adj. garden fence	61.63
Under shed	0.59
Under decking	26.70
Feeding station	72.74
Nest box 1 (wood)	79.79
Nest box 2 (wood; slate roof)	38.37
Nest box 3 (wicker)	39.58