Anthropogenic factors associated with West-European Hedgehog (*Erinaceus europaeus*) survival

Lucy Emma Bearman-Brown

Thesis submitted for the degree of Doctor of Philosophy (PhD)

School of Biological Sciences

Submitted August 2020

DECLARATION OF ORIGINAL AUTHORSHIP

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

Lucy Emma Bearman-Brown

DEDICATION

To Daniel Ball, affectionately known as Tex.

Your love for, and chat about, “hedgies” knew no bounds, so this is dedicated to you.

Rest well my friend.

“The fact is that no species has ever had such wholesale control over everything on earth, living or dead, as we now have. That lays upon us, whether we like it or not, an awesome responsibility. In our hands now lies not only our own future, but that of all other living creatures with whom we share the earth.”

Sir David Attenborough

ABSTRACT

Global biodiversity is declining at a rate comparable to previously documented mass extinctions and does not appear to be slowing despite extensive global collaboration in the academic community and policy change targets. This decline is expected to be greatest in terrestrial ecosystems due to anthropogenic factors particularly in two of the most pervasive forms of land change undertaken by humans; urbanisation and agricultural intensification which will lead to further significant changes in the species composition of ecological communities and abundance of species. For example, the West-European hedgehog (*Erinaceus europeaus*) population is declining substantially across its range as a result of anthropogenic activity, which is explored here.

The degree to which the rural environment has been altered may impact the survival of hedgehogs. As hibernation has previously been described as a high-risk time, over-winter survival and nesting behaviour in the rural, human-dominated landscape was investigated at two contrasting sites. Hedgehogs consistently nested near hedgerows, roads and woodlands, but avoided pasture fields. Differences between the sites were evident for arable fields, amenity grassland and buildings, such that different land management practices might influence hibernation success. Significant differences in survival and percentage mass loss between the two sites indicated that such land management practices may impact upon survival of hedgehogs, although mortalities occurred in autumn and spring, indicating winter is not the high-risk time previously described.

Whilst the value of woodland to hibernating hedgehogs was evident over-winter, methods for detecting hedgehogs in such complex habitats are limited. Therefore, the effectiveness of three methods (infra-red thermal camera, specialist search dog, spotlight) for detecting hedgehogs were compared in three different habitats. Significantly more hedgehogs were detected, and at greater distance, using the camera and dog than the spotlight in amenity grassland and pasture although no hedgehogs were detected in woodland. This could indicate that all three methods are not suitable for surveying in this habitat or that hedgehogs typically avoid woodlands during the summer and autumn, potentially as a strategy to avoid badgers.

To further explore the cause of mortality of hedgehogs, data from wildlife hospitals were analysed. Anthropogenic factors were responsible for up to 47% of admissions, whilst 51% of animals survived to release. Survival was highest for orphans (63%) but lowest for anthropogenic causes (39%). Comparatively few large hospitals (>250 hedgehogs year^{-1}) exist, but care for the majority of hedgehogs. The wild population is increased by an estimated 4-6% of the pre-breeding population nationally by rehabilitators, suggesting rehabilitation could have a marked benefit ameliorating some of the negative impacts of humans.

ACKNOWLEDGEMENTS

I am grateful for the support and guidance of my supervisor Dr Philip Baker (University of Reading) who guided me throughout the completion of this thesis. I am also grateful for the support of Dr Richard Yarnell (Nottingham Trent University) who supported a chapter of this thesis. Further support was provided by Dr Antonio Uzal (Nottingham Trent University) including advice, assistance and guidance with GIS for which I am grateful. Prof. Victoria Melfi (Hartpury University) provided invaluable support during the writing process,. I would also like to thank Louise Wilson (Conservation K9 Consultancy) for her huge contribution; training and handling Henry for the detection dog chapter and developing my understanding of the huge contribution dogs can make to conservation. Dr Vicky Boult provided input for GIS analysis for which I am hugely appreciative.

I would like to thank the People's Trust for Endangered Species (PTES) and British Hedgehog Preservation Society (BHPS) for financial support for two chapters, and extensive guidance throughout my PhD. Their contacts, direction and patience were invaluable. Further, I would like to thank Hartpury University for financial assistance and time to complete this work, as well as access to the estate where much of my fieldwork was completed.

Much of this work would not have been possible without the contribution of the volunteers who assisted with fieldwork. Particular mention must go to Catherine, Becky, Alice, James, Edward, Jenny, Ella, Frankie and Jessica for their extensive nights of surveying.

I am very grateful for the support provided by the Royal Society for the Prevention of Cruelty to Animals (RSPCA) for the provision of their data, which an entire chapter is based upon, and for the time it took the many respondents who completed the questionnaire described here, despite the request being made during the busy hoglet season.

Finally, I would like to thank everyone who has supported and believed in me throughout, particularly my family; Scott and Tia Bearman-Brown and Sue, Adrian, Natalie and Michael Clarke. I am not sure I would have had the resolve to complete this without your ongoing encouragement. Thank you for the patience, humour and love that meant I could finish this.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

APPENDICES

LIST OF FIGURES

CHAPTER ONE

CHAPTER TWO

CHAPTER THREE

CHAPTER FOUR

CHAPTER FIVE

APPENDICES

CHAPTER ONE

Introduction

Global biodiversity is declining at a rate comparable to previously documented mass extinctions (Parmesan, 2006; Firbank *et al.*, 2008; Barnosky *et al.*, 2011; Wagler, 2013; Ceballos and Ehrlich, 2018), and does not appear to be slowing despite extensive global collaboration in the academic community and policy change targets (Butchart *et al.*, 2010; Mace *et al.*, 2012; Tittensor *et al.*, 2014). The decline in biodiversity is greatest in terrestrial ecosystems (Crooks *et al.*, 2017; Sala *et al.*, 2017) due to anthropogenic factors, including, but not limited to: habitat loss, fragmentation and degradation; noise, light and chemical pollution; global climate change; the introduction of non-native species; and over-exploitation (Gurevitch and Padilla, 2004; Davies *et al.,* 2009; Schulte *et al.*, 2010; Barnosky *et al.*, 2011; Oliver *et al.,* 2015; Bond and Grasby, 2017; Stanton *et al.*, 2018). However, variation in cause and impact differs significantly between species and regions (Woinarski *et al.*, 2015; Crees *et al.,* 2016; Harris *et al.,* 2016). For example, Butchart *et al.* (2010) reported changes of: +3% (forest extent); -16% (terrestrial, habitat-specialist birds in Europe and North America); -9% (mangrove extent); -20% (seagrass extent); -31% (global vertebrates); -33% (global shorebirds); and -38% (coral reef condition). No taxon studied showed recent significant reductions in their rate of decline. Furthermore, the impact of these anthropogenic activities is expected to increase as the human population grows and expands (Tilman *et al.*, 2001; Crist *et al.*, 2017).

A major driver of biodiversity decline is habitat loss (Hoekstra *et al.*, 2005; Duro *et al.*, 2014) and two of the most pervasive forms of land change undertaken by humans are urbanisation and agricultural intensification (Burel *et al.*, 2004; Luck, 2007; Grimm *et al.*, 2008; Hahs *et al.*, 2009; Seto *et al.*, 2011), both of which are associated with the destruction of complex natural habitats and associated ecological communities (Hoekstra *et al.*, 2005; Grimm *et al.*, 2008; Seto *et al.*, 2011; Stanton *et al.*, 2018). Agricultural intensification affects biodiversity at all levels (Robinson and Sutherland, 2002), including microbiota (Banerjee *et al.,* 2019), invertebrates (Hallmann *et al.*, 2017), small mammals (Burel *et al.,* 2004) and birds (Hayhow *et al.,* 2017), with further concern expressed regarding the resilience of ecosystems following this depletion (Oliver *et al.*, 2015).

Both agricultural intensification and urbanisation are connected with different effects on soil characteristics and processes. Agriculture is associated with soil erosion, degradation, compaction and desertification, leading to long term declines in productivity and its environment moderating capacity (Lal, 2001; Vanwalleghem *et al.*, 2017). For example, each year, an estimated 24 billion tons of fertile soil are lost due to erosion (Beck *et al.*, 2016). Likewise, the extent of non-porous surfaces in urban areas leads to the urban heat island effect resulting in an average increase of 2.9°C above the non-urban fringe, with a 4.3°C temperature difference in summer and 1.3°C in winter (Imhoff *et al.*, 2010). In agricultural landscapes, complex systems are replaced with monocultures, whilst in urban areas primary producers are substantially reduced in both diversity and coverage; such changes fundamentally alter ecosystem resilience (Matsushita *et al.*, 2016) and ecosystem services (Hahs *et al.*, 2009). Furthermore, changes in urban areas may affect rural landscapes, and vice versa. For example, as increasing amounts of land are covered with non-porous surfaces the water cycle is significantly altered, resulting in poor water quality in agricultural areas and increased rates of water abstraction (Fischer *et al.*, 2007) whilst urban areas suffer from flash flooding and increased levels of water pollution (Hahs *et al.*, 2009).

Pollution is a pervasive element of both agricultural intensification and urbanisation. Urban areas are routinely affected by light and noise pollution, which have the potential to affect the physiology, behaviour and reproduction of a range of plant and animal taxa, including changes in foraging and reproductive behaviours, reduction in fitness, increased risk of predation and reduced reproductive success (Longcore and Rich, 2004; Newport *et al.*, 2014). Agricultural areas are widely affected by chemical pollution from fertilisers and pesticides leaching into ground water (Parris, 2011). Whilst the overall pressure of agriculture on water quality in rivers, lakes, groundwater and coastal waters has eased since the early 1990s due to the decline in nutrient surpluses and pesticide use, for nearly half of the Organisation for Economic Co-operation and Development (OECD) countries absolute levels of agricultural nutrient pollution exceed national drinking water limits (Parris, 2011).

Significant changes in the species composition of ecological communities have been documented in both urbanised and intensively farmed areas (Geiger *et al.*, 2010). The homogenisation of the landscape favours generalist species over specialist species (McKinney, 2006), resulting in some generalist species positively benefitting from the creation of urban and/or agricultural areas. These species, described by Blair (1996) as urban adapters, hold the ability to exploit abundant food subsidies and other resources, which allows them to attain inflated population densities (Bateman and Fleming, 2012). For example, the red fox (*Vulpes vulpes*) occupies the widest geographic range of any species of carnivore, with human-facilitated introduction to both North America and Australia fundamental to its global range expansion (Lewis *et al.*, 1999). Once introduced, the species quickly exploited a wide range of habitats including intensively farmed, and latterly, highly urbanised areas (Lewis *et al.*, 1999; Scott *et al.*, 2014). Agricultural areas are also associated with additional negative effects on mammalian predators arising from the production and protection of livestock, such as deliberate persecution, reduced food web complexity, less stable food webs and the risk of trophic cascades (Freilich *et al.*, 2003; Hooper *et al.*, 2005; Baker *et al.*, 2008a; Otto *et al.*, 2008). As diversity and ecosystem function are more complex at higher trophic levels, understanding of how biodiversity loss may propagate through the ecosystem is crucial where significant anthropogenic change is evident (Thebault and Loreau, 2003; Worm and Duffy, 2003; Hooper *et al.*, 2005).

As the human population increases, both urban areas and agricultural production will inevitably increase, along with the progressive move of large numbers of people from rural areas to urban areas. The rate of urban expansion, driven by growth in GDP and human population expansion, varies globally, peaking at 13% per annum in coastal China (Seto *et al.,* 2011). Fifty-five percent of the global population are now urban dwellers, up from 30% in 1950 and which is projected to reach 68% by 2050 (United Nations, 2019). Associated with this change, agricultural production will also need to approximately double, but for food and for increasing bioenergy use (Beck *et al.*, 2016). Agricultural land covers approximately 38% (4.91 billion hectares) of Earth’s ice-free land, an increase by nearly 3% (154 million hectares) between 1985 and 2005 (Foley *et al.*, 2011). Should historic patterns of human population growth and consumption continue, the extent of natural ecosystems requiring conversion to agricultural land is expected to increase by 10^9 hectares by 2050 (Tilman *et al.*, 2001).

Biodiversity changes in the UK

The decline in biodiversity across the United Kingdom (UK) is well defined (Hayhow *et al.*, 2016; Martay *et al.*, 2017; Defra, 2018). Long-term declines in the relative abundance and range of 75% of the 215 priority species monitored by the Joint Nature Conservation Committee (JNCC) since 1970 have been recorded (Defra, 2018; Figure 1.1), despite extensive financial investments and conservation (Laycock *et al.*, 2011; McCarthy *et al.*, 2012). For example, the hazel dormouse (*Muscardinus avellanarius*), a European Protected Species, has been closely monitored throughout the UK since the late 1980s through the National Dormouse Monitoring Programme. Recent analysis of these data, however, has indicated a population decrease of 72% from 1993 to 2014, equivalent to a mean annual reduction of 6% (Goodwin *et al.,* 2017), even though significant efforts have been made to address the underlying causes of decline (Bright *et al.*, 2006).

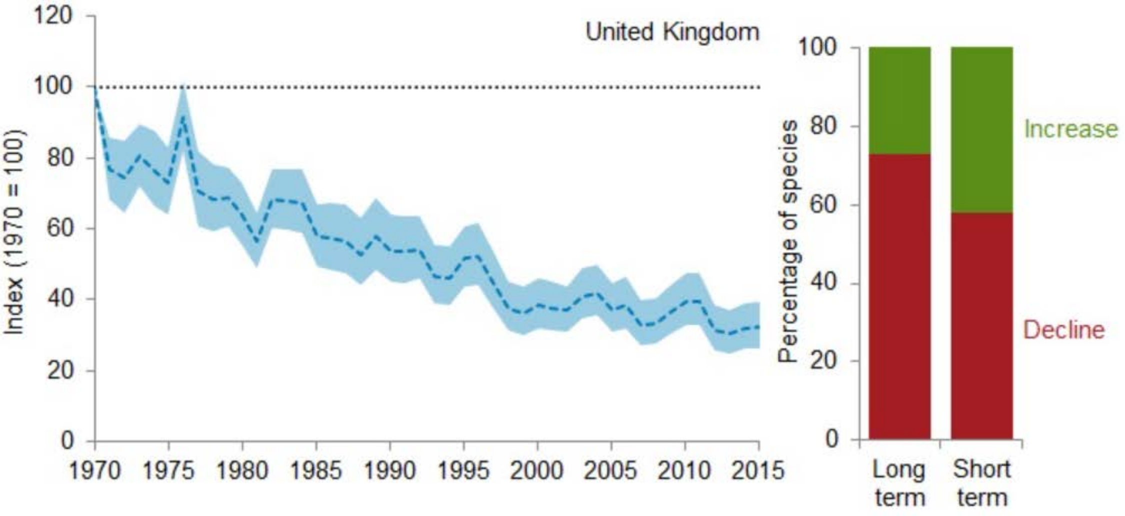


Figure 1.1. Change in the relative abundance of 215 priority species (103 birds, 80 moths, 21 butterflies, 11 mammals) in the UK (Defra, 2018). Counts are standardised to 1970. Bar chart indicates the percentage of species increasing or declining over the long- (1970-2015) and short-term (2010-2015).

The decline in vascular plants was widely reported in 2014 when the first Red List for Vascular Plants was launched (Stroh *et al.,* 2014), highlighting that one fifth of England's wildflower species are under threat, with the majority of these threatened species suffering a decline of 30% or more, many of which were once widely regarded as commonplace; almost one in five species were assessed as threatened. Such declines have been mirrored by invertebrate species, with a 68% decline in the habitat specialist butterflies index and a 30% decline in the index for butterfly species of the wider countryside (Defra, 2019a). Similarly, the status of pollinator index declined by 31% from 1980 to 2016, with a 10% decrease between 2011 and 2016 alone (Defra, 2019b). Invertebrates providing pest control and pollination functions in ecosystems in the UK have shown declines of 16% and 27%, respectively, from 1970 to 2009 (Oliver *et al.,* 2015).

In the same vein, breeding bird abundance has also declined markedly. In the latest review of Birds of Conservation Concern, 20 species were moved to the Red List, a net increase of 16 species since the previous review in 2009; the number of red listed species now stands at 67, its highest ever total (Eaton *et al.*, 2015; Harris *et al.*, 2018). Within this general context, habitat-specific differences are also evident; for example, farmland birds have declined by 9% between 2010 and 2015, woodland birds by 23% since the 1970s and water and wetland birds have declined by 8% since 1975 (Hayhow *et al.,* 2017).

In comparison, the status of mammal species within the UK is less clear. Of 58 species reviewed by Mathews *et al.* (2018) , the geographic range and/or population of just four (7%) and nine (16%) species, respectively, were considered to have declined since the mid-1990s (Harris *et al.,* 1995). However, these parameters could not be estimated for 14 (24%) and 30 (52%) species, respectively, reflecting the difficulties associated with both monitoring mammal populations *per se* and the lack of density estimates for many species. Furthermore, Harris *et al.* (1995) and Mathews *et al.* (2018) employed slightly different analytical techniques such that the data presented in both publications are not directly comparable.

In comparison, data for a subset of nine mammalian species recorded as part of the British Trust for Ornithology's (BTO) *Breeding Bird Survey* (Harris *et al.*, 2020) indicate declines in four (44%) species, including previously common species such as the red fox and the European rabbit (*Oryctolagus cuniculus*). Again, however, these general patterns cannot easily be compared with those of Mathews *et al.* (2018) because of differences in the range of species studied and differences in the methodologies applied.

Despite the caveats associated with comparing data which have been collected, analysed and presented in different ways, these examples illustrate that a broad range of taxonomic groups have experienced declines in the UK over the last 50 years. To help redress these declines, and their potential effects on ecosystem services and resilience (Oliver *et al.,* 2015), a comprehensive understanding of anthropogenic pressures on populations at both local and national scales is fundamental for guiding future conservation efforts (National Research Council, 1992). Obtaining such evidence can, however, be challenging because of financial limitations, but also because of the inherent practical problems associated with studying those species of concern. One such species of interest in the UK at the current time is the West-European hedgehog (*Erinaceus europaeus*) (Linnaeus, 1758).

Evidence for a decline in British hedgehog numbers

The West-European hedgehog is a nocturnal, solitary, insectivorous mammal, native to much of Western Europe, the Iberian Peninsula and Italy northwards into Scandinavia (Morris and Reeve, 2008). To the east, the species is replaced by the Northern white-breasted hedgehog (*Erinaceus roumanicus*) although the range of the two species overlap to a limited degree in Eastern Europe, through the Czech Republic (Reeve, 1994; Amori, 2016), north to Poland and the Baltic countries and southern Russia (Morris, 2018) (Figure 1.2). In southern Spain, the West-European hedgehog is syntopic with the Algerian hedgehog (*Atelerix algirus*); the latter is found throughout North Africa, the south-eastern coastal region of the Iberian Peninsula and the Canary and Balearic Islands. The continental European population of *A. algeirus* is believed to be a recent anthropogenic introduction (Khaldi *et al.,* 2016). The Southern white-breasted hedgehog (*E. concolor*) is distributed from Turkey, to Azerbaijan, south into Jordan and Israel and north to the Caucasus mountains, with no overlap with similar species (Amori, 2016b).

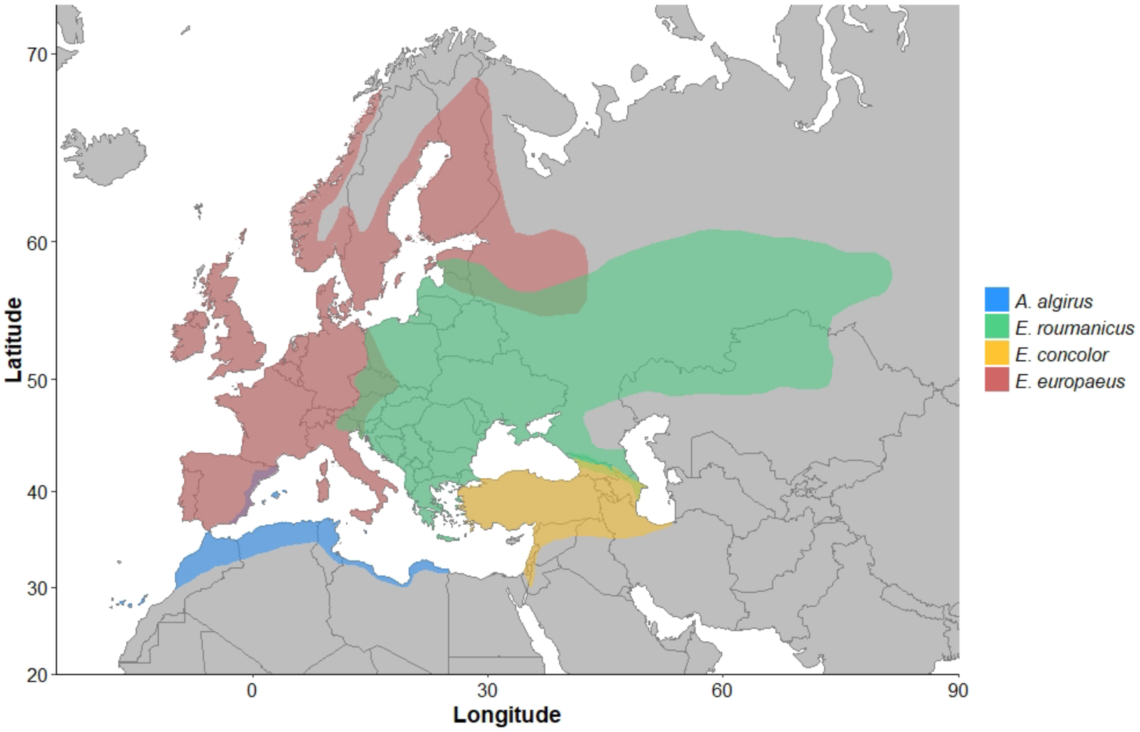


Figure 1.2. The geographical distribution of the Algerian hedgehog (*Atelerix algirus*), Northern white-breasted hedgehog (*Erinaceus roumanicus*), Southern white-breasted hedgehog (*Erinaceus concolor*) and West-European hedgehog (*Erinaceus europaeus*) in Europe (Adapted from: (Amori, 2016a); created by V. Boult).

The West-European hedgehog has also been introduced to many islands within the UK, including the Uist Islands in Scotland, as well as into New Zealand (Reeve, 1994). In some of these areas, the species poses significant conservation problems for native species (Jackson and Green, 2000; Jackson, 2007; Bolfíková *et al.*, 2013), so is controlled as an invasive species (Global Invasive Species Database, 2020).

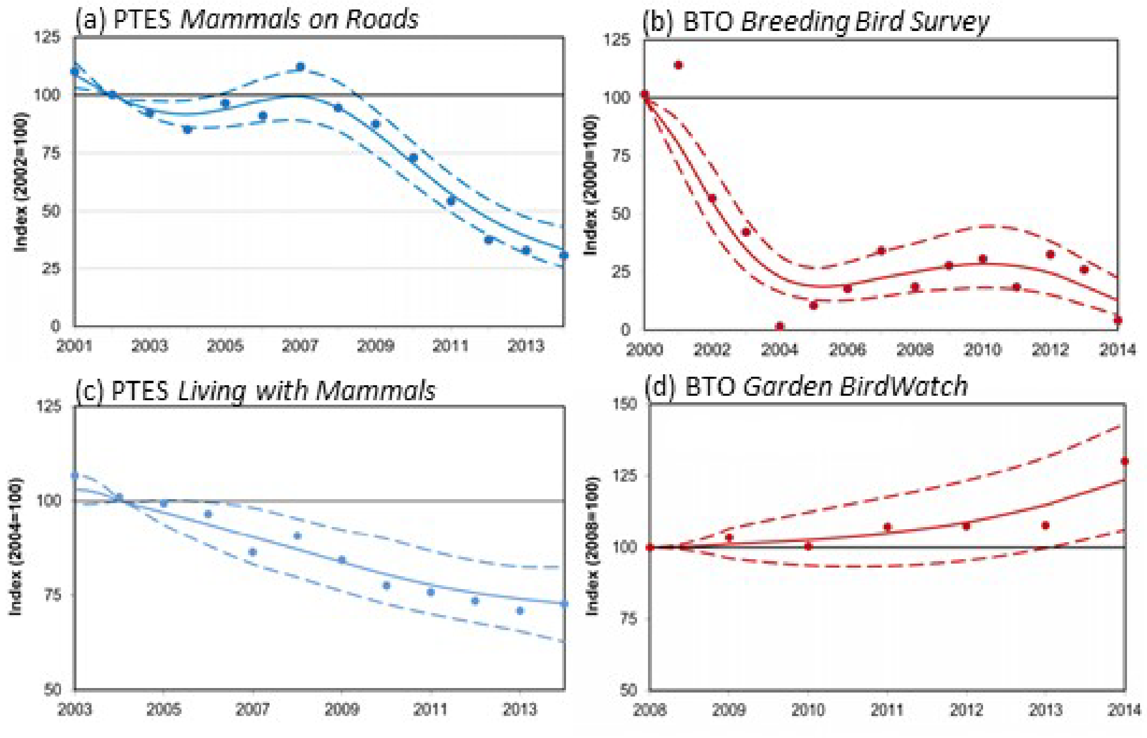
The West European hedgehog (hereafter “hedgehog”) is identified as Least Concern by the International Union for the Conservation of Nature (IUCN), as it is common throughout its extensive range (Amori, 2016a). It is protected under Appendix III (Protected Fauna Species) of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention) (Council of Europe, 1982), and is protected in the UK under the Wildlife and Countryside Act (1981), listed as Schedule 6.

Whilst considered locally common, the population in the UK is believed to be declining (Battersby, 2005; Hof and Bright, 2016; Mathews *et al.*, 2018; Williams *et al.*, 2018a) and has recently been listed as Vulnerable in the IUCN Red List for Great Britain’s Mammals (The Mammal Society, 2020). However, accurate estimates for hedgehog populations are currently not available (Croft *et al.,* 2017), in part because of its elusive, nocturnal behaviour. For example, Harris *et al.* (1995) estimated a British population of 1.5 million, although this was considered of low reliability as it was based on just four estimates of hedgehog density which were then applied to 32 land classes. More recently, Mathews *et al.* (2018a) estimated overall population size by first interpolating the species' geographic range based upon data held in The National Biodiversity Network gateway, local record centres, national and local monitoring schemes and iRecord (Mathews *et al.*, 2018), and then multiplying by habitat-specific density estimates by the extent of these habitats within the geographical range. These authors estimated that the national population may number just 522,000 pre-breeding individuals, although they also assigned their estimate a low reliability score as the volume of habitat-specific density estimates was similarly low; the estimates for urban and gardens and improved grassland were derived from just one study (Parrott *et al.*, 2014), whereas those for arable and horticulture, broadleaved woodland, coniferous woodland and unimproved grassland were taken from the original report by Harris *et al*. (1995).

Despite limitations associated with estimating densities *per se* (but see Schaus *et al.,* 2020), ongoing monitoring programmes consistently indicate that rural hedgehog populations in the UK are continuing to decline, potentially at a rate of 2 - 11% per annum (Wembridge, 2015, 2011; Figure 1.3 a-b). Similar patterns of decline have also been recorded based upon presence-absence data at a 10x10 km^2 grid cell scale across England (5.0-7.4% decline from 1960-2015: Hof and Bright 2016). Mathews *et al.* (2018) notes however, that declines appear to be in the density of populations rather than a contraction of the range, which appears to have remained relatively stable since consideration in the early 1990s (Arnold, 1993). This is consistent with the reduction in occupancy documented by Williams *et al.* (2018a). Comparable declines have been reported in other European countries, including Belgium (Holsbeek *et al.*, 1999), Germany (Müller, 2018), Italy (Canova and Balestrieri, 2019) and the Netherlands (Huijser and Bergers, 2000; Van de Poel *et al.,* 2015).

There are, however, noticeable difference in trends between rural (Figure 1.3 a-b) and urban (Figure 1.3 c-d) landscapes. Hedgehogs were present in 10% (BTO *Breeding Bird Survey*) and 16% (BTO *Waterways Breeding Bird Survey*) of sites surveyed in rural habitats compared to 25% (People's Trust for Endangered Species (PTES) *Living with*

Mammals) and 44% (BTO *Garden BirdWatch*) of sites surveyed in urban habitats. These differences are likely to reflect a combination of factors including variation in population density, habitat suitability and habitat utilisation. Conversely, this may potentially illustrate differences in the detectability of hedgehogs in the two landscapes based upon the survey methodologies used. For example, surveys with a primarily ornithological focus are likely to under-record hedgehogs which are active at night. In addition, volunteers in these bird surveys are also able to decide to record hedgehogs (and other mammal species) or not; such "opt in" approaches may increase the likelihood that surveyors who do detect hedgehogs (e.g. from animals dead on the roads, or through discussions with local landowners) end up choosing to include this species. On the positive side, however, the surveys run by the BTO are generally extensive, and this geographic scope generates large numbers of records throughout England, Scotland and Wales.


(a) PTES *Mammals on Roads*

(b) BTO *Breeding Bird Survey*

(c) PTES *Living with Mammals*

(d) BTO *Garden BirdWatch*

Figure 1.3. Trends in UK hedgehog population as estimated by four different monitoring schemes: (a) PTES *Mammals on Roads* and (b) BTO *Breeding Bird Survey* reflect changes in rural hedgehogs; (c) *PTES Living with Mammals* and (d) *BTO Garden BirdWatch* reflect changes in urban hedgehogs. Solid lines show smoothed trends; dashed lines show 95% confidence limits. Estimates for each year (circles) are calculated as an index relative to the 'base year' indicated by the solid horizontal line (from Wembridge, 2015).

These differences in the direction and/or magnitude of population changes between the two landscapes could result in future differences in population trends (Macdonald and Burnham, 2011). Limited connectivity between patches of suitable habitat and the potential movement of hedgehogs from rural to urban/suburban areas may make this particularly significant (Doncaster *et al.,* 2001; Young *et al.,* 2006; Baker and Harris, 2007; Hubert *et al.,* 2011; van de Poel *et al.,* 2015; Pettett *et al.,* 2017b; Williams *et al.*, 2018a). Estimates of density within improved grassland are considerably lower than those in gardens and urban areas (Parrott *et al.*, 2014: 0.04 km^{-2} and 0.54 km^{-2} respectively; Micol *et al.*, 1994: 3.9 ±0.8 and 0.7 ±0.2 hedgehogs per field respectively). Most recently, Schaus *et al.* (2020) used motion-activated trail cameras and spatial-capture-recapture methods to estimate densities of 4.3 and 32.3 hedgehogs per km^{-2} in rural versus urban habitats, respectively.

The decline of a once common, widespread, generalist species such as the hedgehog is of significant concern (Hof, 2009) as it is likely to indicate a general deterioration in the environmental quality of the landscape, and may have far-reaching implications. Such changes may have more severe implications for less mobile taxa, which have to cope with increasingly fragmented landscapes. Morris (2018) describes hedgehogs as bio-indicators, as their presence is indicative of sustainable populations of macro-invertebrates, whose larvae and adult forms perform vital ecological function for a wide range of other species at all trophic levels.

The species is a generalist predator, focusing largely on macroinvertebrates, but able to consume a broad diet including frogs, bird eggs and chicks, juvenile rodents, carrion and fallen fruit (Reeve, 1994; Morris, 2018;). Soft-bodied prey, such as earthworms, slugs, caterpillars and larvae, are preferentially selected over hard-bodied macroinvertebrates, possibly as a result of increased nutritional value due to decreased chitin, although earwigs and beetles do regularly feature in the diet (Yalden, 1976; Rautio *et al.,* 2016). Hedgehog abundance has been shown to be positively correlated with the earthworm abundance (Doncaster, 1994; Micol *et al.,* 1994; Young *et al.,* 2006).   Throughout urban areas, their diet is heavily supported by anthropogenic foodstuffs, including pet food, sunflower seeds and nuts (Hubert *et al.,* 2011; Rautio *et al.,* 2016; Pettett *et al*., 2017b); some of these may, however, have detrimental effects by increasing dental decay and bone degradation, and urban hedgehogs are also occasionally poisoned through the consumption of rodents and slugs that have been poisoned by householders or pest control personnel.

Factors associated with the decline in UK hedgehog numbers

The decline in the UK hedgehog population has been attributed to a range of factors in both rural and urban landscapes. However, the relative importance of, and interactions between, each of these factors is currently not known. In particular, the underlying biological mechanisms associated with these factors are poorly understood. For example, the negative correlation observed between badgers (*Meles meles*) and hedgehogs could be attributed to competition, predator avoidance and/or predation. Similarly, the increased tendency for hedgehogs to be found in areas associated with human habitation may be a result of, amongst other things: predator avoidance; increased food availability; increased availability of refugia for resting, breeding and hibernation; and micro-habitat differences in ambient temperature.

Factors associated with the decline in hedgehogs in rural landscapes

In rural landscapes, the factors most likely to have had a negative impact on hedgehogs are habitat loss, habitat fragmentation, habitat degradation, climate change and intra-guild predation.

Habitat loss

Agricultural intensification has been a major cause of habitat loss across Europe since 1945, with a move towards a less diverse landscape (Robinson and Sutherland, 2002; Firbank *et al.*, 2008; Stoate *et al.*, 2009; Tscharntke *et al.*, 2012; Veach *et al.*, 2017). The fragmentation of natural or semi-natural habitat through the introduction of areas of arable or pastoral land creates a mosaic habitat, including areas of semi-natural grassland, hedgerows, field margins, ditches, woodland, set-aside and waterways (Robinson and Sutherland, 2002). One habitat that has been notably affected by agricultural intensification, and which is considered intimately important for hedgehogs (the name hedgehog is derived from the Middle English “heyghoge” from “heyg” or “hegge” because of its tendency to be found near hedgerows, and “hoge”or “hogge” from its pig-like snout and grunting noises that it often makes), are hedgerows.

As agricultural production intensified after the Second World War, hedgerows were removed to increase field sizes and facilitate access for farming machinery (Barr and Gillespie, 2000; Benton *et al.*, 2003). It is estimated that 24,600 km of hedgerow (4% of national total) was removed between 1977 and 1984, with a further 121,000 km (22% of national total) removed by 1990 (Barr *et al.,* 1990). In addition to the physical removal of hedgerows, further losses have been attributed to under-management, resulting in successional development into a treeline, or over-management to the point they become little more than a line of shrubs (Barr and Gillespie 2000). One particular change associated with this overall decline was the decrease in the length of single species hedgerows, which are more frequently found between fields rather than along road sides (Barr and Gillespie, 2000).

The loss of hedgerows is likely to have had a multitude of effects on hedgehogs historically as they are likely to have been important for nesting/breeding hibernating, as a source of food, as a refuge from predators and for navigation through the landscape. All of these important roles in the ecology of hedgehogs are still evident today (Hof, 2009; Moorhouse *et al.*, 2014; Pettett *et al.*, 2017b). However, as hedgehogs are generally associated with edge habitats, utilising the boundaries between fields, woodland fragments and areas of grassland (Morris, 1986; Dowie, 1993; Huijser, 2000; Hof and Bright, 2010a, 2012, 2016; Williams *et al.*, 2018a), they are likely to have benefitted (albeit only marginally) from the creation of heterogeneous landscapes. But it is the creation of large tracts of crop monocultures, typically associated with the widespread use of chemicals, that appear to have been especially detrimental (Doncaster, 1994; Haigh *et al.*, 2009; Hubert *et al.*, 2011; Hof and Bright, 2012; Van de Poel *et al.*, 2015; Williams *et al.*, 2018a; but see Pettett *et al.*, 2017b)

Habitat fragmentation

Whilst habitat loss, degradation and fragmentation are frequently concurrent, they are distinct phenomena, and can occur in isolation (Curtis, 1956; Moore, 1962; Fahrig, 2019). Together they lead to a reduction in total suitable habitat availability, resulting in an otherwise heterogeneous habitat becoming divided into smaller, less suitable patches embedded within a landscape of inhospitable space (Fahrig, 1997; Villard *et al.,* 1999; Guerry and Hunter, 2002). The loss in total habitat availability, decline in the quality of that remaining habitat and the isolation of suitable habitat patches have been identified as a significant driver for the loss of global biodiversity and the key cause of biodiversity loss in terrestrial ecosystems (Sala *et al.,* 2017).

Fragmentation, degradation and loss have been identified as threats to a wide range of taxa, and have large scale impacts on landscape dynamics, with the potential to put populations at risk of reaching their extinction threshold (Crooks *et al.,* 2017). For example, 27% of mammalian species globally are threatened with extinction, and the loss and degradation of habitat has been implicated as a primary threat (Schipper *et al.,* 2008). This decline can result from a range of mechanisms, including the creation of detrimental edge effects between habitat patches, limit to the movement of animal and gene flow, and severing of landscape connectivity (Crooks and Sanjayan, 2006). Mammalian species classified as threatened in the World Conservation Union (IUCN) Red List experience higher levels of habitat fragmentation than those classified as Least Concern and Near Threatened (Crooks *et al.,* 2017), indicating the impact of such processes on species survival.

Although the loss of habitats poses a direct risk to hedgehogs at the point that they are physically removed, it is the resultant longer-term reductions in the number of nesting, breeding and hibernation sites, food availability and connectivity between subpopulations (leading to reduced gene flow: Andren, 1999; Morris, 2018) that are ultimately more detrimental. The magnitude of the impact arising from habitat fragmentation is dependent on a range of inter-related components including: the size of remaining fragments and how they meet the needs of individuals; the rate at which sub-populations go extinct; and patterns of dispersal (Moorhouse *et al.*, 2014) and mating between sub-populations. Landscape fragmentation is significant across the European Union (EU): by 2015, around 28% of the landscape in the EU was classified as strongly or very strongly fragmented, equating to approximately 1.127 million km^{-2} (European Environment Agency, 2019).

Globally, the major fragmentation issue affecting wildlife is the creation and expansion of the road network and associated increases in traffic volume (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Eigenbrod *et al.,* 2008; Ibisch *et al.*, 2017; Wright *et al.,* 2020). Traffic usage in the UK increased by 28% from 1993-2018, with 44% of all motor vehicle traffic on rural A and rural minor roads by 2018 (Havaei-Ahary, 2019). Roads can create an impermeable barrier for some wildlife species (Forman and Alexander, 1998; Trombulak and Frissell, 2000), with body mass an influencing factor (Chen and Koprowski, 2019). For example, hedgehogs have been found to be unwilling to cross roads, with 50% of radio-tracked hedgehogs not crossing a single road during observations, and only 25% of observed trajectories crossing roads of any size (Rondinini and Doncaster, 2002). Similarly, hedgehog abundance has been reported to be approximately 30% lower near roads, suggesting factors associated with habitat quality in the vicinity of roads may also be important (Huijser and Bergers, 2000).

Roads also pose a risk of direct mortality through wildlife-vehicle collisions (WVC) (Lesiński *et al.,* 2011; Nelli *et al.,* 2018; Fabrizio *et al.,* 2019), with an estimated one million animals killed on Great Britain's roads annually including 100,000-300,000 hedgehogs (Roos *et al.,* 2012; Wembridge *et al.,* 2016); similar numbers have also been estimated in Belgium (Holsbeek *et al.,* 1999) and the Netherlands (Huijser *et al.,* 1998), and Rautio *et al.,* (2016) also recorded a mean of 0.65 hedgehogs killed per 100 km^{-1} of road transect in their study in Finland. Consequently, WVCs can account for a large proportion of overall deaths in hedgehog populations (Reeve, 1998; Doncaster *et al.*, 2001).

Hedgehog vehicle collisions peak in July, and are at their lowest during the winter months (Holsbeek *et al.*, 1999; Haigh *et al.*, 2014b; Canova and Balestrieri, 2019; Wright *et al.*, 2020), in relation to patterns of mating behaviour, reproductive output and hibernation (Rautio *et al.,* 2016). As outlined above, counts of dead hedgehogs on roads have been used in Great Britain as part of a long-term monitoring programme (Figure 3a), although no study to date has demonstrated that such counts actually reflect population size for this species, although data for other species indicate that they may (Baker *et al.*, 2004; Canova and Balestrieri, 2019). In addition, the location and/or frequency of hedgehog vehicle collisions are also influenced by road and roadside characteristics, as well as correlated with patterns of habitat composition (Hof and Bright, 2009; Pettett *et al.* 2017b; Santos *et al.*, 2018; Wright *et al.*, 2020); these relationships imply that the characteristics of certain locations may increase (or decrease) the likelihood that hedgehogs are killed and/or that more hedgehogs are killed on roads as animal density increases.

Habitat degradation

Food availability in the landscape will undoubtedly affect both the presence and abundance of hedgehogs (Kristiansson, 1984). Within rural landscapes, the widespread use of herbicides, insecticides and molluscicides has led to the reduced abundance of soil macro-invertebrates (Decaëns and Jimenez, 2002; Zhiping *et al.*, 2006; Nkem *et al.*, 2020), and have been proposed as a cause of the lower abundance and reduced distribution of hedgehogs in arable landscapes (Pettett *et al.*, 2017b). However, these effects will vary between different habitats and different taxa within those habitats. For example, Hubert *et al.* (2011) recorded earthworm abundance at approximately three times higher in pasture (933 ± 214 kg/ha) than in arable (284 ± 97 kg/ha) fields, whereas arthropod abundance was four times higher in arable (3325 ± 940 kg/ha) than pasture (852 ± 217 kg/ha) fields. One potential approach to help reduce these effects is through the use of, for example, grassy field margins and beetle banks (Vickery *et al*., 2009; Hof and Bright, 2010a).

However, the effects of food availability on hedgehog distribution, density, reproduction and survival in England and Wales are, at the current time, heavily influenced by badgers, an inter-guild predator (see below), whose numbers have approximately doubled in recent decades (Judge *et al*., 2014, 2017) (data are lacking for other nations within the UK). It is important to note, therefore, that whilst reduced food availability is often cited as a reason for the decline in hedgehog numbers (e.g. Wilson and Wembridge, 2018), the availability of macro-invertebrate prey must have been sufficiently high to sustain this increase. For example, Morris (unpublished data) suggested that one badger could consume the same number of earthworms as seven hedgehogs. Conversely, in their occupancy study, Williams *et al.* (2018a) reported that more than a quarter (27%) of the sites they surveyed had no badger setts nor hedgehogs.

In addition to the use of agricultural chemicals, the increased use of heavy machinery may also have further reduced macroinvertebrate abundance through soil compaction, although there are few data on this.

Climate change

The Intergovernmental Panel on Climate Change (IPCC) defines climate change as a change in the state of the climate that can be identified by changes in the mean and/or the variability of its properties and that persists for an extended period of time, typically decades (IPCC, 2007). Climate change has been identified as a key driver behind extinctions in a wide range of species globally (Thomas *et al.,* 2004; Urban, 2015; Wan *et al.,* 2019) and as a threat to ecosystem function (McCarty, 2001; Nolan *et al.,* 2018). Whilst coral reefs (e.g. Baker *et al.,* 2008b; Hoegh-Guldberg, 2011; Graham *et al.,* 2020) and the polar regions (e.g. Lee *et al.,* 2017; Amélineau *et al.,* 2019; Box *et al.,* 2019) are most widely studied, climate change affects all ecosystems. Such changes may affect species directly, such as through change in temperature making an area inhospitable, or indirectly, such as through changes in food diversity and abundance; these may then lead to e.g. alterations in species' distribution, changes in key demographic variables, population isolation and increased risk of disease (Mawdsley *et al.,* 2009).

Species-specific examples of the impact of climate change are extensive, and represent every major taxon, across the globe. For example, polar bear (*Ursus maritimus*) populations are predicted to suffer drastic declines by the end of the 21st century (Hunter *et al.,* 2010), Mauritius kestrels (*Falco punctatus*) experienced reduced reproductive success during wetter spring seasons (Senapathi *et al.,* 2011), and warmer winters are associated with earlier breeding but reduced female fecundity in the wood frog (*Rana sylvatica*) (Benard, 2015). However, climate change may positively impact reproductive efforts: for example, the population of badgers in Wytham Woods, Oxfordshire, increased from 60 to 228 adults over a 10-year period, as warmer winters are believed to have led to increases in January body weight (Macdonald and Newman, 2006).

In general, warmer conditions have been shown to support greater hedgehog survival and breeding success on the Hebridean island of South Uist (Jackson, 2007). However, warm summers are also associated with an increase in admissions of hedgehogs to wildlife hospitals (Dowding, 2007); this may be associated with reduced food availability at the point many juvenile animals become independent, but is also potentially likely to affect all animals as they try to accumulate sufficient fat reserves prior to hibernation (Rasmussen *et al.,* 2019a). Warm weather during winter may also increase the frequency with which animals rouse from hibernation at a time where natural food availability is low, possibly reducing over-winter survival rates. In addition, by nesting, breeding and hibernating at (or below) ground level, hedgehogs are also vulnerable to the increased frequency of flooding events associated with climate change. This is particularly the case during winter, when rousing from hibernation can take several hours (Walhovd, 1979).

Intra-guild predation

Whilst a range of species including red foxes (*Vulpes vulpes*) (Harris, 1981; Doncaster *et al.,* 1990), domestic dogs (*Canis lupus familiaris*) (Stocker, 2005; Morris and Reeve, 2007) and birds of prey (Sergio *et al.,* 2003; Mikkola and Tornberg, 2014) kill hedgehogs, the Eurasian badger is typically the only one considered to have a significant impact on the population in the UK (Reeve, 1994). Badgers are generalist omnivores, primarily consuming invertebrates and plant matter (Roper, 2010), although they do eat smaller mammals including hedgehogs (Doncaster, 1992, 1994; Micol *et al.,* 1994; Goszczyński *et al.,* 2000; Del Bove and Isotti, 2001; Young *et al.,* 2006); they are the only species known to be able to uncurl and kill a defensive hedgehog (Doncaster, 1992; Ward *et al.,* 1997). Hedgehogs generally occur in the diet of badgers at low proportions, for example: 3% and 12% occurrence in badger scats in Italy (Del Bove and Isotti, 2001) and Poland (Goszczyński *et al.,* 2000) respectively, although as many as four hedgehog remains were found in the stomach of one single adult found in England (Middleton, 1935). Badgers also, however, compete with hedgehogs for food, making them an intra-guild predator (Polis *et al.*, 1989). Badger presence/increased density has been shown to negatively affect the density (Young *et al.*, 2006; Trewby *et al.*, 2014; Hof *et al.*, 2019) and occupancy (Williams *et al.*, 2018a) of hedgehogs in rural landscapes (see also Pettett *et al.*, 2018b).

Following enhanced legal protection in 1974, badger numbers in England and Wales have increased from approximately 250,000 in the 1980s, to 485,000 in 2014 (Judge *et al.*, 2014, 2017). Whilst badger densities are higher in England and Wales than elsewhere in the native range (Johnson *et al.,* 2002), this increase is replicated in continental Europe (van Moll, 2005). In England and Wales the badger population is typically concentrated in lowland pastoral landscapes (Judge *et al.,* 2014, 2017) which is also favourable to hedgehogs in the absence of badgers (Hof *et al.,* 2019). However, hedgehog abundance is now thought to be higher in areas that are generally less suitable, such as areas dominated by arable land, due to a lower abundance of badgers (Hof *et al*., 2019).

Hedgehogs are absent from areas of higher badger abundance (Micol *et al.*, 1994; Young *et al.*, 2006; Parrott *et al.*, 2014; Williams *et al.*, 2018a), and breed at lower levels close to badger setts (Hubert *et al.*, 2011). In the early 1990s Micol *et al.* (1994) postulated that hedgehogs would be absent from most areas with badger sett densities above 0.23 km^{-2}. However, this limit has been exceeded throughout much of England and Wales, with Judge *et al.,* (2014, 2017) recording badger sett densities ranging from 0.26 km^{-2} in upland areas to 5.98 km^{-}2 in undulating pastoral areas. Despite this change, hedgehogs were present in a recent survey of England and Wales in areas where badger sett density was <3.29 main setts km^{-2} (Williams *et al.*, 2018a) suggesting that the species is possibly more able to co-exist with badgers than suggested by Micol *et al.*'s earlier study.

Similarly, hedgehog counts on amenity grassland, a key habitat for hedgehogs (Parrott *et al.*, 2014; Pettett, *et al.*, 2017b), varied from 0.2–1.0 hedgehogs ha^{-1} in areas where badgers were not culled as part of the Randomised Badger Culling Trial to investigate the effect of different culling strategies on the prevalence of bovine tuberculosis in cattle, to 0.9–2.4 ha^{-1} in where badgers were culled (Trewby *et al.,* 2014). The speed and magnitude of this change (mean hedgehog abundance approximately doubled in one year but was then stable for three more years before increasing again) suggest two possible mechanisms. First, the increased number of hedgehogs observed as badger numbers were reduced could reflect increased reproduction and/or survival rates; this mechanism would suggest that the greater impact of badgers is via predation. Second, as hedgehogs actively avoid badger odour when foraging (Ward *et al.,* 1997; Monclús *et al.,* 2006; Hof and Bright, 2012), the increase in hedgehog “numbers” observed could simply reflect the re-colonisation of habitat which they were avoiding; this mechanism would suggest the larger impact of badgers may be via avoidance. Unfortunately, no study to date has quantified how the movement patterns of hedgehogs change in response to the removal of badgers.

One consistent observation from a growing number of studies, however, is that hedgehogs appear to be increasingly common in areas of human habitation, including urban areas, as these are less frequently occupied by badgers (Doncaster, 1992; Young *et al.* 2006; Hubert *et al.* 2011, Van de Poel *et al.* 2015). However, urban areas also offer other additional advantages, but also disadvantages, for hedgehogs. These issues are discussed in the next section.

Factors associated with the decline in hedgehogs in urban landscapes

Other than a reduced abundance of badgers, urban areas are thought to be associated with an increased abundance of invertebrate prey (although there are very few data currently available to substantiate this perception) but especially food accidentally (e.g. refuse) or deliberately supplied by humans (Baker and Harris, 2007). At the very least, hedgehog populations are typically present at much higher densities than in rural habitats (e.g. Hubert *et al.* 2011, Van de Poel *et al.* 2015; Schaus *et al.* 2020) suggesting that food is abundant. However, urban areas are also associated with a range of factors that affect their survival, reproduction and movement patterns, some of which are similar to those seen in rural landscapes whereas other are novel.

Like rural hedgehog populations, urban hedgehog populations are susceptible to the mortality and fragmentation risks associated with roads (Braaker *et al.,* 2014, 2017). However, evidence from Bristol, England, suggests that urban hedgehogs may reduce the mortality risk associated with crossing roads by adjusting their nocturnal activity patterns such that they are most active in the latter half of the night when traffic volume is markedly lower (Dowding *et al.* 2010a). The second form of habitat fragmentation faced by urban hedgehogs is garden fencing: an increase in the quality, style (e.g. those with horizontal gravel boards) and maintenance of garden fences is believed to have reduced the ability of hedgehogs to move easily from garden to garden. Consequently, the PTES and British Hedgehog Preservation Society (BHPS) have launched “Hedgehog Street” (*www.hedgehogstreet.org*), a campaign to persuade householders to cut holes in or under their fences (“hedgehog holes”) to increase inter-garden connectivity. To date, >80,000 of people have signed up this campaign, although preliminary analysis of a questionnaire survey of these “Hedgehog Champions” suggest that only a small minority have actually created a hedgehog hole (A. Gazzard, pers. comm.).

Urban gardens are also associated with a wide range of hazards which can injure or kill hedgehogs, including but not limited to: garden ponds; bonfires; garden strimmers (which cause serious injuries to hedgehogs sleeping in grassy areas); domestic dogs; slug pellets; anticoagulant rodenticides (Dowding *et al.*, 2010b); uncovered drains; discarded elastic bands (these can become trapped around the animal's head and cut through the windpipe); and deliberate acts of cruelty. In addition, even those householders that put food out for hedgehogs can end up injuring or killing them. Historically, hedgehogs were often fed bread and milk, the latter resulting in diarrhoea as hedgehogs are lactose intolerant; despite a widespread campaign in the 1980s, this is still a recurrent problem today. More recent food-related problems relate to the use of bird foods such as unsalted peanuts and sunflower hearts which, along with a high abundance of some sugary fruits in commercially available hedgehog foods, can lead to dental decay or damage if they get stuck in the animal's palate. The most serious issue, however, is the use of mealworms, which hedgehogs favour, but which cause a metabolic disorder whereby key minerals are leached from the animal's bones resulting in brittle and distorted bones; such animals have to be euthanased. As a consequence of all these factors, hedgehogs are the mammalian species most commonly admitted to wildlife hospitals in England (Grogan and Kelly, 2013).

Urban areas in Great Britain are also associated with large numbers of foxes (Scott *et al.*, 2014). Although not historically thought to be a major factor influencing hedgehog populations, Trewby *et al.* (2014) reported an increase in both hedgehogs and foxes in relation to the culling of badgers, and Pettett *et al.* (2017b) found a positive correlation between the number of road-killed hedgehogs and the numbers of dead foxes. Further, Harris and Baker (2001) reported a substantial increase in hedgehogs observed alive and dead following a dramatic reduction in fox numbers due to an outbreak of sarcoptic mange.

Hedgehogs in an anthropogenic world

Whilst data from several different monitoring programmes indicate that British hedgehog populations have declined markedly in recent decades, the magnitude of this decline varies both within and between rural and urban landscapes. Associated with this decline are a broad range of underlying factors related to anthropogenic activities which can be expected to continue to negatively affect hedgehog populations. However, there are relatively few data that definitively support these factors as being detrimental to hedgehog populations, with the possible exception of the role of badgers, although even in that case the underlying biological mechanism(s) is not known. In addition, there is a paucity of information about how these anthropogenic factors influence hedgehog survival rates, in part because of the practical challenges associated with studying this species. The following sections present key information related to the questions addressed in this thesis.

Hibernation as a key period in hedgehog dynamics

Hibernation has typically evolved to enable endothermic species to survive periods of prolonged food shortages as levels of energy expenditure are drastically reduced (Geiser, 2011; Staples, 2014; Ruf and Geiser, 2015). Multi-day bouts of torpor whereby high euthermic body temperature is suspended for periods lasting, on average, more than a week, differentiate hibernating species from those classed as daily heterotherms, which suspend the maintenance of a high euthermic body temperature for ~3-12 hours (Geiser and Ruf, 1995). Hibernating species tend to have slower reproductive rates (Turbill *et al.*, 2011), potentially increasing their long-term vulnerability to human activities, including habitat fragmentation and changing climatic conditions (Inouye *et al.*, 2000; Lane, 2012; Lane *et al.*, 2012; Geiser, 2013).

Hibernation is implemented by hedgehogs to avoid harsh winter conditions throughout much of their range (Reeve, 1994). However, it is a highly flexible strategy, for example Rasmussen *et al.* (2019a) suggested hibernation was delayed by up to one month due to a particularly mild autumn during a study of urban juveniles in Denmark. In the UK, hedgehogs typically hibernate from November to March/April, with some variation dependent upon regional conditions (Reeve, 1994) . At the extreme of its geographical range in Finland, hedgehog have been reported to hibernate continuously for more than 200 days (males: 224 ±4.8 days; females: 223 ± 2.5 days) (Rautio *et al.*, 2014).

Hibernation has typically been identified as a period of high risk for hedgehogs, although evidence to substantiate this assertion is limited and equivocal. Kristiansson (1990) observed that annual mortality rates in rural Sweden varied greatly with both age and season; mortality rates in summer (average 15%; range 2-33%) were markedly lower than in winter for adults (33%: 26%-43%) but especially for juveniles (33%: 6%-94%) (annual average: 34% in juveniles and 47% in adults and sub-adults). However, Walhovd

(1990) described such prior estimates as “over-rated”, and more recent studies suggest that survival rates during hibernation may be higher, e.g. 74% for juveniles in Denmark (Rasmussen *et al.*, 2019a) and 83% survival in England (Yarnell *et al.*, 2019) with the latter study suggesting that mortality in spring, post-hibernation, is the period of peak mortality. Earlier studies to quantify patterns of over-winter survival rates (e.g. Morris, 1988; Kristiansson, 1990) have relied upon capture-mark-recapture techniques, but as these are not able to discriminate between deaths and emigration from the study area they are likely to generate biased estimates of over-winter mortality.

To survive hibernation, hedgehogs must accumulate sufficient subcutaneous fat reserves. Previous estimates suggest this minimum body mass may be as high as 600-650 g (Bunnell, 2002) or as low as 450 g (Morris, 1984); one animal weighing just 175 g reportedly survived hibernation in the western edge of the species’ range in Ireland (Haigh *et al.*, 2012b). During hibernation, animals may lose 20-30% of their body weight (Jensen 2004; Rasmussen *et al.* 2019a), and is likely to increase the more often hedgehogs have to rouse temporarily to move nests in response to e.g. increases in temperature or disturbance.

Hedgehog hibernacula must serve the dual purposes of keeping individuals warmer than the ambient temperature whilst also permitting exchange of respiratory gasses. To avoid physiological damage, hedgehogs must rouse from hibernation if the body temperature drops below 0°C; however, they can minimise the need to do this by building a suitably insulated nest that maintains its internal temperature above this critical threshold. Consequently, hedgehogs need access to suitable materials (mainly the leaves of broadleaved trees) to construct their winter nests (Morris, 2018). In addition, it is also reasonable to assume that nests must be sites in locations that minimise the likelihood of being detected by a predator or trampled accidentally (Morris, 1973). Furthermore, hedgehogs may need to have several suitable sites in close proximity to one another in order to minimise the risks associated with moving location if they have to do so (Reeve and Morris, 1985). Given these requirements, habitat loss, habitat degradation, climate change and fragmentation, as well as disturbance by livestock and humans, could all negatively impact over-winter survival rates of hedgehogs by e.g. reducing the ability of hedgehogs to build up fat reserves, reducing the availability of suitable sites and suitable nest materials, and increasing the frequency with which they move between nest sites.

Wildlife rehabilitation to address anthropogenic losses

Wildlife rehabilitation involves the treatment and temporary care of injured, diseased or orphaned animals and the subsequent release of healthy animals to appropriate habitats in the wild (Miller, 2012). Whilst rehabilitation is a global pursuit, there is little understanding of its role in helping conservation programmes (Pyke and Szabo, 2017) in particular in helping reversing species' declines. Any benefit arising from wildlife rehabilitation will be related to the number of individuals of a given species entering rehabilitation centres, the success rate of rehabilitation practices and the survival rate of animals post-release.

Although hedgehogs are known to be the mammal species most commonly admitted to wildlife hospitals / centres in England (Reeve and Huijser, 1999; Kirkwood, 2003; Grogan and Kelly, 2013), there is no detailed estimate of the numbers involved, although various assessments have been made (Table 1.1). For example, Molony *et al.* (2007) suggested 30,000-40,000 casualties (all bird and mammal species) are admitted to wildlife hospitals annually, whilst Grogan and Kelly (2013) proposed a figure of 71,000 may be more accurate across England and Wales. In addition, Barnes and Farnworth (2016) estimated veterinary professionals may see more than 131,000 animals each year across the UK.

However, none of these authors accounted for the fact that the hedgehog rehabilitation community in Great Britain contains an unknown number of small-scale rehabilitators who operate from their own homes. For example, the BHPS estimates that there may be as many as 800 hedgehog rehabilitators operating in the UK (Morris, 2018), whereas Mullineaux and Kidner (2011) suggested a total of 80 wildlife centres and the estimate of Grogan and Kelly (2013) outlined above was based upon a request to 123 individuals/ organisations.

Table 1.1 Summary of studies outlining the number of hedgehog admissions to European wildlife rescue centres and veterinary practices

Species recorded	**National estimate of treatment**	**Sample size**	**No (%) hedgehogs**	**Rate of survival to release**	**Identified factor for success**	**Citation**
All British wildlife species admitted	>131,000 animals (range 90,0444-173,173) based on 10% of 1706 vet practices responded.	8,081 admissions to 143 practices	1,932 reported (23.9%)	-	-	Barnes and Farnworth, 2016
Badger, blackbird, hedgehog, red fox, tawny owl, starling, house sparrow	Not reported	4 RSPCA hospitals	5,187 over 4 years; 754 (14.5% of all admissions)	39% for all species combined 53% for hedgehogs	Severity of injury	Molony *et al.*, 2007
All British wildlife species admitted	71,000	27	-	40% assumed across all spp.	-	Grogan and Kelly, 2013
All British wildlife species admitted	4,000	1 wildlife hospital	-	None identified	-	Mullineaux and Kidner, 2011
European hedgehog Algerian hedgehog	-	412 over 5 years 78 over 5 years	-	69% survived to release	Cause of admission	Martínez *et al.*, 2014
European hedgehog	-	168 over 3 years	-	74% nestlings 55% juveniles 58% adults 68% overall	-	Bunnell, 2001
European hedgehog	-	1 wildlife hospital (Jersey)	3000	65%	-	Morris, 1998
British wildlife	-	16,000 admissions to BWRC centres	-	42% for all spp. 31% for mammals	-	Kirkwood, 2003
All British wildlife species admitted	-	10,000/yr ~35 centres	16.5% of all admissions	35%	-	Kirkwood and Best, 1998
European hedgehog	-	12,397	16% of all admissions 54% of mammals	-	-	Reeve and Huijser, 1999

Given the possible scale of hedgehog rehabilitation in the UK, information on the numbers of animals admitted annually, the reasons for those admissions, and rates of survival to release are potentially important metrics in understanding how hedgehog populations may be faring but also helping to identify underlying causes. Cross-collaboration between individuals / organisation would also act to enhance triage, treatment and release practices, and maximise animal welfare standards (Mullineaux, 2014). Combining databases across multiple agencies would also increase sample sizes and geographic scope (Martínez *et al.,* 2006; Ancillotto *et al.,* 2013). However, wildlife rehabilitation is largely unregulated in the UK (Mullineaux, 2014; British Zoological Veterinary Association, 2016), with no mandatory requirement to record the number of animals admitted and released, to share good practice or to monitor post-release survival. Furthermore, there is no official requirement for rehabilitators to register with the BHPS, the body that unofficially oversees hedgehog rehabilitation in the UK.

Wildlife hospitals also potentially serve as a useful educational “starting point”. For example, previous studies of admission records have suggested that anthropogenic factors were associated with 40-50% of admissions and 59% of deaths of hedgehogs in wildlife hospitals (Kirkwood and Best, 1998; Reeve and Huijser, 1999; Kirkwood, 2003). As such, wildlife rehabilitators are in the best position to identify risk factors that members of the public need to be informed about in order to help minimise the number of casualties; this is particularly pertinent now, when many people have access to the internet. To date, several such campaigns have been undertaken relating to e.g. the health implications of giving hedgehogs milk to drink, and the risks posed by bonfires on Guy Fawkes Night and New Year’s Eve. In addition, members of the public also need to be able to access information about when not to pick up wild animals (Martínez *et al.,* 2014). At the most basic level, such education strategies require knowledge of the relative importance of each of these factors leading to admission and how these may be changing over time (Pyke and Szabo, 2017).

Overall, therefore, there is evidence to suggest that rehabilitated animals can have post-release survival rates similar to those of wild individuals, but with the potential for high numbers of losses in some circumstances (Vogelnest, 2008). A range of factors can be identified that are likely to affect post-release success related to practices within hospitals themselves but also at release sites, for example: veterinary screening prior to release; release methodology (soft versus hard release); release location (site of origin versus new site) or habitat; or the number of animals released together (Molony *et al.,* 2006).

Ideally, current conservation programmes used to monitor hedgehog populations in the UK would not only help to provide information on the absolute or relative change in population size over time, but also help to inform the reasons for such changes (e.g. variation in summer and winter weather patterns). Such studies do, however, require long-term data sets, but the field is now potentially at the point where these programmes may allow such analyses to be conducted (e.g. several programmes have been running for ~20 years; Figure 2a-c) and data from wildlife rehabilitation organisations such as the Royal Society for the Protection of Animals (RSPCA) may be available for longer time periods (Dowding, 2007). In addition, rehabilitation data would allow a more detailed analysis of some aspects of inter-annual trends in numbers as information on e.g. sex, age and reason for admission are recorded.

Whilst wildlife rehabilitation is widely considered to be primarily for animal welfare rather than conservation (Mullineaux, 2014; Pyke and Szabo, 2017), depending on the scale at which such activities are occurring this view may be challenged. Lunney *et al.* (2004) suggested that with a comparable rate of survival and breeding between wild koalas (*Phascolarctos cinereus*) and those released after burning incidents, rehabilitated animals have the potential to contribute to the recovery of populations depleted by fire. Further, Thomas *et al.* (2013) concluded that following the rescue and release of green sturgeon (*Acipenser medirostris*) in the Sacramento River, California, a population decrease of 7% was predicted as a result of future stranding events with rescue and release, compared to 33% decrease without such interventions.

In summary, wildlife rehabilitators potentially have an important role to play in helping the conservation of wild hedgehog populations by e.g. boosting local populations, enhancing understanding of potential threats, helping identify areas for future research and supporting understanding of underlying ecological mechanisms associated with the decline in hedgehog numbers. However, there is currently limited understanding of how rehabilitators operate, and the scale on which they contribute to the wild population, both of which warrant further investigation.

Post-release monitoring and survival rates

For rehabilitation to be considered successful, those animals which are released should ideally have survival rates comparable to individuals that do not enter hospitals and form part of the local breeding population. In the absence of either of these outcomes, rehabilitation can be considered, at best, a waste of resources; at worst, the presence of rehabilitated animals in the local population could lower overall survival and/or reproductive rates by virtue of negative density-dependent feedback mechanisms (Kirkwood and Sainsbury, 1996). Additional risks associated with wildlife rehabilitation include the introduction of parasitic diseases and potential genetic effects on recipient populations (Mullineaux, 2014).

A range of studies have examined post-release survival rates in a range of habitats in Great Britain. Documented survival rates are: 58% (n = 12) after nine weeks (Morris and Warwick, 1994); 33% (n = 12) after 6 weeks (Sainsbury *et al.,* 1996); and 42% survival after 108 days (n = 12) (Reeve, 1998). Two studies have documented the survival rates of hedgehogs translocated from the Uist Islands in Scotland to mainland Britain. Warwick *et al.* (2006) recorded a 28-day survival rate of 67-80% for animals released into a Scottish Country Park (n = 20). Conversely, survival rates of rehabilitated hedgehogs released into urban Bristol (73% after 8 weeks; n = 20) were comparable to populations of both wild hedgehogs in the city (64-95%; n = 20) and to a population of animals from the Uist Islands that had spent a period of 4 weeks in captivity (n = 23) (Molony *et al.,* 2006). Most recently Yarnell *et al.* (2019) found no significant difference in the survival of rehabilitated hedgehogs (91%; n = 34;) released in winter when compared to wild (82%; n = 23) counterparts over a mean of 133.8 days.

Overall, therefore, there is evidence to suggest that rehabilitated animals can have post-release survival rates similar to those of wild individuals, but with the potential for high numbers of losses in some circumstances (Vogelnest, 2008); factors that could affect post-release success related to practices within hospitals themselves and at release sites include veterinary screening prior to release, release methodology (soft versus hard release), release location (site of origin versus new site), and the number of animals released together (Molony *et al.,* 2006). As such, wildlife rehabilitators potentially have an important role to play in helping the conservation of wild hedgehog populations by e.g. boosting local populations, enhancing understanding of potential threats and helping identify areas for future research. However, there is currently limited understanding of the structure and characteristics of the collective rehabilitation community, and the number of hedgehogs passing through these hospitals on an annual basis.

Methods of hedgehog surveying and detection

Effective estimation of the population size is essential for the development of effective conservation plans, and for determining whether these are successful or not. Both direct (observing the animal itself) and indirect (observing field signs) methods may be required to accurately determine a species' range and abundance (Langbein *et al.* 1999, Wilson and Delahay 2001; Day *et al.* 2016). Indirect counts are based on counts of "field signs" such as refugia (Waters *et al.* 2011; Judge *et al.* 2014), tracks (Alibhai *et al.* 2017; Williams *et al.* 2018a, b), scats (Churchfield *et al.* 2000; Day *et al.* 2016; Cortázar-Chinarro *et al.* 2019; Mwebi *et al.* 2019) and/or feeding signs (Redpath *et al.* 2001; Meek *et al.* 2012), or e.g. counts of animals killed on roads (Baker *et al.* 2004; Seiler *et al.* 2004; Bright *et al.* 2015) or by hunters (Aebischer *et al.* 2011; Aebischer 2019). Such indirect approaches have tended to be used where direct methods are not possible (e.g. the focal species occupies a habitat where direct observation is not possible), or because they are cheaper (Alibhai *et al.*, 2017). The use of indirect measures is, however, predicated on the assumption that they reflect population size *per se* or some relative measure of population size, but it is known that they can be associated with a range of confounding factors that make estimates uncertain and interpretation of data difficult (McDonald and Harris 1999; Bright *et al.* 2015). As a nocturnal, elusive species, surveying hedgehogs can be challenging, but with suspected decline of the UK population accurate recording methods are essential.

Footprint-tunnels provide an indirect measure

The use of footprint tunnels, originally developed to determine the utilisation of burrow systems by burrowing mammals (Mayer, 1957; Lord *et al.,* 1970) provides a cost effective, indirect measure for recording the presence of small mammals. The standard design for surveying hedgehogs is a corrugated plastic board (for hedgehogs a minimum of 50 x 80 cm) folded into a prism, with sheets of A4 white paper attached to each end of the base; strips of masking tape coated in a mix of paraffin or vegetable oil and carbon black is then placed either side of a centrally positioned food bait (cat/hedgehog biscuits, tinned dog food or similar for hedgehogs) (Figure 1.4). When animals walk through the tunnel, their footprints are left on the paper.

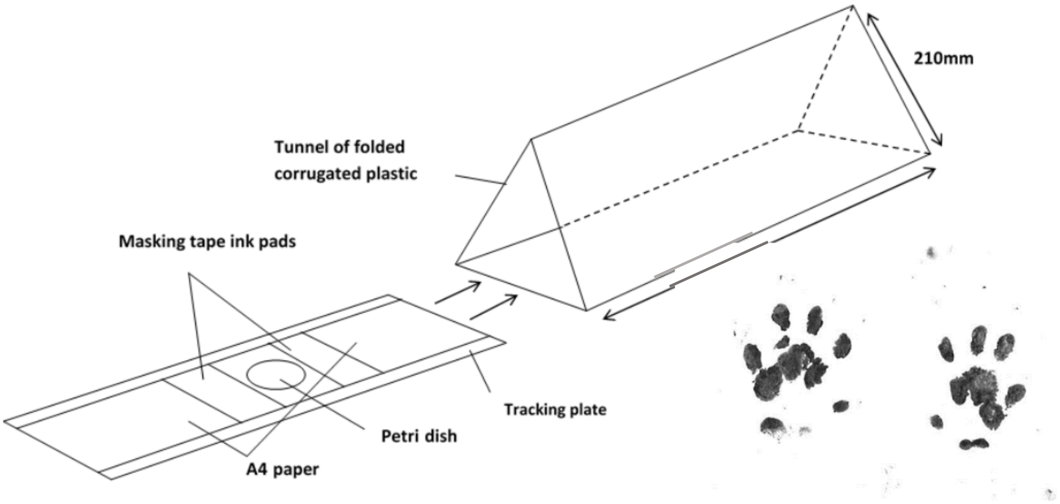


Figure 1.4. Footprint tunnel for detecting hedgehogs with an indication of hedgehog footprints (Thomas and Wilson, 2018)

Footprint-tunnels have been used successfully in studies of both urban (Williams *et al.*, 2018b) and rural (Yarnell *et al.*, 2014; Williams *et al.*, 2018a) populations, with each site surveyed for a continuous five day-period. Whilst tunnels will typically only determine presence or absence, changes in occupancy in the order of 25% would be accurately detected (Yarnell *et al.,* 2014). Success with the method in other studies has, however, been variable. For example, Haigh *et al.* (2012a) only recorded hedgehogs at two of three surveyed sites, and tunnels were not utilised by hedgehogs at all in Regent's Park in London (Gurnell and Bowen, 2016). The reasons for these differences are unknown.

Spotlights

The use of high powered spotlights, typically of 1-2 million candles have been used globally for searching for nocturnal species including great crested newts (*Triturus cristatus*) (Langton *et al.,* 2001), European hares (*Lepus europaeus*) (Santilli and Galardi, 2016), red foxes (Parrott *et al.,* 2012) and badgers (Hof *et al.,* 2012), as well as hedgehogs (e.g. Hof *et al.,* 2012; Pettett *et al.,* 2017b; Rast *et al.,* 2019; Yarnell *et al.,* 2019). In the case of hedgehogs, spotlights can be used to estimate presence/absence but also as a tool to help estimate relative abundance since individuals can be easily captured and marked; to date, however, no one has attempted to use spotlighting as a method for estimating absolute density (e.g. using DISTANCE sampling) because of low contact rates (e.g. Poulton and Reeve, 2010). Marking individuals is usually achieved through the application of 5-10 small plastic markers to spines, attached either with glue (Molony *et al.,* 2006; Dowding *et al.,* 2010a; Abu Baker *et al.,* 2017) or heat (Doncaster, 1993), or through the insertion of a microchip (Doncaster, 1994). However, spotlight surveys which involve the physical capture of the hedgehog itself can only be undertaken under licence from Natural England (or other relevant devolved government agencies) as hedgehogs are listed on Schedule 6 of the Wildlife and Countryside Act, 1981, which restricts the use of dazzling devices as a capture device.

During spotlight counts, sites are typically searched systematically on 3-5 occasions (Micol *et al.*, 1994) often along the margins of fields or amenity grassland (Haigh *et al.,* 2012b) or following a pre-determined transect route. Detection rates vary, with approximately one hedgehog detected per km surveyed (Thomas and Wilson, 2018), although Haigh *et al.*

(2012a) considered spotlighting to be the most effective form of surveying in comparison to footprint tunnels, with a detection time of four nights for spotlighting compared to 48 nights with footprint tunnels. Upon detection, hedgehogs will typically display a predator avoidance response, such as curling into a ball or running for nearby cover.

Farms with woodland have been identified as reporting hedgehogs at a higher rate than those without (Micol *et al.,* 1994), although less time is spent in woodland than in pasture fields (Doncaster, 1993; Pettet *et al.* 2017) and hedgehogs favour woodland edges over other habitats (Doncaster *et al.,* 2001). Detecting hedgehogs in woodland is challenging because of the high vegetation. However, developing a technique capable of detecting hedgehogs in this habitat is particularly important, given that broadleaved woodland is considered to be the most important habitat for hedgehogs nationally (Mathews *et al*., 2018).

VHF/GPS

Very High Frequency (VHF) and Global Positioning System (GPS) tags have been used internationally to study the movements of animals in a wide range of environments and contexts including in dense tropical forest river systems (Martin and Da Silva, 1998), during migration (García-Rippolles *et al.,* 2010), and marine mammals in the open ocean (Kuhn *et al.,* 2009). VHF tags are generally cheaper than GPS tags, but require that the animal is tracked physically by an observer whereas GPS tags allow an animal to be tracked remotely. VHF technologies can also be incorporated within GPS tags to allow retrieval of the latter (Recio *et al.,* 2011).

For tracking hedgehogs, tags can be attached to a clipped portion of spines using dental adhesive or epoxy/acrylic resin (Glasby and Yarnell, 2013; Rautio *et al.*, 2013); alternatively, Barthel *et al.* (2018) suggested attaching a small piece of Velcro® to the spines so that successive tags can be replaced more easily, circumventing problems associated with the limited life span of tracking devices associated with the small body weight of hedgehogs. Total tag weight is typically 7-30 g but should be no more than *c.*

5% of the animal’s body mass in accordance with international guidelines, whilst allowing for changes in mass e.g. during hibernation (Sikes and Gannon, 2011). Consequently, hedgehogs <600 g are rarely tagged (Yarnell *et al.,* 2019).

Both techniques are beneficial in quantifying home range size and distance travelled (Morris, 1988; Rautio *et al.,* 2013), survival rates (Rasmussen *et al.,* 2019a), nesting behaviour (Reeve and Morris, 1985), and patterns of behaviour following release from wildlife rescue centres (Hof and Bright, 2010b; Yarnell *et al.,* 2019).

Thermal cameras

Infra-red thermography (IRT), or thermal imaging cameras (TIC) detect radiation at wavelengths of 9-14 µm on the electromagnetic spectrum, which are emitted by all objects on the Earth (Bowen *et al.,* 2019). The amount of infra-red light emitted varies with temperature, allowing detection of objects of different materials to be visualised in the absence of visible light (Figure 1.5). Such devices are used widely in the medical and natural sciences, providing a safe and non-invasive diagnostics tool for disease detection in plants (Smigaj *et al.,* 2015), and animals (Dunbar *et al.,* 2009), and to assess animal welfare (Yarnell *et al.,* 2013; Foster and Ijichi, 2017).

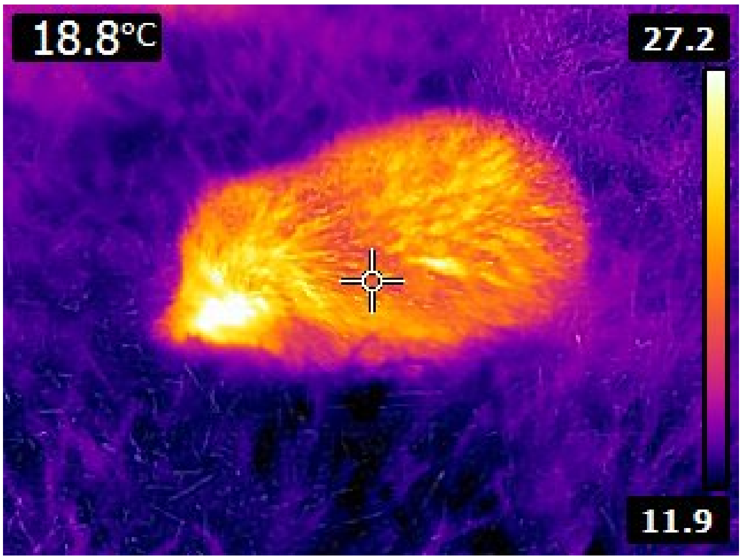


Figure 1.5. Infra-red thermography (IRT) cameras visualise the radiation emitted by all objects, allowing objects to be seen in the absence of visible light, in this instance a hedgehog

IRT has also been utilised for surveying wildlife, and for the detection of wildlife poachers, either passively (Damm *et al.,* 2010) or actively (Keller *et al.,* 2019). IRT cameras can also be attached to aerial drones to increase the area and distance covered (Chrétien *et al.,* 2015). IRT has repeatedly been tested against other survey methods for a wide range of species (Storm *et al.,* 2011; Keller *et al.,* 2019;) and also have the potential to detect animals in dens/nests (Smith *et al.,* 2020), including during hibernation (Bartonička *et al.,* 2017), although there are limitations due to environmental conditions (Smith *et al.,* 2020).

The use of IRT cameras has been assessed in hedgehogs in Regents Park, London, and were found to be more effective than spotlight surveying: 53% of hedgehog sightings were via the use of an IRT camera, compared to 42% by spotlight, 3% by sound and 2% went undetected (Bowen *et al.*, 2019). Detection distance was also greater for IRT cameras than spotlights (IRT camera: mean 30 m, range 1–200 m; spotlights: mean 12 m, range 1–50 m), and volunteers quickly learnt how to use the cameras to detect hedgehogs. In addition, IRT cameras can be used to detect hedgehogs without the requirement for licensing, although they are considerably more expensive than spotlights (£500-£7000 per camera, compared to £40-£174 per torch; Thomas and Wilson, 2018). However, the model of camera used, and its settings, will significantly affect results e.g. Haigh *et al.* (2012a) found that hedgehogs could not be detected at a distance of even 1m using a Testo 880 range camera, whilst Bowen *et al.* (2019) detected hedgehogs over distances of up to 200 m (mean = 30 m, range = 1-200 m, n = 133) with a FLIR E60. This variability reduces the direct comparability of results from different studies.

Summary and thesis outline

Overall, the population status of the hedgehog in Great Britain is uncertain. Whilst there is significant evidence of a decline, potentially up to 50% in some places, questions remain regarding the scale at which this decline is occurring in some habitats, most notably in woodland, potentially due to limitations in survey methods available. Whilst much attention has been given to specific aspects of the species' ecology, such as its interaction with badgers and the impact of urbanisation on hedgehogs, little attention has been paid to anthropogenic interactions that may impact upon survival.

As discussed here, the arable landscape is one that may be particularly inhospitable to this species, during a time of potentially greatest risk: hibernation. Further understanding of how hibernation may affect survival and present critical challenges is key to understanding the annual lifecycle of this mammal of conservation concern. This is therefore a particular focus in this thesis, along with other aspects of human:wildlife interaction, most notably in wildlife rehabilitation. Further understanding of factors that lead to the admission and survival of animals within rehabilitation, and the degree to which this practice can contribute to the survival of the species as a whole, requires further investigation.

The following thesis is written as a series of chapters (Chapters Two to Five), each presented as an individual research paper for submission to peer-reviewed journals, hence some variation in style and formatting, and some degree of repetition. These papers are drawn together with the final chapter (Chapter Six) to provide overarching discussion and recommend areas of further research. This work has been undertaken in collaboration with external organisations, most notably People's Trust for Endangered Species (PTES) and the British Hedgehog Preservation Society (BHPS), as well as with collaborators at University of Reading, Nottingham Trent University, Keele University and Conservation K9 Consultancy.

CHAPTER TWO

As outlined previously, hibernation has been proposed (Kristiansson, 1990) and debated as (Rasmussen *et al.,* 2019a; Yarnell *et al.,* 2019) a potentially high risk time for hedgehogs, and the arable landscape is suggested as particularly unfavourable (Hof and Bright, 2012; Hof and Bright, 2016; Williams, *et al.*, 2018a), so determining how effectively hedgehogs survive hibernation in this landscape is important to establishing the degree to which survival occurs. Hibernation success may be dependent upon a range of habitat factors associated with agricultural intensification and climate change, which may affect: changes in body mass during hibernation and during the rest of the year, changes in mortality rates and changes in the way hedgehogs utilise the landscape for nesting, both in relation to the sites selected for nests and how frequently they move between nests.

Therefore, in this chapter, data regarding the movements between nests of hedgehogs at two contrasting rural sites over two winters are considered. In this study I utilised radio tracking to quantify: (i) habitat factors associated with nest site selection and movements in the rural landscape over-winter; (ii) over-winter changes in body mass; (iii) patterns of nest-site occupancy and movement; (iv) over-winter survival rates.

The manuscript presented in this chapter has been submitted for publication in the journal *Animals*, in a special issue: Applied Hedgehog Conservation.

My contribution to the work:

I undertook all survey work at the Hartpury campus and conducted the analysis with input from Dr Richard Yarnell and Dr Antonio Uzal at Nottingham Trent University, and from Dr Luke Evans and Dr Philip Baker at Reading University. I wrote the manuscript with Dr Philip Baker, with editorial input from all co-authors.

Article reference:

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-winter survival and nest site selection of the west-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. *Animals*, *10*, 1449. https://doi.org/10.3390/ani10091449

Over-Winter Survival and Nest Site Selection of the West-European Hedgehog (*Erinaceus europaeus*) in Arable Dominated Landscapes

Simple Summary: Hedgehogs (*Erinaceus europaeus*) have declined markedly in the UK in recent decades. One key stage that could affect their population dynamics is the annual winter hibernation period. Therefore, we studied two contrasting populations in England to examine patterns of winter nest use, body mass changes and survival during hibernation. On average, animals at both sites weighed the same prior to, and used the same number of nests, during hibernation. There was a marked difference in survival rates between the two sites, but no animals died during hibernation; all deaths occurred prior to or after the hibernation period, mainly from predation or vehicle collisions. Hedgehogs consistently nested in proximity to some habitats (hedgerows, roads, woodlands) but avoided others (pasture fields); the use of other habitats (arable fields, amenity grassland, buildings) varied between the two sites. These data suggest: (i) that hibernation was not a period of significant mortality at either site for individuals that had attained a sufficient weight (>600 g) in autumn; but that (ii) habitat composition did significantly affect the positioning of winter nests, such that different land management practices (historic and current) could influence hibernation success.

Abstract

The West-European hedgehog (*Erinaceus europaeus*) has declined markedly in the UK. The winter hibernation period may make hedgehogs vulnerable to anthropogenic habitat and climate changes. Therefore, we studied two contrasting populations in England to examine patterns of winter nest use, body mass changes and survival during hibernation. No between-site differences were evident in body mass prior to hibernation nor the number of winter nests used, but significant differences in overwinter mass change and survival were observed. Mass change did not, however, affect survival rates; all deaths occurred prior to or after the hibernation period, mainly from predation or vehicle collisions. Hedgehogs consistently nested in proximity to hedgerows, roads and woodlands, but avoided pasture fields; differences between sites were evident for the selection for or avoidance of arable fields, amenity grassland and buildings. Collectively, these data indicate that hibernation was not a period of significant mortality for individuals that had attained sufficient weight (>600 g) pre-hibernation. Conversely, habitat composition did significantly affect the positioning of winter nests, such that different land management practices (historic and current) might potentially influence hibernation success. The limitations of this study and suggestions for future research are discussed.

Keywords: *Erinaceus europaeus*; farmland; habitat fragmentation; hedgerow; hibernacula; hibernation; mammal; nest

Introduction

Agricultural intensification and climate alteration are two anthropogenic processes that have profound impacts on natural ecological systems (Parmesan, 2006; Firbank *et al.*, 2008; Tscharntke *et al.*, 2012; Tuck *et al.*, 2014; Veach *et al.*, 2017; Zabel *et al.*, 2019). The effects arise from a wide range of underlying causal factors including: habitat destruction, fragmentation and degradation (Ellis *et al.*, 2010; Crooks *et al.*, 2011); the introduction of livestock, diseases and non-native biological control agents (Robinson *et al.*, 2014; Wiethoelter *et al.*, 2015; Gordon, 2018; Howell *et al.*, 2019; Öllerer *et al.*, 2019); the management of wildlife where they conflict with human interests (Eklund *et al.*, 2017; van Eeden, *et al.*, 2018a); the application of chemical biocides (Garcês *et al.*, 2020); and changes in the phenology of key biological events (Brown *et al.*, 2013; Kharouba *et al.*, 2018). Collectively, these factors have led to the decline, extirpation and extinction of large numbers of species (Butchart *et al.*, 2010; Hoffmann *et al.*, 2010; Di Marco *et al.*, 2014; Maxwell *et al.*, 2016; Dudley and Alexander, 2017; Stanton *et al.*, 2018), but also increases in the abundance and geographic range of others (e.g. Long, 2003; Clout and Russell, 2007).

One group of species that might be expected to be particularly affected by agricultural practices and changing climatic conditions are hibernators (Inouye *et al.*, 2000; Lane, 2012; Lane *et al.*, 2012; Geiser, 2013). Hibernation has typically evolved to enable species to survive periods of prolonged food shortages by dramatically reducing levels of energy expenditure (Geiser, 2011; Staples, 2014). One consequence of this is that hibernating species tend to have slower reproductive rates (Turbill *et al.*, 2011), potentially increasing their long-term vulnerability to human activities.

The West-European hedgehog (*Erinaceus europaeus*, hereafter 'hedgehog') is a medium-sized (<1.2 kg) insectivorous mammal found from the Iberian Peninsula and Italy northwards into Scandinavia (Morris and Reeve, 2008). In Great Britain, hedgehogs were historically found throughout a broad range of agricultural landscapes (Burton, 1969; Tapper, 1992; Arnold, 1993; Lovegrove, 2007), but rural populations have declined markedly in recent decades (Hof and Bright, 2016; Mathews *et al.*, 2018; Williams, *et al.*, 2018a). Consequently, hedgehogs are now increasingly found within areas of human habitation in this country (Young *et al.*, 2006; Parrott *et al.*, 2014; Pettett *et al.*, 2017b) and elsewhere (Hubert *et al.*, 2011; Van de Poel *et al.*, 2015). Associated with this decline has been a substantial reduction in the availability (Robinson and Sutherland, 2002) and quality (Carey *et al.*, 2008; Wright, 2016; Dover, 2019) of hedgerows, an important habitat for foraging (Hof and Bright, 2010b), dispersal (Moorhouse *et al.*, 2014) and refuge (Hof *et al.*, 2012), and a substantive increase in the numbers of badgers (*Meles meles*) (Judge *et al.*, 2014, 2017), an intra-guild predator (Trewby *et al.*, 2014).

During hibernation, hedgehogs face specific challenges. First, they need to accumulate sufficient fat reserves to survive for a period of many months; in Great Britain, hedgehogs typically hibernate from October/November to March/April (Morris and Reeve, 2008), although the exact timing is dependent on a combination of both temperature and food availability (Morris, 2018). Second, they need to find enough appropriate building material(s) to construct a hibernaculum that will maintain the environment within the nest at an appropriate temperature; nests are preferentially constructed from the leaves of broadleaved trees (Morris, 1973). Third, the habitat must be sufficiently diverse that it offers a range of nesting locations in close proximity to one another so that an individual can relocate safely if necessary. In addition, by nesting at ground level, hedgehogs are susceptible to a range of other factors such as flooding, trampling by livestock, and disturbance by e.g. land managers, walkers and domestic dogs (*Canis familiaris*). Finally, changes in temperature patterns throughout winter may cause hedgehogs to rouse from hibernation when natural food availability is limited.

Hibernation success is, therefore, dependent on several factors, all of which may be negatively affected by agricultural intensification and/or climate change. For example: hot dry summers, soil compaction from heavy machinery and the application of pesticides and molluscicides may all reduce food availability prior to hibernation and, therefore, limit the ability of animals to acquire sufficient fat reserves to successfully complete hibernation; habitat loss and degradation may limit the number of suitable sites for hibernacula, meaning that hedgehogs may be forced to use alternative locations/habitats where preferred nesting materials are not available or whether the risk of disturbance is greater; and warmer, wetter and/or more variable winters may cause animals to rouse more often and move between nests more frequently thereby depleting fat reserves and increasing susceptibility to some forms of mortality. Ultimately, such effects would be evident as: reductions in body mass before, and increased mass loss during, hibernation; an increase in the number of winter nests used and their placement in the environment; and an increase in over-winter mortality rates. These parameters would be expected to vary between areas undergoing different types of land management practice, and potentially between sexes (e.g. females may enter hibernation in poorer condition because of the energetic burden of rearing offspring, whilst males may finish hibernating earlier so that they can put on weight before the mating season).

Given the wide range of ways in which human activities could affect this phase, hibernation could represent a key critical period in the dynamics of hedgehog populations (Morris, 1984; Kristiansson, 1990;). Despite its potential importance, little research has been conducted on the hibernation behaviour of hedgehogs in Great Britain in the last 40 years (Morris and Reeve, 2008; Yarnell *et al.*, 2019). Therefore, in this study, we radio-tracked hedgehogs at one arable-dominated and one pasture-dominated site in England over the hibernation period to quantify differences in: (i) the number of winter nest sites used; (ii) patterns of habitat selection for nests; (iii) over-winter survival rates; and (iv) over-winter changes in body mass.

Materials and Methods

Data were collected from: (1) the Brackenhurst Campus (332 ha) of Nottingham Trent University, Nottinghamshire, UK (Universal Transverse Mercator (UTM): 53°03′47″N , 000°57′50″W); and (2) Hartpury University and College campus (339 ha), Gloucestershire, UK (UTM: 51°54′18″N , 002°18′37″W). Both sites were mixed commercial farms alongside a university campus, managed under the Entry level Environmental Stewardship Scheme (Natural England, 2013). Brackenhurst is dominated by arable fields (68.7%), with pasture fields, amenity grassland and woodland covering 24%, 2% and 3% of total land area, respectively. In contrast, Hartpury is dominated by pasture (35%) and amenity grassland (17%) with higher woodland (8%) and lower arable (31%) coverage. Hedgerow length at each site is 27.1 km^{-1} (Brackenhurst) and 16.9 km^{-1} (Hartpury). Badgers were present at both locations. Hedgehog densities estimated in 2017 using two different methods were 5.6-9.4 km^{-2} at Brackenhurst and 4.3-12.5 km^{-2} at Hartpury (Schaus *et al.*, 2020).

Fieldwork was conducted from August 2015-May 2016 and August 2016-May 2017, inclusive. Hedgehogs were captured by hand at night under licence from Natural England (ref: 20130866) using a 1-million candlepower spotlight to systematically search arable fields, pasture fields and areas of amenity grassland. Sites were surveyed at least twice per week during August and September. Once captured, animals were sexed, given a visual health check and weighed using digital scales (Salter 1035 platform scales, Salter, UK). Healthy animals weighing ≥600 g were fitted with a VHF radio transmitter (10 g: <2% of body mass; Biotrack Ltd, UK) glued to a region of clipped dorsal spines. All animals, regardless of body mass, were marked with coloured heat shrink tubing attached to 10 dorsal spines in a unique location; tubing was attached using a portable soldering iron. The capture location was recorded with a handheld GPS unit (Garmin GPS 60, Garmin, UK). Animals were released at the point of capture, typically within 15 minutes.

Nesting Behaviour

Determining the onset of hibernation for each individual using radio-tracking is difficult. Previous authors have tended to use either a criterion based on the number of successive days a single nest was used, although these have been variable (e.g. seven days (Haigh *et al.*, 2012b), one month (Rautio *et al.*, 2014)), or based upon a defined time period (Yarnell *et al.*, 2019). In this study, the latter approach was used as it was not possible to definitively identify the onset of hibernation based upon patterns of nest use alone (see Results) and because it was plausible that hibernating animals may have moved nests following e.g. disturbance by human activities.

Consequently, radio-tracking data were divided into three phases in line with the time periods defined by Yarnell *et al.* (2019): August-October (pre-hibernation); November-March (hibernation period); and April (post-hibernation). In the pre-hibernation phase, animals were located one night each week to record body mass and check transmitter attachment, and once per week during the day to determine the position of nests. In the hibernation phase, animals were located two-three times each week to determine the position of nests: searches were a minimum of two days apart. Radio-tracking was conducted using a Sika radio-tracking receiver and handheld, three element Yagi antenna (Biotrack).

The location of nests was recorded with a GPS unit and marked with a cane close to the nest for future identification. The position of nests was considered in the context of its specific location (e.g. in an animal burrow, hedgerow, next to or underneath a building) and the surrounding habitats (e.g. gardens, pasture, woodland). Where possible, nests were examined once they had been vacated to identify the dominant and secondary nesting materials. After examination, all nest material was left in position for future use, as hedgehogs have been found to return to nests or to occupy those of other individuals (Morris, 2014).

The number of nests used by each hedgehog was calculated for the time period 1st November-31st March inclusive. Where an individual had not been tracked before 1st November (n = 3) or up to 31st March (n = 3), one extra nest was added to the actual number recorded in line with the pattern of nest use observed for other animals. Differences in the number of nests used by males and females within and between the two sites were analysed using a Kruskal-Wallis test as the data were not normally distributed.

Patterns of habitat selection for winter nests were quantified by comparing the characteristics of observed (used) nest locations with those of randomly selected locations within the area available to hedgehogs. Data for each site were analysed separately. The available area was defined as the minimum convex polygon (MCP) encompassing all the diurnal and nocturnal locations from all hedgehogs radio-tracked during the study period at that site; this was used to incorporate areas outside each individual's home range (McClean *et al.*, 1998), and is a more objective reflection of the area used by each hedgehog population collectively than an arbitrarily predefined study area (Uzal *et al.*, 2013). Available nest locations were randomly sampled (10 times the number of used locations) within the MCP for each study area to create an available versus used dataset. The habitat characteristics of used and available nest locations were obtained by calculating the minimum Euclidian distances to each of the seven main land cover types (amenity grassland, arable fields, buildings and associated hard-standing (hereafter ‘buildings’), hedgerows, pasture fields, roads and road verges (hereafter ‘roads’), woodland) found in both areas. All GIS analyses were carried out using ArcMap 10.3.1 software (Environmental Systems Resource Institute) .

Resource Selection Functions (RSFs; Manly *et al.*, 2007) based on generalised linear models for each site were used to quantify habitat selection. A logistic regression for each site was fitted, with the response variable being the used (1: GPS nesting locations) and available locations (0: random location within the MCP area defined above). Collinearity among explanatory variables was assessed using the Pearson correlation coefficient. At Brackenhurst, but not Hartpury, the minimum distances to amenity grassland and buildings were highly correlated (r = 0.7). Therefore, two different RSFs were built: Model A included amenity grassland but not buildings; Model B included buildings but not amenity grassland. Both amenity grassland and buildings were included in the Hartpury model.

Akaike’s Information Criterion (AIC) (Burnham and Anderson, 2002; Zuur *et al.*, 2009) was used for model selection. Parameter values were averaged across models within two AIC units of the best fitting model (Burnham and Anderson, 2002).

Patterns of survival

Survival rates were compared between sites using Kaplan-Meier analysis (Kaplan and Meier, 1958). Sexes and years were combined because of relatively small sample sizes (Brackenhurst n = 10; Hartpury: n = 21), and because there was no apparent difference in the number of males and females that died at each site (see Results). Because animals were captured at different times, a staggered entry (Pollock *et al.*, 1989) design was used: the first animal was captured (Day 1) on August 1st. To avoid potential biases associated with the *ad hoc* recovery of untagged individuals, only radio-tagged individuals were included in this analysis. Differences in survival between the two sites were quantified using a log-rank test.

Body Mass Changes

Differences in overwinter changes in mass were compared between sites and sexes using a series of general linear models. Mass loss was calculated using each individual’s mass at capture as close to the start and end of the hibernation period as possible; on average, animals were captured 15.5 days before November 1st and 2.6 days after March 31st.

Statistical models compared differences in body mass at the start of hibernation, and absolute and percentage mass change during hibernation. All models included SITE and SEX as fixed factors and included a SEX*SITE interaction term. Linear correlation was also used to compare the number of nest sites used during hibernation with absolute mass loss over the hibernation period.

Data Analysis

General linear modelling and Kruskal-Wallis analyses were conducted using MINITAB version 19.1.1 and SPSS version 25, respectively. Survival analysis and RSF analyses were undertaken in R 3.3.3 (R Core Team, 2016) using lme4 and MuMIn packages (Bates *et al.*, 2015; Barton, 2019). All data were checked to ensure they conformed to the underlying assumptions of the tests used. All results are presented as mean (± SD) unless otherwise specified. As it was not possible to e.g. re-capture all tagged animals or access all nest sites, and because some animals perished during the course of the study, sample sizes vary between analyses.

Results

Forty hedgehogs were found during nocturnal surveys: 33 were fitted with radio transmitters (Table 2.1). Data on nesting behaviour during the hibernation period were collected from 21 hedgehogs. In total, 448 nocturnal locations, 138 nests, and 1028 diurnal locations were recorded.

Table 2.1. Number of hedgehogs captured and radio-tagged at each site, the total number of nocturnal and diurnal locations recorded, and the number of nest sites identified.

	Brackenhurst		Hartpury		TOTAL
	2015-2016	**2016-2017**	**2015-2016**	**2016-2017**	
No. captured & marked	7 (4♀:3♂)	3 (2♀:1♂)	22 (12♀: 10♂)	8 (3♀: 5♂)	40 (21♀:19♂)
No. radio-tagged	7 (4♀:3♂)	3 (2♀:1♂)	18 (9♀:9♂)	5 (3♀:2♂)	33 (18♀:15♂)
No. tracked during hibernation	7 (4♀:3♂)	3 (2♀:1♂)	7 (4♀:3♂)	4 (2♀:2♂)	21 (12♀:9♂)
Total no. of nests recorded (% accessible for recording composition)	54 (59%)	12 (100%)	50 (66%)	16 (75%)	138 (65%)
No. of nocturnal locations recorded	103	74	210	61	448
No. of diurnal locations recorded	408	114	360	146	1028

Nesting Behaviour

The pattern of nest use was highly variable, with several animals using the same nest site for extended periods before and/or during the hibernation period (Figure 2.1). There was no significant difference in the number of nests used by males and female within and between the two sites (Kruskal-Wallis test: H = 0.60, DF = 3, P = 0.896). Combining the data, hedgehogs used a median of five nests (mean ± SD = 5.5 ± 2.3) across the 151-day hibernation period. Thirteen animals (62%) used at least one site for ≥89 days.

RSF analyses indicated that woodland, roads, pasture and, to a lesser extent, hedgerows, were consistently included in the top (ΔAIC < 2) ranked models at both sites (Figure 2.2; Table 2.2). At both sites, hedgehogs selected nest locations closer to hedgerows, in vegetation alongside roads and in woodlands, but avoided pasture fields (Table 2.3). Between-site differences were evident for arable fields (neither selected nor avoided at Brackenhurst; avoided at Hartpury) and both amenity grassland and buildings (both selected for at Brackenhurst in each model where these habitats were included; neither selected nor avoided at Hartpury, or not retained in top-ranked models).

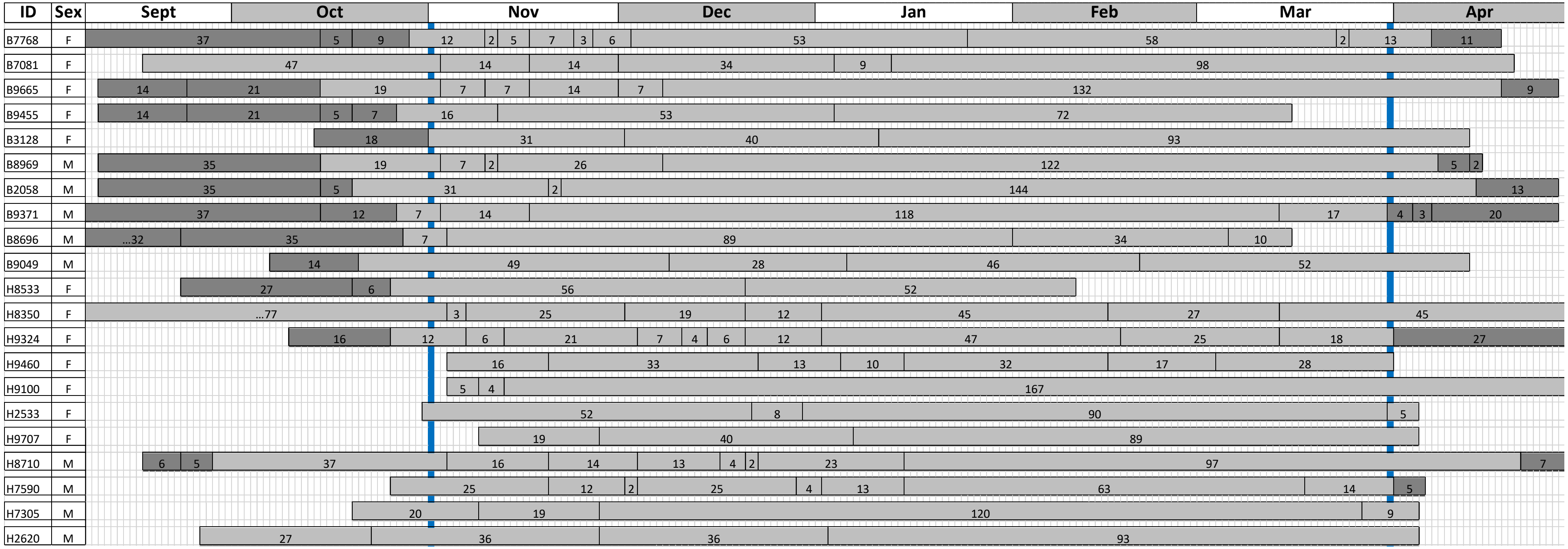


Figure 2.1. Pattern of occupation of winter nests by hedgehogs at Brackenhurst (ID numbers prefixed by "B") and Hartpury (ID numbers prefixed by "H"). Figures in horizontal bars indicate the number of days that each nest was estimated to be occupied based upon the sampling regime (see text for details). Vertical blue columns indicate the start (November 1st) and end (March 31st) of the hibernation period: dark and light shaded bars indicate nests excluded from and included in the analysis of the number of nests used over the hibernation period, respectively.

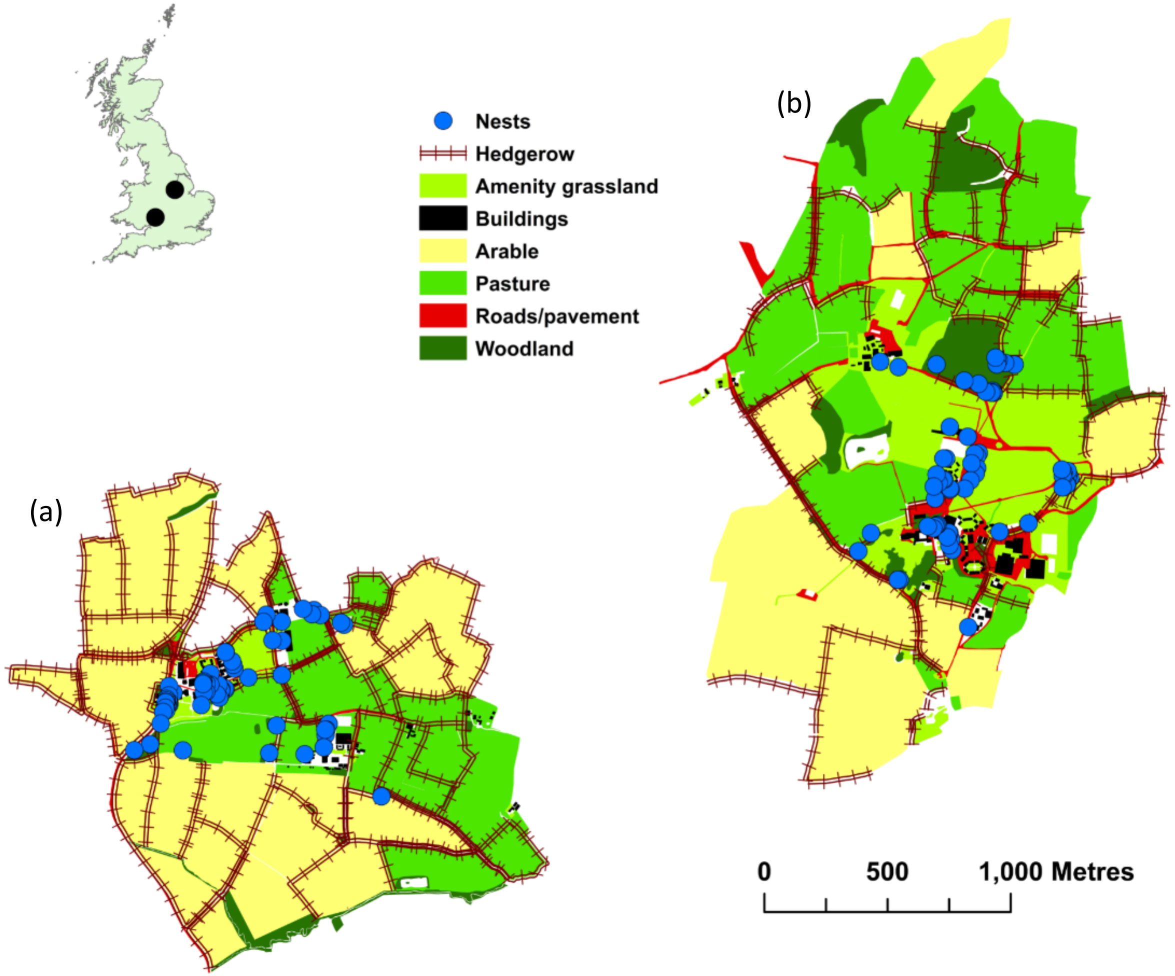


Figure 2.2. Position of hedgehog winter nest sites (blue dots) at **(a)** Brackenhurst and **(b)** Hartpury in relation to habitat composition.

Table 2.2. Results of the top five *a-priori* models for predictors of habitat selection of hedgehog winter nests. Models are ranked based on their AIC values. Null model is also provided for comparison. Models indicated in bold were selected to build average models. Brackenhurst had two alternative maximal models, one including distance to amenity grassland (Brackenhurst Model A) and another including distance to buildings (Brackenhurst Model B). Habitats included in each of the top-ranking models are indicated by the "✓" symbol.

<table>
<tr><th colspan="10">Brackenhurst Model A</th></tr>
<tr><td colspan="10">Models (N = 64)</td></tr>
<tr><th>Amenity grassland</th><th>Buildings</th><th>Hedgerows</th><th>Pastures</th><th>Roads</th><th>Woodland</th><th>Arable</th><th>AIC</th><th>ΔAIC</th><th>AIC_w</th></tr>
<tr><td>✓</td><td>Not included</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td></td><td>357.5</td><td>0.00</td><td>0.38</td></tr>
<tr><td>✓</td><td>Not included</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>358.2</td><td>0.75</td><td>0.26</td></tr>
<tr><td>✓</td><td>Not included</td><td></td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>359.4</td><td>1.94</td><td>0.14</td></tr>
<tr><td>✓</td><td>Not included</td><td></td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>360.8</td><td>3.33</td><td>0.07</td></tr>
<tr><td>✓</td><td>Not included</td><td>✓</td><td>✓</td><td></td><td>✓</td><td>✓</td><td>362.2</td><td>4.67</td><td>0.04</td></tr>
<tr><td colspan="7">NULL</td><td>491.2</td><td>134.00</td><td><0.01</td></tr>
<tr><th colspan="10">Brackenhurst Model B</th></tr>
<tr><td colspan="10">Models (N = 64)</td></tr>
<tr><th>Amenity grassland</th><th>Buildings</th><th>Hedgerows</th><th>Pastures</th><th>Roads</th><th>Woodland</th><th>Arable</th><th>AIC</th><th>ΔAIC</th><th>AIC_w</th></tr>
<tr><td>Not included</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td></td><td>350.2</td><td>0.00</td><td>0.41</td></tr>
<tr><td>Not included</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>351.1</td><td>0.90</td><td>0.26</td></tr>
<tr><td>Not included</td><td>✓</td><td></td><td>✓</td><td>✓</td><td>✓</td><td></td><td>352.1</td><td>1.89</td><td>0.16</td></tr>
<tr><td>Not included</td><td>✓</td><td></td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>352.6</td><td>3.44</td><td>0.07</td></tr>
<tr><td>Not included</td><td>✓</td><td>✓</td><td>✓</td><td></td><td>✓</td><td>✓</td><td>354.3</td><td>4.09</td><td>0.05</td></tr>
<tr><td colspan="7">NULL</td><td>491.2</td><td>141.00</td><td><0.01</td></tr>
<tr><th colspan="10">Hartpury</th></tr>
<tr><td colspan="10">Models (N = 128)</td></tr>
<tr><th>Amenity grassland</th><th>Buildings</th><th>Hedgerows</th><th>Pastures</th><th>Roads</th><th>Woodland</th><th>Arable</th><th>AIC</th><th>ΔAIC</th><th>AIC_w</th></tr>
<tr><td></td><td></td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>395.6</td><td>0.00</td><td>0.49</td></tr>
<tr><td></td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>397.4</td><td>1.80</td><td>0.20</td></tr>
<tr><td>✓</td><td></td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>397.6</td><td>2.04</td><td>0.18</td></tr>
<tr><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>✓</td><td>399.4</td><td>3.84</td><td>0.07</td></tr>
<tr><td></td><td></td><td>✓</td><td>✓</td><td></td><td>✓</td><td>✓</td><td>401.2</td><td>5.61</td><td>0.03</td></tr>
<tr><td colspan="7">NULL</td><td>464.4</td><td>68.8</td><td><0.01</td></tr>
</table>

Table 2.3. Model averaged values of the best *a priori* models (ΔAIC <2) investigating habitat selection for winter nest sites. SE = standard error. Brackenhurst had two alternative models, one including distance to amenity grassland but excluding buildings (Brackenhurst Model A) and another including distance to buildings but excluding amenity grassland (Brackenhurst Model B). Negative values indicate a higher probability of nesting closer to that specific habitat.

Brackenhurst Model A (3 best *a-priori* models)					Brackenhurst Model B (3 best *a-priori* models)				
Variable	Estimate	SE	z	p value	Variable	Estimate	SE	z	p value
(Intercept)	-0.281	0.439	0.640	0.522	(Intercept)	-0.113	0.432	0.261	0.794
Hedgerows	-0.013	0.006	2.000	<0.05	Hedgerows	-0.013	0.006	2.000	<0.05
Pasture	0.017	0.006	2.942	<0.01	Pasture	0.017	0.006	2.877	<0.01
Roads	-0.012	0.005	2.544	<0.05	Roads	-0.010	0.004	2.443	<0.05
Woodland	-0.020	0.003	5.919	<0.001	Woodland	-0.020	0.003	5.607	<0.001
Arable	0.002	0.002	1.127	0.260	Arable	0.002	0.002	1.062	0.288
Buildings (not included)					Buildings	-0.01	0.003	3.412	<0.001
Amenity grassland	-0.008	0.003	2.527	<0.05	Amenity grassland (not included)				

Hartpury (2 best *a-priori* models)				
Variable	Estimate	SE	z	p value
(Intercept)	-2.514	0.515	4.879	<0.001
Hedgerows	-0.008	0.003	3.204	<0.01
Pastures	0.010	0.003	3.748	<0.001
Roads	-0.016	0.006	2.590	<0.01
Woodland	-0.013	0.003	3.774	<0.001
Arable	0.005	0.001	3.436	<0.001
Buildings	0.001	0.001	0.488	0.626
Amenity (not selected by top models)				

Winter nests were primarily constructed from broad leaves (major component in 45% of nests at Brackenhurst and 51% of nests at Hartpury: Appendix 1: Supplementary Table 1). Major differences in the relative proportion of nests containing different materials were, however, evident. For example, litter and/or plastic waste was present in 20 nests (24%)

at Hartpury, although never as the dominant material, but was never recorded at Brackenhurst.

Patterns of Survival

Nine animals died during the study, with no apparent sex difference in mortality risk (Brackenhurst: 1♂; Hartpury: 4♀:4♂). The overall survival rate was significantly lower at Hartpury (Log-rank test: $X^2_1 = 9.46$, $P = 0.002$). All deaths occurred before or after the hibernation period (Figure 2.3). The most common known cause of death was predation by badgers (Appendix 1: Supplementary Table 2).

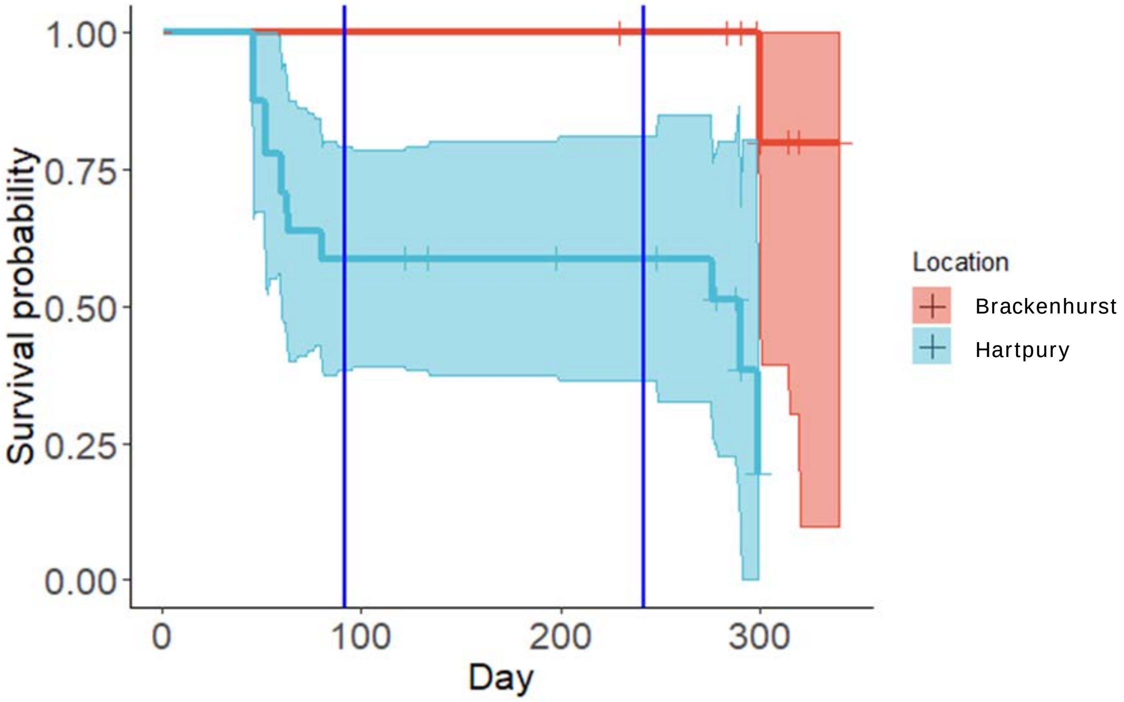


Figure 2.3. Kaplan-Meier survival functions for hedgehogs at Brackenhurst (Site 1: n = 10) versus Hartpury (Site 2: n = 21). Data from sexes and years (2015-2016 and 2016-2017) combined. Vertical blue lines indicate the start (November 1st) and end (March 31st) of the hibernation period.

Body Mass Changes

Data on body mass changes across the study were available for 21 individuals. There were no significant SITE ($F_{1,17} = 3.75$, P = 0.069), SEX ($F_{1,17} = 0.78$, P = 0.389) or SITE*SEX ($F_{1,17} = 3.75$, P = 0.943) differences in mean body mass at the start of the hibernation period (Appendix 1: Supplementary Table 3); collectively, hedgehogs weighed 869 ± 133 g (females:

843 ± 144 g; males: 898 ± 120 g). During hibernation, 16 individuals lost mass (Brackenhurst - 5♀:3♂; Hartpury - 5♀:3♂), whilst five (Brackenhurst - 2♂; Hartpury - 1♀:2♂) gained mass. Absolute mass change ($F_{1,17}$ = 4.65, P = 0.046) but not percentage mass change ($F_{1,17}$ = 4.22, P = 0.056) differed significantly between the sexes at each site, although the latter was close to significance. At Brackenhurst, females lost 242 ± 150 g (-25%) on average whilst males gained a small amount of weight (4 ± 89 g; +1%); Figure 2.4); male and female hedgehogs at Hartpury lost 117 ± 121 g (-14%) and 110 ± 141 g (-15%), respectively (Appendix 1: Supplementary Figure 1).

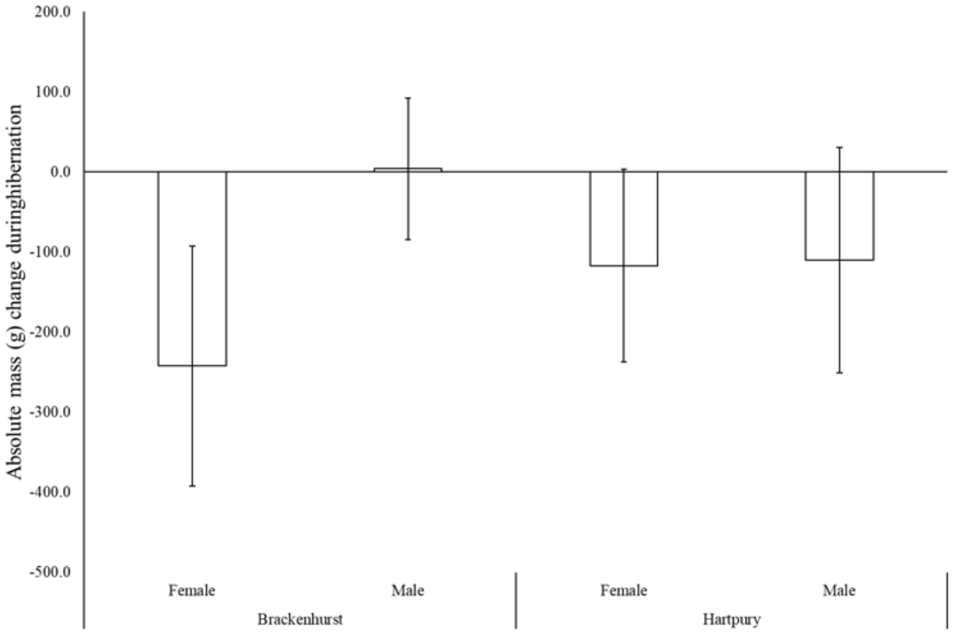


Figure 2.4. Mean (±SD) absolute mass change during the hibernation period (November 1st – March 31st) in relation to site and sex (Brackenhurst: n = 5♀:5♂; Hartpury: n = 6♀:5♂)

There was a negative correlation between the number of nest sites used and the absolute loss in body mass, although this was not significant (r = -0.409, n = 21, P = 0.066; Figure 2.5). However, this was dependent on the extreme loss exhibited by a single female at Brackenhurst (432 g); excluding this female, the relationship is significant (r = -0.561, n = 20, P = 0.010).

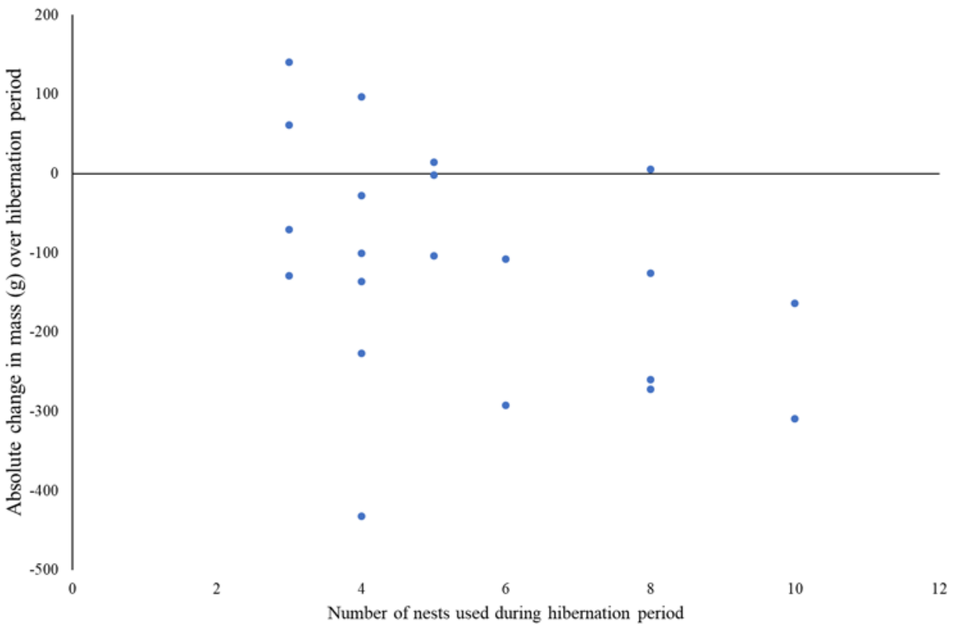


Figure 2.5. Relationship between number of nests used during the hibernation period (November 1st–March 31st) and the corresponding absolute change in mass (g) over the hibernation period (n = 21).

Discussion

In this study, we investigated four factors associated with the winter hibernation period of hedgehogs that could potentially be affected by agricultural land-use and climate change: (i) patterns of body mass change; (ii) frequency of winter nest use; (iii) habitat selection for winter nest sites; and (iv) over-winter survival. Between the two sites studied, one dominated by arable crop production and the other by pasture and amenity grasslands, there were no apparent differences in body mass at the start of hibernation, the number of nest sites used during winter, and the selection for and avoidance of many, but not all, major habitats as nesting locations. In contrast, there were significant differences between the study sites with respect to sex-specific changes in body mass, the use of hedgerows and buildings for nesting, and patterns of survival.

Change in body mass

Estimated body mass of radio-tagged animals at the outset of the hibernation period was not significantly different between Brackenhurst and Hartpury, with animals weighing, on average 869 ± 133 g. This is likely due, in part, to the fact that we only radio-tagged individuals ≥600 g in accordance with guidance relating to the release of rehabilitated hedgehogs by the major wildlife welfare organisation in the UK (RSPCA, 2013). This reliance on radio-tagged individuals to ensure that individuals captured before hibernation could be re-captured afterwards does, however, preclude obtaining data on animals below this threshold weight.

Acknowledging this caveat, the general pattern of mass loss observed (mean of 100-240 g within most site-sex divisions, equivalent to a mean of 14-25% of pre-hibernation mass) is within the range recorded in previous studies (Table 2.5). However, there was a substantial difference in sex-specific patterns of mass change at the two sites. At Hartpury, both males and females lost approximately the same amount of weight (Figure 2.4). Conversely, females at Brackenhurst lost markedly more weight than any other division, whereas males, on average, gained a small amount of weight. In fact, five (23.8%) animals across both sites gained weight across the hibernation period. This could indicate that individuals may have been able to access sufficient food resources during the winter period to offset the fat reserves used during hibernation, or that some animals may have already stopped hibernating and resumed typical foraging activity before they were recaptured in March/April. Although we are not able to discriminate between these possibilities, it is clear that the magnitude of these average changes are within the survivable range documented for this species.

Absolute mass loss was also negatively correlated with the number of nests used in the winter period (Figure 2.5), although not significantly (P = 0.066). The lack of significance may, in part, be attributable to the relatively small sample size (n = 21), the highly variable changes in mass recorded, and the presence of one female that lost >400 g (40% of her body mass). Although this is among one of the largest percentage mass losses ever recorded (Table 2.4) and was >100 g more than any other individual in this study, this individual survived to spring. As rousing from hibernation is energetically expensive (Tähti and Soivio, 1977), hedgehogs would be expected to avoid doing so unnecessarily to avoid depleting their fat reserves. Rousing is likely to occur in response to environmental fluctuations, including both rises or falls in temperature (Morris, 2018), but in anthropogenic landscapes, it may also occur in response to human disturbance. To date, however, there are very few data on the extent to which disturbances affect hedgehog hibernation, either by causing them to move nests or rouse but remain in the same nest (Walhovd, 1979), and what impacts these may have on energy consumption and mortality risk.

Table 2.4. Summary of body mass changes recorded in previous studies of the West-European hedgehog over the winter hibernation period.

Country	**Habitat**	**Years studied**	**Sample size & composition**	**Mass loss recorded over winter**	**Minimum weight to survive hibernation**	**Reference**
England	Urban parkland	1963 - 1968	105	25%	Recommends 450 g (550 g in more northern areas)	Morris, 1984
Denmark	Rural	2001 - 2002	10 (5♀:5♂); (3A:7J)	30 ± 7% (A) 22 ± 10% (J)	513 g	Jensen, 2004
Ireland	Rural	2008 - 2009	8 (7A:1J)	301 ± 3.9 g (♀) (range: 15-38%) 108 ± 2.6 g (♂) (range: 3-6%)	475 g in Nov	Haigh *et al.*, 2012b
Denmark	Suburban	2014 - 2015	8 (8J)	16 ± 3% (J)	-	Rasmussen *et al.*, 2019a
England	Various	2010 - 2014	55 (19♀:30♂:16?); (20A:35J)	98.6 ± 35.6 g (♀) 160.8 ± 40.5 g (♂) 111.4 ± 33.0 g (A) 162.2 ± 43.3 g (J) 14.1 ± 3.1% (All animals)	Recommends >600 g for release, but one individual weighing 391 g survived release and hibernation	Yarnell *et al.*, 2019
England	Various	2015-2017	21 (11♀:10♂)	Site 1: 240 ± 150 g (25 ± 13%) (♀) Site 1: -4 ± 89 g (1 ± 9%) (♂) Site 2: 117 ± 121 g (14 ± 16%) (♀) Site 3: 110 ± 141 g (15± 19%) (♂)	-	Present study

Nesting behaviour

Hedgehogs used a median of 5 (mean: 5.5) nests during the 151-day hibernation period. This is markedly higher than that observed in other studies (Table 2.5). Drawing direct comparisons between the number of nests used in such studies is, however, problematic because of the methodological differences used to define the onset and duration of hibernation, coupled with latitudinal differences in weather and/or temperature which extend or shorten the overall length of the hibernation period. It is worth noting, however, that the mean number of nests used by the animals in this study was more than twice that (1.74 nests per 100 days = 2.6 nests over 151 days) recorded in the most recent study of hedgehogs in England and which utilized the same dates for defining the hibernation period (Yarnell *et al.*, 2019).

The increased number of nests used in our study was associated with periods during November, December and/or January where several individuals used a series of nests in quick succession (Figure 2.1). Although some of these periods of frequent movements between nests could be interpreted as indicating that an individual had not yet started hibernating, the patterns of nest retention exhibited throughout the study as a whole were extremely variable such that it is difficult to identify clear general trends. The possible exception to this is that the majority (62%) of animals used a single nest location for >89 days, with many of these used for the first time in November or December; this is markedly higher than the 21% of nests (n = 167) occupied for ≥3 months reported by Morris (Morris, 1973) in west London.

Table 2.5. Summary of over-winter nesting behaviour in previous studies of the West-European hedgehog. Studies are listed in chronological order.

Country	**Habitat**	**Years studied**	**Sample size & composition**[1]	**Duration of hibernation (days)**	**Number of nests used**	**Reference**
England	Urban park	1963 - 1967	167 nests	Not recorded	Mean occupation time = 1.4 months (range 0-6 months)	Morris, 1973b
Denmark	Rural	2001 - 2002	10 (3A:7J)	197.7 ± 2.2 (A) 178.8 ± 13.1 (J)	2.2 (range: 1-4)	Jensen, 2004
Ireland	Rural	2008 - 2010	8 (7A:1J)	167.3 ± 10.5 (♀) 148.6 ± 10.2 (♂) 155.4 ± 9.0 (A) 157 (J)	2.0 ± 0.6 (♀) 3.2 ± 0.6 (♂) 2.4 ± 0.7 (A) 5.0 (J)	Haigh *et al.*, 2012b
Finland	Urban	2004 - 2006	11 (11A) (5♀:6♂)	223 ± 2.5 (♀) 224 ± 4.8 (♂)	1.0 (♀) 1.0 (♂)	Rautio *et al.*, 2014
Denmark	Urban	2014 - 2015	8 (8J)	138.0 ± 5.6 (J)	1.8 ± 0.14 (J)	Rasmussen *et al.*, 2019a
England	Various	2010 - 2014	55 (20A:35J); (19♀:30♂:16?)	Not recorded	2.2 ± 0.5 (♀)[2] 1.7 ± 0.4 (♂)[2] 1.8 ± 0.4 (A)[2] 2.6 ± 0.6 (J)[2]	Yarnell *et al.*, 2019
England	Arable	2015 - 2017	21A (12♀:9♂)	Not recorded	5.8 ± 2.6 (♀) 5.0 ± 1.9 (♂)	Present study

[1] Data were recorded by the authors either in terms of the number of nests studied or the number of individuals studied: A = adult; J = juvenile; ? = unknown sex.

[2] Figures are the number of nests used per 100 days.

Clear patterns in nest location were evident for most, but not all, habitats. Hedgehogs consistently avoided nesting near pasture fields, whilst favouring hedgerows, woodlands and roads. In contrast, differing patterns of selection were evident for arable fields, buildings and amenity grassland. At Brackenhurst, nests were preferentially located near to amenity grassland and near buildings, although these habitats were strongly correlated with one another, whereas arable fields were neither selected nor avoided. Conversely, at Hartpury, arable fields were avoided, buildings were neither selected nor avoided and amenity grassland was not retained in the top-ranked models. These data imply that agricultural habitats were generally unsuitable for hibernation, a finding consistent with behaviour outside the hibernation period that has been attributed to a combination of reduced food availability (Hof and Bright, 2010a) and increased risk of predation from and competition with badgers (Young *et al.*, 2006; Hubert *et al.*, 2011; Parrott *et al.*, 2014; Trewby *et al.*, 2014; Van de Poel *et al.*, 2015; Pettett *et al.*, 2017a, ; Williams *et al.*, 2018a).

Hedgerows and woodland were an important habitat for nesting, a pattern that is evident in both summer and winter seasons in other studies (Jensen, 2004; Riber, 2006; Rautio *et al.*, 2014; Pettett *et al.*, 2017b). Similarly, the selection for roads in this study is also most probably associated with the presence of hedgerows as borders along roads at both sites. In addition to acting as nesting sites, hedgerows are also recognised as an important refuge habitat whilst foraging where badgers are present (Hof *et al.*, 2012; Pettett *et al.*, 2017b) and for orientation through fragmented landscapes (Moorhouse *et al.*, 2014). As such, the general loss and degradation of hedgerows in the UK (Sutherland *et al.*, 2006; Cornulier *et al.*, 2011) is likely to have negatively affected hedgehog populations due to impacts at multiple stages in their annual cycle, although the exact mechanisms are unknown because of the relative paucity of data on rural hedgehog populations and behaviour since the 1950s (Harris *et al.*, 1995).

Similarly, there are few data on the importance of woodlands for hedgehogs. For example, woodlands were not identified as a factor affecting patterns of occupancy in a national survey of England and Wales (Williams *et al.*, 2018a), they were the least selected habitat in a radio-tracking study in arable landscapes (Pettett *et al.*, 2017b), and no hedgehogs were detected in woodland in a pilot project on the Hartpury campus investigating the efficacy of three different methods for surveying hedgehogs (Bearman-Brown *et al.*, 2020b; Chapter

Five): all these studies were, however, conducted in the summer. The preference for woodlands as sites for hibernation observed in this study, and the reliance on broad leaves as nesting material, may suggest that hedgehogs tend to avoid woodlands during the summer months but use them as sites for hibernating during the winter months. As outlined above, one possible reason for these seasonal differences is the presence of badgers, which favour woodlands and plantations as sites for their setts (Wilson *et al.*, 1997) but undergo a period of torpor in winter (Roper, 2010). Consequently, hedgehogs could be avoiding woodlands during the summer when badgers are active but using them as hibernation sites in the winter when the risk from badgers is markedly lower. As such, woodlands may represent a key resource for hedgehogs but only during one phase of their annual cycle. The impact of historical changes in the coverage of different types of woodland (Hopkins and Kirby, 2007; Amar *et al.*, 2010), their management and their interaction with an increasing badger population (Judge *et al.*, 2014, 2017) on hedgehog populations are unknown but require investigation. For example, in their recent report, Mathews *et al.* (2018) estimated that 37% of the British hedgehog population was supported by broadleaved woodland.

The affinity for amenity grassland as a foraging habitat has been well documented in Great Britain, most notably in the context of responses to the culling of badgers as a means for managing bovine tuberculosis in cattle (Young *et al.*, 2006; Parrott *et al.*, 2014; Trewby *et al.*, 2014). During winter these areas are likely to be associated with low levels of badger activity (due to torpor) but also possibly marginally higher average temperatures than surrounding areas due to their proximity to buildings, and provision of food either accidentally (discarded refuse) or deliberately (although we were not aware of anyone deliberately feeding hedgehogs on either campus). However, amenity areas on university campuses are likely to experience high levels of pedestrian activity except in particularly poor weather and over the Christmas holiday period. The presence of buildings on these two sites also enabled hedgehogs to use some unusual nest locations, including piles of building materials and underground heating tunnels.

Over-winter survival

Survival across the study period as a whole (August-May) was significantly lower at Hartpury versus Brackenhurst. However, this was not associated with differences in mortality during the hibernation period itself, but rather mortality prior to the onset of hibernation and in the period after animals had resumed foraging in spring: in fact, none of the tagged animals in this study (n = 31) died during the hibernation period itself (Figure 2.3). Consequently, mortalities were not related to body mass *per se* but stochastic events such as predation by badgers and road traffic accidents (although it could be argued that animals which have not yet accumulated sufficient fat reserves and/or those that leave hibernation having lost a large amount of weight might be expected to take greater risks when foraging). However, it must be emphasised that these survival data are based on animals that were in good physical condition (visually health-checked and ≥600 g) prior to hibernation in accordance with welfare guidelines; this is substantially higher than the minimum threshold of 450-513 g outlined in Table 2.4, and which would tend to elevate survival rates.

The survival rate observed at Hartpury, when measured from August to April (approximately 65%), was lower than that recorded in Sweden (57-96%, mean = 71%) over seven years in the 1970s (Kristiansson, 1990), whereas the survival rates at both sites when measured from October to April were comparable to studies from England (83%), Ireland (100%), Denmark (89-90%) and Finland (100%) conducted between 2001 and 2017 (Jensen, 2004; Rautio *et al.*, 2013; Yarnell *et al.*, 2019). Overall, this body of evidence suggests that, in general terms, the survival rate of animals that have accumulated sufficient fat reserves prior to hibernation is likely to be high, but that site-specific pressures associated with movements in autumn and spring can substantially increase mortality rates (Yarnell *et al.*, 2019).

Conclusions

This study has identified key similarities and differences in four key parameters associated with the winter hibernation of hedgehogs across two sites associated with different patterns of land management. Most notably, the period of hibernation itself, when hedgehogs are generally inactive within hibernacula, is not associated with high levels of mortality. Conversely, it is the periods before and after entering hibernation that pose significant risks, predominantly from stochastic factors such as badger predation and vehicle collisions. In addition, hedgehogs at both sites consistently avoided nesting in proximity to pastoral fields during winter, but favoured locations near to hedgerows, woodlands and roads. Selection for or avoidance of arable fields, buildings, amenity grasslands and hedgerows varied between the two sites.

However, this study was associated with several practical limitations. Data could only be reliably collected from radio-tagged individuals and radio-tags can only be fitted to animals weighing ≥600 g for welfare reasons. Radio-tracking is also limited in the extent to which the start and end of the hibernation period (for each individual) can be identified reliably, and the ease with which data on short-term patterns of movement between nests can be collected given that animals are inactive for many successive days. Future studies, therefore, need to consider the use of other technologies, such as GPS tracking devices (Glasby and Yarnell, 2013) and animal-mounted bio-loggers (Chmura *et al.*, 2018), to overcome these constraints. In particular, such studies need to focus on: (i) quantifying patterns of survival of animals weighing <600g; (ii) identifying factors associated with nest movements and whether this affects mass change during hibernation; and (iii) the role of woodlands in the annual cycle of hedgehogs in both arable and pastoral dominated landscapes.

CHAPTER THREE

Chapter Two discussed factors associated with the rural landscape which may affect survival of hedgehogs, particularly over-winter. The association of hedgehogs increasingly with the urban landscape is discussed in Chapter One, and was also evident in Chapter Two, with the presence of badgers a possible explanation for this.

This progression into urban and sub-urban habitats may bring hedgehogs into greater contact with humans, increasing the risk of mortality and injury. Having determined that where mortality does occur, it is during the active months, I sought to explore this further by considering if this is also evident in the condition of animals arriving with wildlife rehabilitators.

In order to explore this further I undertook an analysis of data from one of Europe's largest animal welfare organisations: the Royal Society for the Prevention of Cruelty to Animals (RSPCA) to examine the pattern of hedgehog admissions over 13 years to quantify: the age and sex composition of hedgehogs admitted annually and seasonally; age and sex differences between causes of admission; patterns of mortality and survival in relation to cause of admission; and the effect of age, sex and cause of admission on the probability of survival to release. Determining the extent to which animals can be returned to the wild, as a key characteristic of wildlife rehabilitation, is paramount for this practice to have any value in addressing some of the anthropogenic causes of decline reported in the literature.

Therefore, in this chapter I aimed to explore: (i) how admission numbers are affected by season, sex, and age; (ii) how cause of admission and duration of care varies with season; and (iii) factors associated with long term fluctuations in the number and outcome of admissions.

The manuscript presented in this chapter has been prepared for publication in *European Journal of Wildlife Research.*

My contribution to the work:

I designed the project and conducted all analysis with assistance from Dr Philip Baker. I prepared the manuscript with assistance from Dr Philip Baker.

An investigation of factors associated with the admission of hedgehogs (*Erinaceus europeaus*) to, and survival rates in, RSPCA wildlife centres in England and Wales 2006-2018

Abstract

Wildlife rehabilitation could have important benefits for formerly common species that are declining rapidly; analysis of admission records could help to identify underlying natural and/or anthropogenic reasons for such declines. In this study, we examined records from >23,000 hedgehogs (*Erinaceus europaeus*), a species that has declined by up to 40% in the last 20 years in Great Britain, admitted to the Royal Society for the Prevention of Cruelty to Animals between 2006-2018. Significantly more males (1.06♂:1.00♀) and juveniles were admitted, but the number of adults and juveniles admitted annually was positively correlated. Natural causes, anthropogenic causes, orphaned dependent young and attacks by other animals comprised 46%, 15%, 19% and 3% of admissions, respectively; however, given the indirect impacts of humans, anthropogenic factors could have been responsible for up to 47% of cases. In total, 51% of animals survived to be released, but 31% of animals that died or were euthanased perished >48h after being admitted, suggesting that existing triage procedures potentially need to be reviewed. Survival probabilities were equivalent for males and females, but significantly lower for adults versus juveniles. In relation to underlying causes, survival probabilities were highest for orphans (63%) and lowest for anthropogenic causes (39%). The dataset used did, however, contain a lot of missing data: the implications of this, and the other associated limitations of wildlife admissions data, are discussed. Overall, these data suggest that hedgehog rehabilitators are likely to have a marked benefit ameliorating some of the negative impacts caused by humans.

Keywords: wildlife causalities; rehabilitation; hedgehog; mortality; injury; anthropogenic

Introduction

Wildlife rehabilitation (WR) involves the treatment and temporary care of injured, diseased, orphaned and displaced wild animals (mostly, but not exclusively, indigenous species) and the subsequent release of healthy individuals into appropriate wild habitats (Miller, 2012). Estimates of the numbers of animals taken into care annually at a national level typically run into the tens of thousands. For example, within the UK, wildlife hospitals and rehabilitators have been estimated to receive 30,000 (Molony *et al.*, 2006) to >71,000 animals per annum (Grogan and Kelly, 2013), with a further 130,000 wild animals treated by veterinarians each year (Barnes and Farnworth, 2016). Similarly, Garcês *et al.* (2020) estimated that approximately 12,000 wild birds had been admitted to wildlife rehabilitation centres in northern Portugal during the 10-year period 2008-2017, while the National Wildlife Rehabilitators' Association in the United States reported treating 105,000 animals and birds in a single year (cited in Loyd *et al.*, 2017). Based upon these figures, it is reasonable to assume that, at an international level and across the broad range of taxa involved, the total number of individuals entering WR facilities is likely to be in the order of millions each year.

This volume of animals potentially represents a substantive source of information and / or specimens for use in a broad range of contexts. For example, in addition to improving practices associated with the rehabilitation process itself, such as triage and release protocols (Robertson and Harris, 1995; Molony *et al.*, 2007; Kelly *et al.*, 2008, 2010; Champagnon *et al.*, 2012; Yarnell *et al.*, 2019), data on the number of animals admitted and the reasons for those admissions could be used to answer questions related to a wide range of health, welfare and conservation related questions. This might include: disease, pollution and ecotoxicology surveillance (Dowding *et al.*, 2010b; Mullineaux and Kidner, 2011; Silpa *et al.*, 2015; Rasmussen *et al.*, 2019b; Delogu *et al.*, 2020); assessment of the relative importance of different causes of morbidity and mortality, and how these may vary with age and sex (Leighton and Grogan, 2011; Williams *et al.*, 2017; Garcês *et al.*, 2019); identifying the positive or negative impacts of anthropogenic activities such as wildlife management programmes, habitat alterations, legislative changes and climate change (Goldsworthy *et al.*, 2000; Lunney *et al.*, 2004); and perhaps even for population monitoring (Pyke and Szabo, 2018). Furthermore, although contested, WR may also have conservation benefits for some species; in particular, wildlife rehabilitators may receive large numbers of species that are widespread and relatively common, but which are declining rapidly. For these species, analysis of archival data on the numbers of animals entering their facilities, and the reasons why, may help to identify reasons for such declines, whilst also helping to promote the sharing of best practice between rehabilitators (Tribe and Brown, 2000; Wimberger and Downs, 2010; Schenk and Souza, 2014).

The West-European hedgehog (*Erinaceus europeaus*) is a small (<1.5 kg), insectivorous mammal found throughout Spain, Portugal and Italy north to Scandinavia (Morris, 2018). In several countries within this range, hedgehog populations are estimated to have declined by up to 40% over the last two decades (Holsbeek *et al.*, 1999; Huijser and Bergers, 2000; Van de Poel *et al.*, 2015; Hof and Bright, 2016; Müller, 2018; Williams *et al.*, 2018a; Wilson and Wembridge, 2018); within Great Britain, the species was recently upgraded to Vulnerable by Mathews *et al.* (2018). Despite these changes, hedgehogs are still one of the most common species entering wildlife hospitals in England and Wales (Reeve and Huijser, 1999; Grogan and Kelly, 2013). This is due, in part, to the fact that they are widely found in residential gardens in urban areas (Hof and Bright, 2009) and that they are one of the easier species that members of the public can capture by hand.

Within the UK wildlife rehabilitation is not a licenced activity (Mullineaux, 2014), and is practiced by a large number of autonomous individuals working from their own homes through to several large hospitals (Chapter Four); all work in collaboration with external or on-site veterinary surgeons, and many are registered as charities. The largest organisation in England and Wales undertaking WR activities is the Royal Society for the Prevention of Cruelty to Animals (RSPCA) which runs four wildlife hospitals in England along with a range of other animal welfare activities. Given the wide variation in the range of people rehabilitating hedgehogs, and their varied presence on social media, it is difficult to estimate how many hedgehogs are “rescued” each year in the UK, but it could be as many as 40,000-59,000 individuals (Chapter Four). In the context of a national estimated pre-breeding population of 522,000 animals (Mathews *et al.*, 2018), this is a substantial number. Consequently, wildlife rehabilitators could have a significant role in helping this species at the current time and for the foreseeable future.

As wild hedgehogs enter wildlife hospitals because they are injured, orphaned or in ill-health, collating information on the underlying reasons for these admissions means that it is possible to identify the relative importance of both natural and anthropogenic causes and how these may change over time. Previously, Reeve and Huijser (1999) analysed 11,541 records from 20-30 wildlife hospitals collated by the British Wildlife Rehabilitation Council from 1993-1997: of these, 28% were classified as orphans and 28% were attributed to natural causes, but 25% were considered “unnatural” as they were associated with human activities or their pets. Since that time, however, there have been substantive changes within Great Britain/the UK in a range of factors that could potentially have impacted hedgehogs. For example, between 1998 and 2018: the human population increased from 58.4 million to 66.4 million (an increase of 14%: www.ons.gov.uk; data are for UK); the total length of roads increased from 388,641 km^{-1} to 397,021 km^{-1} (+2%: www.gov.uk; data are for Great Britain); road traffic volume increased from 284.9 billion to 328.1 billion vehicle miles (+15%: www.roadtraffic.dft.gov.uk; data are for Great Britain); the number of households increased from 24.0 million to 27.6 million (+15%: www.ons.gov.uk; data are for Great Britain); and the ten hottest years on record have all occurred since 2002 (www.metoffice.gov.uk; data are for the UK).

Therefore, in this study we examined the pattern of hedgehog admissions to the RSPCA across the 13-year period 2006-2018 to determine whether there have been any marked changes in the pattern of admissions since the earlier investigation by Reeve and Huijser (1999). Specifically, we quantified: (i) the age and sex composition of hedgehogs admitted annually; (ii) seasonal differences in the numbers of animals in different age-sex classes; (iii) age and sex differences between different causes of admission; (iv) patterns of mortality and survival in relation to cause of admission; and (v) the effect of age, sex and cause of admissions on the probability of survival to release. Differences in these parameters are then (vi) compared to the results of similar previous analyses.

Methods

Admissions records of hedgehogs admitted to the four RSPCA wildlife centres in England (East Winch, Norfolk; Mallydams Wood, East Sussex; Stapeley Grange, Cheshire; West Hatch, Somerset) were obtained, from January 2006 to December 2018 inclusive. The following information was recorded for each animal: age (adult, juvenile, unknown); sex (female, male, unknown); reason for admission (21 categories: abnormal behaviour (including out in the day), attacked by other animal, attacked by human, blind, caught/entangled, collision with vehicle, disease, flystrike, garden accident, geriatric, inexperienced juvenile, injury (cause uncertain), oiled/other contaminant, orphaned, other reason, parasite, poisoned, shot, starvation, unknown, weakness); admission date; outcome (released, euthanased, died, transferred to other organisation); and outcome date. Prior to analysis, the data were checked for errors and any anomalous records were removed (e.g. if the admission date was later than the outcome date, if no definitive outcome was listed, etc.). The outcome and admission date were used to determine whether animals died, were euthanased or released within three time periods: at admission (difference between outcome and admission date =0), within 48 hours (difference = 1-2 days) or after 48 hours (≥3 days). This 48 hour time period is used as part of the overall triage process (e.g. the decision to euthanase or treat an individual may be deferred for 1-2 days thereby giving staff the opportunity to make a more informed decision as the animal's likely chances of surviving). No specific licences were required for this work as it was a retrospective analysis of data recorded by the RSPCA as part of their normal practices.

The sex and age composition of those animals admitted each year, and collectively, were compared using a series of chi-squared tests; animals of unknown sex or age were excluded from these analyses. The relationship between the numbers of adults and juveniles admitted each year were analysed using a Pearson's correlation. The seasonal (spring: March - May; summer: June - August; autumn: September - November; winter: December - February) pattern of admission was then compared separately for adult males, adult females, juvenile males and juvenile females using repeated-measures ANOVAs: data for each age-sex class was checked to see if it conformed to the assumption of sphericity; where this assumption was not upheld, degrees of freedom were adjusted using the Greenhouse-Geisser correction.

Causes of admission

Differences in the age and sex composition for each of the 21 causes for admission listed above were quantified using a series of chi-squared test; tests were not conducted if sample sizes were too small, or if the cause of admission was specific to one age class (e.g. orphaned juveniles). In addition, to increase comparability with the previous study of Reeve and Huijser (1999), these 21 causes for admission were also merged into six categories: natural causes (abnormal behaviour, blind, disease, flystrike, geriatric, inexperienced juvenile, parasite, starvation, weakness); anthropogenic causes (attacked by human, caught/entangled, collision with a vehicle, garden accident, injury (cause uncertain), shot); orphaned juvenile; attacked by another animal; poison or pollutant; and other/unknown. Seasonal differences in the number of animals admitted for natural causes, anthropogenic causes, orphans and following an attack by another animal were compared using repeated-measures ANOVAs (the Greenhouse-Geisser correction was applied if the assumption of sphericity was violated).

Patterns of survival to release

The pattern of survival within each of the RSPCA's 21 admission classes, and the six major groupings of these classes, was determined by collating the number of animals that died, were euthanased or were released within each of the three time periods (at admission, within 48 hours of admission, more than 48 hours after admission). The effect of sex, age and cause of admission (major grouping) on the probability that an animal survived to release was analysed using a binary logistic regression. This model included only main terms, as some major divisions (e.g orphans) were specific to just one age class. In addition, a Kruskal-Wallis test was used to compare the median time individuals spent in care within all admission classes and the six major groupings.

Data analysis

Statistical analyses were undertaken using MINITAB version 19 and SPSS version 25.

Results

A total of 24,419 hedgehogs were received by the RSPCA during 2006-2018. However, 477 records (2%) were omitted: 9 cases where the dates of admission and release were contradictory; 31 cases where the animal had been in captivity for more than one year; 88 cases where the individual was dead at arrival; 248 cases where no cause of admission was listed; 42 cases where the outcome date was not recorded; and 59 cases where the outcome was not listed. This left 23,942 cases for analysis. On average, 1842 hedgehogs were submitted annually (range: 1381-2518; Table 3.1).

Sex and age composition

Sex was not recorded for 13,727 (57.3%) individuals; of the remainder, 5253 (21.9%) were male and 4962 (20.7%) were female. This cumulative sex ratio (1.06♂:1.00♀) across the sample as a whole is significantly different from parity (Chi-squared test: $X^2_1 = 8.29$, $P = 0.004$). However, the sex ratio of animals of known sex within a given year was typically not significantly different from 1:1 ratio, with the exception of one year (Table 3.1).

Table 3.1. Sex and age composition of hedgehogs submitted to RSPCA wildlife centres 2006-2018. Chi-squared tests relate to animals of known sex and known age only.

Year	**Sex composition**				**Age composition**				**Total**
	Male	**Female**	**Unknown**	**Chi-squared test**	**Adult**	**Juvenile**	**Unknown**	**Chi-squared test**	
2006	262	228	891	$X^2_1 = 2.36$, $P = 0.125$	272	883	226	$X^2_1 = 323.22$, $P < 0.001$	1,381
2007	357	336	1,246	$X^2_1 = 0.66$, $P = 0.425$	361	1,260	318	$X^2_1 = 498.58$, $P < 0.001$	1,939
2008	417	427	809	$X^2_1 = 0.12$, $P = 0.731$	334	1,183	136	$X^2_1 = 475.15$, $P < 0.001$	1,653
2009	414	370	876	$X^2_1 = 2.47$, $P = 0.116$	311	1,206	143	$X^2_1 = 528.03$, $P < 0.001$	1,660
2010	468	417	802	$X^2_1 = 2.94$, $P = 0.086$	327	1,254	106	$X^2_1 = 543.54$, $P < 0.001$	1,687
2011	372	341	783	$X^2_1 = 1.35$, $P = 0.246$	362	1,058	76	$X^2_1 = 341.14$, $P < 0.001$	1,496
2012	513	453	1,057	$X^2_1 = 3.73$, $P = 0.054$	452	1,405	166	$X^2_1 = 489.07$, $P < 0.001$	2,023
2013	298	308	795	$X^2_1 = 0.17$, $P = 0.685$	336	945	120	$X^2_1 = 289.53$, $P < 0.001$	1,401
2014	379	379	1,119	$X^2_1 = 0.00$, $P = 1.000$	384	1,319	174	$X^2_1 = 513.34$, $P < 0.001$	1,877
2015	462	457	1,118	$X^2_1 = 0.03$, $P = 0.869$	464	1,391	182	$X^2_1 = 463.25$, $P < 0.001$	2,037
2016	473	413	1,369	$X^2_1 = 4.06$, $P = 0.044$	516	1,530	209	$X^2_1 = 502.45$, $P < 0.001$	2,255
2017	469	475	1,574	$X^2_1 = 0.04$, $P = 0.845$	537	1,590	391	$X^2_1 = 521.30$, $P < 0.001$	2,518
2018	369	358	1,288	$X^2_1 = 0.17$, $P = 0.683$	418	1,104	493	$X^2_1 = 309.20$, $P < 0.001$	2,015
Total	5,253	4,962	13,727	$X^2_1 = 8.29$, $P = 0.004$	5,074	16,128	2,740	$X^2_1 = 5763.18$, $P < 0.001$	23,942

Significantly more juvenile animals than adults were consistently admitted each year (Table 3.1), although the numbers of adults versus juveniles submitted annually was significantly positively correlated (Pearson correlation coefficient: r = 0.753, P < 0.001: Figure 3.1). There was a 1.8-fold difference between the smallest number of juveniles submitted in a single year (2006: n = 883) and the largest number submitted in a single year (2017: n = 1590).

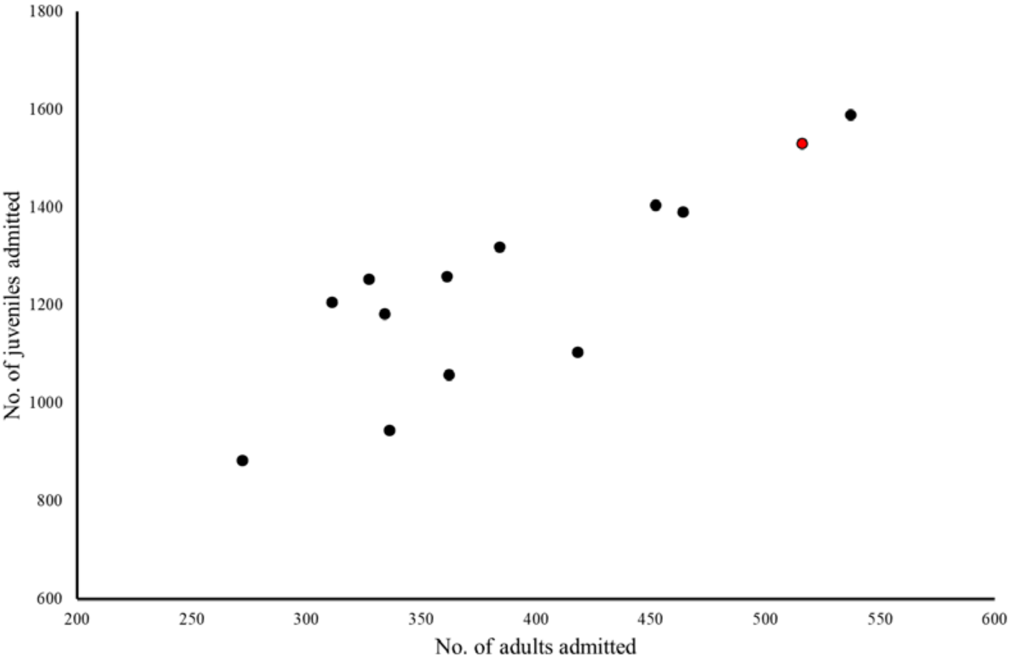
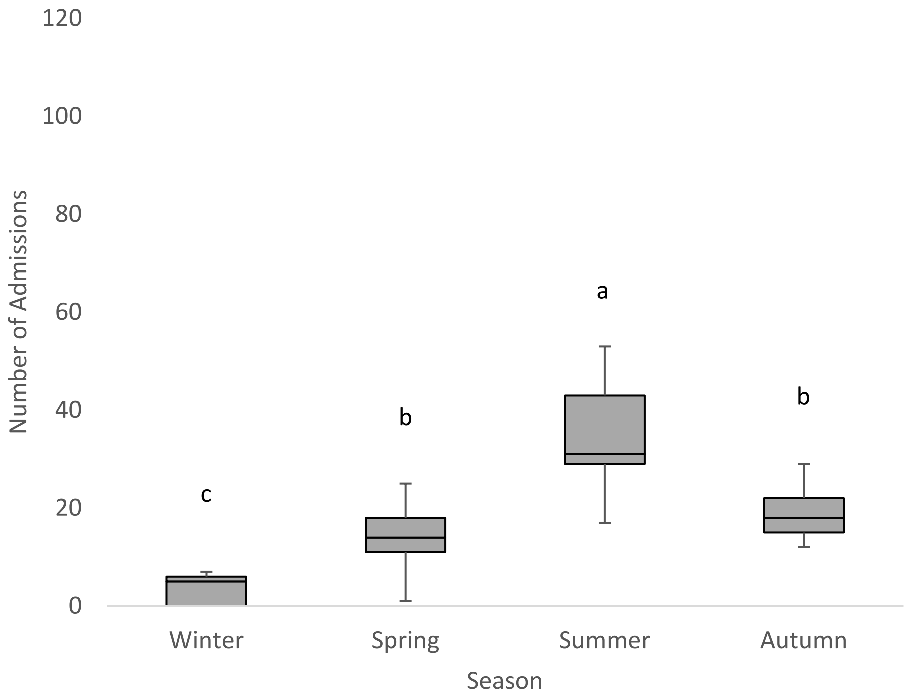


Figure 3.1. Correlation between the number of adult (n = 5074) and juvenile (n = 16,128) hedgehogs submitted each year. The year 2016 is indicated by the red data point, as the only year where a significant difference in sex composition was detected.

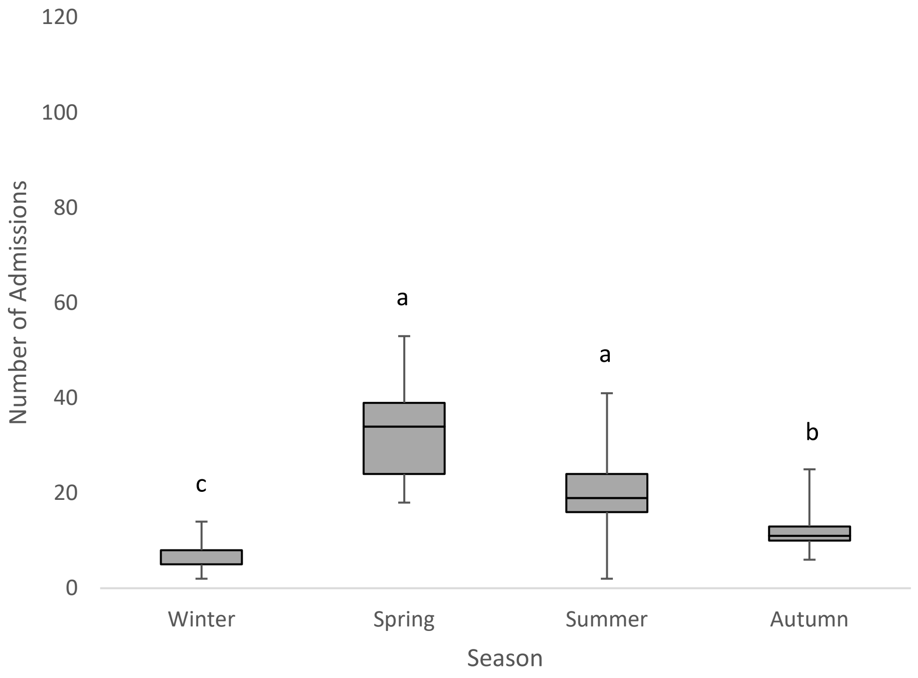
Seasonality of admissions by age and sex

Information on both age and sex was recorded for 9711 (39.8%) animals. There was a significant difference in the number of animals admitted each season in all four age-sex classes (Repeated-measures ANOVA: adult females: $F_{3,\,36}$ = 86.393, P < 0.001, n = 1317; adult males: $F_{3,\,36}$ = 66.071, P < 0.001, n = 1303; juvenile females: $F_{2.048,\,25.472}$ = 143.694, P < 0.001, n = 3398; juvenile males: $F_{1.984,\,499.461}$ = 141.548, P < 0.001, n = 3693), although the seasonal pattern was different between most age classes (Figure 3.2). Adult animals were most frequently admitted in summer due to a peak in female admissions (Figure 3.2a): male admissions were comparable in both spring and summer (Figure 3.2b). The number of adults admitted then declined slightly during autumn and was lowest in winter (Figures 3.2a & 3.2b). Juvenile males and females had similar patterns of admission (Figures 3.2c & 3.2d), with numbers increasing markedly from spring to summer and then peaking in autumn: admissions in winter were intermediate to those seen in spring and summer.

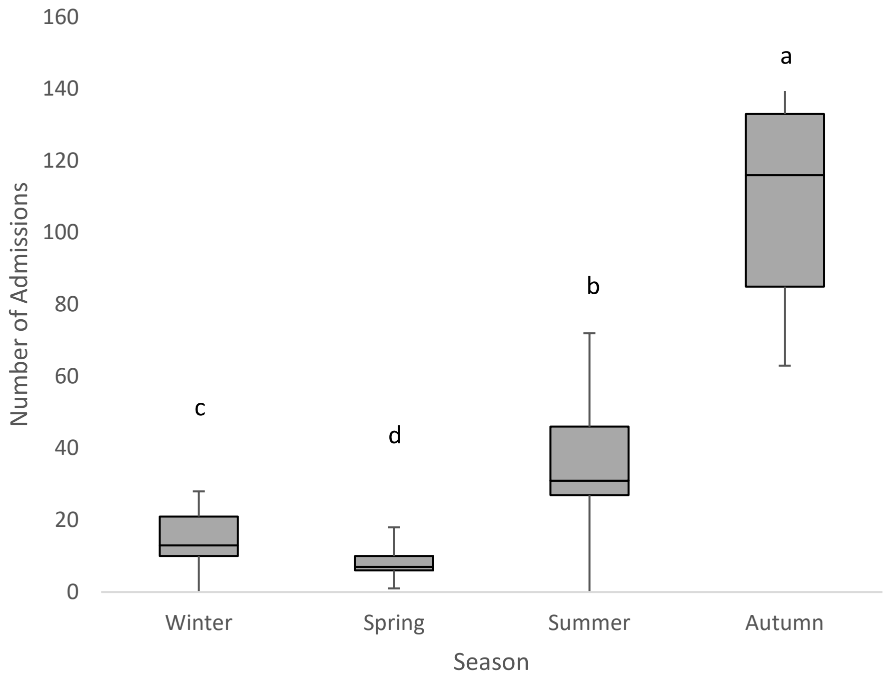
(a) Adult females



(b) Adult males



(c) Juvenile females



(d) Juvenile males

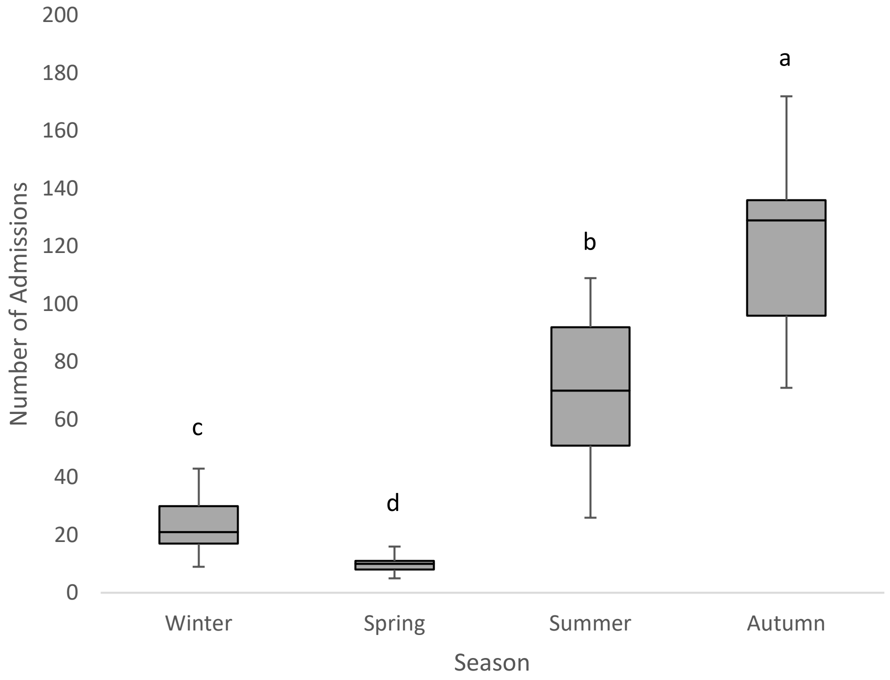


Figure 3.2. Median (±IQR) number of hedgehogs admitted to RSPCA wildlife centres each season during the period 2006-2018 (inclusive) in relation to age and sex: (a) adult females (n = 1317); (b) adult males (n = 1303); (c) juvenile females (n = 3398); and (d) juvenile males (n = 3693). Letters denote *post hoc* groupings from a series of repeated-measures ANOVAs.

Causes of admission

Cause of admission was predominantly as a result of natural causes (46%), anthropogenic causes (15%) and orphaned dependent young (19%) (Table 3.2). Very few animals were admitted following an attack by another animal (3%) or because they were poisoned or exposed to some other contaminant (<1%). However, the cause for admission was not recorded for 17% of individuals.

Significant sex differences in the numbers of animals admitted were evident for natural causes, orphans and those attacked by another animal (Table 3.2): males were more likely to have been admitted for natural causes or having been orphaned, whereas more females were admitted following an attack by another animal. Significantly more males were also admitted in two sub-categories: caught/entangled and collision with a vehicle. Collectively, however, there was no sex difference in the numbers of hedgehogs admitted for anthropogenic causes, nor within the poison/pollutant or other/unknown categories.

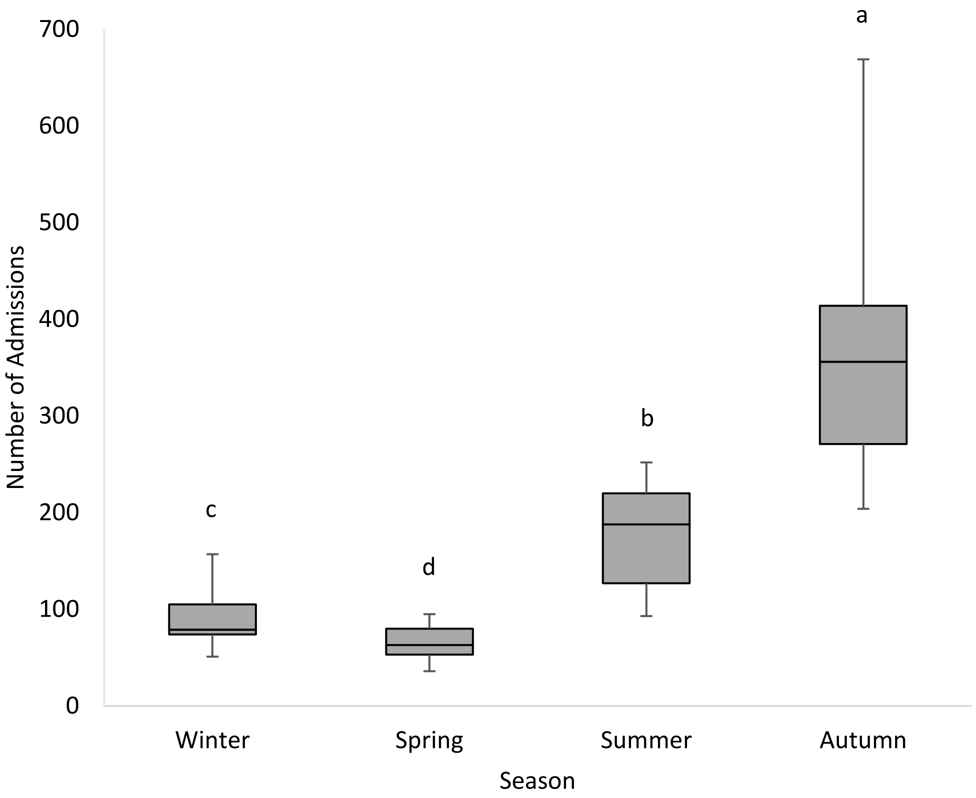
Age-related differences in the causes of admission were evident in every major category (Table 3.2). Juveniles were more likely to have been admitted for natural causes, following an attack by another animal and, by default, as orphans; adults were more likely to have been admitted for anthropogenic causes and because they were poisoned or exposed to a contaminant. Juveniles were also more prevalent in the other/unknown category. Significant differences were also evident in the majority of sub-categories: notably, significantly more juveniles were admitted for exhibiting abnormal behaviour and because they were starving, whereas more adults were attacked by humans, following a collision with a vehicle and because of an injury of unknown origin.

There was a significant difference in the seasonal pattern of admissions classified as natural causes (Repeated-measures ANOVA: $F_{1.391,16.689} = 98.26$, $P < 0.001$), anthropogenic causes ($F_{3,36} = 159.93$, $P < 0.001$), an attack by another animal ($F_{1.991,23.895} = 64.85$, $P < 0.001$) and orphan ($F_{1.241,14.890} = 243.37$, $P < 0.001$). Admissions for anthropogenic causes, attacks by other animals and orphans peaked in summer, whereas those for natural causes were highest in autumn (Figure 3.3). Numbers of admissions for all these causes were generally much lower in winter and spring.

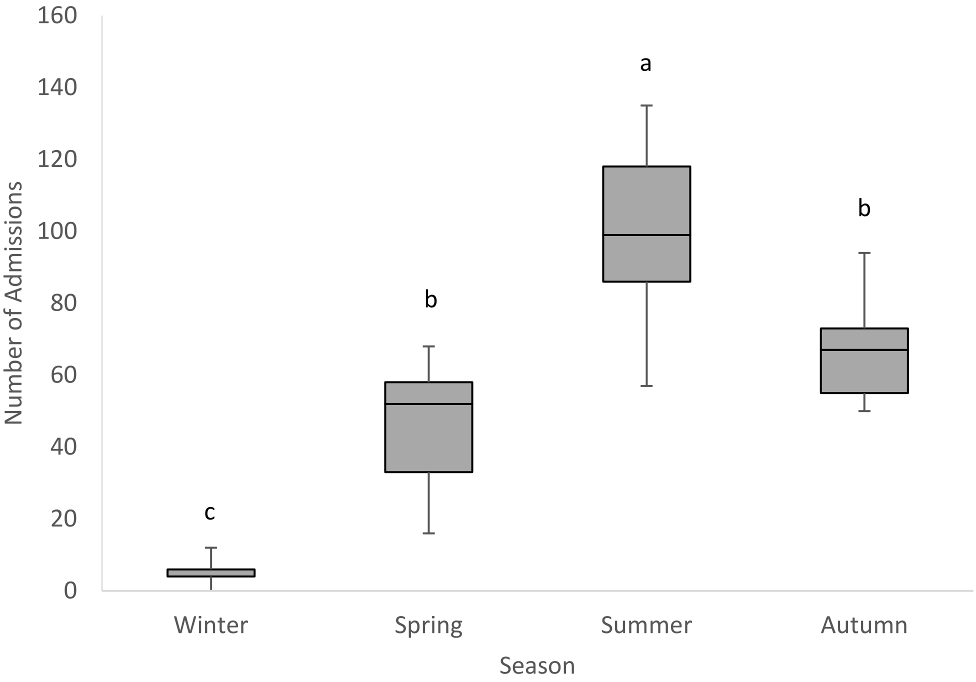
Table 3.2. Sex and age composition of hedgehogs (N = 23,942) admitted to RSPCA wildlife centres during 2006-2018 in relation to reason for admission. M = male; F = female; J = juvenile; A = adult; U = unknown. Chi-squared tests were only performed on animals of known sex and known age. Where no test results are presented, this is either because sample sizes were too small or because the sub-category was specific to one age class (e.g. orphaned juveniles).

Major cause for admission	**Sub-category**	**N (%)**	**Sex composition**					**Age composition**				
			M	**F**	**U**	**X^2_1**	**P**	**J**	**A**	**U**	**X^2_1**	**P**
NATURAL CAUSES	Abnormal behaviour	5351 (22.3%)	1069	1008	3274	1.79	0.181	3377	1267	707	958.68	<0.001
	Blind	52 (0.2%)	17	14	21	0.29	0.590	9	40	3	19.61	<0.001
	Disease	482 (2.0%)	134	148	200	0.70	0.404	206	221	55	0.53	0.468
	Flystrike	205 (0.9%)	39	25	141	3.06	0.080	133	45	27	43.51	<0.001
	Geriatric	77 (0.3%)	33	25	19	1.10	0.294	6	68	3	-	-
	Inexperienced juvenile	1032 (4.3%)	172	153	707	1.11	0.292	1005	3	24	-	-
	Parasitism	125 (0.5%)	19	19	87	0.00	1.000	62	43	20	3.44	0.064
	Starvation	3106 (13.0%)	901	834	1371	2.59	0.108	2753	150	203	2334.00	<0.001
	Weakness	598 (2.5%)	119	95	384	2.69	0.101	312	176	110	37.90	<0.001
	Total	11,028 (46.1%)	2503	2321	6204	6.87	0.009	7863	2013	1152	3465.22	<0.001
ANTHROPOGENIC CAUSES	Attacked by human	26 (0.1%)	5	12	9	2.88	-	5	17	4	6.55	0.011
	Caught/entangled	861 (3.6%)	228	182	451	5.16	0.023	352	383	126	1.31	0.253
	Collision with vehicle	262 (1.1%)	70	48	144	4.10	0.043	61	166	35	48.57	<0.001
	Garden accident	185 (0.8%)	39	46	100	0.58	0.448	79	67	39	0.99	0.321
	Injury (cause uncertain)	2239 (9.4%)	476	467	1296	0.09	0.769	780	990	469	24.92	<0.001
	Shot	2 (<0.1%)	0	1	1	1.00	-	1	1	0	-	-
	Total	3,575 (14.9%)	818	756	2001	2.44	0.118	1278	1624	673	41.25	<0.001
ORPHANED YOUNG	Orphan	4573 (19.1%)	873	772	2928	6.20	0.013	4451	0	122	-	-
	Total	4573 (19.1%)	873	772	2928	6.20	0.013	4451	0	122	-	-
ATTACK BY ANIMAL	Attacked by other animal	726 (3.0%)	136	174	416	4.66	0.031	335	263	128	8.67	0.003
	Total	726 (3.0%)	136	174	416	4.66	0.031	335	263	128	8.67	0.003
POISON / POLLUTANT	Oiling/other contaminant	36 (0.2%)	7	12	17	1.32	-	10	19	7	2.79	0.095
	Poisoning	12 (<0.1%)	3	3	6	0.00	-	2	7	3	2.78	0.096
	Total	48 (0.2%)	10	15	23	1.00	0.317	12	26	10	5.16	0.023
OTHER	Other	3946 (16.5%)	904	914	2128	0.06	0.815	2174	1118	654	338.74	<0.001
	Unknown	46 (0.2%)	9	10	27	0.05	-	15	30	1	5.00	0.025
	Total	3992 (16.7%)	913	924	2155	0.07	0.797	2189	1148	655	324.75	<0.001
Total		23,942	5253	4962	13,727			16,128	5074	2740		

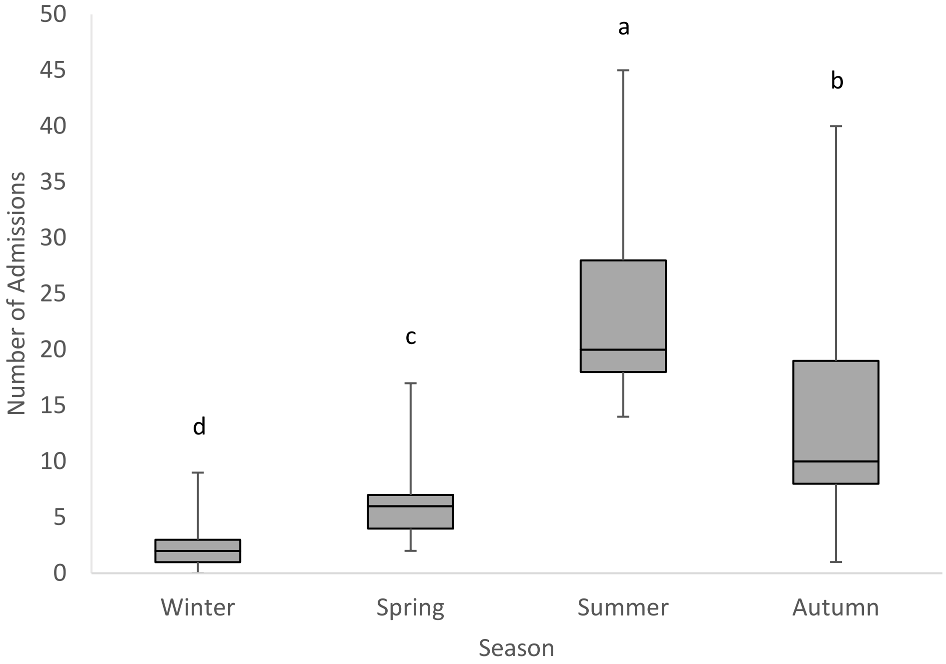
(a) Natural causes



(b) Anthropogenic causes



(c) Attack by another animal



(d) Orphan

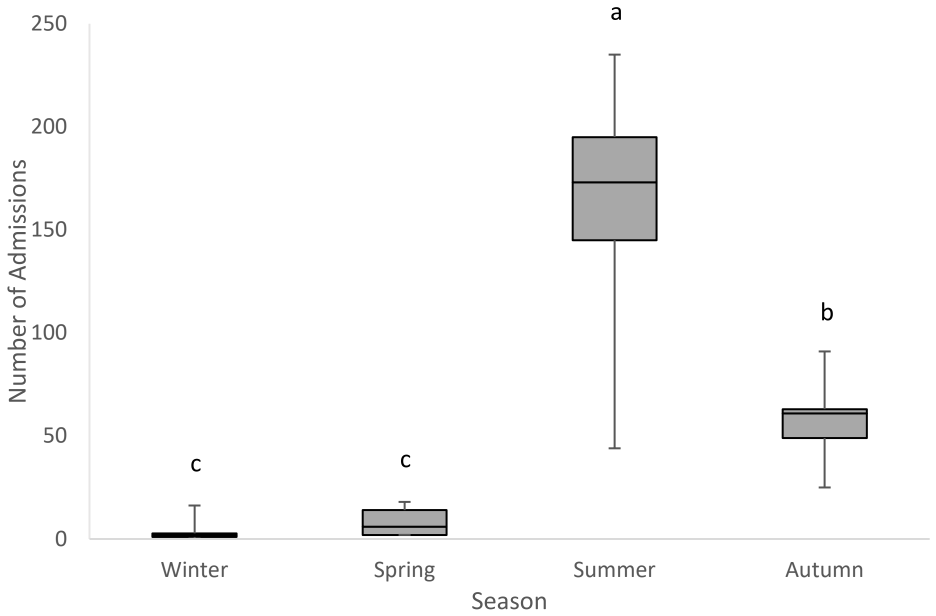


Figure 3.3. Median (±IQR) number of hedgehogs admitted to RSPCA wildlife centres each season during the period 2006-2018 inclusive in relation to cause for admission: (a) natural causes (n = 11,028); (b) anthropogenic causes (n = 3575); (c) juvenile females (n = 3398); and (d) juvenile males (n = 3693). Letters denote *post hoc* groupings from a series of repeated-measures ANOVAs

Patterns of survival to release

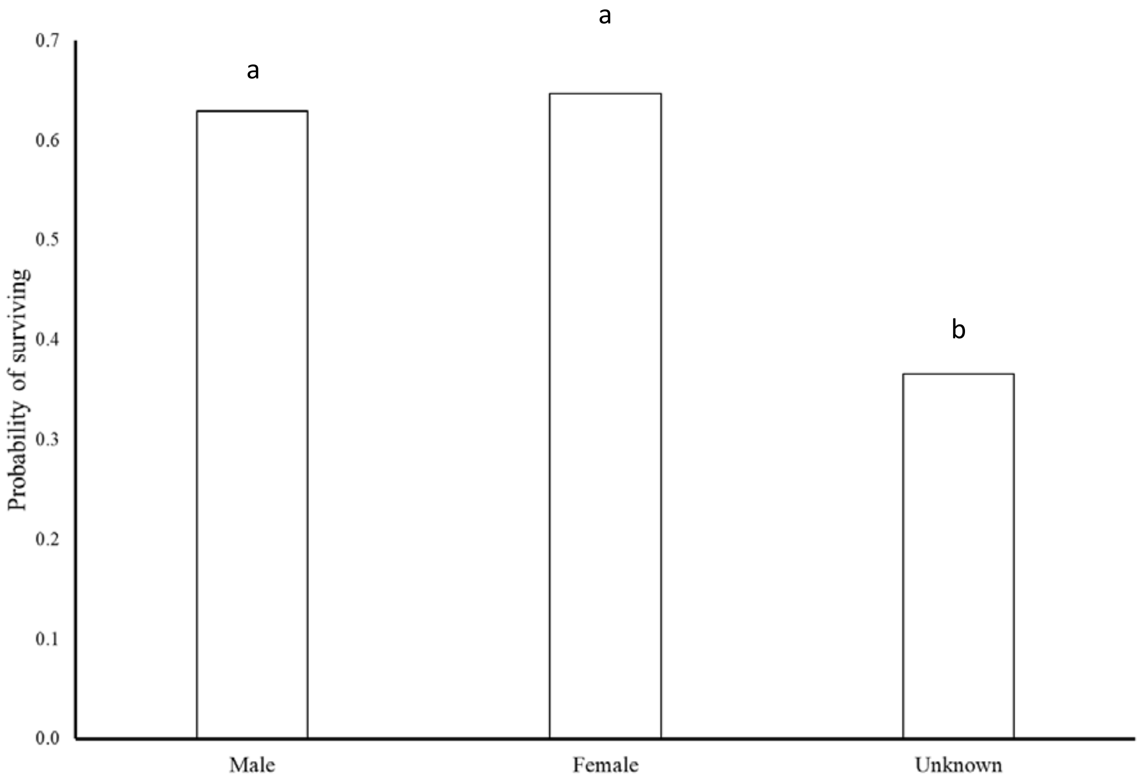
Collectively, 51% of hedgehogs admitted survived to be released (Table 3.3): 12% died or were euthanased at admission, 22% within 48 hours and 15% after 48 hours of admission. There was no significant difference in the mean number of days that animals were in care across the six major subdivisions (Kruskal-Wallis test: $H_5 = 4.86$, $P = 0.433$) with animals spending a median of 15.0 (IQR = 1.0-46.0) days in care; the maximum recorded stay was 313 days.

The probability of survival was significantly affected by sex ($X^2_2 = 1540.79$, $P < 0.001$), age ($X^2_2 = 173.20$, $P < 0.001$) and cause of admission ($X^2_5 = 399.20$, $P < 0.001$). Animals of unknown sex were significantly less likely to have survived than males and females (Figure 3.4a), whereas juvenile hedgehogs were significantly more likely to have survived than adults of unknown sex (Figure 3.4b). Orphaned individuals had the highest probability of surviving, whilst those admitted for anthropogenic causes were least likely to have survived (Figure 3.4c).

Table 3.3. Pattern of survival of hedgehogs admitted to RSPCA wildlife centres during 2006-2018 in relation to the cause for admission. Data indicate the number of animals that died (D), were euthanased or were released (R) within three time periods: at admission, within 48 hours of admission, and more than 48 hours after admission. The survival rate is the overall percentage of animals that survived to be released. Days in care is the mean number of days before death, euthanasia or release.

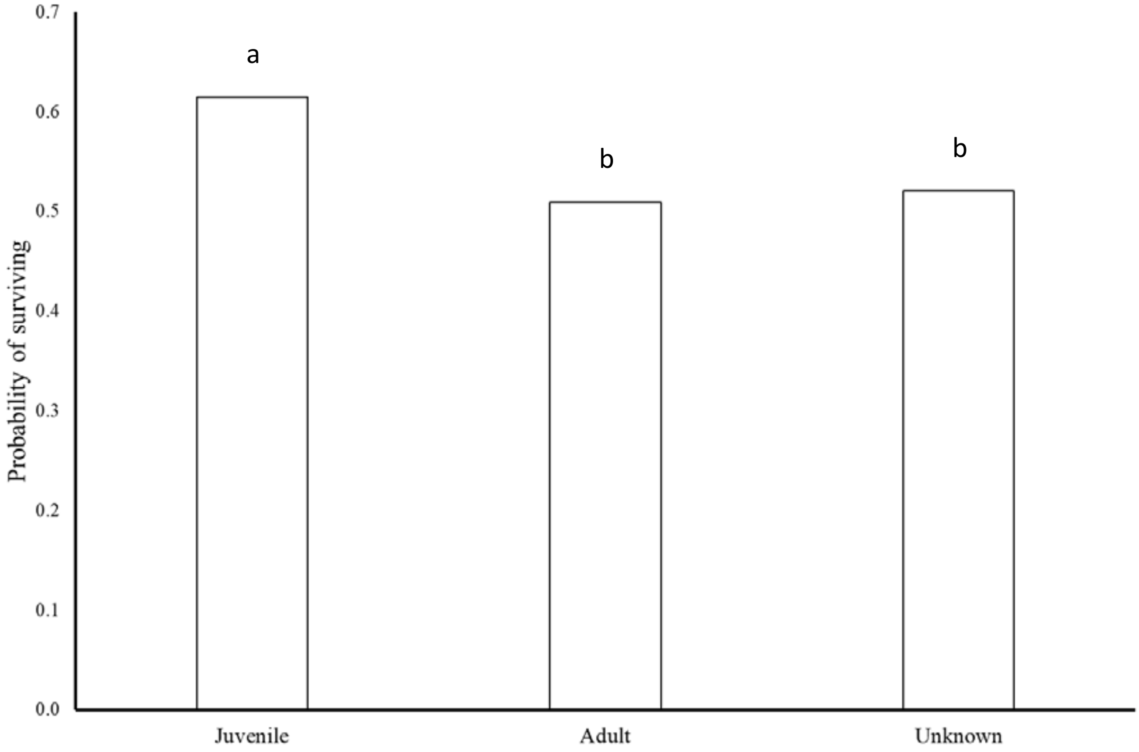
Major cause for admission	Sub-category	At admission			Within 48 hours			After 48 hours			N	Survival rate	Days in care	
		D	E	R	D	E	R	D	E	R			Mean	Median
NATURAL CAUSES	Abnormal behaviour	67	522	29	1041	478	22	501	458	2233	5351	43%	28.5	14.0
	Blind	0	6	0	4	15	0	0	24	3	52	6%	24.0	6.0
	Disease	9	63	0	81	59	1	45	88	136	482	28%	29.4	18.0
	Flystrike	5	79	0	49	21	0	5	10	36	205	18%	26.3	18.0
	Geriatric	1	14	0	7	17	0	5	21	12	77	16%	30.7	22.0
	Inexperienced juvenile	1	31	7	94	54	7	70	85	683	1032	68%	28.7	16.0
	Parasitism	0	22	0	15	6	0	6	15	61	125	49%	31.9	18.0
	Starvation	46	54	5	509	59	0	240	57	2136	3106	69%	29.4	16.0
	Weakness	17	82	0	172	69	2	33	43	180	598	30%	29.9	16.0
	Total	146	873	41	1972	778	32	905	801	5480	11,028	50%	28.9	15.0
ANTHROPOGENIC CAUSES	Attacked by human	2	1	0	3	2	1	1	0	16	26	65%	16.1	1.0
	Caught/entangled	12	73	23	43	46	23	30	52	559	861	70%	30.6	15.0
	Collision with vehicle	7	100	1	28	47	0	11	18	50	262	20%	28.1	15.0
	Garden accident	1	46	0	14	22	1	6	14	81	185	44%	26.0	9.0
	Injury (cause uncertain)	34	861	5	221	373	2	46	218	479	2239	22%	30.1	18.0
	Shot	0	0	0	0	1	0	0	1	0	2	0%	43.0	43.0
	Total	56	1081	29	309	491	27	94	303	1185	3575	35%	29.8	16.0
ORPHANED YOUNG	Orphan	49	188	40	488	148	5	545	385	2725	4573	61%	28.8	14.0
	Total	49	188	40	488	148	5	545	385	2725	4573	61%	28.8	14.0
ATTACK BY ANIMAL	Attacked by other animal	16	125	10	88	53	4	18	43	369	726	53%	30.5	18.0
	Total	16	125	10	88	53	4	18	43	369	726	53%	30.5	18.0
POISON / POLLUTANT	Oiling/other contaminant	1	1	0	2	0	0	5	5	22	36	61%	37.7	27.0
	Poisoning	0	3	0	5	1	0	0	0	3	12	25%	43.7	14.5
	Total	1	4	0	7	1	0	5	5	25	48	52%	39.2	22.0
OTHER	Other	76	327	46	610	248	30	270	284	2055	3946	54%	28.7	14.0
	Unknown	1	2	0	23	1	0	6	1	12	46	26%	37.5	31.5
	Total	77	329	46	633	249	30	276	285	2067	3992	54%	28.8	15.0
TOTAL		345	2600	166	3497	1720	98	1843	1822	11,851	23,942	51%	29.1	15.0

(a) Sex



Probability of surviving
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
a
a
b
Male
Female
Unknown

(b) Age



Probability of surviving
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
a
b
b
Juvenile
Adult
Unknown

(c) Cause of admission

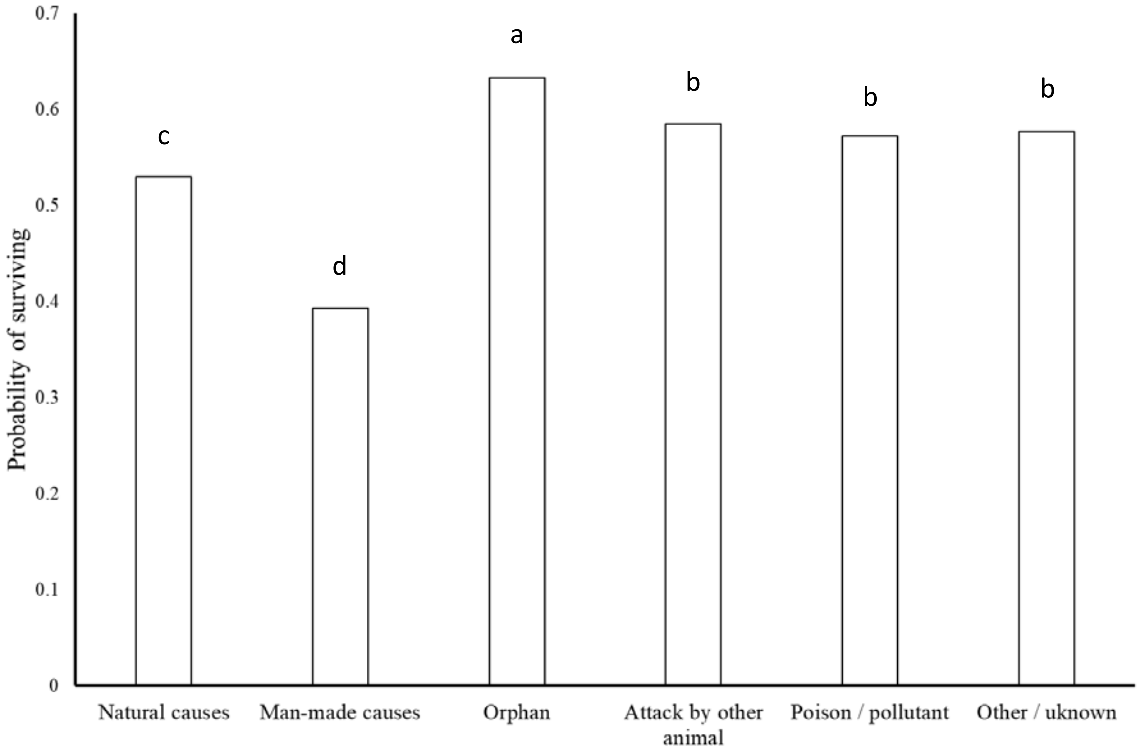


Figure 3.4. Probability that hedgehogs survived to release from binary logistic regression model incorporating (a) sex, (b) age and (c) cause of admission. Letters denote *post hoc* groups.

Discussion

This is one of the most comprehensive datasets on hedgehog admissions into wildlife rehabilitation centres analysed to date (Reeve and Huijser, 1999; Kirkwood, 2003; Molony *et al.*, 2007; Grogan and Kelly, 2013; Garcês *et al.*, 2020), consisting of >23,000 records spanning a 13-year period. However, the dataset contained a substantial amount of unrecorded information for several variables that would be important for any statistical analysis. For example, 477 cases had to be discarded due to missing or inconsistent data: of the remaining 23,942 cases, data on sex and age were missing for 57% and 11% of individuals, respectively, and data on both age and sex were present for only 40% of hedgehogs. This is likely to reflect the fact that the records have been completed by many different individuals with varying degrees of clinical experience over the 13 year period, as is typical in this sort of working environment (e.g. Leighton and Grogan, 2011).

Such a high “error rate” does, however, create two problems. First, it reduces statistical power, although with very large datasets this may not be overly problematic, although it may reduce the number of variables that can be included in any single analysis. Second, and more importantly, it could substantially distort the results if these missing data are not random. In this study, however, we were not able to investigate whether such biases exist or not, but it is important to acknowledge that they may; the following conclusions are therefore based on the assumption that where an individual’s age or sex was not recorded, this occurred randomly.

The data from these four RSPCA wildlife centres exhibit several marked differences from the study of Reeve and Huijser (1999) who collated data (n = 11,541) from 20-30 centres from 1993-1997. These differences include: an 11% increase in the mean number of hedgehogs admitted each year (1656 versus 1841) despite a substantive difference in the number of hospitals contributing information (≥20 versus 4, respectively); a markedly lower, but still significantly different, male-biased sex ratio (1.06♂:1♀ versus 1.2♂:1♀); and an overall release rate of 50% compared to 35%, although this is much lower than the ~68% reported by Molina-Lopez *et al.* (2017).

The most marked difference, however, was in the relative importance of different underlying reasons for admission, although there is some confusion relating to the figures presented by Reeve and Huijser (1999). These authors concluded that admissions were attributable to the following: natural causes, 28%; anthropogenic causes, 22%; orphaned, 28%, dogs and cats, <1%; poisoned, 2%; and other reasons, 13%. These values sum to 93%, and it is not possible to discern whether the remaining 7% represent another distinct category. Therefore, for the purposes of comparing these data with our own, we have redistributed the “missing” 7% in accordance with the observed distribution as reported by the authors (Table 3.4).

Significant differences are evident in the relative proportion of all six categories (Table 3.4). In the current dataset, the relative importance of natural causes has increased by a factor of 1.56, whereas anthropogenic causes and orphans have decreased by a factor of 0.37 and 0.36, respectively. Similarly, attacks by other animals increased markedly in importance in the most recent data, whereas poison/pollution declined in importance. It is of course, however, extremely difficult to draw direct comparisons between these sets of figures because of likely variation in the criteria used to assign animals to different categories and how these may have been interpreted by different people at different hospitals at different times. For example, Reeve and Huijser (1999) only presented data relating to attacks by cats and dogs, whereas the RSPCA record attacks across a broad range of other animals. Therefore, although it is reasonable to assume that these more recent data are likely to relate primarily to attacks by companion animals, given that these are particularly prevalent in urban areas (Murray *et al.*, 2010; Stanley *et al.,* 2015), an unknown proportion of these are also likely to relate to attacks by e.g. badgers and foxes and, unfortunately, humans.

Table 3.4. Summary of the relative importance of different causes of admission in the study of Reeve and Huijser (1999) versus the current study, using a z-score test. The minimum value is that reported by the authors; maximum values were calculated by re-distributing the "missing" 6.8% in accordance with the frequency of the originally cited figures. The z and P values listed are from a series of comparisons of two proportions. % are shown to 1d.p. as the analysis was based on these data.

Source	**Reeve and Huijser (1999) (n = 11,541)**		**This study (n = 23,942)**	**Comparison of two proportions**
Cause	**Minimum**	**Maximum**		
Natural causes	27.5%	29.5%	46.1%	z=-29.736; P < 0.001
Anthropogenic causes	22.1%	23.7%	14.9%	z=20.272; P < 0.001
Orphan	27.9%	29.9%	19.1%	z=22.729; P < 0.001
Attack by other animal	0.7%	0.8%	3.0%	z=-12.949; P < 0.001
Poison/pollution	1.8%	1.9%	<0.1%	z=17.342; P < 0.001
Other/unknown	13.2%	14.2%	16.7%	z=-6.019; P < 0.001
Total	93.2%	100.0%	100.0%	

Furthermore, the assignment to a specific category ignores potential overlap between categories. For example, an individual that is debilitated by a parasitic infection or starving might be more likely to get run over by a vehicle as it forages for food. In addition, the RSPCA recording system includes several generic divisions that do not easily indicate the specific underlying cause for the animal's admission (e.g. abnormal behaviour, inexperienced juvenile, weakness). In these instances, it would be useful if more detailed information could be recorded as the animal's treatment progress or at *post mortem*; alternatively, a detailed analysis of a randomly selected subset of these animals (*sensu* Molony *et al.*, 2007) may help to identify commonalities between individuals in the same sub-category.

These figures also do not represent the relative importance of these causes as sources of mortality in the wider population. This is primarily related to the ease with which animals affected by these different causes will be found and submitted to the RSPCA by members of the public. For example, an animal that has consumed a lethal dose of anticoagulant rodenticide may perish in a position where it is unlikely to be discovered, even if this takes several days, whereas an animal that is injured by a garden strimmer may be noticed immediately. Given these caveats, caution must be taken when interpreting what these data indicate for hedgehog populations themselves, rather than the subset of hedgehogs that find their way to rehabilitation centres.

At first glance, anthropogenic causes appear to be a relatively minor cause for admission in the 2006-2018 data (15%). This is perhaps surprising given the media (and social media) coverage devoted to issues such as road traffic collisions and garden related accidents (e.g. drowning, bonfires, garden strimmers). However, presenting the data in this format excludes the underlying pervasive impact that humans may be having on hedgehog populations. For example, starvation was recorded as the cause for admission of 28% of those individuals in the ‘natural causes’ category. Although competition for food is a natural process, and one that is often associated with negative density-dependent feedback mechanisms (Sinclair and Pech, 1996) such that starvation could reflect a healthy population, this is also possibly indicative of a reduced abundance of natural foods in both rural and urban landscapes. For example, urbanisation is associated with a substantial reduction in vegetative cover (Millennium Ecosystem Assessment (MEA), 2005), and recent trends in low maintenance gardening have reduced this even further (Smith, 2008; van Heezik *et al.*, 2013). At present, however, there are few data on the abundance of macro-invertebrate prey in British urban areas, although Pettett (2015) reported that the prey taxa consumed by hedgehogs did not vary along the buildings to rural gradient studied, but all hedgehogs had consumed pet food suggesting that natural foods could be limited.

Similarly, orphaned hedgehogs are also most commonly admitted to wildlife hospitals after they have been accidentally disturbed by human activity (e.g. clearing vegetation, dismantling sheds) or by companion animals; as such, this indicates an underlying anthropogenic cause. Poisoning and other forms of contaminant would also fall into this category. Consequently, summing these various major and minor categories together imply that humans may be responsible directly or indirectly for 47% (n = 11,302) of overall cases in this dataset. As such, and to reiterate the point made by Reeve and Huijser (1999), anthropogenic factors are responsible for a marked proportion of admissions to wildlife hospitals, and this is despite widespread media coverage in the intervening 20 years on several of these aspects specifically, and the continuing decline of hedgehogs in the country as a whole generally.

Intra- and inter-annual patterns of admissions

There was a 1.8-fold difference between the lowest (n = 1381) and highest (n = 2518) number of hedgehogs admitted, a pattern which was consistent across both adults (272-537 = 2.0-fold difference) and juveniles (883-1590: a 1.8-fold difference). Consequently, differences in overall admissions appear to relate to simultaneous changes in both adult and juvenile animals (Figure 3.1), rather than from one age class alone. This pattern is consistent with both an increase in the underlying population itself ("more animals available to be affected") or the result of an underlying cause that has wide-ranging effects ("more animals affected in a population of a given size"). One possible factor that could affect animals on an inter-annual basis is prevailing weather conditions. For example, prolonged periods of hot dry weather in the summer could reduce food availability which would be expected to affect both adult and juvenile animals. Analyses of admission numbers in relation to patterns of weather are, therefore, warranted.

Admissions were dominated by juveniles (76% of animals of known age), with pronounced peaks evident in the summer and autumn associated primarily with orphaned dependent young (Figures 3.2c & 3.2d; Figures 3.3a & 3.3d). In addition, these seasons were also associated with increased admissions associated with attacks from other animals and anthropogenic causes (Figures 3.3b & 3.3c), which could be linked to the increased ranging behaviour of newly independent offspring. Overall, therefore, these inter-annual and intra-annual patterns suggest that the summer and autumn seasons are key stages for hedgehog populations, but which can be adversely affected by changes in food availability and associated secure refugia; both of these could be positively impacted by persuading to adopt strategies that increase access into more gardens (e.g. www.hedgehogstreet.org) but also adopting hedgehog-friendly gardening practices. The latter need to focus on promoting the year-round availability of ground-level and soil macro-invertebrates, as well as offering secure rest sites which cannot be accessed by dogs; promoting responsible dog ownership to make owners aware of the risk posed by their pets would also be an important consideration (Schenk and Souza, 2014). To date, the Hedgehog Street campaign has attracted more than 80,000 signatories, although this is still a relatively small number in the context of the 27.2 million households in Great Britain (Office for National Statistics, 2017). In addition, it is not even clear how many of these have actually created a hedgehog highway in their own garden (A. Gazzard, pers. comm.) which is the primary aim of this programme.

Survival to release was significantly affect by age, sex and cause of admission. As reported by Molony *et al.* (2007), there was no significant difference between males and females (Figure 3.4a) and juvenile animals were more likely to survive than adults (Figure 3.4b). However, there was a difference in survival probability between animals of known age and sex versus animals of unknown age and sex: animals of unknown sex had a survival probability almost half that of males and females, whereas animals of unknown age had a survival probability comparable to that of adults but significantly lower than that of juveniles. As outlined above, these results could be indicative of the fact that these unknown animals are not a random sample of the hedgehogs admitted and they could be masking important age or sex differences in survival; at the very least, they would act to reduce the survival probabilities of the animals whose sex and age is known.

The pattern of survival within causes for admission (Figure 3.4c) did not reflect their relative importance as a cause of admission (Table 3.2). The highest survival rate was evident for orphans, indicating that rehabilitators are extremely proficient at rearing even the smallest hoglets. Similarly, the survival rate of hedgehogs attacked by other animals, which is presumably a reflection of the proficiency of their protective coats. Conversely, significantly lower survival probabilities were evident for anthropogenic causes, indicating that these are often associated with greater levels of physical trauma or unusual injuries (e.g. netting wrapped around their neck) which their coat cannot protect them from, or which in some circumstances makes things worse.

Welfare implications

The 50% release rate for hedgehogs is amongst the highest for species most commonly admitted to the RSPCA's wildlife centres in England and Wales (Grogan and Kelly, 2013). In the context of welfare during the rehabilitation process is the adoption of effective triage procedures, whereby animals that are likely to perish are identified as early as possible so that they can be humanely destroyed. In this study, of all animals admitted, 12% died or were euthanased at admission, 22% died or were euthanased within 48 hours and 15% died or were euthanased after 48 hours of admission. The figures related to 25% (at admission), 44% (<48 hours) and 31% (>48 hours) of the 11,827 animals that did not survive. Although the RSPCA have made efforts to improve their triage protocols (Molony *et al.*, 2007), the number of fatalities at all stages are indicative of a need that further improvements need to be made.

Mean time in care was 15 days, although some animals were in captivity for hundreds of days. In the context of wildlife rehabilitation generally, this can lead to the individuals to become imprinted on or habituated to humans (Fàbregas *et al.*, 2020), with these individuals more likely to become aggressive or a nuisance after release (Beringer *et al.*, 2004). Admission is highly stressful as animals are exposed to humans and disease, which may cause further ill health and long-term stressor exposure or chronic stress. Such factors can lead to weight loss, immunosuppression, reproductive failure and psychological distress (Sapolsky *et al.*, 2000). Stress can also have a detrimental impact on immunological function, which can lead to animals contracting disease whilst in care (Fischer and Romero, 2019), which may further extend their stay. Furthermore, the considerable fluctuations in number of admissions, length of stay and rate of survival are important considerations for practitioners to be able to manage expectations and finances, as the expense of housing and food for animals within the rehabilitation environment are acknowledged as the most significant costs (Wimberger *et al.*, 2010). One additional consideration with the rehabilitation of juveniles is whether they can be sufficiently prepared for independent survival in the wild (Baker, 2002; Guy *et al.*, 2013), with the suggestion that rehabilitation as a group can be beneficial (Schwartz *et al.*, 2016).

For hedgehogs, the rapid turnover of animals transferred from the Uist Islands in Scotland and their subsequent release in Bristol, England was associated with low post-release survival rates due partly to stress while in captivity but also an inability to put on sufficient fat reserves prior to their release (Molony *et al.*, 2006). Conversely, animals that were held in captivity for longer were able to accumulate sufficient fat reserves to survive the transition to the new habitat. For this species, therefore, an intermediate time in care is likely to be beneficial.

However, one concern that has been raised in the rehabilitation community is that prolonged periods in care in close proximity to humans can reduce their ‘fear’ reflex whereby they roll up in a ball when they detect danger (Reeve, 1994). One possible consequence of this is that it may make them more vulnerable to dogs and foxes. The latter, it has been suggested, have increasingly “learnt” that they can kill hedgehogs by rapidly biting the hedgehog’s leg before it curls up; the animal is then debilitated. The efficiency of this hunting technique, whether it is increasing in frequency, and whether rehabilitated animals are more vulnerable are all unknown.

Conclusion

Records of animals entering wildlife rehabilitation centres potentially represent a useful means for identifying anthropogenic and natural factors impact wild animal populations, although they are associated with difficulties relating to e.g. the non-independence of causal factors and detection probabilities. In this study, these issues were further exacerbated by incomplete information in some fields of the dataset, notably age and sex, as well as the use of generic admission categories (e.g. inexperienced juvenile, abnormal behaviour) that do not provide definitive information on the underlying reason for admission. The former problem could lead to sampling biases that mask important relationships. These issues could be redressed by greater emphasis on ensuring the record for each animal is complete; this is likely to include the need to revisit the information recorded at the time of admission while the animal is in care, so that an accurate and comprehensive record is generated.

Despite extensive media coverage outlining the threats posed to hedgehogs, anthropogenic causes are still responsible for a substantial proportion of hedgehogs admitted to the RSPCA (up to 47%); some of these are, however, likely to be associated with habitat quality, and which may be further exacerbated by e.g. inter-annual variation in weather conditions. The relationship between the number of admissions and environmental factors requires further examination.

Overall, 51% of hedgehogs admitted survived to release, although this varied markedly between different causes of admission. The highest survival probability was associated with orphaned juveniles (63%), and the lowest with anthropogenic causes (39%). Patterns of mortality during the rehabilitation process indicated that significant improvements in welfare could be achieved with more stringent triage procedures.

CHAPTER FOUR

Chapter Three presented the rate of rehabilitation to release one of Europe’s largest animal welfare organisations but it is not known on what scale wildlife rehabilitation is practiced across the country. Whilst the RSPCA handles substantial numbers, the BHPS reports in excess of 800 wildlife rehabilitators are operating, although the degree to which these facilities contribute to the care of hedgehogs has not previously been established.

As discussed in Chapter One, Molony *et al*. (2007) suggested 30,000-40,000 casualties of a range of British bird and mammal species are admitted to wildlife hospitals annually, whilst Grogan and Kelly (2013) proposed a figure of 71,000 may be more accurate. In addition, Barnes and Farnworth (2016) estimated veterinary professionals may see more than 131,000 animals each year. Little more specific detail exists currently regarding the status of hedgehogs in rehabilitation so in this chapter I undertook a questionnaire with hedgehog rehabilitators across the UK to estimate: (i) the number of individuals/organisations rehabilitating hedgehogs in Great Britain, and (ii) the number of hedgehogs admitted to wildlife hospitals in a single year. The questionnaire also requested a range of information relating to the structure and practices of these individuals and organisations to identify how British hedgehog rehabilitation is structured, to gain a greater insight into its operation and the degree to which the practice of rehabilitation may support the conservation of the species, as well as the welfare of individual animals.

The manuscript presented in this chapter has been prepared for publication in *Anthrozoös.*

My contribution to the work:

I designed the project, undertook data collection and conducted all analysis with assistance from Dr Philip Baker. I prepared the manuscript with assistance from Dr Philip Baker.

An estimate of the scale and composition of the hedgehog (*Erinaceus europeaus*) rehabilitation community in Great Britain and the Channel Islands

Abstract

The conservation benefits of wildlife rehabilitation are equivocal but could be substantial for formerly common species that are declining rapidly but which are still commonly admitted to wildlife hospitals. In Great Britain, one such species is the West-European hedgehog (*Erinaceus europaeus*). In this study, we used a questionnaire survey to estimate the number of practitioners (individuals or organisations) involved in rehabilitating hedgehogs and the number of animals entering hospitals in one benchmark year (2016); practitioners were identified using an internet search and snowball sampling. 304 rehabilitators were identified; 148 (48.6%) replied to the questionnaire. The latter consisted of 63% small (≤50 hedgehogs admitted per year^{-1}), 17% medium-sized (51-250 year^{-1}) and 21% large (>250 year^{-1}) hospitals; however, these accounted for 5%, 12% and 83% of hedgehog admissions, respectively. Small hospitals were significantly less likely to be registered as a charity, have paid staff, have a business-related social media account, to use a computer for record keeping and carry out post-release monitoring; conversely, they were more likely to operate from their own personal residence and to have been established for ≤5 years (74%). The known sample of 148 hospitals admitted 25,540 hedgehogs in 2016; extrapolations using two different methods suggest that all hospitals could have admitted 40,000-59,000 hedgehogs, a much larger number than previous estimates. Assuming 50% of hedgehogs would survive to release, this would be equivalent to 4-6% of the pre-breeding population nationally, suggesting this practice could have a positive impact on both the population and on animal welfare.

Keywords: Animal welfare, conservation, *Erinaceus europaeus,* European hedgehog, wildlife hospital, wildlife rehabilitation.

Introduction

The International Wildlife Rehabilitation Council defines wildlife rehabilitation (WR) as ‘the treatment and temporary care of injured, diseased, and displaced indigenous animals, and the subsequent release of healthy animals to appropriate habitats in the wild’ (Miller, 2012).

Although specific data are lacking, it is reasonable to assume that the practice of rehabilitating wild animals has increased at an international level as a result of the increasing negative impact of humans on natural ecosystems (Morner, 2002; Molina-López *et al.*, 2011; Grogan and Kelly, 2013; Schenk and Souza, 2014; Mcruer, *et al.* 2017; Montesdeoca, *et al.*, 2017; Tejera *et al.*, 2018; Taylor-Brown *et al.*, 2019). Although widely perceived as helping wildlife, the role of WR as a conservation tool is contested (Kirkwood, 2003). For example, it can be argued that most animals that enter wildlife hospitals tend to be species that are common and widespread (Molony *et al.*, 2007; Wimberger *et al.*, 2010) and that the money spent on their care is money that cannot be spent on conservation actions such as habitat preservation (Kirkwood, 1992). Similarly, unless released individuals have survival rates comparable to those of individuals that have not required similar treatment, the cost-effectiveness of human intervention could be questioned (Miller, 2012; Guy *et al.*, 2013, 2014; Pyke and Szabo, 2017). Consequently, WR has more often been portrayed as an animal welfare issue or for the "benefit of the individual" than for conservation (Kirkwood and Sainsbury, 1996; Kirkwood and Best, 1998; Dubois, 2003; Kirkwood, 2003; Guy *et al.*, 2013).

However, WR does potentially offer resources that can aid conservation in a more general context such as aiding education (Dubois, 2003; Wimberger *et al.*, 2010; Wimberger and Downs, 2010; Guy *et al.*, 2013; Pyke and Szabo, 2017), disease surveillance (Trocini *et al.*, 2008; Randall *et al.*, 2012; Camacho *et al.*, 2016; Yabsley, 2020), monitoring of environmental pollutants (Jaspers *et al.*, 2006) and the development of a broad range of capture, treatment and release protocols that can subsequently be applied to species of conservation concern (Molony *et al.*, 2006; Soorae, 2013). In addition, it can help reduce the impacts of catastrophic events such as oil spills and wildfires where large numbers of individuals within a breeding population may be affected in a very short space of time (Goldsworthy *et al.*, 2000; Newman *et al.*, 2003; Lunney *et al.*, 2004; Griffith *et al.*, 2013). Furthermore, although high conservation status is often perceived in the context of rarity, it can also result from rapid declines in species that were formerly abundant and widespread (Rodríguez *et al.*, 2012; Monadjem *et al.*, 2013). In this context, wildlife rehabilitators may continue to receive large numbers of individuals which, if successfully rehabilitated and released, could potentially contribute to the conservation of that species. The magnitude of this benefit is dependent, in part, on the number of individuals rehabilitated and released in relation to population size (Guy *et al.*, 2013; Pyke and Szabo, 2018).

Quantifying the numbers of different species which are rehabilitated and released can, however, be challenging because of the way that WR is often practised. In many instances, the wildlife rehabilitation community of a country can encompass single individuals, charitable and non-charitable NGOs and/or government agencies, some of which may focus on wildlife generally whilst others focus on just one or a few species (Molony *et al.*, 2007; Wimberger *et al.*, 2010; Guy *et al.*, 2013). In any given country, therefore, some rehabilitators may only treat a handful of animals each year, whereas larger organisations may treat thousands. In addition, not all countries require that wildlife rehabilitators are licenced or registered (Wimberger *et al.*, 2010; Mullineaux, 2014), such that even identifying the number of wildlife rehabilitators operating at any given time is problematic. This issue is currently of interest in Great Britain in the context of the rehabilitation of West-European hedgehogs (*Erinaceus europeaus*; hereafter 'hedgehog'), a species of increasing conservation concern (Mathews *et al.*, 2018).

The hedgehog is a small (<1.5kg), insectivorous mammal found throughout western Europe (Morris, 2018). In Great Britain, it can be found in a wide range of human-dominated landscapes, including arable and pastoral farmland as well as urban areas (Hof and Bright, 2009, 2012; Van de Poel *et al.*, 2015; Pettett *et al.*, 2017b, 2018; Williams *et al.*, 2018a). Evidence from a range of different long-term surveys suggest that populations may have declined by up to 40% in some habitats in the last few decades (Wembridge, 2011, 2015, 2018; Hof and Bright, 2016; Pettett *et al.*, 2017b; Williams *et al.*, 2018a), with declines to varying degrees also present throughout Europe (Holsbeek *et al.*, 1999; Huijser and Bergers, 2000; Van de Poel *et al.*, 2015; Müller, 2018). Factors likely to be associated with this decline include: habitat loss, fragmentation and degradation; the application of chemical biocides; an increase in the size of road networks and associated traffic volume; the increased abundance of an intra-gild predator, the Eurasian badger (*Meles meles*); and climate change (Doncaster, 1994; Whalen *et al.*, 1998; Huijser and Bergers, 2000; Rondinini and Doncaster, 2002; Molony *et al.*, 2006; Young *et al.*, 2006; Dowding *et al.*, 2010a; Geiger *et al.*, 2010; Moorhouse *et al.*, 2014; Trewby *et al.*, 2014). Despite this substantial decline, hedgehogs are frequently the most common mammal species admitted to wildlife hospitals in Great Britain (Kirkwood, 2003; Molony *et al.*, 2007; Morris, 2018), and are also commonly taken to veterinary surgeons by members of the public for treatment (Barnes and Farnworth 2016).

Most recently, Mathews *et al.* (2018) estimated that the British hedgehog population numbers approximately 0.52 million individuals, down from a similar estimate of 1.56 million in the mid-1990s (Harris *et al.*, 1995), which triggered its status to be upgraded to Vulnerable to extinction (The Mammal Society, 2020). However, both estimates were reliant upon extrapolating data on hedgehog density and/or occupancy within specific land classes (Harris *et al.*, 1995) or habitats (Mathews *et al.*, 2018) to the country as a whole, whilst acknowledging that such data were extremely limited and/or dated. For example, Mathews *et al.* (2018) were still reliant on density estimates collated by Harris *et al.* (1995) for four major habitat classes and were only able to update estimates for two habitats based on one further study in the intervening 20 years (Parrott *et al.*, 2014). Consequently, both sets of authors gave low reliability scores for their respective estimates.

Hedgehog rehabilitation in Great Britain

Whilst the specific details of wildlife legislation in Great Britain are complex, in general terms these allow members of the public to take any injured (or orphaned) wild animal into captivity for the purposes of treatment (including euthanasia) or care prior to its subsequent release; whilst in captivity, the animal must receive appropriate husbandry and be taken to e.g. a veterinary surgeon for examination if necessary (Mullineaux, 2014; Jones and Chapman, 2019). At the point the animal is deemed fit enough to survive in the wild, it should be released (Miller, 2012). The selection of a suitable release site, and e.g. the time of year it is released, are therefore additional considerations (Molony *et al.*, 2006; Miller, 2012; Yarnell *et al.*, 2019). For example, although animals can often be released at the site where they were found, this is not always possible or advisable e.g. standardised release protocols for hedgehogs emphasise that they should not be released at locations with high badger numbers. Furthermore, the release of some non-native species is not permitted. For those individuals that cannot be released because they are unlikely to survive, many rehabilitators recommend euthanasia, whereas others consider retention in captivity an acceptable option (although it is illegal to keep some species in captivity) (Bullen, 2010; Miller, 2012; Grogan and Kelly, 2013; Jones and Chapman, 2019).

The wildlife rehabilitation community in Great Britain is large, diverse and, in some respects, disjointed (Kirkwood, 2003). At one end of the spectrum is the Royal Society for the Protection of Animals (RSPCA) (www.rspca.org.uk), the largest animal welfare organisation in England and Wales, and the Scottish Society for the Protection of Animals (SSPCA) (www.scottishspca.org), which operates in Scotland. Both organisations investigate and enforce cases associated with animal welfare and animal cruelty, including wild animals, but also rehabilitate injured wild animals; the RSPCA has four wildlife centres based in England, and the SSPCA has one based in Clackmannanshire. Similarly, Tiggywinkles Wildlife Hospital (www.sttiggywinkles.org.uk) in Oxfordshire, England is considered the largest purpose-built wildlife hospital in Europe. Individually, these three organisations may each admit >1000 hedgehogs each year.

However, there are a substantial number of smaller organisations and individuals who also rehabilitate hedgehogs in Great Britain. For example, the British Hedgehog Preservation Society (BHPS) (www.britishhedgehogs.org.uk), a charitable organisation that has a specific focus on hedgehog rehabilitation, maintains a service whereby members of the public can call them to ask for the contact details of their nearest hedgehog carer/rehabilitator. Under UK data protection rules, this information cannot be disseminated to researchers, but it is estimated that this list may contain up to 800 different individuals and organisations (F. Vass, CEO of the BHPS, pers. comm.; Morris, 2018). These are often individuals working from their own private residence, with hedgehogs in care housed within their home itself or in a shed or purpose-built unit in their garden. Given the widespread interest in the plight of hedgehogs in Great Britain, and the availability of training courses associated with treating and rehabilitating hedgehogs (www.valewildlife.org.uk/courses/), the numbers of these individuals/smaller organisations is likely to have grown in recent years.

Despite earlier recommendations about the scientific merits of collecting and collating data from animals entering wildlife hospitals (Grogan, 2009; Grogan and Kelly, 2013), relatively few data currently exist on the numbers of animals that are admitted to wildlife hospitals in Great

Britain. For example, Molony *et al.* (2007) reported that an estimated 30,000-40,000 casualties are admitted to wildlife hospitals annually, with the most common species being the red fox (*Vulpes vulpes*), Eurasian badger (*Melels meles*), hedgehog and blackbird (*Turdus merula*). More recently, Grogan and Kelly (2013) reported 71,000 animals (of a wide range of British species) were admitted to the RSPCA's four wildlife centres and 23 other wildlife hospitals in 2011. Given this paucity of information, and the potentially increasing importance of rehabilitation as hedgehog numbers continue to decline, in this study, we used a structured internet search and questionnaire survey to estimate (i) the number of individuals and organisations rehabilitating hedgehogs in Great Britain, and (ii) the number of hedgehogs admitted to wildlife hospitals in a single year. The questionnaire also requested a range of information relating to the structure and practices of these individuals and organisations to identify how British hedgehog rehabilitation is structured at the current time: (iii) their charitable status; (iv) the numbers of paid and unpaid personnel involved; (v) patterns of veterinary support; (vi) how long they had been established; (vii) the physical infrastructure used; (viii) their use of social media; (ix) how they recorded information on the hedgehogs admitted; and (x) whether or not they conducted post-release monitoring. In addition, we highlight the challenges associated with deriving estimates of the number of rehabilitators practising and the numbers of hedgehogs admitted in the context of similar future studies.

Materials and Methods

Terminology

For brevity, we use the term 'rehabilitator' to collectively refer to any individual or organisation which treats and releases hedgehogs; in Great Britain, this is also synonymous with the term "carer". The terms 'hospital' or 'centre' refer to any building or structure from which a rehabilitator operates; this includes private households, buildings in private premises such as a garden shed, and large purpose-build facilities.

Internet search

A systematic search was undertaken from September 2016-January 2017 using the online search engines Google and Bing, websites for known rehabilitators, online databases (e.g.

www.helpwildlife.co.uk/directory) and the social media platforms Facebook and Twitter to create a database of hedgehog rehabilitators and rehabilitation organisations. Search terms included: “wildlife hospital”, “wildlife rescue”, “hedgehog hospital”, “hogspital” and “hedgehog rescue”. Where available, the name and contact details of each rehabilitator were provisionally recorded if they had an online presence in any form, such as a social media profile, had been mentioned in a local or national media, or had a fundraising campaign advertised. However, because online information may be out of date (e.g. a rehabilitator had ceased practising), each rehabilitator was only classified as active if their online information indicated that they were still operating in 2016; where this information was not immediately evident, the rehabilitator was contacted directly by email or via social media.

Following this online search, snowball sampling was used to help identify additional rehabilitators. This was done by searching the social media associates of each provisionally identified rehabilitator, and by also asking them to forward/advertise the resultant questionnaire (see below) to their personal contacts. This approach would help identify rehabilitators that had no obvious online social media presence, including individuals that had only recently started practising.

Questionnaire survey

A self-administered questionnaire was distributed via SmartSurvey from January 2017-December 2017 to obtain information on the composition of the hedgehog rehabilitation community in Great Britain and to estimate the number of animals admitted in 2016. The questionnaire was publicised through social media using a number of established web pages associated with wildlife and hedgehog rehabilitation, and contacting the rehabilitators identified above directly. The questionnaire was further publicised via newsletters published by the British Hedgehog Preservation Society (BHPS), British Wildlife Rehabilitation Council and the People’s Trust for Endangered Species. The BHPS promoted the questionnaire to the ~800 carers on their database. All centres were contacted at least once via email or a social media message, depending on their preferred mode of communication as advertised on their website or social media, with a request to complete the questionnaire. Information requested included: their name; whether they were a registered charity or not; how many paid personnel they employed; how many unpaid staff (volunteers) worked at their hospital; whether they had a full-time veterinary surgeon on staff or worked in conjunction with an external veterinary practice; the year they had started rehabilitating hedgehogs; whether their hospital was run from their personal residence or from a purpose built rehabilitation centre; whether they had a personal and/or business social media account for advertising their hospital to the general public; and whether they used paper records or a computer to record information about the animals they have cared for.

Respondents were then asked to indicate how many hedgehogs they had received each year for the 5-year period 2012-2016, inclusive; as 2016 was the most recent year for which respondents would have had complete information, this was taken as the benchmark year for estimating the number of animals admitted. Finally, respondents were asked to indicate whether they undertook post-release monitoring of any sort and, if so, what methods they used (radio-tags, GPS-tags, injected microchips (PIT tags), ear tags, marking spines with numbered tags (Reeve *et al.*, 2019) or nail varnish). Ethical approval was provided by the University of Reading.

Estimating the number of hedgehog admissions

To estimate the total number of hedgehogs admitted in 2016 by all active rehabilitators identified, we first categorised those hospitals for which we had data on the number of admissions into three size classes: small, medium and large. These divisions were estimated retrospectively based upon the frequency distribution of the numbers of hedgehogs admitted: these were assigned to reflect both the pattern of admissions but also to ensure that sufficient numbers of hospitals (both from the original searches and from snowball sampling) were in each division to enable statistical analysis. Differences in the relative numbers of hospitals in each of the three size classes identified in the online searches versus the snowball sampling were compared using a chi-squared test. Differences in the median number of hedgehogs admitted in 2016 within each size class in the online searches versus snowball sampling were compared using a series of Mann-Whitney tests.

Two models were used to estimate the numbers of hedgehogs admitted by those hospitals for which there was no data available. In Model 1, the data from both the online searches and snowball sampling were merged and treated as a homogenous sample. These combined data were used to estimate: the proportion of small, medium and large hospitals; and the median number of hedgehogs admitted by those hospitals in each size class. The total sample of hospitals with missing data was then divided in accordance with the proportions identified in the known sample: the resulting number of hospitals in each size class was then multiplied by the associated median value to estimate the total number of hedgehogs admitted in each class. These three totals were then summed and added to the number of known hedgehogs admitted by those hospitals for which data were available.

Model 2 followed a similar approach, except that the data from the online searches and snowball sampling were treated separately, as there was evidence that the composition of each sample varied with respect to the proportion of hospitals in each size class and the median number of hedgehogs admitted within each size class (see Results). In this model, therefore, the proportion of small/medium/large hospitals and the median number of hedgehogs admitted within each size class were estimated separately for those hospitals identified in the online search versus those identified by snowball sampling. The estimated numbers of hedgehogs admitted within each of these two samples were then summed and added to the total number of known hedgehogs admitted by those hospitals for which data were available.

Structure of the rehabilitation community

Differences in the characteristics of small, medium and large hospitals were quantified using data from those rehabilitators where we had both an estimate of their size and who had completed the questionnaire survey; rehabilitators who had completed the questionnaire but who had not indicated the numbers of hedgehogs admitted in 2016 were excluded. Similarly, rehabilitators who had failed to answer a specific question were excluded from the analysis relating to that question.

A series of chi-squared tests were used to compare differences between the three hospital classes with respect to: whether they were a registered charity or not; the type of veterinary care they had (five categories: none; work with an external veterinary practice; work with external wildlife hospital; they themselves are a veterinary nurse or veterinary surgeon; onsite veterinary surgeon); how long they had been established (data merged into two categories: ≤5 years and >5 years); where hedgehogs were housed during rehabilitation (three categories: building in private grounds e.g. garden shed; in their private residence; a purpose-built facility); the type of social media account(s) that they had (three categories: none; only one or more personal social media accounts; one or more business accounts, with or without personal accounts as well); how they kept records of the hedgehogs admitted (two categories: fully or partly on paper; fully or partly on computer. NB: the option "partly paper" indicates that the majority of records were recorded on paper with a minority on computer, whereas "partly computer" indicates that the majority of records would have been recorded on computer with a minority on paper); and whether they did or did not undertake any form of post-release monitoring.

In addition, we quantified the number of paid and unpaid (volunteers) staff working in each hospital size class. The number of unpaid staff was divided into three categories (1 volunteer; 2 volunteers; ≥3 volunteers) and analysed using a chi-squared test; where hospitals were run by just one unpaid person, this would be the person in charge of that hospital who was running it on a voluntary basis. The distribution of paid staff was very uneven, with very few hospitals employing paid personnel at all, such that we were not able to analyse these data statistically. Therefore, we have summarised these data by indicating: the percentage of hospitals within each size class that employed one or more paid staff; and the mean number of paid staff in those hospitals where they were present.

Temporal trends in the annual number of admissions from 2012-2016 were investigated for each size category to identify whether 2016 was potentially an atypical year for the number of admissions. Median (±inter-quartile range (IQR)) numbers of admissions were plotted separately for small, medium and large hospitals utilising all the data available. However, it was not possible to analyse these data as some hospitals only supplied data for some years within the overall five-year period, whereas others provided data for all five years; consequently, the data were neither truly independent nor truly repeated. Therefore, Friedman tests were used to identify whether there were any between-year differences for those subsets of hospitals within each size class where data were available for all five years.

Data analyses

All statistical analyses were conducted using MINITAB version 19.1.1 and SPSS version 25. Nonparametric tests were used throughout as the data were not normally distributed. Data were therefore presented as medians ±IQR unless otherwise specified.

Results

Overall, 239 rehabilitators were provisionally identified through online searches; 179 were considered active in 2016, 47 were considered not active and 13 were of unknown status. Of the 179 that were active, information on the number of hedgehogs admitted was available from 59 (33.0%). A further 125 rehabilitators were identified by snowball sampling, all of which were considered active; 115 (92.0%) provided information on admissions. Therefore, we had data on the number of admissions in the benchmark year for 174 hospitals but did not have equivalent data for 130 hospitals, consisting of 120 hospitals identified from the online searches and 10 from snowball sampling.

Based on the pattern of admissions in 2016 (Figure 1), small, medium and large hospitals were defined as those which admitted ≤50 (n = 109: 62.6%), 51-250 (n = 29: 16.7%) and >250 (n = 36: 20.7%) hedgehogs, respectively. Significantly more small hospitals and fewer large hospitals were detected by snowball sampling compared to the original online search (Chi-squared test: $X^2_2 = 67.18$, $P < 0.001$; Figure 4.1).

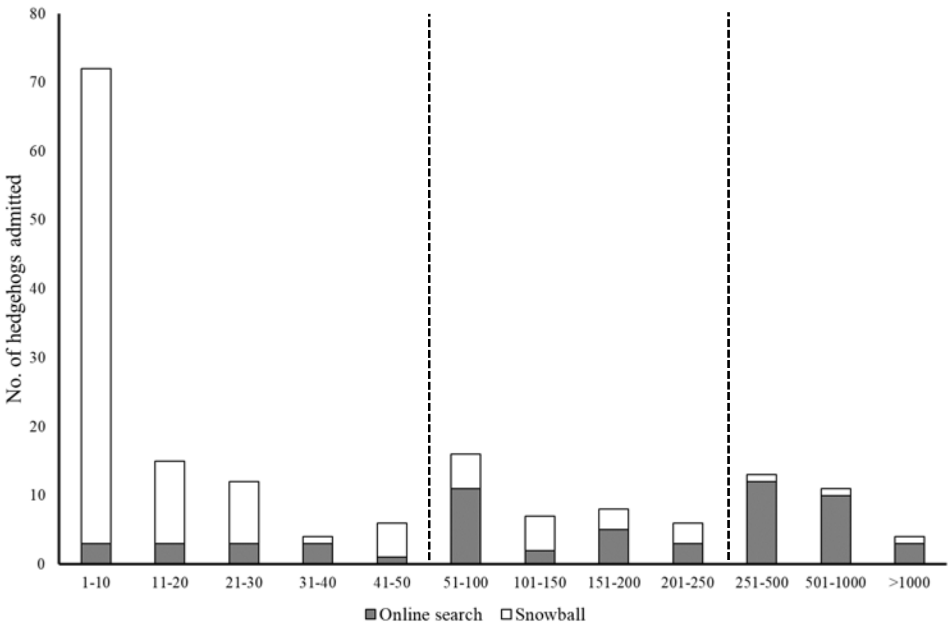


Figure 4.1. Frequency distribution of small, medium and large rehabilitation organisations identified from original online searches versus snowball sampling. Size categories were defined on the basis of the number of hedgehogs admitted in 2016: small = ≤50 admissions; medium = 51-250 admissions; and large = >250 admissions.

Estimating the number of hedgehog admissions

Overall, the 174 rehabilitators for which data were available admitted 25,540 hedgehogs in 2016, with large hospitals dealing with much larger numbers (n = 21,145; 82.8%), than medium-sized (n = 3,169; 12.4%) or small (n = 1,226; 4.8%) hospitals. Significantly fewer hedgehogs were admitted to small hospitals depending on whether they had been identified by snowball sampling versus those that had been identified in the original online search (Table 4.1); no significant differences were evident for medium-sized or large hospitals.

Extrapolating from the data summarised in Table 4.1, the number of hedgehogs admitted by all 304 active hospitals in the combined sample was estimated to range from 40,991 (Model 1 where the data from the online search and snowball sample were treated as homogenous and merged) to 59,308 (Model 2 where the data from the online search and snowball sample were considered separately) individuals (Table 4.2).

Table 4.1. Summary of the median (±IQR) number of hedgehogs admitted to small (≤50 admissions per annum), medium (51-250 admissions) and large (>250 admissions) in 2016 for those hospitals identified in the original online search (n = 59) versus those identified by snowball sampling (n = 115).

	Small	**Medium**	**Large**
Online	25.0 (10.0-32.0) (n = 13)	97.0 (67.5-156.5) (n = 17)	500.0 (346.0-701.0) (n = 29)
Snowball	6.0 (2.0-12.8) (n = 96)	121.0 (59.0-143.0) (n = 12)	235.0 (201.0-582.0) (n = 7)
Combined	6.0 (2.5-16.0) (n = 109)	97.0 (63.5-145.0) (n = 29)	478.0 (261.0-645.0) (n = 36)
Mann-Whitney test	W = 1124.00, P < 0.001	W = 256.50, P = 0.965	W = 578.50, P = 0.097

Table 4.2. Estimated number of hedgehogs admitted to the active wildlife hospitals identified by the online search (n = 179) and snowball sampling (n = 125) based upon two extrapolations. Model 1 is based on the assumption that the combined data from the online search and snowball sample are a representative sample of the hospitals where data on hedgehog admissions in 2016 were not available (n = 125). Model 2 is based on the assumption that the hospitals identified from the online search and snowball sample were not comparable, such that estimates for those hospitals where data were not available in each sample (n = 120 and n = 5, respectively) had to be calculated separately. The size of hospitals is defined on the basis of the number of hedgehogs admitted in 2016: small = ≤50 admissions; medium = 51-250 admissions; and large = >250 admissions.

Model 1: combined sample is representative

	Small	**Medium**	**Large**
Total no. of hospitals identified (excluding closed & unknown)	304 (n = 179 + 125)		
Total no. of hospitals where number of hedgehogs admitted is known	174 (n = 59 + 115)		
No. of hospitals where number of hedgehogs admitted is known	109 (62.6%)	29 (16.7%)	36 (20.7%)
Total known number of hedgehogs admitted	1,226	3,169	21,145
No. of hospitals where number of hedgehogs admitted is not known	130 (n = 120 + 10)		
Estimated number of hospitals in size division	81.4 (130 * 0.626)	21.7 (130 * 0.167)	26.9 (130 * 0.207)
Estimated median number of hedgehogs admitted per sample	6	97	478
Estimated number of additional hedgehogs	488 (81.4 * 6)	2,105 (21.7 * 97)	12,858 (26.9 * 478)
Estimated total number of hedgehogs in size division	1,714	5,274	34,003
Estimated total number of hedgehogs admitted	40,991		

Model 2: estimates need to be derived independently

	Small	Medium	Large
(a) Hospitals identified through online search			
Total no. of hospitals identified (excluding closed & unknown)	179		
Total no. of hospitals where number of hedgehogs admitted is known	59		
No. of hospitals where number of hedgehogs admitted is known	13 (22.0%)	17 (28.8%)	29 (49.2%)
Total known number of hedgehogs admitted	299	1,833	18,070
No. of hospitals where number of hedgehogs admitted is not known	120		
Estimated number of hospitals in size division	26.4 (120 * 0.220)	34.6 (120 * 0.288)	59.0 (120 * 0.492)
Estimated median number of hedgehogs admitted per sample	25	97	500
Estimated number of additional hedgehogs	660 (26.4 * 25)	3,356 (34.6 * 97)	29,500 (59.0 * 500)
Estimated total number of hedgehogs in size division	959	5,189	47,570
Estimated total number of hedgehogs admitted	53,718		
(b) Hospitals identified through snowball sampling			
Total no. of hospitals identified (excluding closed & unknown)	125		
Total no. of hospitals where number of hedgehogs admitted is known	115		
No. of hospitals where number of hedgehogs admitted is known	96 (83.5%)	12 (10.4%)	7 (6.1%)
Total known number of hedgehogs admitted	927	1,336	3,075
No. of hospitals where number of hedgehogs admitted is not known	10		
Estimated number of hospitals in size division	8.4 (10 * 0.835)	1.0 (10 * 0.104)	0.6 (10 * 0.061)
Estimated median number of hedgehogs admitted per sample	6	121	135
Estimated number of additional hedgehogs	50 (8.4 * 6)	121 (1.0 * 121)	81 (0.6 * 135)
Estimated total number of hedgehogs in size division	977	1,457	3,156
Estimated total number of hedgehogs admitted	5,590		
(c) All hospitals combined			
Total no. of hospitals identified (excluding closed & unknown)	304 (n = 179 + 125)		
Estimated total number of hedgehogs admitted	59,308		

Structure of the hedgehog rehabilitation community

Of the 304 active rehabilitators contacted, 153 completed the questionnaire survey indicating an overall return rate of 50%. However, 5 of these had to be omitted from the analyses of community structure as they did not provide information about the number of hedgehogs admitted in 2016, so we could not determine their size. Therefore, all analyses were based on a maximum sample size of 148 rehabilitators (49%). Responses from two rehabilitators in the Channel Islands were received and have been included here for completeness, whilst acknowledging these are not in Great Britain.

Hospitals varied significantly with respect to their charitable status, the number of unpaid staff working at the hospital, the length of time they had been established, where hedgehogs were housed during the rehabilitation process, their social media presence, patterns of record-keeping but not patterns of veterinary care and whether they conducted post-release monitoring (Table 4.3). In general terms, small and medium-sized hospitals were less likely to be registered as a charity, more likely to have been established within the five years prior to 2016 (Figure 4.2), and more likely to operate out of the rehabilitator's private residence (Table 4.3). Furthermore, smaller hospitals were most commonly staffed by just one unpaid person (Figure 4.3), less likely to have a business social media presence, more likely to rely on paper records, and less likely to carry out post-release monitoring (Table 4.3): post-release monitoring by all hospitals was predominantly via the use of spinal tags or nail varnish (n = 65 of 70 hospitals that conducted post-release monitoring). All three categories of hospital relied extensively on support from an external veterinary practice. Paid staff were present in <5% of small and medium-sized hospitals, but >40% of large hospitals (Table 4.3).

The median number of hedgehogs submitted annually throughout the period 2012-2016 appeared to increase for small (Figure 4.4a) and medium-sized (Figure 4.4b) hospitals, and to a lesser degree for large hospitals (Figure 4.4c). Considering only those hospitals where there were five years' worth of data (n = 28), the median number of hedgehogs submitted in 2016 was significantly higher than in both 2012 and 2013 (Friedman test: $H = 22.94$, $DF = 4$, $P < 0.001$; Figure 4.4d).

Table 4.3. Summary of the characteristics of small (≤50 hedgehogs admitted in 2016), medium-sized (51-250 hedgehogs admitted) and large (>250 hedgehogs admitted) wildlife hospitals based on the online questionnaire survey (n = 148). Sample sizes vary for individual analyses if respondents did not answer that question.

Characteristics		**Small (n = 108)**	**Medium (n = 22)**	**Large (n = 18)**	**Chi-squared results**
Registered charity (n = 148)	No	96%	86%	28%	$X^2_2 = 61.98$, $P < 0.001$
	Yes	4%	14%	72%	
No. of paid staff (n = 146)	% of hospitals with paid staff	5%	0%	44%	-
	Mean no. of paid staff (range)	1.2 (1-2)[1]	-	6.4 (1-30)	
No. of unpaid staff (n = 148)	1 volunteer	84%	46%	22%	$X^2_4 = 74.70$, $P < 0.001$
	2 volunteers	15%	18%	-	
	3 or more volunteers	2%	36%	78%	
Veterinary care (n = 148)	None	3%	-	-	$X^2_8 = 13.03$, $P = 0.111$
	Work with external vet practice	82%	100%	89%	
	Work with external rescue/hospital	12%	-	-	
	I am a veterinary nurse / vet	2%	-	-	
	Have an onsite vet	2%	-	11%	
Duration (n = 137)	≤5 years	79%	69%	12%	$X^2_2 = 30.03$, $P < 0.001$
	>5 years	21%	32%	88%	
Housing (n = 148)	Building in private grounds	4%	18%	11%	$X^2_4 = 41.53$, $P < 0.001$
	Personal residence	94%	77%	50%	
	Purpose-built facility	2%	5%	39%	
Social Media (n = 148)	No social media account(s)	57%	5%	11%	$X^2_4 = 52.46$, $P < 0.001$
	Only personal account(s)	26%	18%	6%	
	Business and/or personal account(s)	18%	77%	83%	
Record-keeping (n = 132)	Paper (partly or fully)	78%	46%	50%	$X^2_2 = 12.42$, $P = 0.002$
	Computer (partly or fully)	22%	56%	50%	
Post-release monitoring (n = 145)	No	59%	38%	24%	$X^2_2 = 9.17$, $P = 0.010$
	Yes	41%	62%	77%	

[1] Two small hospitals based at higher education establishments were excluded from these figures as they listed the number of paid staff as “lots” and “4,000” which presumably refers to the students at these establishment

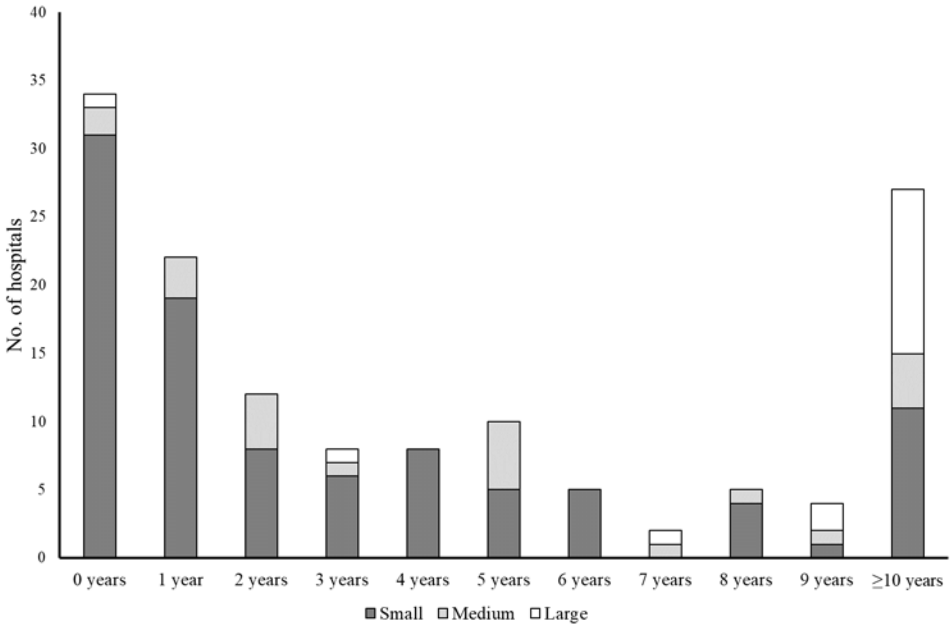


Figure 4.2. Number of years that small (≤50 admissions; n = 98), medium-sized (51-250 admissions; n = 22) and large (>250 admissions; n = 17) hospitals had been established in 2016.

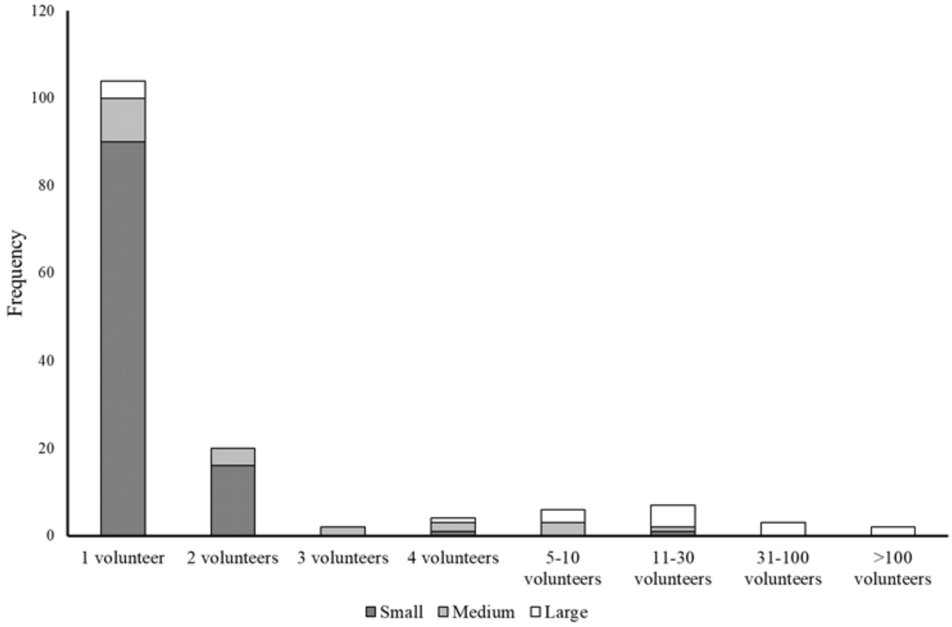
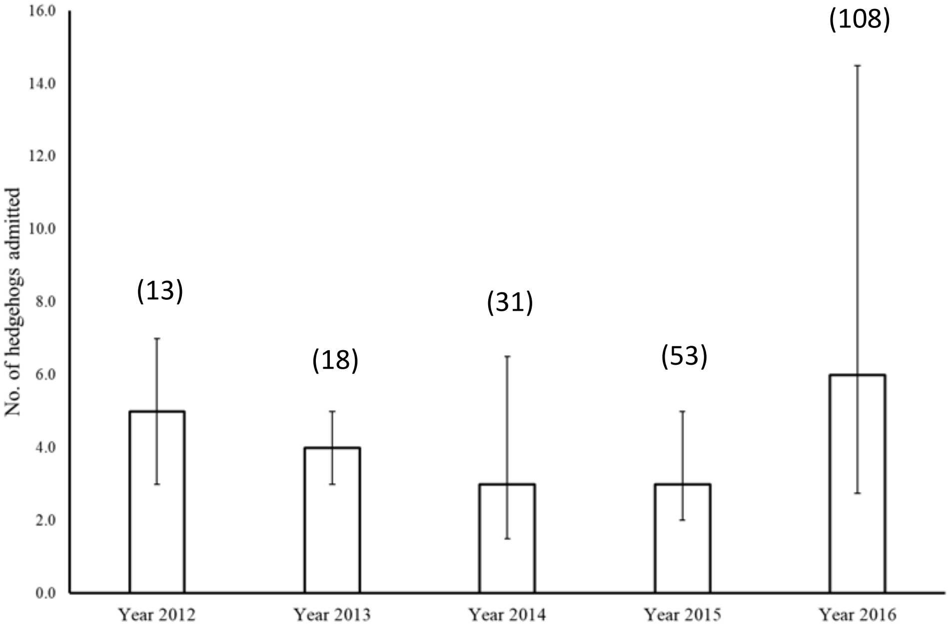
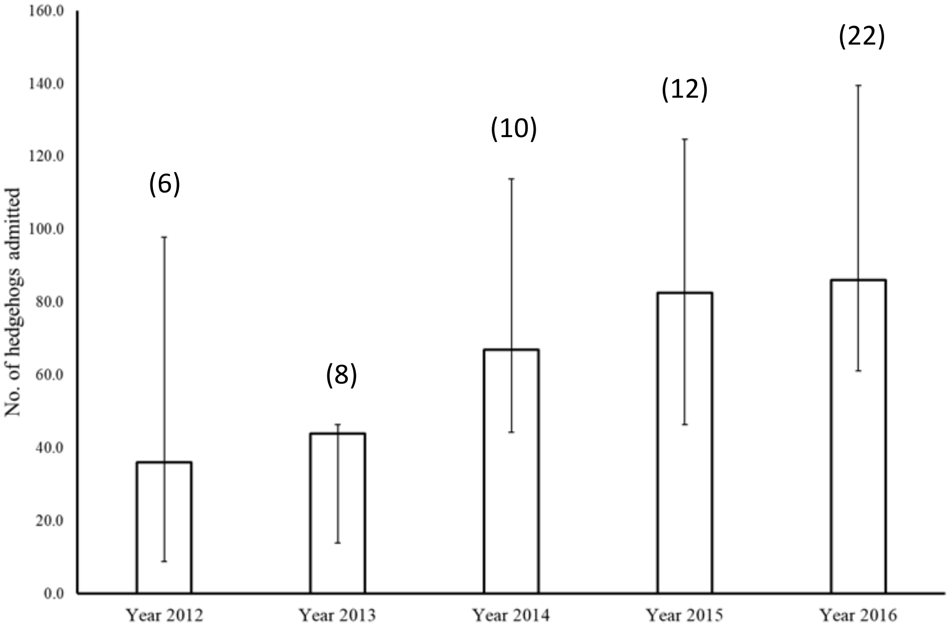


Figure 4.3. Frequency plot of the number of unpaid staff (volunteers) working at small (≤50 admissions; n = 108), medium-sized (51-250 admissions; n = 22) and large (>250 admissions; n = 17) hospitals.

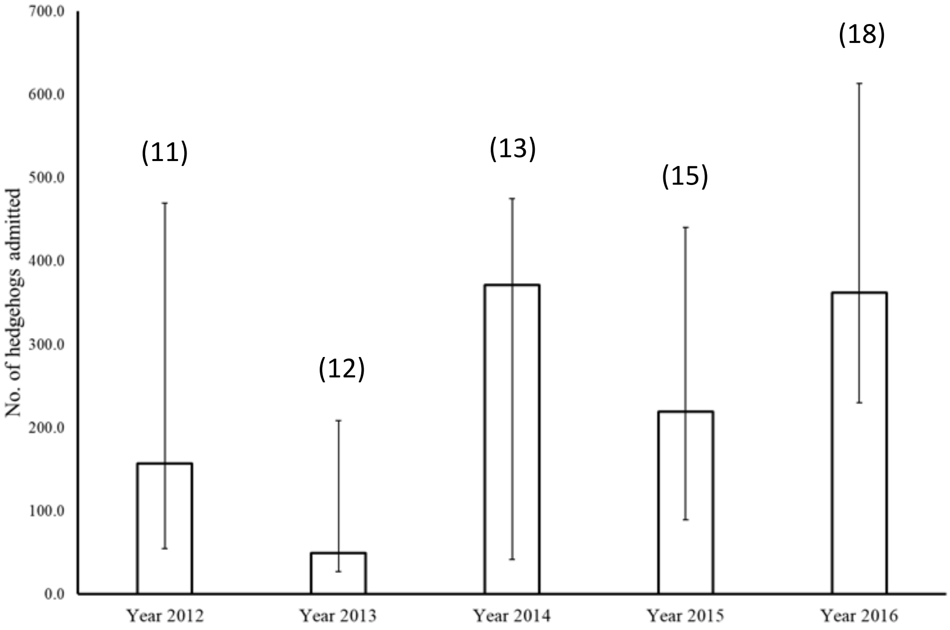
(a) Small hospitals



(b) Medium-sized hospitals



(c) Large hospitals



(d) Hospitals with 5 years' data (n = 28)

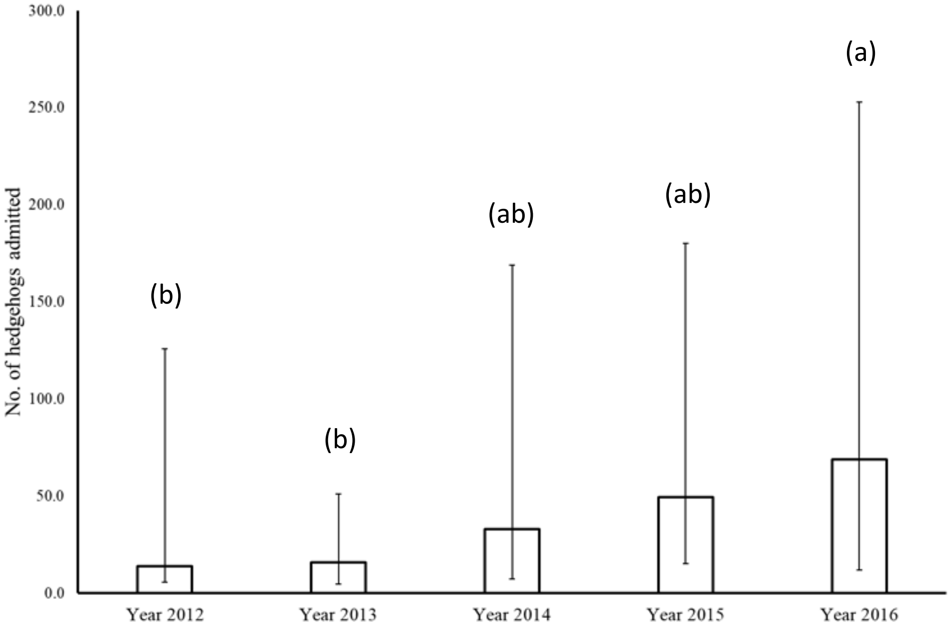


Figure 4.4. Median (±IQR) number of hedgehogs admitted annually to (a) small (≤50 admissions), (b) medium (51-250 admissions) and (c) large (>250 admissions) hospitals each year in the five-year period 2012-2016; figures above columns indicate sample sizes. (d) Number of hedgehogs admitted annually for those hospitals (n = 28) that provided data for all five years; letters above columns indicate *post hoc* groups from Friedman test.

Discussion

This study is, to the best of our knowledge, the first to attempt to estimate the number of practitioners involved in the rehabilitation of hedgehogs in Great Britain and the number of hedgehogs admitted into their care. At one level, searching for rehabilitators via the internet should be straightforward: as members of the public need to be able to locate and contact individuals or organisations who take in and care for injured or orphaned hedgehogs, it would be expected that practitioners would maintain an active social media presence advertising their services. However, this did not seem to be the case. Overall, we identified 304 active rehabilitators, but only 59% (n = 179) were identified in the original online searches; the remaining 41% (n = 125) were only identified by snowball sampling i.e. relying on provisionally identified practitioners to further advertise our request for information to their personal contacts. This potentially indicates that a large proportion of hedgehog rehabilitators in Great Britain rely on indirect contact networks (e.g. referrals from other rehabilitators) or “word of mouth” in order to be found by members of the public. This increases the possibility that they will not be identified in studies like this one; therefore, the numbers presented in this study should be considered minimum estimates.

In terms of the number of hospitals, the hedgehog rehabilitation community in Great Britain is dominated by small hospitals (63%), with many fewer medium-sized (17%) and large (21%) establishments. This does, in part, reflect the approach we used to group hospitals into different size classes, but it is clear that a very large number of rehabilitators deal with relatively small numbers of admissions annually (Figure 4.1). This pattern is further reflected in a wide range of associated characteristics. For example, small hospitals were: less likely to be a registered charity; likely to consist of just one unpaid member of staff; to operate out of their house or a building such as a shed in their garden; to rely on paper records rather than a computer; and not to carry out post-release monitoring. Collectively, these characteristics are consistent with the image of a passionate hedgehog enthusiast operating out of their own home or garage whilst working full- or part-time.

Furthermore, the majority of recent growth in the size and structure of this rehabilitation community is associated with smaller hospitals. For example, 74% of the small hospitals in our survey sample had been in operations for ≤5 years (equivalent to a start within the period 2012-2016). In contrast, comparable figures for medium-sized and large hospitals were 10% and 18%, respectively. Despite their prevalence, however, the number of hedgehogs admitted into care across these small hospitals was comparatively small; of the 25,540 hedgehogs admitted by the 174 rehabilitators for which data were available, only 5% were associated with small hospitals compared to 12% for medium-sized and 83% for large hospitals. The relatively low number of hedgehogs entering small hospitals is likely to reflect a range of limiting factors acting upon practitioners including space, time and funding. Furthermore, new rehabilitators may also purposefully only take on a limited number of patients, with the intention of expanding their capacity as they become more experienced; as such, individual hospitals may, over time, move between the (arbitrary) size classes we have defined.

In addition, the numbers of hedgehogs handed in to any single rehabilitator is also likely to be dependent upon the size of their "catchment area", how the hedgehog population in this area fluctuates over time and differences in the prevalence of factors which lead to hedgehogs being injured, orphaned or in ill-health. Consequently, the magnitude of the benefit of rehabilitating a given number of hedgehogs is contingent on the density and dynamics of the associated population; as such, the successful treatment and release of even moderate numbers of individuals into the local area could have marked value. Furthermore, the abundance of smaller rehabilitators may increase the likelihood that a sick or injured hedgehog is actually taken into care, as members of the public are sometimes reluctant to travel long distances (pers. obs.).

The number of admissions relative to population size: a national perspective

Extrapolating from the data derived from the questionnaire survey, we estimated that a total of 40,000-59,000 hedgehogs may have been admitted to the 304 wildlife rehabilitators active in 2016. However, there is a substantial disparity between these estimates, suggesting that they are sensitive to the modelling approaches used. For example, Model 2 was particularly affected by the proportion of large hospitals identified in the online searches (49%) which was then used to estimate the corresponding number in the sample of 120 hospitals for which no data were available; this calculation suggested that we had missed 59 large hospitals in these initial searches. We consider this unrealistic, as large rehabilitators typically had business related social media accounts meaning that they were relatively straightforward to identify. This is also reflected in the fact that only three large hospitals were identified by snowball sampling. Therefore, we believe the lower estimate of 40,000 is more plausible.

This number is substantially greater than implied by previous estimates. For example, Molony *et al.* (2007) and Grogan and Kelly (2013) reported estimates of 30,000-40,000 and 71,000 admissions per annum across the full range of bird and mammal species (there are >200 species of bird (Harris *et al.*, 2020) and >40 species of mammal in Great Britain (Mathews *et al*., 2018), many of which end up in wildlife hospitals, several in large numbers (e.g. Grogan and Kelly, 2013; Baker *et al.*, 2018)). Furthermore, it is important to note that: (i) the figures outlined above do not include the 31,000 hedgehogs admitted to veterinary surgeons (Barnes and Farnworth, 2016), although merging these two estimates together is not straightforward since there would be some element of double-accounting as some individuals would subsequently be transferred to rehabilitators for further care prior to release, whilst some vets in Barnes and Farnworth's (2016) study would have been working in collaboration with a rehabilitator; and (ii) the 304 active rehabilitators that we identified is substantially lower than the list of 800 hedgehog carers purportedly held by the BHPS, although we were not able to verify this number. If this latter figure is correct, then the number of hedgehogs admitted to wildlife hospitals in the benchmark year may have been markedly higher, although we would suggest that many of these additional hospitals would be considered small and therefore associated with relatively low median numbers of admissions.

The most recent estimate of the pre-breeding hedgehog population in Great Britain is 522,000 (Mathews *et al.*, 2018). At the most basic level, our estimate of 40,000-59,000 admissions is therefore equivalent to 8-11% of this total. However, only approximately 50% of those animals admitted are likely to survive to be released (Grogan and Kelly, 2013), implying that rehabilitators may collectively be saving 20,000-29,500 hedgehogs that would otherwise have been expected to perish (equivalent to 4-6% of the pre-breeding population). Yet, even this lower value is large relative to the rate at which the British hedgehog population is estimated to be declining based upon data from two long-term citizen science programmes run by the People's Trust for Endangered Species: trends in the size of rural hedgehog populations have been quantified using counts of dead hedgehogs on roads (*"Mammals on roads":* 2001-2017), whilst urban populations have been monitored by recording patterns of presence-absence in different habitats (*"Living with mammals"*; 2003-2017), in particular gardens (Wembridge and Langton, 2016; Wilson and Wembridge, 2018). Although converting these data to absolute changes in population size is difficult, these data suggest annual declines in the order of 3% in rural habitats and 2% in urban habitats. In this context, it can be argued that the hedgehog rehabilitation community could indeed be having a positive impact at a population level, rather than being merely a service related to animal welfare as some authors have previously suggested (Kirkwood and Sainsbury, 1996; Kirkwood and Best, 1998; Dubois, 2003; Guy *et al.*, 2013).

Nevertheless, any benefits associated with rehabilitation are not likely to be experienced by rural and urban hedgehog populations equally. For example, a growing body of evidence suggests that hedgehogs are increasingly associated with areas of human habitation, both in Great Britain (Young *et al.*, 2006; Hof and Bright, 2009; Pettett *et al.*, 2017b; Schaus *et al.*, 2020) and elsewhere (Hubert *et al.*, 2011; Van de Poel *et al.*, 2015), and relatively uncommon in rural areas (Young *et al.*, 2006; Trewby *et al.*, 2014; Williams *et al.*, 2018a). As >80% of people in Great Britain live in urban areas (Statista, 2020), and that urban hedgehogs are most commonly found in residential gardens (Hof and Bright, 2009; Dowding *et al.*, 2010a; Wembridge and Langton, 2016), it is perhaps unsurprising that most underlying reasons for hedgehogs being taken to wildlife hospitals are associated with garden-related factors (Chapter Three). Further, even in rural landscapes hedgehogs tend to be found near buildings (Pettett *et al.*, 2017b), suggesting that most rehabilitated hedgehogs are likely to originate from areas of human habitation. This is despite the fact that <1% of the hedgehog population nationally is thought to be found in urban areas (Mathews *et al.*, 2018).

Limitations and future work

The figures presented above assume that the benchmark year (2016) was typical whilst acknowledging that the number of admissions is likely to fluctuate inter-annually as the result of changes in population size, reproductive output, the number of practising rehabilitators, and factors likely to cause hedgehogs to enter hospitals (e.g. disease outbreaks, climatic conditions). For those hospitals where we did have a continuous set of data across the five-year period, the number admitted in 2016 was significantly higher than in 2012 and 2013 potentially suggesting that admissions in the last year were larger than normal. Alternatively, these differences could have partly reflected the ease/accuracy with which rehabilitators could collate information on the number of hedgehogs they admitted each year, 2016 being the year closest to the time when the questionnaire was distributed. This is likely to be more time-consuming for rehabilitators that only have paper records which may get damaged, lost, or disposed of because rehabilitators do not have the space to store them or because they are not aware of the potential scientific usefulness of this information. Also, as individuals would need to physically trawl through their written record to extract the data, rehabilitators that rely on paper records may also be less likely to respond to questionnaires requesting detailed information; this is potentially one reason why half of the rehabilitators contacted actually completed the questionnaire survey. Strategies which focussed on increasing the number of rehabilitators who store their data electronically would facilitate similar future studies.

The ultimate measure of the success of rehabilitation is the degree to which released individuals integrate into the wild population and reproduce. Although numerous studies have previously quantified post-release survival rates (e.g. Morris and Warwick, 1994; Morris, 1997; Molony *et al.*, 2006; Yarnell *et al.*, 2019) most have relied on radio-tagging individuals: although this enables each individual's definitive fate to be identified, these studies typically only last 8-10 weeks and they typically do not even encompass the released animal's first winter hibernation period. On a positive note, 48% of the rehabilitators who answered the questionnaire stated that they were conducting post-release monitoring, but most of this was via the use of numbered tags or nail varnish/correction fluid painted onto the spines; these are likely to be short-term as they will be lost when the spines are shed. Furthermore, lots of animals need to be marked to get sufficient observations from which to estimate post-release survival rates. For example, of 1,002 hedgehogs ear-tagged on the island of Jersey, only 156 (16%) were "recaptured", but this did indicate that approximately 6% of animals survived for more than three years after being released (Morris, 2018). One major problem with relying solely on rehabilitators to collect post-release data, however, is that there is a strong dependence on released animals re-entering wildlife hospitals, implying that they have experienced further problems. One way around this would be for better collaborations between rehabilitators and researchers in areas where long-term monitoring of individually-marked hedgehogs is already taking place; in these situations, scientists may be able to use a wider range of methods to quantify patterns of survival.

Conclusion

This study was the first to attempt to directly estimate the number, and characteristics, of practitioners rehabilitating hedgehogs in Great Britain and the Channel Islands, and the number of hedgehogs that enter their hospitals annually in comparison to the size and rate of decline of the national population. A minimum of 304 rehabilitators were identified: most (63%) of these admitted ≤50 hedgehogs annually, whereas the majority of hedgehogs (83%) were admitted by the small number of large hospitals. However, the growth of the hedgehog rehabilitation community is mostly associated with the creation of these smaller hospitals. Overall, the collective number of hedgehogs admitted to (40,000-59,000), and potentially released from (20,000-29,500), these wildlife hospitals was large relative to both the size of the estimated breeding population and annual rate of decline implying that rehabilitation could be an important conservation action. However, further information is required on the long-term survival and reproductive rates of released hedgehogs.

CHAPTER FIVE

As determined in Chapter Two, detection of hedgehogs in woodland is at a lower rate than in other habitats. Further, in Chapters Three and Four, trauma is a significant cause of admission to wildlife rehabilitators. This is as a result of garden tools, during mowing etc. possibly due to the camouflaged nature of the hedgehog nest in long grass. Detection of hedgehogs, either active or in the nest, in these complex habitats cannot be achieved through current methods, and monitoring population declines relies on robust, effective survey methods suited to a range of different habitats. Therefore, this chapter sought to determine the effectiveness of detecting hedgehogs with a conservation detection dog, in comparison to widely used detection methods. I conducted a pilot study to compare the effectiveness of a thermal camera, a detection dog and spotlighting as methods for locating hedgehogs in a rural landscape. This focused on key measures: (i) the absolute number of hedgehogs detected by each method in three different habitats (amenity grassland, pasture, woodland); (ii) the mean detection distance of each method in each habitat; and (iii) the effect of vegetative ground cover on detection distance. This then considers (iv) observations of using a detection dog for the first time as a method for locating hedgehogs; and (v) the costs and benefits associated with each of the three methods in the context of future studies.

In this chapter I explored the use of three different methods for the detection of hedgehogs, namely spotlight, infra-red thermal cameras and conservation detection dogs, with a view to developing a method that could be used for detection of hedgehogs in the nest. Whilst the former two methods have been considered in the literature (Haigh *et al.*, 2012a; Bowen *et al.*, 2019), and spotlights are widely used for hedgehog detection (e.g. Hof *et al.*, 2012; Pettett *et al.*, 2017a), the use of detection dogs has not be fully explored for active hedgehogs and has not be described previously for those in the nest. Recent research demonstrated the benefit of dogs for the detection of small cryptic, nocturnal mammals (Karp, 2020), albeit those which inhabit more open areas of the landscape than is typically for the hedgehog, and consideration of the animal in the nest is limited.

My contribution to the work

I designed the project and conducted all field work, with the detection dog handled and trained by Louise Wilson of Conservation K9 Consultancy. I prepared the manuscript with assistance from Dr Philip Baker. Statistical analysis was conducted by myself, with assistance from Dr Philip Baker and Dr Luke Evans.

Publication reference

The manuscript presented in this chapter has been submitted for publication in the *Journal of Vertebrate Biology: Detection Dog special issue.*

Bearman-Brown, L. E., Wilson, L. E., Evans, L., & Baker, P. J. (2020). Comparing non-invasive surveying techniques for elusive, nocturnal mammals: a case study of the West European hedgehog (*Erinaceus europaeus*). *Journal of Vertebrate Biology*, 69(3), 20075. https://doi.org/10.25225/jvb.20075

Comparing non-invasive surveying techniques for elusive, nocturnal mammals: a case study of the West European hedgehog (*Erinaceus europaeus*)

Abstract

Monitoring changes in populations is fundamental for effective management. The West-European hedgehog (*Erinaceus europeaus*) is of conservation concern in the UK because of recent substantial declines. Surveying hedgehogs is, however, problematic because of their nocturnal, cryptic behaviour. We compared the effectiveness of three methods (infra-red thermal camera, specialist search dog, spotlight) for detecting hedgehogs in three different habitats. Significantly more hedgehogs were detected, and at greater distance, using the camera and dog than the spotlight in amenity grassland and pasture; no hedgehogs were detected in woodland. Increasing ground cover reduced detection distances, with most detections (59.6%) associated with bare soil or mown grass; the dog was the only method that detected hedgehogs in vegetation taller than the target species' height. Current data on rural hedgehog movements suggest that the additional value of surveying with an infra-red camera or detection dog is most likely to be realised in areas where badgers (*Meles meles*), an intra-guild predator, are absent, and where ground cover enables hedgehogs to forage further from refuge habitats. Further consideration of the effectiveness of detection dogs for finding hedgehogs in nests, as well as developing techniques for monitoring this species in woodland, is warranted.

Key words: Conservation dog; detection dog; infra-red camera; mammal monitoring; scent dog; thermal camera

Introduction

Wildlife management and conservation interventions are becoming increasingly important globally as extensive anthropogenic changes are made to the environment (Vitousek *et al.* 1997, Millennium Ecosystem Assessment (MEA) 2005, Sutherland 2013, Veach *et al.* 2017) and biodiversity is threatened (Butchart *et al.* 2010, Wagler 2013, Tittensor *et al.* 2014, Ceballos and Ehrlich 2018). The effective development and implementation of conservation and/or management strategies is, in part, dependent upon quantifying the distribution and abundance of populations and how they are changing spatially and/or temporally (Warren *et al.* 2000, Wilson and Delahay 2001, Grenyer *et al.* 2006, Schipper *et al.* 2008).

Methods for estimating temporal and spatial variation in population size and distribution can be broadly split into direct versus indirect methods (Langbein *et al.* 1999, Wilson and Delahay 2001, Day *et al.* 2016). Direct methods are associated with counts of live animals themselves, whereas indirect counts are based on counts of “field signs” such as refugia (Waters *et al.* 2011, Judge *et al.* 2014), tracks (Alibhai *et al.* 2017, Williams *et al.* 2018a, b), scats (Churchfield *et al.* 2000, Day *et al.* 2016, Cortázar-Chinarro *et al.* 2019, Mwebi *et al.* 2019) and feeding signs (Redpath *et al.* 2001, Meek *et al.* 2012), or e.g. counts of animals killed on roads (Baker *et al.* 2004, Seiler *et al.* 2004, Bright *et al.* 2015) or by hunters (Aebischer *et al.* 2011, Aebischer 2019). These indirect approaches have tended to be used where direct methods are not possible (e.g. the focal species occupies a habitat where direct observation is not possible), or because they are cheaper (Alibhai *et al.*, 2017). The use of indirect measures is, however, predicated on the assumption that they reflect population size *per se* or some relative measure of population size, but it is known that they can be associated with a range of confounding factors that make estimates uncertain and interpretation of data difficult (McDonald and Harris 1999, Bright *et al.* 2015). Converting counts of relative abundance to measures of absolute abundance is particularly problematic.

In addition to counting animals for population monitoring, capturing individuals may also be an important component of scientific studies. For example, radio- and satellite-tracking have revolutionised our understanding of animal movement patterns (Craighead and Craighead 1972, Deutsch *et al.* 1998, Marzluff *et al.* 2001) and the attachment of bio-loggers and animal-mounted video cameras enable scientists to obtain data that would otherwise be impossible to get (Yasuhiko 2004, Ropert-Coudert and Wilson 2005, Loyd *et al.* 2013, Volpov *et al.* 2015, Wilmers *et al.* 2015). Handling animals also enables morphological, physiological, isotopic, reproductive and parasitological data to be collected (Wassenaar and Hobson 2000, Elledge *et al.* 2008, Telfer *et al.* 2010, Wikenros *et al.* 2016), as well as being crucial to the application of techniques such as the use of doubly labelled water for estimating energy consumption (Lifson *et al.* 1955, Lifson and McClintock 1966, Nagy 2001, Pettett *et al.* 2017a). Typically, animals are captured using devices such as nets, traps and snares (Flowerdew *et al.* 2004, Hill and Greenaway 2005, Tyrrell *et al.* 2009): this is often expensive, time-consuming, and associated with significant animal welfare and legal issues (Putman 1995, Lane and McDonald 2010, Brown *et al.* 2013). Consequently, the development of novel methods for locating animals that improve welfare standards and enable the collection of robust data is important for designing successful management plans.

The West-European hedgehog (*Erinaceus europeaus*, hereafter 'hedgehog') is a species of increasing conservation concern in Great Britain (Mathews *et al*., 2018), and elsewhere (Haigh 2011, Van de Poel *et al.* 2015), because of a substantial decline in recent decades (Holsbeek *et al.* 1999, Huijser and Bergers 2000, Van de Poel *et al.* 2015, Hof and Bright 2016, Mathews *et al.* 2018, Müller 2018, Pettett *et al.* 2018b, Williams *et al.* 2018a, Wilson and Wembridge 2018). This has been widely attributed to a range of factors, including: a substantial reduction in the extent and quality of hedgerows (Carey *et al.* 2008, Moorhouse *et al.* 2014); increased predation and competition pressure from badgers (*Meles meles*) (Young *et al.* 2006, Judge *et al.* 2014); direct or indirect impact of roads (Huijser and Bergers 2000, Rondinini and Doncaster 2002) and the extensive use of pesticides (Battersby, 2005), which have resulted in direct poisoning (Dowding *et al.*, 2010b) or a decline in the abundance and variety of invertebrate prey (Geiger *et al.* 2010, Hof and Bright 2010a, b). The magnitude of this decline is, however, equivocal because of problems associated with quantifying hedgehog density.

To date, researchers and NGOs have generally relied upon spotlighting, footprint-tunnels, trapping and/or counts of dead animals on roads to either (i) capture hedgehogs (mainly for marking and to attach radio-tracking or GPS-tracking devices) or (ii) estimate relative abundance or hedgehog presence-absence (Young *et al.* 2006, Poulton and Reeve 2010, Trewby *et al.* 2014, Pettett *et al.* 2017a, b, Williams *et al.* 2018 a, b). However, these approaches have often varied in their efficacy and are associated with factors that may affect their robustness or usefulness. In addition, most studies have relied on a single technique, preventing comparison of the efficacies of different techniques. For example, footprint-tunnels have been used successfully in both urban and rural areas in the UK (Yarnell *et al.* 2014, Williams *et al.* 2018a, b) but have had limited uptake in other studies (Haigh *et al.* 2012a, Gurnell and Bowen 2016). Similarly, spotlight surveys were the most effective method for locating hedgehogs in Regent's Park, London (Gurnell and Bowen, 2016), whereas Poulton and Reeve (2010) dismissed this method for surveying hedgehogs, as when applied, they only detected hedgehogs in 14 of 97 visits across 30 sites in Great Britain. The latter could, however, have simply reflected low patterns of occupancy at the sites surveyed rather than a limitation of spotlighting *per se*; this is supported by spotlights and footprint-tunnels providing consistent results across 17 of 19 (89%) sites surveyed in spring, 15 of 18 (83%) in summer and 6 of 17 (94%) in autumn, respectively, by Yarnell *et al.* (2014: authors' unpublished data). Finally, footprint-tunnels and counts of dead hedgehogs do not provide information about hedgehog density, and the latter may be influenced by road size (Rondinini and Doncaster, 2002). Consequently, there is a need to consider novel survey methods that overcome the limitations associated with these current methods, but also to compare their relative efficacy by conducting standardised surveys at the same site(s).

Two methods that could potentially be used to survey hedgehogs more efficiently are infra-red thermal cameras and detection dogs. Infra-red thermal (IRT) cameras display an image of the scene using emitted heat (infra-red radiation) rather than visible light (Cilulko *et al.*, 2013). In the context of surveying for animals, this approach is particularly useful at night when the contrast between the heat of the animal and the surrounding vegetation is large (Sabol and Hudson 1995, Mayle *et al.* 1999, Butler *et al.* 2006, Bowen *et al.* 2019). This overcomes issues associated with using visible light, such as from a spotlight or torch, to detect species that are cryptically camouflaged and those, such as with hedgehogs, which "freeze" or curl up when feeling threatened (Reeve 1994, Nottingham *et al.* 2019). However, like spotlights, IRT cameras are not as effective in dense vegetation, which blocks the heat signature (Ditchkoff *et al.*, 2005); this is particularly problematic for small species where even short grass may obscure individuals (Boonstra *et al.* 1994, Karp 2020).

Specially trained dogs have been used for conservation purposes since the 1890s when they were used to locate New Zealand kiwi (*Apreyx* spp.) and kakapo (*Strigops habroptilus*) (Helton, 2009). Since these pioneering projects, dogs have been trained to detect the presence of a wide array of biological organisms and associated structures and ejecta, including: plants (Goodwin *et al.*, 2010); large mammal faeces (Vynne *et al.* 2011, de Oliveira *et al.* 2012, Arandjelovic *et al.* 2015); reptiles (Stevenson *et al.* 2010, Nielsen *et al.* 2016); nests (Cablk and Heaton 2006, O'Connor *et al.* 2012); carcasses

(Paula *et al.* 2011, Mathews *et al.* 2013); and owl pellets (Wasser *et al.* 2012). Dogs rely on detecting the focal animal/object by scent rather than sight and are able, therefore, to detect these even if they are not in direct line of sight e.g. in vegetation (Leigh and Dominick 2015, Karp 2020), and at a greater distance than humans (Goodwin *et al.* 2010, de Oliveira *et al.* 2012). Furthermore, dogs trained to detect particular scents mean that they are better able to discriminate between objects/structures that challenge human observers. For example, dogs were 153% more accurate and 19 times faster at identifying koala (*Phascolarctos cinereus*) scat than experienced human surveyors (Cristescu *et al.*, 2015), and accurately identified 90% of burrows containing nests of desert tortoises (*Gopherus agassizii*) (Cablk and Heaton 2006).

Both IRT cameras and dogs have previously been used to locate hedgehogs. For example, dogs were used in the search for hedgehogs on the island of North Uist in Scotland during a removal programme to protect ground-nesting birds (Scottish Natural Heritage, unpublished); overall, over 1129 searches with dogs were undertaken, although no figure of the number of hedgehogs found during that time is available. Similarly, Warwick (1987) briefly used a dog during initial surveys in North Ronaldsey (Orkney Islands, Scotland) where it effectively found hedgehogs in a familiar area but not elsewhere. Finally, Morris (1988) also mentions success in finding hedgehogs with a dog although this is not described in detail. IRT cameras have been used successfully in Regent's Park, London, UK (Bowen *et al.* 2019) and forest fragments in Auckland, New Zealand (Nottingham *et al.* 2019). Conversely, Haigh *et al.* (2014a) concluded that the IRT camera they used was ineffective.

The efficacy of these two techniques have not, however, been compared, nor have these techniques been applied in non-urban habitats within Great Britain. Therefore, in this study, we conducted a pilot project to compare the effectiveness of an IRT camera, a detection dog and spotlighting as methods for locating hedgehogs in a rural landscape. Specifically, we compared: (i) the absolute number of hedgehogs detected by each method in three different habitats (amenity grassland, pasture, woodland); (ii) the median detection distance of each method in each habitat; and (iii) the effect of vegetative ground cover on detection distance. We then go on to: (iv) discuss our observations of using a detection dog for the first time as a method for locating hedgehogs; and (v) consider the costs and benefits associated with each of the three methods in the context of future studies.

Materials and Methods

Data were collected on the Hartpury University and College campus, Gloucestershire, UK (UTM: 51°54′18″N, 002°18′37″W), a 360 ha^{-1} mixed commercial farm used for agricultural teaching and research. Previous studies had confirmed that hedgehogs were present (Bearman-Brown *et al.*, 2020a; Chapter Two). The site was surveyed on 18 separate nights during May-October 2019 following a standardised transect route (approx. 6km long; but see Results) which encompassed three specific habitat types (HABITAT): amenity grassland, pasture and woodland. Surveys were conducted using three different methods (METHOD): spotlighting; infra-red thermal (IRT) camera; and a trained conservation detection dog. Only one method was used on any given night, with six replicates performed for each method. All three habitats were surveyed once each night, with habitats visited in a random order.

Surveys started approximately one hour after sunset and were conducted on nights with minimal rain and wind as these may have affected hedgehog behaviour and reduced the efficiency of one or more of the survey methods. Two measures of survey effort were recorded within each habitat: survey duration (TIME: maximum 40 minutes) and distance travelled (DISTANCE). Air temperature and humidity were recorded at the start and end of each survey and each time a hedgehog was located.

Spotlight and thermal camera surveying

Spotlight (1 million candle-power Clulite CB2 Clubman, Clulite Engineering Ltd., Petersfield, Hampshire, UK) and infra-red thermal camera (FLIR E53, FLIR Systems UK, West Malling, Kent, UK) surveys were conducted on foot by an experienced hedgehog surveyor (LBB). The surveyor was accompanied by a second person for safety reasons but who was instructed to remain silent throughout; any hedgehogs missed by the surveyor but observed by the safety person were recorded at the end of the surveying (i.e. they were not recorded as a "detection" for the purposes of the current study). The spotlight was not filtered as in some other studies (Pettett *et al.* 2017a,b).

Both the spotlight and IRT camera were used intermittently, with the surveyor walking ten paces then stopping to slowly scan the surrounding area; this approach was adopted to minimise the risk of tripping, as the IRT camera may not indicate hazards that have equal thermal properties to the surrounding area. Batteries on both devices were changed after approximately 1.5 hours. The thermal camera was recently calibrated, and set up according to the following parameters (Bowen *et al.*, 2019): emissivity setting set to a custom setting of 0.95; distance 20 m; relative humidity 50%; atmospheric temperature 20°C; and window compensation off.

Dog-team surveying

One male rescue springer spaniel dog was trained to search for, and quietly indicate upon, the scent of hedgehog: training was conducted using hedgehog spines taken from specimens found dead on roads. The dog had previously been trained to detect a range of wildlife odours and worked in a commercial capacity for a consultancy undertaking wildlife surveys. Consequently, he was only available for the current project outside these other commitments. The alert behaviour was to sit near (≥0.5 m) the source of the odour and remain there quietly until called away, at which point he received the reward (tennis ball). He was handled by an experienced, trained detection dog handler (LW).

The dog and handler team were despatched on different nights to the human surveyors to ensure the dog was not following the scent of human surveyors. The dog worked on an 8m long line to ensure close control at all times. The handler followed the standardised transect route, but the dog was allowed to lead the handler when an odour was detected. Once the odour trail had been followed to ensure all areas had been covered, the dog-handler team would then return to the point at which they had departed from the transect.

As the primary focus of this study was to determine the reliability of the dog in detecting hedgehogs in a range of habitats, the dog-handler team was followed at a distance of 15-20 m by a second surveyor with the thermal camera. This allowed the area to be checked unobtrusively to determine if any hedgehogs had been missed by the dog. The handler was not informed if any hedgehogs had been missed until the surveys had been completed.

The dog team worked for a maximum of three hours per night for welfare reasons, with 40 minutes survey time followed by a 20 minute break. During the break period, the dog's harness was removed, and he was put in his kennel in a van as a clear indication that it was time to rest. Water was offered at regular intervals during surveying in accordance with environmental temperature and humidity to ensure that his mucous membranes remained moist and that he was working effectively.

Data recording

To minimise disruption to surveying during the current project, a period of prior surveying was undertaken on site using the thermal camera to locate, capture and mark hedgehogs for identification purposes. By doing this, any hedgehog captured during the study could be identified and released quickly; unmarked animals, however, did need more extensive handling as these also needed to be marked for future studies. This period also provided opportunity to determine the most appropriate settings for the thermal camera under different environmental conditions.

All hedgehogs detected during the study were captured by hand under licence from Natural England, as the use of dazzling devices such as high-powered spotlights for detecting hedgehogs is restricted under Schedule 6 of the Wildlife and Countryside Act, 1981 (licence number: 2017-31042-SCI-SCI). At their initial capture, all animals were weighed, sexed, given a health check and marked using sections of numbered plastic tubing (Printasleeve Ltd, Crewkerne, Somerset, UK) glued to five individual spines on the nape of the neck. Animals caught for the first time were released at the point of capture within 15 minutes; previously marked animals that had been re-caught were typically released within ≤5 minutes. The time taken to process each animal was excluded from the 40 minute survey period.

The capture location of each hedgehog was recorded using a handheld GPS device (Garmin GPS 60). The height of vegetation in the area immediately surrounding the hedgehog was categorised as: (1) bare ground or mown grass; (2) less than the height of the back of the hedgehog (approx. <15 cm); (3) ≤0.5 m tall; (4) ≤1 m tall; or (5) >1 m tall. These categories were condensed to two levels for analysis (low: Category 1; high: Categories 2-5 combined) because of small sample sizes in the latter divisions.

For spotlighting and the IRT camera, detection distance was measured as the straight-line distance from the surveyor to the position of the hedgehog when it was first sighted. For the dog team, detection distance was taken as the straight-line distance from the dog to the hedgehog at the point the handler believed it was clear the dog had caught the animal's scent.

Data analysis

Survey effort

As the number of hedgehogs detected by each method may vary in relation to the method itself but also the density of hedgehogs in the different habitats and survey effort, preliminary analyses were conducted to determine whether survey effort was consistent. A general linear model was used to analyse the effects of HABITAT and METHOD on distance walked (DISTANCE): this model included a HABITAT*METHOD interaction term. Both predictor variables were modelled as fixed factors. Data were checked to ensure that they conformed to the underlying assumptions of the test (Grafen and Hails, 2002). Data for the duration of surveying (TIME) were not normally distributed, so a Kruskal-Wallis test was used to compare median values across all nine HABITAT-METHOD subgroups.

The relationship between DISTANCE and TIME was analysed using Pearson correlation as these are likely to be inter-related, which can cause problems with multicollinearity in statistical models (Grafen and Hails 2002, Field 2017). Initially, data across all three habitats were compared. A further correlation was conducted for those data from amenity grassland and pasture but excluding woodland as the latter was excluded from the analysis comparing the survey methods since hedgehogs were not detected in woodland by any method (see Results).

Comparison of survey methods

The effect of METHOD, HABITAT, TIME, DISTANCE, air TEMPERATURE and HUMIDITY on the number of hedgehogs detected was analysed using a generalised linear model (GLM) assuming a Poisson error distribution. As no hedgehogs were detected in woodland using any method, these data were both uninformative for evaluating the influence of the covariates and caused under-dispersion; they were, therefore, removed prior to analysis. An initial global model containing all covariates was fitted and then AIC based multi-model selection (Burnham and Anderson, 2002) was applied using the *MuMin* package (Barton, 2019) in R version 3.3.3 to find the best fitting models; models with ΔAICc values <2 were assumed to have equal support (Burnham and Anderson, 2004).

The assumptions of the GLM were then tested for the global model and the single best-fitting model, using a goodness-of-fit deviance test and a residual dispersion test for a Poisson error distribution through the *DHARMa* package (Hartig, 2017).

Factors affecting detection distance

It was not possible to incorporate METHOD, HABITAT type (amenity grassland, pasture) and ground COVER (low, high) into a single analysis because of e.g. the inherent limitations of the methods themselves and how this influenced sample sizes in different categories (see Appendix 2: Supplementary Figure 2). For example, surveyors are less likely to be able to detect hedgehogs in dense cover using a spotlight or IRT camera because the animal is physically hidden from view, whereas this may not be the case for a detection dog. Therefore, we used a combination of Kruskal-Wallis and Mann-Whitney tests to compare differences in the distance over which hedgehogs were first detected in relation to (a) survey method, (b) ground cover and (b) habitat.

General linear model, Kruskal-Wallis and Mann-Whitney analyses were conducted using Minitab version 19 and SPSS version 25. Data are presented as mean (±SD) or median (±IQR) in accordance with the statistical tests used.

Results

Survey effort

Survey DISTANCE was not significantly affected by METHOD (General linear model: $F_{2,45} = 0.05$, $P = 0.952$) or the interaction between METHOD*HABITAT ($F_{4,45} = 0.99$, $P = 0.424$) but was significantly affected by HABITAT ($F_{2,45} = 60.74$, $P < 0.001$). Distance walked was significantly higher in pasture (2.27 ± 0.20 km) than in amenity grassland (1.73 ± 0.19) and woodland (1.67 ± 0.14).

There was also a significant difference in the duration of surveying (TIME) across the nine HABITAT and METHOD subgroups (Kruskal-Wallis test: $H = 20.72$, DF = 8, $P = 0.008$). Although there was a lot of overlap between subgroups, this difference was principally due to a longer survey time in pasture (all surveys lasted 40 minutes regardless of survey method) compared to mean survey times of 38.9 (range: 36-40) minutes for amenity grassland and 36.8 (range: 32-40) minutes for woodland.

Survey duration and distance walked were significantly positively correlated when data from all three habitats were considered (Pearson correlation: r = 0.41, n = 54, P = 0.002), but not when woodland was excluded (r = 0.31, n = 36, P = 0.064).

Comparison of survey methods

Hedgehogs were detected on 47 occasions across the 54 transect surveys (mean (±): 0.87 ± 1.20; range: 0-5). There was a marked difference in the number of animals detected within each habitat (Table 5.1). Most notably, no hedgehogs were detected by any method in woodlands; 2.6 times as many hedgehogs were detected in amenity grassland versus pasture. On no occasion did the dog fail to detect a hedgehog that was located by the second surveyor following behind with the IRT camera.

Table 5.1. Number of hedgehogs recorded within each habitat using each survey method. Six transect surveys were conducted in each habitat using each method.

Method	**Habitat**			**Total**	**Mean (±SD)**	**Median [Range]**
	Amenity grassland	**Pasture**	**Woodland**			
Camera	15	4	0	19	1.06 ± 1.55	0.0 [0-5]
Dog	12	8	0	20	1.11 ± 1.02	1.0 [0-3]
Spotlight	7	1	0	8	0.44 ± 0.86	0.0 [0-3]
Total	34	13	0	47	0.87 ± 1.20	0.0 [0-5]
Mean (±SD)	1.89 ± 1.32	0.72 ± 0.89	0.00	0.87 ± 1.20		
Median [Range]	2.0 [0-5]	0.5 [0-3]	0.0 [-]			

Across all models, there were significantly fewer hedgehogs detected in pasture than in amenity grassland (Table 5.2; Figure 5.1). In three out of the five top-ranked models, including the best overall model, METHOD of detection was retained, with more hedgehogs detected with the infra-red camera and the dog compared to spotlighting (Table 5.2; Figure 5.1). DISTANCE walked and TEMPERATURE were retained in two and one of the best models, respectively, although neither were significant.

Table 5.2. Estimated regression parameters (± standard error) from the general linear model predicting the number of hedgehogs detected. Reference level for 'Habitat' is amenity grassland; reference level for 'Method' is spotlight. Models presented are those with ΔAICc < 2. Full and conditional model averages are presented beneath. Asterisks denote: * < 0.05, ** < 0.01, *** <0.001.

Intercept	Distance (km)	Habitat (Pasture)	Method (Camera)	Method (Dog)	Start temperature (°C)	df	AICc	ΔAICc
-0.04 (± 0.37)		-0.96** (± 0.33)	0.87* (± 0.42)	0.92* (± 0.42)		32	102.1	0.00
0.66 (± 0.70)		-0.89* (± 0.33)	0.97* (± 0.43)	0.87* (± 0.42)	-0.05 (± 0.04)	31	103.5	1.33
0.64*** (± 0.17)		-0.96** (± 0.32)				34	103.5	1.42
1.47 (± 1.35)	0.84 (± 0.75)	-1.39** (± 0.51)	0.83 (± 0.42)	0.86 (± 0.42)		31	103.6	1.46
-1.29 (± 1.35)	1.10 (± 0.76)	-1.56** (± 0.53)				33	103.9	1.73
-0.22 (± 1.18)	0.30 (± 0.62)	-1.11* (± 0.47)	0.61 (± 0.54)	0.61 (± 0.54)	-0.01 (± 0.03)	Full average		
-0.22 (± 1.18)	0.96 (± 0.77)	-1.10* (± 0.47)	0.88* (± 0.42)	0.89* (± 0.42)	-0.05 (± 0.04)	Conditional average		

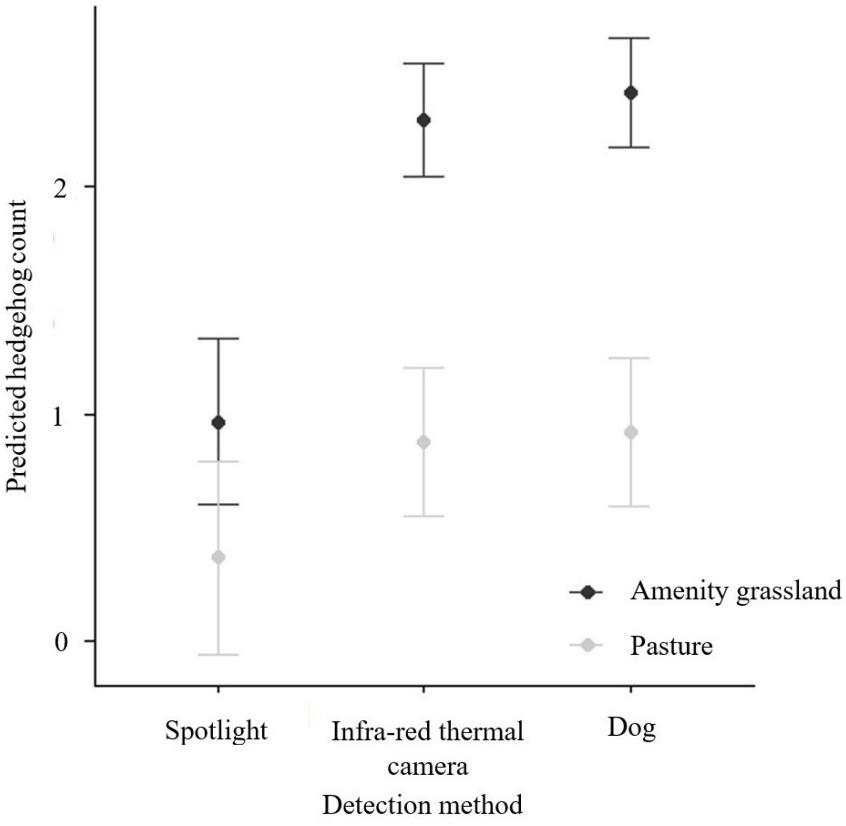


Figure 5.1. The predicted number (± SE) of hedgehogs detected per transect across HABITAT and METHOD from the single best model (Table 5.2).

Factors affecting detection distance

On average, the minimum detection distance was significantly greater for the IRT camera compared to the spotlight, with the detection dog intermediate to these two methods (Kruskal-Wallis test: H = 8.21, DF = 3, P = 0.016; Figure 5.2). However, there was a lot of overlap in the detection distances (Figure 5.3). Hedgehogs were generally detected by spotlighting at a distance of 1-10 m, although one individual was first detected at 20 m. Similarly, hedgehogs tended to be detected by the dog within 4-15 m, but with two detection events at 25 m and 30 m; it must be noted, however, that these values are likely to be conservative estimates as the point at which the hedgehog was first detected was sometimes hard to estimate based upon a clear change in the dog's behaviour. Detection distance was most variable using the IRT camera, ranging from 4-50 m; this method was associated with the majority of long-distance detections (>15 m).

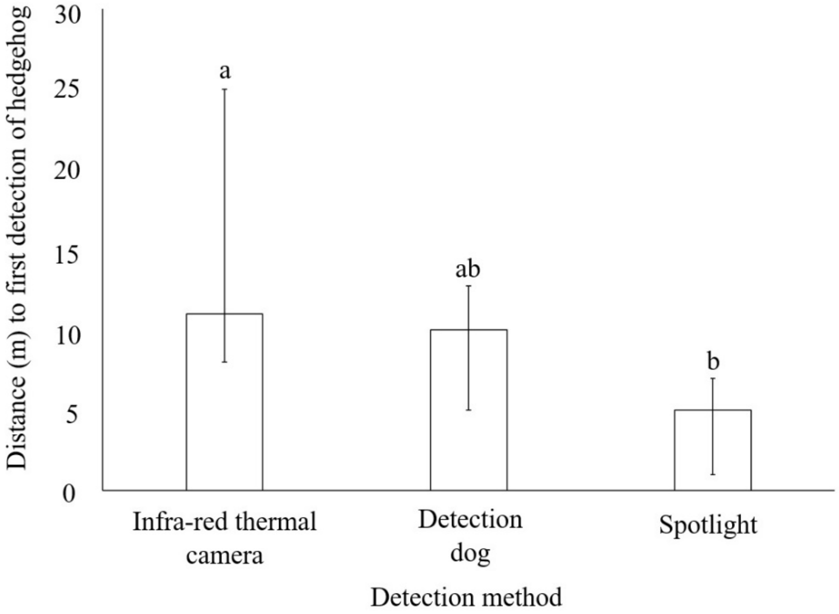


Figure 5.2. Median (±IQR) distance hedgehogs were first detected using an infra-red thermal camera (n = 19), detection dog (n = 20) or spotlight (n = 8). Data from different habitats and different levels of ground cover combined. Letters denote post hoc groupings from a Kruskal-Wallis test.

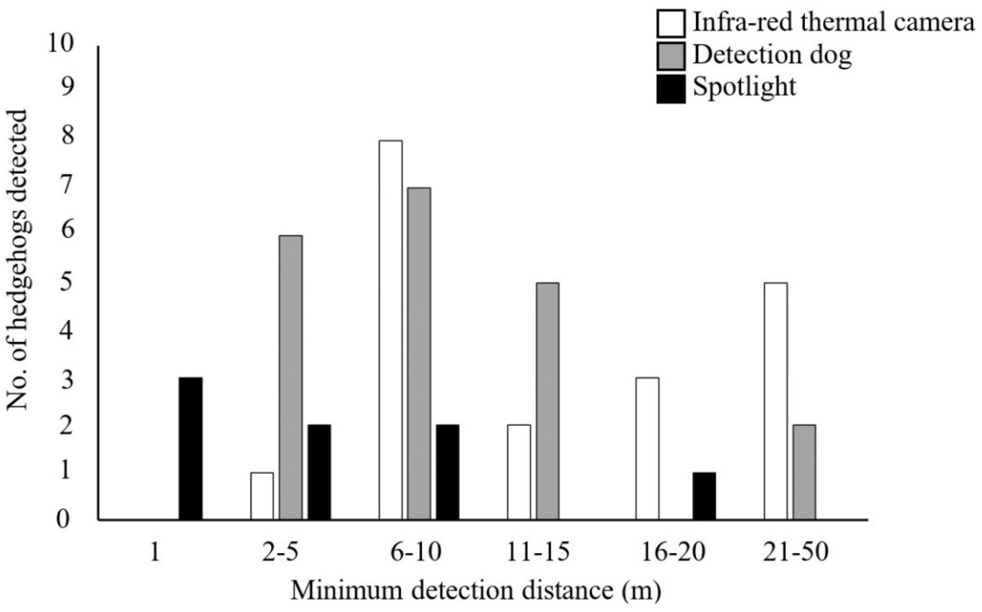
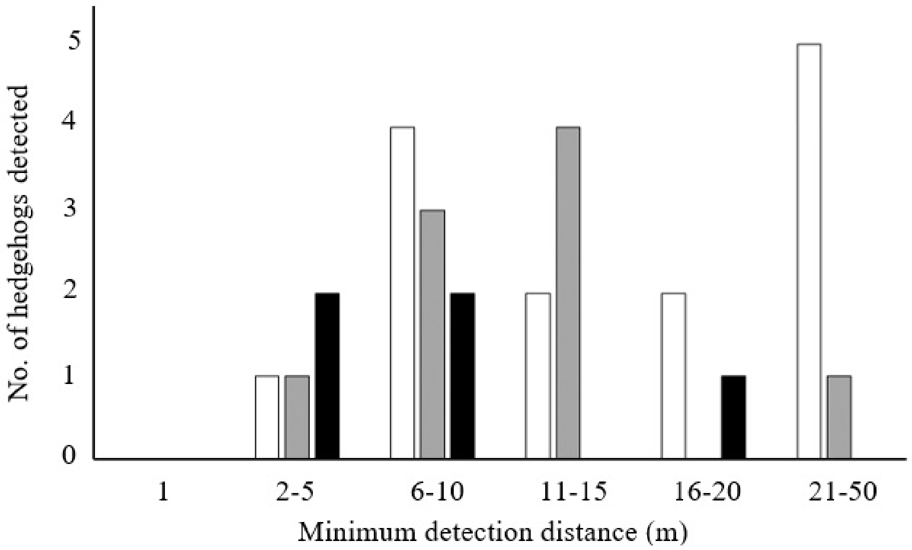


Figure 5.3. Pattern of minimum detection distance (m) in relation to survey method: infra-red thermal camera (n = 19), detection dog (n = 20) and spotlight (n = 8). Data from different habitats and different levels of ground cover combined.

Most detections (n = 28) were associated with low ground cover (bare ground or mown grass): hedgehogs tended to be detected using the spotlight at distances of 5-10 m, dog at 5-15 m and IRT camera at 8-30 m, respectively (Figure 5.4a). In comparison, spotlights were only able to detect hedgehogs in higher vegetation at very short distances (1 m) whereas the detection distances for both the IRT camera and dog were much higher (IRT camera: 6-18 m and dog: 4-25 m; Figure 5.4b). The dog was the only method that detected hedgehogs in vegetation greater than the height of the hedgehog (Categories 3-5; n = 4). Given these patterns, the median detection distance was significantly greater in low ground cover (Mann-Whitney test: U = 120.50, n = 47, P = 0.002; Figure 5.5).

(a) Low ground cover



(b) High ground cover

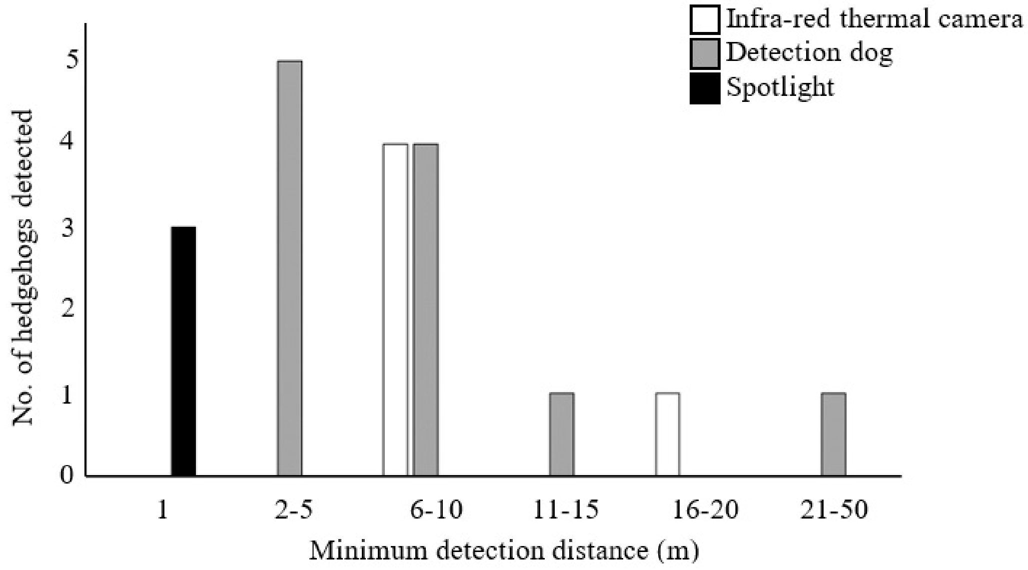


Figure 5.4. Pattern of minimum detection distance (m) in relation to survey method in (a) low (n = 28) and (b) high (n = 19) ground cover. Data from different habitats combined.

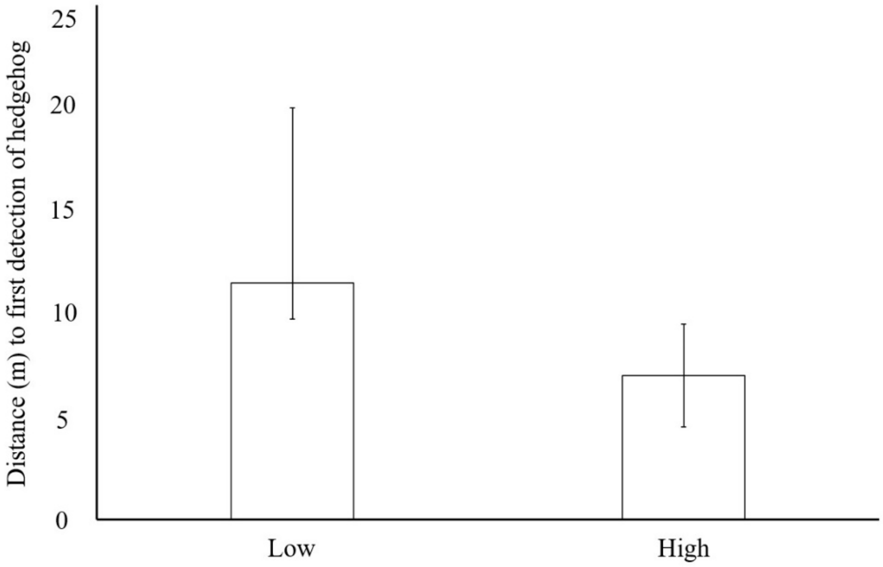


Figure 5.5. Distance to first detection of hedgehogs across all habitats, with all methods combined. Low vegetation is equivalent to bare ground or mown grass; high vegetation was equivalent to vegetation greater than 15cm in height.

Discussion

This pilot study is the first to compare the efficacy of an infra-red thermal camera, a detection dog and spotlighting as methods for locating hedgehogs in three common rural habitats in Great Britain: amenity grassland, pasture and woodland. To standardise survey effort, surveyors walked the same transect route in each habitat, trying to walk at a consistent speed for a maximum of 40 minutes. In addition to affecting survey effort, differences in walking speed in different habitats could affect the amount of noise made by surveyors, thereby affecting the number of animals detected; this is particularly true for hedgehogs which generally tend to freeze or curl into a ball when they feel threatened, although some individuals will actively run away (Reeve 1994, Morris 2018).

However, significant differences were evident for both the distance walked and survey duration within each of the three habitats. Distance walked during surveying was significantly higher in pasture (mean: 2.27 km^{-1}) than in both amenity grassland (1.73 km^{-1}) and woodland (1.67 km^{-1}), whereas survey duration was lower in woodlands (mean: 36.8 minutes) compared to amenity grassland (38.9 minutes) and pasture (40.0 minutes). Consequently, surveyor speed was markedly greater in pasture (3.4 kmh^{-1}) than in the other habitats (amenity grassland: 2.7 kmh^{-1}; woodland: 2.7 kmh^{-1}). At one level, these data indicate the need to record both measures of survey effort in these sorts of studies, but also those where a single technique is used to derive an estimate of the relative abundance of hedgehogs. Standardising survey distance and time may be particularly important in large-scale surveys involving volunteers, where surveyor skill may be a particular issue for cryptic species such as the hedgehog. To date, however, survey effort has not typically been recorded in hedgehog studies in the UK and/or incorporated into the resultant statistical analyses (e.g. Young *et al.* 2006, Poulton and Reeve 2010, Trewby *et al.* 2014, Bowen *et al.* 2019). In this study, distance walked but not survey time was retained in two of the five best-ranked models investigating factors associated with the number of hedgehogs detected (Table 5.2).

Approximately twice as many hedgehogs were located, on average, using the IRT camera and detection dog than spotlighting in both amenity grassland and pasture (Figure 5.1). In addition, the minimum detection distance was greater for the IRT camera (median: 11 m) and, to a lesser degree, the detection dog (10 m) than the spotlight (5 m: Figure 5.2). These distances for the IRT camera and spotlight are markedly lower than those reported by Bowen *et al.* (2019) from their study in Regent's Park London. In that study, the thermal camera detected hedgehogs at a mean distance of 30.0m, but with a maximum distance of 200 m; comparable figures for the torch used were a mean and maximum of 12.0 m and 50 m, respectively.

Drawing specific comparisons between studies is, however, difficult. For example, in addition to differences associated with the make and model of the thermal camera and torch used in different studies, and the number of surveyors applying each method at any given time (e.g. Bowen *et al.* (2019) utilised 3-4 surveyors for torch surveys compared to one person for their IRT camera), it is also necessary to consider differences in hedgehog density, habitat structure and the wider landscape. One major difference between our study and Bowen *et al.*'s (2019) study is the potential impact of the presence of badgers: these are absent from Regent's Park but are present at Hartpury. Many previous studies have documented changes in the density (Young *et al.* 2006, Hubert *et al.* 2011, Trewby *et al.* 2014, Van de Poel *et al.* 2015) and movement behaviour (Hof *et al.* 2012, Pettett *et al.* 2017b) of hedgehogs in the presence versus absence of badgers. Notably, hedgehogs tend to remain in closer proximity to areas of cover where badgers are present, which would tend to have the effect of reducing detection distances because animals would be less likely to be in open habitats a long way from protective vegetation.

None of the three methods detected any hedgehogs in woodland. This could indicate an inability of all three methods to work effectively in very cluttered habitats, or that woods are not a favoured habitat for hedgehogs at this time of the year. Although the data are limited, there is some evidence that supports the latter hypothesis. For example, woodlands were the least selected habitat in a radio-tracking study of hedgehogs in arable landscapes (Pettett *et al.*, 2017b) and were not identified as a factor significantly affecting patterns of hedgehog occupancy in a national survey of England and Wales (Williams *et al.*, 2018a). As outlined above, one possible factor affecting the use of woodlands is the likelihood of encountering badgers, which favour woodlands and plantations as habitats for their setts (Wilson *et al.*, 1997). This aspect of hedgehog ecology requires urgent attention as two previous national estimates of the total number of hedgehogs in Great Britain (Harris *et al.* 1995, Mathews *et al.* 2018) have both relied upon an estimate of 40 hedgehogs/km^2 for broadleaved woodland, with this single habitat harbouring 37% of the national population.

Detection distances were, however, significantly affected by the amount of ground cover. In fact, we had to merge all categories of ground cover other than bare ground or mown grass (60% of all detection events) for analysis because of the small number of detections in categories where even small amounts of grass were present. Not surprisingly, therefore, the median detection distance was significantly higher (11.5 m) at the lowest level of ground cover compared to more vegetated areas (7.0 m). In the presence of vegetative cover, the detection dog out-performed the other two methods, accounting for 11 of 19 (58%) detections, and was the only method where hedgehogs were detected when they were surrounded by vegetation taller than they were.

Performance of the detection dog

As biological organisms, detection dogs are potentially susceptible to a range of limitations not evident with other forms of survey “equipment” including fatigue, distraction and potential risk to the focal animals themselves. In this study, we therefore adapted the surveying protocol to minimise some of these issues. For example, we ensured that the dog had a 20 minute rest period after each habitat had been surveyed and did not work for more than three hours each night. In addition, as the detection of animals by scent can be affected by environmental conditions, leading to inconsistencies in detection ability (Gutzwiller 1990, Cablk *et al.* 2008), we only surveyed when the air temperature was above ~10^{o}C (mean 15.4^{o}C; range 9.3-24.1^{o}C) and conditions were dry (humidity: mean 68%; range 40-100%). As a result, humidity was not significant in the analysis of factors affecting the numbers of hedgehogs detected, but air temperature at the start of surveying was retained in one of the five top-ranking models: in that model, air temperature was negatively related to the number of hedgehogs located but the parameter was not significant (Table 5.2). This partly corroborates the observation of Pettett *et al.* (2017a) that hedgehogs were more likely to be further from cover in colder temperatures.

Whilst in many instances dogs have been used to detect scats (e.g. Smith *et al.*, 2005, Long *et al.*, 2007, Vynne *et al.*, 2011) or carcasses (e.g. Paula *et al.*, 2011, Alasaad *et al.*, 2012, Mathews *et al.*, 2013), the use of a dog to locate and approach live (potentially) prey animals poses additional challenges. These include the potential for the dog to injure the animal, for the animal to injure itself in attempts to escape, and/or for the transmission of disease. In this context, both the selection of a dog with a low prey drive and rigorous training is critical (Karp, 2020). In this study, the dog never approached a hedgehog closer than approximately 0.5 m as trained, and never attempted to pursue any other animal encountered during surveying (e.g. rabbits *Oryctolagus cunniculus*). Upon approach by the dog, all hedgehogs demonstrated a freeze or curl response suggesting the risk of injury to the hedgehogs was low, as attempts to escape were not evident; all animals also demonstrated the same responses when spotlights were used, as has been previously reported (Bowen *et al.*, 2019). However, a flee response was observed on two occasions when using the IRT camera; in both cases, the animals were already only a short distance from cover.

To further ensure the safety of the hedgehogs and the dog itself, the dog remained on a long line as recommended by Mathews *et al.*, (2013). However, previous authors have suggested that allowing a dog to search freely allows for more natural movement and search patterns for the target (de Oliveira *et al.*, 2012, Glen *et al.*, 2018, Thomas *et al.*, 2020) and dogs have been found to be more effective off-lead in controlled trials searching for scats (Cristescu *et al.*, 2015); the use of dogs to find live, nocturnal animals at night has also been recently reported (Karp, 2020).-Therefore, future studies could examine whether the use of an unrestricted dog could further increase hedgehog detection rates; this could be particularly important in habitats, such as woodlands, where the presence of the surveyor may impede the dog's movement. However, it must be noted that on no occasion did the dog in this study fail to detect a hedgehog that was also detected by the second surveyor carrying the IRT camera, such that detection reliability in both amenity grassland and pasture was not negatively impacted by being restrained.

The dog in this study was used to detect free-roaming hedgehogs. However, the ability to detect hedgehogs in their nests could offer both scientific and practical benefits. For example, they could facilitate studies investigating the use of different habitats as sites for summer nests and winter hibernacula (Morris 1973, Reeve and Morris 1985); they may be especially helpful in helping obtain data from smaller individuals that cannot be fitted with radio-tags on welfare grounds, but which may be more vulnerable to variation in food availability (*sensu* Rasmussen *et al.* 2019a). Nesting hedgehogs are also vulnerable to a range of human activities including mowing, bonfires and the clearance of land for development (Reeve 1994, Reeve and Huijser 1999, Rasmussen *et al.* 2019a). In these contexts, detection dogs offer one possible means of locating nesting animals which could then be moved out of harm's way; currently no option exists to do this.

Cost-benefit comparisons

Both the IRT camera and the detection dog enabled surveyors to detect more hedgehogs and at greater distances than spotlighting, and the IRT camera detected more hedgehogs at greater distances than the dog in areas of low ground cover, but this was reversed in areas of high ground cover. As such, thermal cameras and detection dogs both offer distinct advantages over spotlighting in terms of both capturing hedgehogs and for surveying and monitoring populations, but also some disadvantages including price and practicability. For example, the IRT camera and spotlight models (including battery packs) used in this study retailed at a cost of approximately £4600 and £270, respectively. In comparison, the detection dog cost £470 per night (£350 fee, £80 transport and £40 accommodation) to hire. These figures translate to a unit-cost of £242 (dog), £34 (spotlight) and £141 (IRT camera) per hedgehog detected. However, the cost of both the IRT camera and the spotlight are fixed, such that the financial reward of purchasing these devices would increase each time they are used; this is not the case for the detection dog.

However, the added value of the camera and the dog are the additional number of animals that would be detected per unit effort. From a scientific perspective, these extra detection events would lead to more robust data, including increased statistical power (Mayle *et al.*, 1999). Unfortunately, quantifying the magnitude of this added value from the current study is complicated because of how the data were collected: because the focus of the study was to compare the ability of the three methods to detect live hedgehogs, and especially because the IRT camera is dependent on identifying body heat, we had to collect data on live hedgehogs in real time. It was also not possible to use all three methods simultaneously for practical reasons, but also because having three sets of surveyors in the field in the same place at the same time would likely increase levels of disturbance and perhaps raise difficulties in maintaining the independence of observations. Consequently, we used one technique each night, which meant that the distribution of hedgehogs was not consistent across each night of surveying. In addition, the increased detection distance associated with the camera and dog would not increase the value of these methods if they simply detected hedgehogs earlier than the spotlight, but which would have been detected by the latter in due course e.g. they were in front of the surveyor on the general trajectory of the transect; this was the case for most of the detections in this study. Conversely, the increased detection range of the camera and dog would be an advantage if hedgehogs displayed an aversive reaction to the sound of an approaching surveyor; there are currently no data on whether this is a problem or not.

Furthermore, data from radio-tracking studies suggest that, in areas where badgers are present, hedgehogs are typically in close proximity to refuge habitats such as hedgerows. For example, (Hof *et al.*, 2012) recorded mean distances to cover of 8 m at sites with badgers versus 28 m at sites without badgers. Similarly, Pettett *et al.* (2017a) recorded that hedgehogs were, on average, 13 m closer to hedgerows and 7 m closer to buildings, when badgers were present. In the context of, for example, a citizen-science project to estimate hedgehog abundance across a large spatial scale (*sensu* Williams *et al.* 2018b), surveyors would likely be instructed to follow hedgerows and other linear habitats because of the increased likelihood of detecting hedgehogs, but also to avoid damaging crops or disturbing livestock. In these circumstances, spotlight searches may represent a cheap and effective method for surveying hedgehogs, although surveyors would need to be licensed in accordance with the Wildlife and Countryside Act which is unlikely to be granted to novice surveyors. Conversely, a licence is not required for IRT cameras.

However, hedgehogs are also known to forage further from refuge habitats if badgers are absent and if other cover is available. For example, the mean distance to cover increased from 4 m to 42 m in Hof and Bright's (2012) study, and from 12 m when arable crops were less than 50 cm tall, to 38 m when they were >1 m tall. In these circumstances, the IRT camera and dog would be advantageous, e.g. being able to locate hedgehogs much further into a pasture field even where a transect follows the field margin. A detection dog, in particular, would be able to locate hedgehogs in taller vegetation than an IRT camera or spotlight, which would help extend the amount of time surveys could be conducted throughout the year as vegetation grows; although, it is questionable whether farmers would allow surveyors to approach hedgehogs in arable fields if this was likely to damage the crop.

The current availability of just a single commercial “hedgehog dog” is a limitation for the widespread use of this approach in future studies, especially for extensive studies where multiple sites need to be surveyed within a single field-season. However, having demonstrated that dogs can be successfully trained to locate active hedgehogs, further individuals may become available in due course. It is important to acknowledge that performance can vary between dogs and handlers (Cablk and Heaton, 2006, Jamieson *et al.*, 2017, DeMatteo *et al.*, 2019), and even one dog’s performance may change with different handlers (Jamieson *et al.*, 2018). As such, this dog/handler variation would need to be incorporated into the design of future studies.

Conclusion

Spotlights have conventionally been used to locate hedgehogs for tagging and marking and to estimate relative abundance. In this study, however, significantly more hedgehogs were detected using an infra-red thermal camera and a detection dog, and at greater distances, in amenity grassland and pasture. Nevertheless, the benefits of an IRT camera and dog for surveying hedgehog populations are likely to be dependent on the typical pattern of hedgehog foraging behaviour. One factor known to significantly affect the distance hedgehogs range from cover is the presence/absence of badgers: in the presence of badgers, IRT cameras and dogs may offer limited benefits as hedgehogs are likely to stay close to cover, within the typical detection range of a spotlight; in the absence of badgers, IRT cameras and dogs may enable hedgehogs to be detected at much greater distances from transect lines.

No hedgehogs were detected in woodland by any method. This could indicate that all three methods are not suitable for surveying in this habitat or that hedgehogs typically avoid woodlands during the summer and autumn. Future studies, therefore, need to determine whether woodlands are an important habitat for hedgehogs and, if so, identify a suitable method for surveying them. In this context, detection dogs may be suitable as they were the only method in this study to detect hedgehogs in vegetation greater than the height of a hedgehog.

This study has demonstrated that detection dogs can be trained to successfully and safely locate free-ranging hedgehogs, with a performance comparable to, or greater than, current technologies, although they are associated with markedly higher costs. Further consideration should, therefore, be given to improving this technique e.g. by comparing the effectiveness when the dog is not confined to a leash; this may be particularly true for habitats with high ground cover. Additional attention should also be focused on investigating the effectiveness of detecting hedgehogs when they are in summer and/or winter nests, as this may have applied benefits for this declining species.

Acknowledgments

We would like to thank the volunteers who assisted with field work and to Hartpury University and College for access to the site where data collection was undertaken. This study was funded by the People’s Trust for Endangered Species and British Hedgehog Preservation Society, for which we are very grateful. We note that Louise Wilson is a professional detection dog handler.

CHAPTER SIX

General Discussion

With much of the world altered through anthropogenic activity it is of little surprise that biodiversity is declining at an alarming rate. Changes in land use, such as agricultural intensification and increases in urbanisation result in habitat fragmentation and degradation, pollution and climate change, which have led to mass extinctions and ecological changes in all well studied marine, freshwater and terrestrial groups (Parmesan, 2006; Firbank *et al.*, 2008; Barnosky *et al.*, 2011; Bond and Grasby, 2017). Agriculture is considered to have the greatest negative impact on biodiversity of all human activities (Balmford *et al.*, 2012; Kleijn *et al.,* 2012), and this is only likely to increase as the human population expands increasing the requirement for food (Tilman *et al.*, 2011). Moreover, urbanisation is leading to a substantial decline in natural and semi-natural habitat availability (UK National Ecosystem Assessment, 2014; Hayhow *et al.,* 2019). It seems apparent that supporting an increasing human population and maintaining space for biodiversity are somewhat mutually incompatible. However, there is increasing understanding amongst the scientific community (Chan *et al.*, 2016) and beyond, of the impact of such changes, and the need to safeguard the natural world has been recognised, in order to protect ecosystem services fundamental to biodiversity at all levels (Brown *et al.*, 2007; Daily *et al.*, 2009; Schindler and Lee, 2010; Hautier *et al.*, 2015).

Biodiversity in the UK is catalogued to a greater degree than possibly anywhere else in the world, with significant amounts of the data regarding species' distribution and abundance collected by voluntary citizen scientists (Pearce-Higgins *et al.*, 2018), demonstrating a keen interest by members of the public in biodiversity. However, the extent to which anthropogenic activity may negatively impact the natural world is also widely evident, as discussed in Chapter One and the extent to which Great Britain has changed in the last twenty years in discussed in Chapter Three. It is therefore not surprising that many species are declining across the country. It has therefore become more important than ever to understand the impact of interaction between humans and wildlife on the welfare, survival and existence of all concerned.

The aim of this thesis was to explore a range of ways in which hedgehogs are affected by anthropogenic activity, be it through the survival of hedgehogs in a landscape significantly altered by humans (Chapter Two); through activity where hedgehogs are brought into the direct care of humans as a result of anthropogenic factors (Chapters Three and Four); or how different methods can be used to understand changes in the range and abundance of the hedgehog in the rural landscape (Chapter Five).

Whilst it is widely reported that the hedgehog population is in decline (Chapter One), particularly in the rural landscape, much of the data that the recent review of British mammal populations used (Mathews *et al.* 2018) was obtained twenty five years ago (e.g. Harris *et al.*, 1995), and is likely to be out of date, particularly in light of such substantive changes to the British landscape as those outlined previously. It is therefore pertinent that new methods which facilitate greater accuracy in animal detection are explored to expand the tool kit available to conservation biologists to answer the most basic of biological questions; (i) where does a species occur; and (ii) where could that species occur (Peterson and Dunham, 2003). Addressing the first question reliably requires appropriate methods for accurate detection in the field, and the focal species considered within this thesis presents key challenges around that. Its small size, nocturnal behaviour and elusive nature could result in large numbers of animals going undetected, particularly in a landscape abundant with badgers, where hedgehogs remain closer to vegetation allowing easy access to refugia (Hof *et al.*, 2012).

Whilst prior methods have allowed for the detection of hedgehogs in open ground using technology (Bowen *et al.*, 2019), field signs such as footprints (e.g. Yarnell *et al.*, 2014; Williams *et al.*, 2018a) or their presence after death on road kill surveys (Huijser and Bergers, 2000), finding them in dense vegetation or in the nest has to date not been possible. The use of a conservation detection dog has been shown here to be practical, safe and effective. As discussed in Chapter Five, further research is required in the development of this method, particularly in relation to the impact of hibernation nest location and the scent picture released by the hedgehog. As discussed in Chapter Two, hibernation nests can be difficult to access, such as in areas of dense bramble or under buildings, and so ensuring the dog can get sufficiently close to nests to reliably indicate will be a potential barrier. However, given much land clearance occurs overwinter to avoid breeding birds in hedgerows, for example, this method warrants further consideration if it could prevent harm to hibernating hedgehogs.

Chapter Five sought to evaluate the use of conservation detection dogs for locating active hedgehogs, with a view to developing a method for detection in the nest. The use of dogs to find ejecta and carcasses has been widely practiced (Chapter Five), but their use to find cryptic mammals whilst active has only been very recently described (Karp, 2020). This chapter demonstrated their value in locating hedgehogs, particularly when used in combination with a thermal camera. The recent corroboration of the use of IRT cameras (Bowen *et al.*, 2019) enhanced this by determining that IRT cameras were reliable to validate the detection dog's effectiveness, rather than simply provide a comparison between three methods.

The use of the thermal camera in Chapter Five added further weight to the value of this tool in hedgehog surveying, whilst exploring some of its key limitations. Whilst these cameras are valuable for detecting hedgehogs in open habitats, they are less useful in more dense, cluttered areas. There were notable differences in the detection distance between this study and that of Bowen *et al.* (2019) in Regent's Park, London, but this can be explained by differences in the landscape features at the two sites. The complexity of the site chosen for this study was greater than much of Regent's Park, with fewer large open areas, more mature hedgerow and more undulating terrain. Therefore, whilst the weight of the evidence favours thermal cameras for the detection of hedgehogs in the open landscape, they are not well suited to more complex or closed areas, where hedgehogs may be inclined to reside, particularly in the presence of badgers. Consideration of the quality of the equipment used is also essential, as illustrated by the lack of detection success described by Haigh *et al.* (2012a).

Chapter Two identified that, contrary to prior research (Kristiansson, 1990), hibernation appears a comparatively safe time for hedgehogs where they have achieved a body weight ≥600 g. There is clearly still work to do to understanding the survival of hedgehogs below this weight, particularly in the rural landscape after Rasmussen *et al.* (2019a) considered urban juveniles (although in Denmark rather than Great Britain). Clear guidance regarding the weight at which hedgehogs are unlikely to survive hibernation in the wild can be provided to rehabilitators and the public, and to determine landscape features particularly important to this survival, as that of Morris (1984) is widely disputed as too low by many wildlife rehabilitators (*pers. obs.*) and suggested as too high by recent overwinter research (Haigh *et al.*, 2012b; Rasmussen *et al.*, 2019a). Further, with the correlation between number of nests and loss in body mass over winter the impact of disturbance on hedgehogs, both in the rural and the urban landscape, is of concern (Chapter Two).

Increasing public understanding of the issues associated with hedgehogs, and all wildlife more generally, in the anthropogenic landscape could be key to the protection of wildlife, such as how the public can provide the best care when animals are sick or injured, how injuries and fatalities can be avoided, and how to provide sufficient resources within the garden to support a local population. Chapter Four identified the substantial number of hedgehogs that are admitted to wildlife hospitals for a wide range of natural and anthropogenic causes, but most frequently as a result of being underweight juveniles, orphans, or otherwise in a state of poor physical condition. For wildlife rehabilitation to have any value for conservation, release rates must be sizeable, and those animals returned to the wild must have survival and breeding rates similar to their wild counterparts. Data presented here indicate high numbers of animals are admitted (Chapter Four; in the order of 8-11% of the British population per annum) and release of those animals back into the wild is commonplace (Chapter Three; 51%). Success comparable to wild counterparts has recently been demonstrated; the survival of rehabilitated animals is comparable to their wild counterparts, even when released during winter (Yarnell *et al.,* 2019). These studies together, therefore, add weight to the argument that wildlife rehabilitation can, in fact, have benefit for wildlife conservation.

There is debate, however, regarding whether it is morally right to interfere with events in nature (e.g. Kirkwood and Sainsbury, 1996). The high number of admissions to wildlife hospitals as a result of anthropogenic causes (Chapter Four; up to 47%) presents an opportunity to mitigate against some of the harm caused by anthropogenic activities. Whilst those associated with direct action by humans, such as road traffic collisions or attack by humans, are clearly as a result of such human activity, the picture is more complex when the degree to which the landscape has been changed by anthropogenic activity is considered. As discussed in Chapter One, habitat fragmentation, degradation and loss are key causes of the loss of biodiversity and may lead to insufficient food availability, reduced foraging opportunities and isolation of small localised populations, all of which may lead to substantive issues in the population as a whole.

Seasonal fluctuations in survival were evident both in the wild and in the admissions to RSPCA hospitals, with an increase in mortality in the autumn and spring identified in Chapter Two. In the wild, the periods before and after hibernation were found to be when death is most likely to occur (as previously described by Yarnell *et al.,* 2019), with deaths on roads and predation by badgers most frequently recorded. In spring, when hedgehogs are at decreased body mass following hibernation, they may be more inclined to take risks during foraging, putting them at greater chance of predation, or they may struggle to regain weight in a landscape limited in foraging opportunities. The relationship between badgers and hedgehogs is clearly a complex one (e.g. Doncaster, 1992; Trewby *et al.*, 2008; Dowding *et al.,* 2010a; Pettett *et al.*, 2017a; Williams *et al.*, 2018a), and undoubtedly depends on factors wider than simply whether they occupy the same space. The attraction of hedgehogs to areas of human habitation (as seen as Brackenhurst in Chapter Two and discussed in depth by others (e.g. Hubert *et al.*, 2011; Hof *et al*., 2019)) has been proposed as an attempt to seek refuge from such predation pressure. This may be later compromised by the increasing badger population in urban areas (Harris *et al*., 2010) but presents important questions regarding the quality of the rural habitat, and management strategies that may facilitate the co-existence of the two species.

In Chapter Three the role of the RSPCA in rehabilitating substantial numbers of hedgehogs was discussed, leading to the release of more than 50% of those admitted, which is equal to or greater than survival rates for a range of species reported elsewhere (e.g. Reeve and Huijser, 1999; Tribe and Brown, 2000; Molony *et al.*, 2007; Molina-López *et al.,* 2017; Baker *et al.,* 2018). Factors leading to increased risk of admission were identified, particularly noting a higher number of males than females, more juveniles than adults, and seasonal peaks, particularly for adult females in summer and juveniles of both sexes in autumn. Such increases in admissions at these key periods may indicate the environment is insufficient for meeting the needs of these animals, particularly for females during lactation and juveniles gaining sufficient weight prior to hibernation.

Cause of admission could be attributed to anthropogenic factors in up to 47% of cases, although greater clarification is needed in the record keeping and admission process in order to support further analysis. Gaps in records and little detail in the cause of admission removed the possibility of analysis in a large number of cases. Wider issues related to record keeping were discussed in Chapter Four, whereby a paucity of data was evident in the responses of many rehabilitators. This is an area whereby considerable future work is required with the rehabilitation community to ensure such data are reliable, accurate and complete for similar future studies. There is a wealth of information regarding the status of animals in the wild, early warnings regarding biochemicals and disease and indications of the causes of mortality evident within these data, should they be complete and accessible to researchers.

Comparisons drawn between the RSPCA data and the findings of Reeve and Huijser (1999) illustrated differences in the cause of admission, with significantly more hedgehogs admitted to RSPCA hospitals as a result of natural causes, as a result of anthropogenic causes, and as orphans particularly. Possible reasons for this have been discussed previously (Chapter Three). The increase in the number of animals following poor condition may be reduced through public education campaigns, such as Hedgehog Street and those run by many smaller scale hedgehog rehabilitators, although the degree to which feeding by members of the public can artificially support the wild population is open to debate.

Implications for hedgehog conservation

The hedgehog has been shown to be in decline across its extensive range, however due to challenges associated with recording this illusive mammal the extent and causes of this decline are not fully understood. Only through the development of new methods of detection can this be addressed. This thesis has added weight to the use of IRT cameras in the detection of hedgehogs, and tested for the first time under controlled conditions the use of conservation detection dogs for finding active hedgehogs. The validation of this method here provides essential groundwork the development of a new protocol, including the training of the first professional “hedgehog dog” which is now available for commercial use, and others which are currently in training now the method has been demonstrated as viable.

The role of woodlands has been further highlighted as important to hedgehogs during winter, although their lack of detection during the summer months in the same woodland sheds further light on the potential impact that badgers have on the annual cycle of hedgehogs. This helps to support the previously published body of work (Young *et al.*, 2006; Hof *et al.*, 2012; Parrott *et al.*, 2014; Trewby *et al.*, 2014; Williams *et al.*, 2018a; Hof *et al.*, 2019) that shows that following such high levels of anthropogenic alteration the rural landscape is unable to accommodate these two intra-guild species; the dominant known cause of death for animals in Chapter Two was predation by badgers. Whilst the control of one native species to protect another has been evidenced as effective (Trewby *et al.*, 2014), this is unlikely to be popular with the British public and does not take into account the co-existence of these two species for millennia; the innate fear of badger odour shown in naïve hedgehogs is testament to this (Ward *et al.*, 1997). It is more likely that the scale at which the rural landscape has been modified for anthropogenic benefit leads this intra-guild predatory relationship to be one that is so heavily skewed. Once the interaction between these two species is understood in more detail, further mitigation measures can be implemented to facilitate the survival of both species, such as through measures associated with agri-environment schemes particularly hedgehog management and protection (MacDonald *et al.*, 2007; Hof and Bright, 2010b; Moorhouse *et al.*, 2014).

Further, the increasing badger population in the rural landscape is leading to a move of hedgehogs from the rural to the urban landscape (Hubert *et al.*, 2011; Van de Poel *et al.*, 2015), and Chapter Two demonstrated this with the importance of roads and buildings to hibernating hedgehogs in two sites where badgers are known to reside. With increased food abundance in sub-urban and urban areas through residents providing supplementary provisions (deliberately or otherwise) hedgehog populations are able to survive, and potentially even thrive (Hubert *et al.*, 2011). Whilst this may provide a much-needed refuge, it is not without its concerns, including the move of badgers into the urban landscape, and the potential for increased contact with humans, which has been shown here (Chapters Three and Four) to lead to extensive numbers of injuries (and deaths) through trauma caused in gardens and on roads, or lead orphans and underweight juveniles to be taken into care.

The degree to which hedgehog rehabilitation occurs has previously been substantially under-reported (Chapter Three and Four) so this study provides an important insight into this practice. Whilst it is without doubt advantageous that there are experienced, knowledgeable individuals across the country readily willing to provide the care required by those animals, as evidenced by the huge numbers of animals released back into the wild, it does cause unease regarding the lack of regulation of wildlife rehabilitation in the UK. The majority of care has been shown to be undertaken within private residential facilities, by individuals working in isolation (Chapter Four) and it is this that may present cause for concern, in significant contrast to the large-scale wildlife hospitals, usually dealing with a wide range of species of British wildlife. Major challenges with gaining access to records have been identified here, and this alone creates alarm as this lack of record keeping would contravene both veterinary and conservation-based legislation. A key recommendation as a result of this thesis would be that organisation with relevant oversight or influence within the wildlife rehabilitation sector (be it the RSPCA, British Wildlife Rehabilitation Council (BWRC), BHPS or others) investigate strategies for supporting these rehabilitation facilities in developing best practice and supporting record keeping. Lack of knowledge regarding who is qualified to undertake this care, and the impact this may have on humans and the wider hedgehog population also require further consideration to prevent harm, potentially through registration or regulation of practitioners.

Recommendations for further work

Here, I summarise and add to recommendations for future work that I believe would be beneficial and which build on the work in this thesis.

1. Gain greater understanding of fluctuations in mortality of hedgehogs, particularly in relation to seasonal variations and differences between life stages. Whilst I have established here that there is considerable variation in mortality rates between seasons, with a peak evident in spring post-hibernation this does warrant further consideration with a year-round radio-tracking study on a larger scale, particularly of rural hedgehogs. Survival amongst animals during their first year has been shown to be high in the sub-urban landscape (Rasmussen *et al.*, 2019a) but further consideration of this in the rural landscape is needed, where hedgehogs may be under greater pressure from badgers (Hof and Bright, 2012; Trewby *et al.*, 2014), reduced food availability and quality (Hof and Bright, 2010a), agricultural biocides (Dowding *et al.*, 2010b; Sánchez-Barbudo *et al.*, 2012) and habitat degradation (Hof, 2009).
2. Greater understanding of the experience of hedgehogs during hibernation is required, particularly the impact of disturbance on physiological function, and how this differs to natural fluctuations in torpor. The correlation found between the number of nests used and absolute loss in body mass (Chapter Two) is one of particular concern in a human-dominated landscape, when disturbance during this critical period may be frequent and substantial. In this study it was not possible to determine to what extent animals roused without leaving the nest during hibernation, but as the cost of arousal is significant the impact of such disturbance may be substantial, even when the animal is not moving between nests. The wider availability of small, lightweight data loggers and accelerometers than when these data were collected provides opportunity for greater exploration of the animal's behaviour within the nest.
3. Develop greater understanding of the experience of hedgehogs in rehabilitation to determine the extent to which they are affected by the close proximity to conspecifics and humans. As has been determined here (Chapters Three and Four) hedgehogs are being rehabilitated in significant numbers, and the extent of the interaction they have

with humans will affect the degree to which they become habituated and the level of stress they may experience.

4. The use of detection dogs for finding hedgehogs warrants further consideration, specifically for finding them in the nest as this is where they are particularly vulnerable. There are also questions regarding whether dogs need to be specifically trained to detect the odour during hibernation, as research finding animals in hibernation is limited, and the change in biochemistry may result in a change in the scent picture. Hedgehog nests may also be harder to access (as per Chapter Two whereby 35% of nests could not be accessed for examination), which may prevent the dog locating the hedgehog, or physically gaining access to the immediate location of the nest.
5. Develop greater understanding of the survival rate of hedgehogs upon release following rehabilitation to add to current understanding. Whilst it has been recently determined the survival of hedgehogs released during winter is comparable to wild counterparts (Yarnell *et al.*, 2019), particular consideration is needed regarding the minimum weight at which hedgehogs can reasonably be expected to survive hibernation following release, to further lighten the load on rehabilitators, and how survival differs for animals considerably smaller than the 600 g requirement in the study presented here (Chapter Two). Whilst Morris (1984) has long since advocated the admission to rehabilitation of animals under 450-550 g to human care, these figures are based upon an estimation of mass lost over winter, rather than true values of mass loss. As shown in Chapter Two, hedgehog mass loss can vary significantly, with the potential for either no loss over winter due to frequent feeding bouts, or rapid mass gain upon emergence from hibernation clouding the picture further. As radio tracking tags decrease in size, tracking ever smaller individuals will be possible within ethical boundaries, facilitating a greater degree of accuracy to this figure. The use of detection dogs for studying these smaller animals has also been proposed (Chapter Five).
6. Wildlife rehabilitators have a wealth of data that is largely untapped. Whilst issues around accessing records, and the reliability of those data have been discussed here (Chapters Three and Four), myriad questions could be explored through such records, for example, study of maternal behaviour and data on litter size and sex ratio could be

recorded in rehabilitation centres without the need for a licence or to disturb wild hedgehogs, to gain greater understanding regarding mortality prior to dispersal.

7. Whilst current advice is to return animals to their site of origin it seems apparent that this is often not the case. The extent to which this impacts upon gene flow is unknown, as is the impact on potential transmission of disease and parasites (Chipman *et al.*, 2008; Saldanha *et al.*, 2019). With such large numbers of hedgehogs admitted to care the impact release practice may have on the wild population could be significant. For example, the wild population could be artificially supported with healthy animals, or negatively impacted if these artificially supported animals are genetically inferior to the rest of the population, particularly if animals are always released in particular sites, such as the neighbourhood of the hospital.
8. With so many unofficial/informal rehabilitators operating, the likelihood of comprehensive health assessments for all animals by a veterinary surgeon prior to release is unlikely, and so therefore consideration of the potential impact of such practice on the wild population is paramount.
9. The substantial number of rehabilitators working with hedgehogs may be of concern, depending upon the extent to which they are connected to paraprofessionals and an experienced veterinary team. Whilst wildlife rehabilitation is long considered to be based on trial and error, the scale of hedgehog care discussed here, often in short term facilities in residential accommodation, could present significant welfare issues, for both the animals and humans concerned. For example, Sangster *et al.* (2016) identified the public health risk associated with close encounters with hedgehogs due to the detection of zoonotic subtypes of *Cryptosporidium parvum* in the wild population presenting risk to physical health for rehabilitators. Further, the potential impact of isolation of individuals caring for such animals could increase the risk of compassion fatigue, burn out and grief (Neumann, 2010; Englefield *et al.*, 2018). Further to this, greater understanding of the variation in practices undertaken within rehabilitation centres is needed, such as considering where and how animals are returned to the wild (e.g. soft versus hard release, selection criteria around choosing appropriate locations). Such understanding of rehabilitation would support the argument for or against licencing of wildlife rehabilitators in the UK.

10. Greater understanding regarding return rates of animals to rehabilitation centres through wide-scale marking of released animals with PIT tags would provide valuable insight into the rate at which hedgehogs are readmitted into care, how they disperse and their long-term survival post-release. Currently such large-scale studies are not available for either hedgehogs or other species. This would provide important insight into whether individuals are repeatedly admitted but not identified as marking is not used (as discussed in Chapter Three) or when admitted by different hospitals in the same locality. In the absence of a national database recording such identification aids for any species of wildlife it is largely unknown on what scale animals return to care.
11. Further consideration of reliable methods for detecting hedgehogs in woodlands is required, as no hedgehogs were detected using three different methods here (Chapter Five). In this study the dog was handled on lead, which has been shown to affect the effectiveness of searching, and so further consideration of the method, with searches conducted off lead would be recommended. The woodland utilised in this study had a dense understory, and so may have presented particular challenges for the methods tested, so surveying alternative woodlands would be beneficial. Radio tracking of hedgehogs has shown woodlands to be of significant value to the hibernating hedgehog (Chapter Two) and thus reliable survey methods are required for this habitat.
12. More detailed consideration of the interaction between badgers and hedgehogs in woodland is paramount to determine the extent to which hedgehogs may fall foul of competitive exclusion, and understanding of the value of this habitat in the annual cycle of hedgehogs is needed.

Conclusions

In this thesis I have explored a range of factors affecting the survival of the hedgehog in the anthropogenic landscape, with particular consideration for: survival at a time of year previously considered to be high risk; how the rehabilitation process affects them; and how surveying methods can be advanced through the use of non-invasive methods to better understand the population. The substantial numbers of hedgehogs admitted to wildlife hospitals has been shown to potentially have a significant impact on the population, even though rehabilitation has previously been considered to be a practice for animal welfare rather than conservation. However, it is clear from the studies presented here that further research needs to be undertaken within the rehabilitation environment. There are substantial challenges associated with this though, as the lack of regulation does little to facilitate even knowing where this practice is undertaken, let alone the number of animals treated. The unregulated nature of the rehabilitation sector in the UK could present significant risks if training, veterinary support and investment are not taken sufficiently seriously. Issues related to data reliability have been discussed here, and sample sizes in two chapters were reduced considerably as a result of inaccessible or incomplete records, potentially skewing analysis. However, this study has brought such issues to light and thus lead to strategies to mitigate such problems to support future research.

Gaining data regarding this small, elusive mammal, be it in the wild or in captivity, certainly has its challenges, and in order to fully understand how this species is affected by changes seen across the human-dominated landscape ongoing work is required: for example, in relation to detection methods in the wild, and the way in which hedgehogs are treated in captivity, the impact of release practices and how behaviour, once returned to the wild, is affected by anthropogenic activity. If the decline of hedgehogs across their range is to be reversed greater understanding and accommodation of their needs is critical. Without doubt, however, the potentially positive impact of the practices discussed here provide some hope for the future; be it in the hundreds of individuals working to rehabilitate and release thousands of sick and injured animals each year, to the conservation detection dog teams providing greater insight into many species of threatened wildlife.

Appendix 1

Supplementary Table 1. Summary of the dominant materials used in winter nest construction at Brackenhurst and Hartpury. Data for 2015-2016 and 2016-2017 combined. Figures in parentheses are the number of nests where the material was recorded as a secondary material. Sample sizes are less than the total number of nests used by study animals as not all nests were accessible.

Material	Brackenhurst	Hartpury	Total
Broad leaves	32 (49)	42 (42)	74 (91)
Conifer	0 (5)	0 (0)	0 (5)
Grass	12 (20)	5 (9)	17 (29)
Herbaceous plants	1 (18)	0 (1)	1 (19)
Ivy	7 (14)	0 (0)	7 (14)
Litter / plastic	0 (0)	0 (20)	0 (20)
Moss	1 (4)	0 (1)	1 (5)
Ornamental bush	2 (7)	0 (1)	2 (8)
Ornamental grass	2 (2)	3 (2)	5 (4)
Shredded garden waste	2 (2)	0 (0)	2 (2)
Soil	1 (1)	0 (0)	1 (1)
Stones	1 (1)	0 (0)	1 (1)
Straw	1 (3)	0 (2)	1 (5)
Twigs	0 (3)	0 (5)	0 (8)
Unknown	9 (1)	32 (0)	41 (1)
Total	71	82	153

Supplementary Table 2. Cause of death (n = 9) from a sample of 31 individuals followed over two winter hibernation periods (2015-2016 or 2016-2017).

Cause	Brackenhurst	Hartpury	Total
Badger predation	0	3	3 (38%)
Road traffic	0	2	2 (22%)
Natural causes	0	1	1 (11%)
Euthanased[1]	0	1	1 (11%)
Unknown	1	1	2 (22%)
Total	1	8	9

[1] Animal was euthanased by a veterinary surgeon because of a large facial tumour

Supplementary Table 3. General linear models comparing site and sex differences in (**a**) body mass (g) at the start of the hibernation season, and (**b**) absolute and (**c**) percentage mass change during the hibernation period (n = 21).

(a) Body mass at the start of the hibernation period

Variable	Degrees of freedom	Adjusted sum of squares	Adjusted mean sum of squares	F statistic	P
SITE	1	60668	60668.0	3.75	0.069
SEX	1	12647	12646.5	0.78	0.389
SITE*SEX	1	85	84.9	0.01	0.943
Error	17	274767	1612.7		
Total	20	351287			

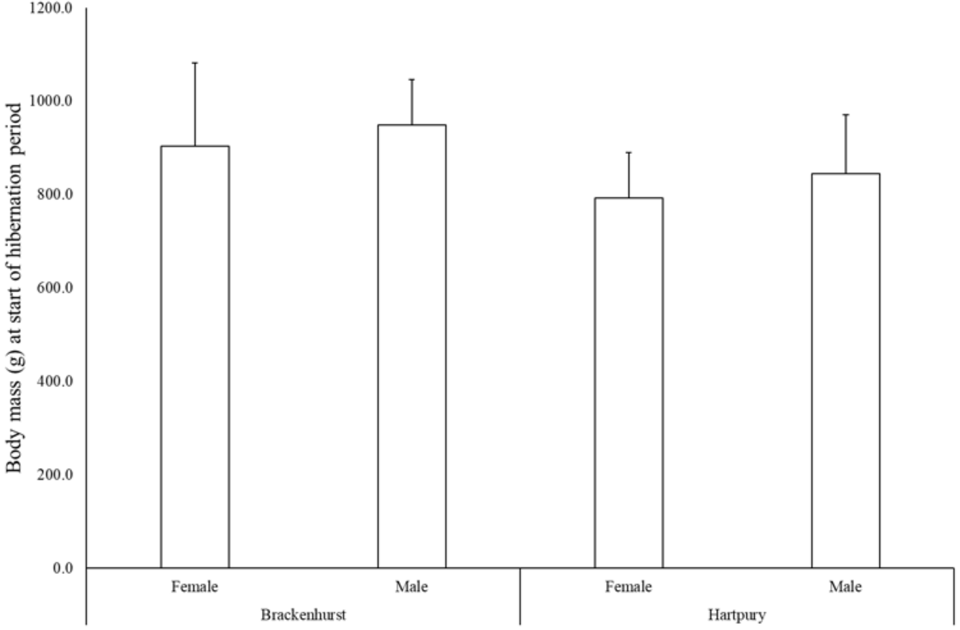
(b) Absolute mass change during hibernation

Variable	Degrees of freedom	Adjusted sum of squares	Adjusted mean sum of squares	F statistic	P
SITE	1	170	169.5	0.01	0.919
SEX	1	83754	83754.2	5.21	0.036
SITE*SEX	1	74755	74755.3	4.65	0.046
Error	17	273349	16079.4		
Total	20	425417			

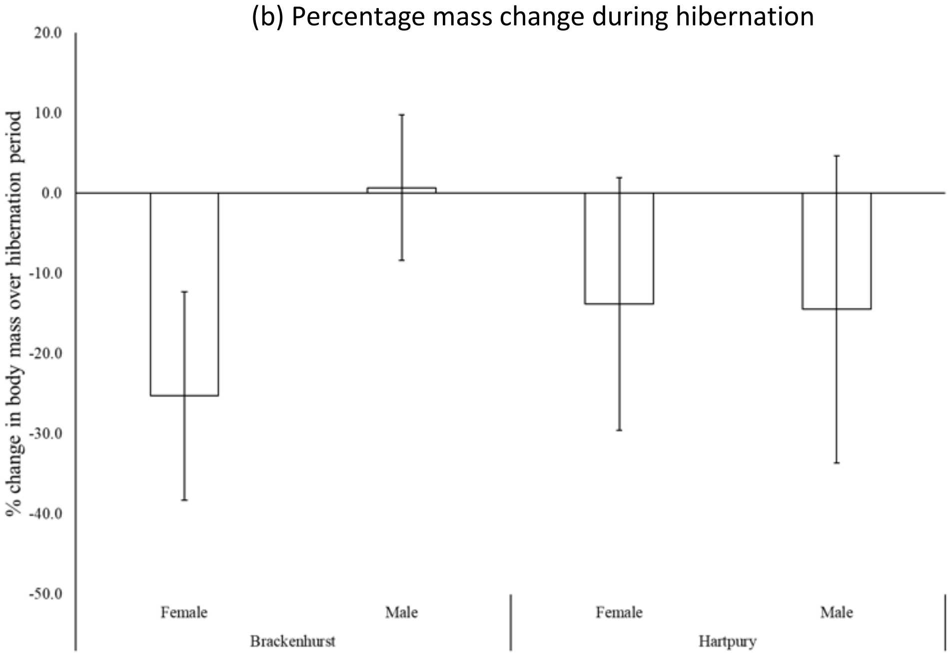
(c) Percentage mass change during hibernation

Variable	Degrees of freedom	Adjusted sum of squares	Adjusted mean sum of squares	F statistic	P
SITE	1	18.26	18.26	0.08	0.776
SEX	1	835.16	835.16	3.81	0.067
SITE*SEX	1	923.28	923.28	4.22	0.056
Error	17	3721.86	218.93		
Total	20	5424.88			

(a) Body mass at the start of hibernation

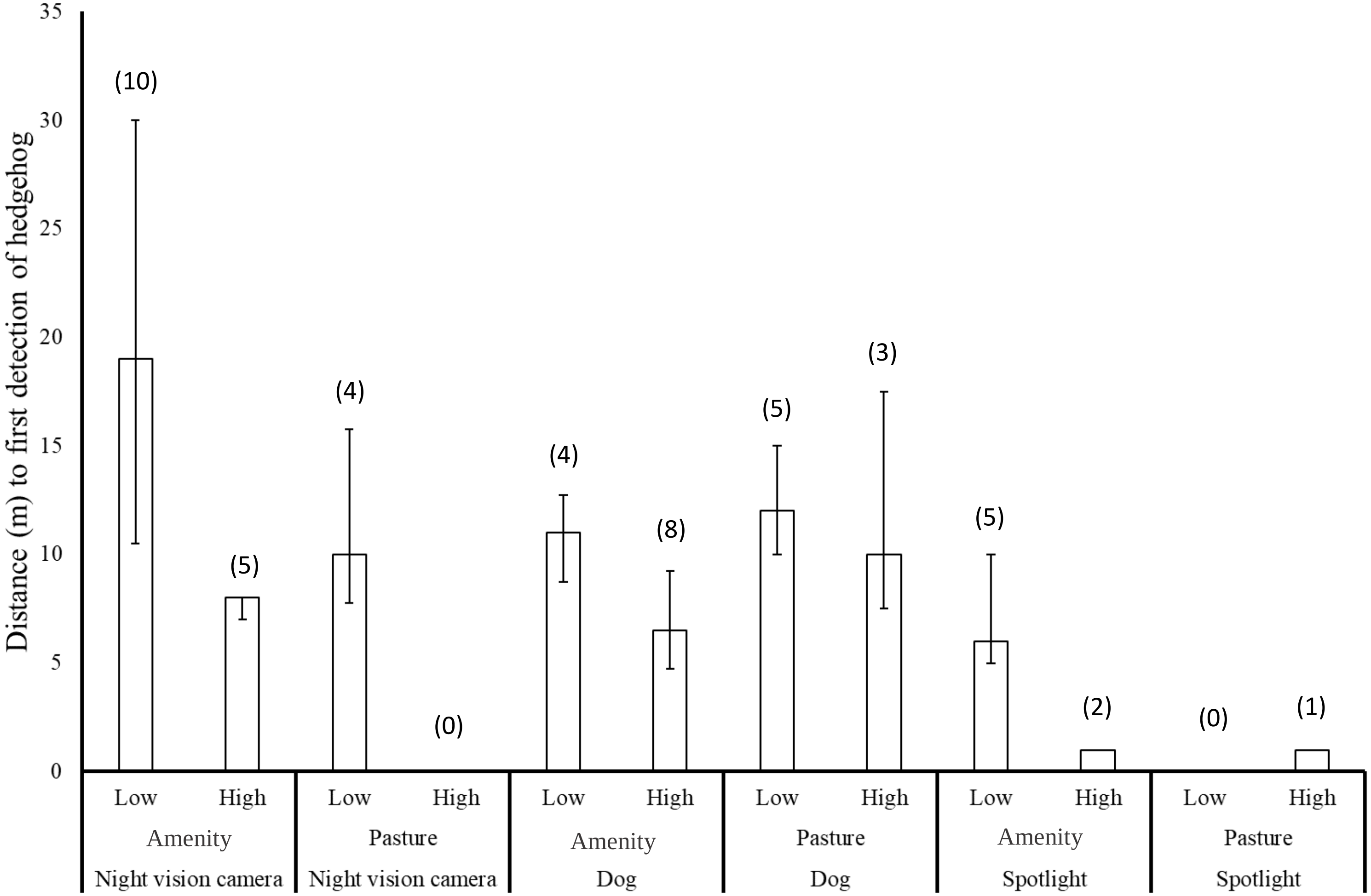


(b) Percentage mass change during hibernation



Supplementary Figure 1. Mean (±SD) (a) body mass (g) at the start of the hibernation season, and (b) percentage mass change during the hibernation period in relation to site and sex (Brackenhurst: n = 5♀:5♂; Hartpury: n = 6♀:5♂)

Appendix 2



Supplementary Figure 2. Median (±IQR) of initial detection distance to hedgehog in relation to method (infra-red thermal camera, detection dog, spotlight), habitat (amenity grassland, woodland) and ground cover (low: bare ground or mown grass; high: less than the height of the hedgehog or higher). Figures above columns are the number of hedgehogs detected

REFERENCES

Abu Baker, M.A., Reeve, N.J., Conkey, A.A.T., Macdonald, D.W., Yamaguchi, N., 2017. Hedgehogs on the move: Testing the effects of land use change on home range size and movement patterns of free-ranging Ethiopian hedgehogs. PLoS One 12, 1–18. https://doi.org/10.1371/journal.pone.0180826

Aebischer, N.J., 2019. Fifty-year trends in UK hunting bags of birds and mammals, and calibrated estimation of national bag size, using GWCT's National Gamebag Census. Eur. J. Wildl. Res. 65, 64. https://doi.org/10.1007/s10344-019-1299-x

Aebischer, N.J., Davey, P.D., Kingdon, N.G., 2011. National Gamebag Census: Mammal Trends to 2009. Game & Wildlife Conservation Trust, Fordingbridge, Hampshire.

Alasaad, S., Permunian, R., Gakuya, F., Mutinda, M., Soriguer, R.C., Rossi, L., 2012. Sarcoptic-mange detector dogs used to identify infected animals during outbreaks in wildlife. BMC Vet. Res. 8. https://doi.org/10.1186/1746-6148-8-110

Alibhai, S., Jewell, Z., Evans, J., 2017. The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. PLoS One 12, e0172065. https://doi.org/10.1371/journal.pone.0172065

Amar, A., Smith, K.W., Butler, S., Lindsell, J.A., Hewson, C.M., Fuller, R.J., Charman, E.C., 2010. Recent patterns of change in vegetation structure and tree composition of British broadleaved woodland: Evidence from large-scale surveys. Forestry 83, 345–356. https://doi.org/10.1093/forestry/cpq017

Amélineau, F., Grémillet, D., Harding, A.M.A., Walkusz, W., Choquet, R., Fort, J., 2019. Arctic climate change and pollution impact little auk foraging and fitness across a decade. Sci. Rep. 9, 1–15. https://doi.org/10.1038/s41598-018-38042-z

Amori, G., 2016a. Erinaceus europaeus: The IUCN Red List of Threatened Species 2016: e.T29650A2791303. [WWW Document]. URL https://www.iucnredlist.org/species/29650/2791303 (accessed 5.3.20).

Amori, G., 2016b. Erinaceus concolor (Southern White-breasted Hedgehog) [WWW Document]. IUCN Red List Threat. Species 2016. URL https://www.iucnredlist.org/species/40605/115174497 (accessed 7.15.20).

Ancillotto, L., Serangeli, M.T., Russo, D., 2013. Curiosity killed the bat: Domestic cats as bat predators. Mamm. Biol. 78, 369–373. https://doi.org/10.1016/j.mambio.2013.01.003

Andren, H., 1999. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. NCASI Tech. Bull. 71, 12–13. https://doi.org/10.2307/3545823

Arandjelovic, M., Bergl, R.A., Ikfuingei, R., Jameson, C., Parker, M., Vigilant, L., 2015. Detection dog efficacy for collecting faecal samples from the critically endangered Cross River gorilla (Gorilla gorilla diehli) for genetic censusing. R. Soc. Open Sci. 2, 140423. https://doi.org/10.1098/rsos.140423

Arnold, H.R., 1993. Atlas of Mammals of Britain. HMSO, London, UK.

Baker, A.C., Glynn, P.W., Riegl, B., 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar. Coast. Shelf Sci. 80, 435–471. https://doi.org/10.1016/j.ecss.2008.09.003

Baker, L.R., 2002. Guidelines for Nonhuman Primate Re-introductions, Reintroduction News 21.

Baker, P.J., Boitani, L., Harris, S., Saunders, G., White, P.C.L., 2008. Terrestrial carnivores and human food production: Impact and management. Mamm. Rev. 38, 123–166. https://doi.org/10.1111/j.1365-2907.2008.00122.x

Baker, P.J., Harris, S., 2007. Urban mammals: What does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. Mamm. Rev. 37, 297–315. https://doi.org/10.1111/j.1365-2907.2007.00102.x

Baker, P.J., Harris, S., Robertson, C.P.J., Saunders, G., White, P.C.L., 2004. Is it possible to monitor mammal population changes from counts of road traffic casualties? An analysis using Bristol’s red foxes Vulpes vulpes as an example. Mamm. Rev. 34, 115–130. https://doi.org/10.1046/j.0305-1838.2003.00024.x

Baker, P.J., Thompson, R., Grogan, A., 2018. Survival rates of cat-attacked birds admitted to RSPCA wildlife centres in the UK: Implications for cat owners and wildlife rehabilitators. Anim. Welf. 27, 305–318. https://doi.org/10.7120/09627286.27.4.305

Balmford, A., Green, R., Phalan, B., 2012. What conservationists need to know about farming.

Proc. R. Soc. B Biol. Sci. 279, 2714–2724. https://doi.org/10.1098/rspb.2012.0515

Banerjee, S., Walder, F., Büchi, L., Meyer, M., Held, A.Y., Gattinger, A., Keller, T., Charles, R., van der Heijden, M.G.A., 2019. Agricultural intensification reduces microbial network complexity and the abundance of keystone taxa in roots. ISME J. 13, 1722–1736. https://doi.org/10.1038/s41396-019-0383-2

Barnes, E., Farnworth, M.J., 2016. Perceptions of responsibility and capability for treating wildlife casualties in UK veterinary practices. Vet. Rec. 108, 197. https://doi.org/10.1136/vr.104052

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57. https://doi.org/10.1038/nature09678

Barr, C., Howard, D., Bunce, B., Gillespie, M., Hallam, C., 1990. Changes in hedgerows in Britain between 1984 and 1990. A report published by the Institute of Terrestrial Ecology. Cumbria, UK.

Barr, C.J., Gillespie, M.K., 2000. Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. J. Environ. Manage. 60, 23–32. https://doi.org/10.1006/jema.2000.0359

Barthel, L.M.F., Hofer, H., Berger, A., 2019. An easy, flexible solution to attach devices to hedgehogs (Erinaceus europaeus) enables long-term high-resolution studies. Ecol. Evol. 9, 672–679. https://doi.org/10.1002/ece3.4794

Barton, K., 2019. Package "MuMIn" R Package version 1(6) [WWW Document]. URL https://cran.r-project.org/web/packages/MuMIn/index.html

Bartonička, T., Bandouchova, H., Berková, H., Blažek, J., Lučan, R., Horáček, I., Martínková, N., Pikula, J., Řehák, Z., Zukal, J., 2017. Deeply torpid bats can change position without elevation of body temperature. J. Therm. Biol. 63, 119–123. https://doi.org/10.1016/j.jtherbio.2016.12.005

Bateman, P.W., Fleming, P.A., 2012. Big city life: Carnivores in urban environments. J. Zool. 287, 1–23. https://doi.org/10.1111/j.1469-7998.2011.00887.x

Bates, D., Machler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Battersby, J., 2005. UK mammals: Species status and population trends, JNCC/Tracking Mammals Partnership. JNCC/Tracking Mammals Partnership, Peterborough, UK.

Bearman-Brown, L.E., Baker, P.J., Scott, D., Uzal, A., Evans, L., Yarnell, R.W., 2020a. Over-winter survival and nest site selection of the west-European hedgehog (Erinaceus europaeus) in arable dominated landscapes. Animals 10, 1449. https://doi.org/10.3390/ani10091449

Bearman-Brown, L.E., Wilson, L.E., Evans, L., Baker, P.J., 2020b. Comparing non-invasive surveying techniques for elusive, nocturnal mammals: a case study of the West European hedgehog (Erinaceus europaeus). J. Vertebr. Biol. 69, 20075. https://doi.org/10.25225/jvb.20075

Beck, A., Haerlin, B., Richter, L., 2016. Agriculture at a crossroads: IAASTD findings and recommendations for future farming. Foundation on Future Farming, Berlin, Germany. https://doi.org/10.1126/science.1158390

Benard, M.F., 2015. Warmer winters reduce frog fecundity and shift breeding phenology, which consequently alters larval development and metamorphic timing. Glob. Chang. Biol. 21, 1058–1065. https://doi.org/10.1111/gcb.12720

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: Is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Beringer, J., Mabry, P., Meyer, T., Wallendorf, M., Eddleman, W.R., 2004. Post-release survival of rehabilitated white-tailed deer fawns in Missouri. Wildl. Soc. Bull. 32, 732–738. https://doi.org/10.2193/0091-7648(2004)032

Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6, 506–519. https://doi.org/10.2307/2269387

Bolfíková, B., Konečný, A., Pfaffle, M., Skuballa, J., Hulva, P., 2013. Population biology of establishment in New Zealand hedgehogs inferred from genetic and historical data: Conflict or compromise? Mol. Ecol. 22, 3709–3720. https://doi.org/10.1111/mec.12331

Bond, D.P.G., Grasby, S.E., 2017. On the causes of mass extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 478, 3–29. https://doi.org/10.1016/j.palaeo.2016.11.005

Boonstra, R., Krebs, C.J., Boutin, S., Eadie, J.M., 1994. Finding Mammals Using Far-Infrared Thermal Imaging. J. Mammal. 75, 1063–1068. https://doi.org/10.2307/1382490

Bowen, C., Reeve, N.J., Pettinger, T., Gurnell, J., 2019. An evaluation of thermal infrared cameras for surveying hedgehogs in parkland habitats. Mammalia 84, 12–14. https://doi.org/10.1515/mammalia-2019-0100

Box, J.E., Colgan, W.T., Christensen, T.R., Schmidt, N.M., Lund, M., Parmentier, F.J.W., Brown, R., Bhatt, U.S., Euskirchen, E.S., Romanovsky, V.E., Walsh, J.E., Overland, J.E., Wang, M., Corell, R.W., Meier, W.N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., Olsen, M.S., 2019. Key indicators of Arctic climate change: 1971-2017. Environ. Res. Lett. https://doi.org/10.1088/1748-9326/aafc1b

Bright, P.W., Balmforth, Z., Macpherson, J.L., 2015. The effects of changes in traffic flow on mammal road kill counts. Appl. Ecol. Environ. Res. 13, 171–179. https://doi.org/10.15666/aeer/1301_171179

Bright, P.W., Morris, P.A., Mitchell-Jones, T., 2006. The Dormouse Conservation Handbook, 2nd ed, English Nature. English Nature, Peterborough, UK.

British Zoological Veterinary Association, 2016. Good Practice Guidelines for Wildlife Rehabilitation Centres. British Zoological Veterinary Association.

Brown, D.D., Kays, R., Wikelski, M., Wilson, R., Klimley, A., 2013. Observing the unwatchable through acceleration logging of animal behavior. Anim. Biotelemetry 1. https://doi.org/10.1186/2050-3385-1-20

Brown, T.C., Bergstrom, J.C., Loomis, J.B., 2007. Defining, valuing, and providing ecosystem goods and services. Nat. Resour. J. 47, 329–376.

Bullen, K., 2010. Hedgehog Rehabilitation. British Hedgehog Preservation Society, Ludlow, UK.

Bunnell, T., 2002. The assessment of British hedgehog (Erinaceus europaeus) casualties on arrival and determination of optimum release weights using a new index. J. Wildl. Rehabil. 25, 11–22.

Bunnell, T., 2001. The incidence of disease and injury in displaced wild hedgehogs (Erinaceus europaeus). Lutra 44, 3–14.

Burel, F., Butet, A., Delettre, Y.R., Millan de La Peña, N., 2004. Differential response of selected taxa to landscape context and agricultural intensification. Landsc. Urban Plan. 67, 195–204. https://doi.org/10.1016/S0169-2046(03)00039-2

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. https://doi.org/10.1177/0049124104268644

Burnham, K.P., Anderson, D.R., 2002. Model selection and multi-model inference: A practical information-theoretic approach. Springer-Verlag, New York.

Burton, M., 1969. The Hedgehog. Andre Deutsch, London, UK.

Butchart, S.H.M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.C., Watson, R., 2010. Global Biodiversity: Indicators of recent declines. Science. 328, 1164–1169. https://doi.org/10.1126/science.1187512

Butler, D.A., Ballard, W.B., Haskell, S.P., Wallace, M.C., 2006. Limitations of thermal infrared imaging for locating neonatal deer in semiarid shrub communities. Wildl. Soc. Bull. 34, 1458–1462.

Cablk, M.E., Heaton, J.S., 2006. Accuracy and reliability of dogs in surveying for desert tortoise (Gopherus agassizii). Ecol. Appl. 16, 1926–1935. https://doi.org/10.1890/1051-0761(2006)016[1926:AARODI]2.0.CO;2

Cablk, M.E., Sagebiel, J.C., Heaton, J.S., Valentin, C., 2008. Olfaction-based detection distance: a quantitative analysis of how far away dogs recognize tortoise odor and follow it to source. Sensors 8, 2208–2222. https://doi.org/10.3390/s8042208

Camacho, M.C., Hernández, J.M., Lima-Barbero, J.F., Höfle, U., 2016. Use of wildlife rehabilitation centres in pathogen surveillance: A case study in white storks (Ciconia ciconia). Prev. Vet. Med. 130, 106–111. https://doi.org/10.1016/j.prevetmed.2016.06.012

Canova, L., Balestrieri, A., 2019. Long-term monitoring by roadkill counts of mammal populations living in intensively cultivated landscapes. Biodivers. Conserv. 28, 97–113.

https://doi.org/10.1007/s10531-018-1638-3

Carey, P.D., Wallis, S.M., Emmett, B., Maskell, L.C., Murphy, J., Norton, L.R., Simpson, I.C., Smart, S.M., 2008. Countryside Survey: UK Headline Messages from 2007. Centre for Ecology & Hydrology, Wallingford, UK.

Ceballos, G., Ehrlich, P.R., 2018. The misunderstood sixth mass extinction. Science. 360, 1080–1081. https://doi.org/10.1126/science.aau0191

Champagnon, J., Guillemain, M., Elmberg, J., Massez, G.G., Cavallo, F.F., Gauthier-Clerc, M.M., 2012. Low survival after release into the wild: Assessing “the burden of captivity” on Mallard physiology and behaviour. Eur. J. Wildl. Res. 58, 255–267. https://doi.org/10.1007/s10344-011-0573-3

Chan, K.M.A., Balvanera, P., Benessaiah, K., Chapman, M., Díaz, S., Gómez-Baggethun, E., Gould, R., Hannahs, N., Jax, K., Klain, S., Luck, G.W., Martín-López, B., Muraca, B., Norton, B., Ott, K., Pascual, U., Satterfield, T., Tadaki, M., Taggart, J., Turner, N., 2016. Why protect nature? Rethinking values and the environment. Proc. Natl. Acad. Sci. U. S. A. 113, 1462–1465. https://doi.org/10.1073/pnas.1525002113

Chen, H.L., Koprowski, J.L., 2019. Can we use body size and road characteristics to anticipate barrier effects of roads in mammals? A meta-analysis. Hystrix, Ital. J. Mammal. 30, 1–7. https://doi.org/10.4404/hystrix–00185-2018

Chipman, R., Slate, D., Rupprechf, C., Mendoza, M., 2008. Downside risk of wildlife translocation. Dev. Biol. (Basel). 131, 223–232.

Chmura, H.E., Glass, T.W., Williams, C.T., 2018. Biologging physiological and ecological responses to climatic variation: New tools for the climate change era. Front. Ecol. Evol. 6, Article 92. https://doi.org/10.3389/fevo.2018.00092

Chrétien, L.P., Théau, J., Ménard, P., 2015. Wildlife multispecies remote sensing using visible and thermal infrared imagery acquired from an unmanned aerial vehicle (UAV). Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci. - ISPRS Arch. XL-1/W4, 241–248. https://doi.org/10.5194/isprsarchives-XL-1-W4-241-2015

Churchfield, S., Barber, J., Quinn, C., 2000. A new survey method for Water Shrews (Neomys fodiens) using baited tubes. Mamm. Rev. 30, 249–254. https://doi.org/10.1046/j.1365-2907.2000.00074.x

Cilulko, J., Janiszewski, P., Bogdaszewski, M., Szczygielska, E., 2013. Infrared thermal imaging in studies of wild animals. Eur. J. Wildl. Res. 59, 17–23. https://doi.org/10.1007/s10344-012-0688-1

Clout, M.N., Russell, J.C., 2007. The invasion ecology of mammals: A global perspective. Wildl. Res. 35, 180–184. https://doi.org/10.1071/WR07091

Cooper, C.B., Dickinson, J., Phillips, T., Bonney, R., 2007. Citizen Science as a Tool for Conservation in Residential Ecosystems. Ecol. Soc. 12, 11.

Cornulier, T., Robinson, R.A., Elston, D., Lambin, X., Sutherland, W.J., Benton, T.G., 2011. Bayesian reconstitution of environmental change from disparate historical records: Hedgerow loss and farmland bird declines. Methods Ecol. Evol. 2, 86–94. https://doi.org/10.1111/j.2041-210X.2010.00054.x

Cortázar-Chinarro, M., Halvarsson, P., Virgós, E., 2019. Sign surveys for red fox (Vulpes vulpes) censuses: evaluating different sources of variation in scat detectability. Mammal Res. 64, 183–190. https://doi.org/10.1007/s13364-018-0404-y

Council of Europe, 1982. Convention on the Conservation of European Wildlife and Natural Habitats Annexe III - Protected fauna species [WWW Document]. URL https://rm.coe.int/168097eb57 (accessed 5.3.20).

Craighead, F.C., Craighead, J.J., 1972. Grizzly bear prehibernation and denning activities as determined by radiotracking. Wildl. Monogr. 32, 3–35. https://doi.org/10.2307/3830629

Crees, J.J., Collins, A.C., Stephenson, P.J., Meredith, H.M.R., Young, R.P., Howe, C., Price, M.R.S., Turvey, S.T., 2016. A comparative approach to assess drivers of success in mammalian conservation recovery programs. Conserv. Biol. 30, 694–705. https://doi.org/10.1111/cobi.12652

Crist, E., Mora, C., Engelman, R., 2017. The interaction of human population, food production, and biodiversity protection. Science. 356, 260–264. https://doi.org/10.1126/science.aal2011

Cristescu, R.H., Foley, E., Markula, A., Jackson, G., Jones, D., Frère, C., 2015. Accuracy and efficiency of detection dogs: A powerful new tool for koala conservation and management. Sci. Rep. 5, 1–6. https://doi.org/10.1038/srep08349

Croft, S., Chauvenet, A.L.M., Smith, G.C., 2017. A systematic approach to estimate the distribution and total abundance of British mammals. PLoS One 12, 1–21. https://doi.org/10.1371/journal.pone.0176339

Crooks, K.R., Burdett, C.L., Theobald, D.M., King, S.R.B., Di Marco, M., Rondinini, C., Boitani, L., 2017. Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. Proc. Natl. Acad. Sci. U. S. A. 114, 7635–7640. https://doi.org/10.1073/pnas.1705769114

Crooks, K.R., Burdett, C.L., Theobald, D.M., Rondinini, C., Boitani, L., 2011. Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos. Trans. R. Soc. B Biol. Sci. 366, 2642–2651. https://doi.org/10.1098/rstb.2011.0120

Crooks, K.R., Sanjayan, M.A., 2006. Connectivity Conservation. Cambridge University Press, Cambridge, UK.

Curtis, J.T., 1956. The Modification of Mid-latitude Grasslands and Forests by Man, in: Thomas, W.L. (Ed.), Man’s Role in Changing the Face of the Earth. University of Chicago Press, Chicago, IL, pp. 721–736.

Daily, G.C., Polasky, S., Goldstein, J., Kareiva, P.M., Mooney, H.A., Pejchar, L., Ricketts, T.H., Salzman, J., Shallenberger, R., 2009. Ecosystem services in decision making: Time to deliver. Front. Ecol. Environ. 7, 21–28. https://doi.org/10.1890/080025

Damm, P.E., Grand, J.B., Barnett, S.W., 2010. Variation in detection among passive infrared triggered-cameras used in wildlife research. Annu. Conf. Southeast Assoc. Fish Wildl. Agencies 64, 125–130.

Davies, Z.G., Fuller, R.A., Loram, A., Irvine, K.N., Sims, V., Gaston, K.J., 2009. A national scale inventory of resource provision for biodiversity within domestic gardens. Biol. Conserv. 142, 761–771. https://doi.org/10.1016/j.biocon.2008.12.016

Day, C.C., Westover, M.D., Hall, L.K., Larsen, R.T., McMillan, B.R., 2016. Comparing direct and indirect methods to estimate detection rates and site use of a cryptic semi-aquatic carnivore. Ecol. Indic. 66, 230–234. https://doi.org/10.1016/j.ecolind.2016.01.039

de Oliveira, M.L., Norris, D., Ramírez, J.F.M., Peres, P.H.F., Galetti, M., Duarte, J.M.B., 2012. Dogs can detect scat samples more efficiently than humans: An experiment in a continuous Atlantic Forest remnant. Zoologia 29, 183–186. https://doi.org/10.1590/S1984-

46702012000200012

Decaëns, T., Jimenez, J.J., 2002. Earthworm communities under an agricultural intensification gradient in Colombia. Plant Soil 240, 133–143.

Defra, 2019a. UKBI - C6. Insects of the countryside | JNCC - Adviser to Government on Nature Conservation [WWW Document]. URL https://jncc.gov.uk/our-work/ukbi-c6-insects-of-the-countryside/ (accessed 5.3.20).

Defra, 2019b. UKBI - D1c. Pollinating insects | JNCC - Adviser to Government on Nature Conservation [WWW Document]. URL https://jncc.gov.uk/our-work/ukbi-d1c-pollinating-insects/ (accessed 5.3.20).

Defra, 2018. UK Biodiversity Indicators 2018 [WWW Document]. URL www.jncc.defra.gov.uk/ukbi (accessed 5.3.20).

Del Bove, E., Isotti, R., 2001. The European badger (Meles meles) diet in a Mediterranean area. Hystrix, Ital. J. Mammal. 12, 19–25. https://doi.org/10.4404/hystrix-12.1-4167

Delogu, M., Cotti, C., Lelli, D., Sozzi, E., Trogu, T., Lavazza, A., Garuti, G., Castrucci, M.R., Vaccari, G., De Marco, M.A., Moreno, A., 2020. Eco-virological preliminary study of potentially emerging pathogens in hedgehogs (Erinaceus europaeus) recovered at a wildlife treatment and rehabilitation center in Northern Italy. Animals 10. https://doi.org/10.3390/ani10030407

DeMatteo, K.E., Davenport, B., Wilson, L.E., 2019. Back to the basics with conservation detection dogs: fundamentals for success. Wildlife Biol. 2019, 1–9. https://doi.org/10.2981/wlb.00584

Deutsch, C.J., Bonde, R.K., Reid, J.P., 1998. Radio-tracking manatees from land and space: tag design, implementation, and lessons learned from long-term study. Mar. Technol. Soc. J. 32, 18–29.

Di Marco, M., Boitani, L., Mallon, D., Hoffmann, M., Iacucci, A., Meijaard, E., Visconti, P., Schipper, J., Rondinini, C., 2014. A Retrospective evaluation of the global decline of carnivores and ungulates. Conserv. Biol. 28, 1109–1118. https://doi.org/10.1111/cobi.12249

Ditchkoff, S.S., Raglin, J.B., Smith, J.M., Collier, B.A., 2005. Capture of white-tailed deer fawns using thermal imaging technology. Wildl. Soc. Bull. 33, 1164–1168. https://doi.org/10.2193/0091-7648(2005)33[1164:ftfcow]2.0.co;2

Doncaster, C.P., 1994. Factors regulating local variations in abundance: Field tests on hedgehogs, Erinaceus europaeus. Oikos 69, 182–192. https://doi.org/10.2307/3546136

Doncaster, C.P., 1993. Influence of predation threat on foraging pattern: The hedgehog's gambit. Rev. d'Ecologie Terre la Vie 48, 207–213.

Doncaster, C.P., 1992. Testing the role of intraguild predation in regulating hedgehog populations. Proc. Biol. Sci. 249, 113–117.

Doncaster, C.P., Dickman, C.R., Macdonald, D.W., 1990. Feeding ecology of red foxes (Vulpes vulpes) in the city of Oxford. J. Mammal. 71, 188–194.

Doncaster, C.P., Rondinini, C., Johnson, P.C.D., 2001. Field test for environmental correlates of dispersal in hedgehogs Erinaceus europaeus. J. Anim. Ecol. 70, 33–46. https://doi.org/10.1046/j.1365-2656.2001.00471.x

Dover, J.W., 2019. The Ecology of Hedgerows and Field Margins. Routledge, Abingdon, UK.

Dowding, C.V., 2007. An Investigation of Factors Relating to the Perceived Decline of European Hedgehogs (Erinaceus europaeus) in Britain. University of Bristol.

Dowding, C.V., Harris, S., Poulton, S.M.C., Baker, P.J., 2010a. Nocturnal ranging behaviour of urban hedgehogs, Erinaceus europaeus, in relation to risk and reward. Anim. Behav. 80, 13–21. https://doi.org/10.1016/j.anbehav.2010.04.007

Dowding, C.V., Shore, R.F., Worgan, A., Baker, P.J., Harris, S., 2010b. Accumulation of anticoagulant rodenticides in a non-target insectivore, the European hedgehog (Erinaceus europaeus). Environ. Pollut. 158, 161–166. https://doi.org/10.1016/j.envpol.2009.07.017

Dowie, M.T., 1993. The Spatial Organisation and Habitat Use of the European Hedgehog, Erinaceus europaeus L., on Farmland. PhD Thesis. University of London, London, UK.

Dubois, S., 2003. A survey of wildlife rehabilitation goals, impediments, issues, and success in British Columbia, Canada. Masters Thesis. The University of Victoria, British Columbia, Canada.

Dudley, N., Alexander, S., 2017. Agriculture and biodiversity: A review. Biodiversity 18, 45–49. https://doi.org/10.1080/14888386.2017.1351892

Dunbar, M.R., Johnson, S.R., Rhyan, J.C., McCollum, M., 2009. Use of Infrared Thermography to Detect Thermographic Changes in Mule Deer (Odocoileus hemionus) Experimentally Infected with Foot-and-Mouth Disease. J. Zoo Wildl. Med. 40, 296–301. https://doi.org/10.1638/2008-0087.1

Duro, D.C., Girard, J., King, D.J., Fahrig, L., Mitchell, S., Lindsay, K., Tischendorf, L., 2014. Predicting species diversity in agricultural environments using Landsat TM imagery. Remote Sens. Environ. 144, 214–225. https://doi.org/10.1016/j.rse.2014.01.001

Eaton, M.A., Brown, A.F., Hearn, R., Noble, D.G., Musgrove, A.J., Lock, L., Stroud, D., Gregory, R.D., 2015. Birds of conservation concern 4: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. Br. Birds 108, 708–746.

Eigenbrod, F., Hecnar, S.J., Fahrig, L., 2008. Accessible habitat: An improved measure of the effects of habitat loss and roads on wildlife populations. Landsc. Ecol. 23, 159–168. https://doi.org/10.1007/s10980-007-9174-7

Eklund, A., López-Bao, J.V., Tourani, M., Chapron, G., Frank, J., 2017. Limited evidence on the effectiveness of interventions to reduce livestock predation by large carnivores. Sci. Rep. 7, 1–9. https://doi.org/10.1038/s41598-017-02323-w

Elledge, A.E., Allen, L.R., Carlsson, B.L., Wilton, A.N., Leung, L.K.P., 2008. An evaluation of genetic analyses, skull morphology and visual appearance for assessing dingo purity: Implications for dingo conservation. Wildl. Res. 35, 812–820. https://doi.org/10.1071/WR07056

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D., Ramankutty, N., 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Glob. Ecol. Biogeogr. 19, 589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x

Englefield, B., Starling, M., McGreevy, P.D., 2018. A review of roadkill rescue: Who cares for the mental, physical and financial welfare of Australian wildlife carers? Wildl. Res. 45, 103–118. https://doi.org/10.1071/WR17099

European Environment Agency, 2019. Landscape fragmentation pressure and trends in Europe [WWW Document]. URL https://www.eea.europa.eu/data-and-maps/indicators/mobility-and-urbanisation-pressure-on-ecosystems-2/assessment (accessed 7.21.20).

Fàbregas, M.C., Fosgate, G.T., Ganswindt, A., Bertschinger, H., Hofmeyr, M., Meyer, L.C.R., 2020.

Rehabilitation method affects behavior, welfare, and adaptation potential for subsequent release of orphaned white rhinoceros. Acta Ethol. 23, 105–114. https://doi.org/10.1007/s10211-020-00343-w

Fabrizio, M., Di Febbraro, M., D'Amico, M., Frate, L., Roscioni, F., Loy, A., 2019. Habitat suitability vs landscape connectivity determining roadkill risk at a regional scale: A case study on European badger (Meles meles). Eur. J. Wildl. Res. https://doi.org/10.1007/s10344-018-1241-7

Fahrig, L., 2019. Habitat fragmentation: A long and tangled tale. Glob. Ecol. Biogeogr. 28, 33–41. https://doi.org/10.1111/geb.12839

Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. J. Wildl. Manage. 61, 603–610.

Field, A., 2017. Discovering Statistics Using IBM SPSS Statistics, 5th ed. SAGE Publications Ltd., London, UK.

Firbank, L.G., Attwood, S., Eory, V., Gadanaski, Y., Lynch, J.M., Sonnino, R., Takahashi, T., 2018. Grand challenges in sustainable intensification and ecosystem services. Front. Sustain. Food Syst. 2, 7. https://doi.org/10.1038/nclimate2916

Firbank, L.G., Petit, S., Smart, S., Blain, A., Fuller, R.J., 2008. Assessing the impacts of agricultural intensification on biodiversity: A British perspective. Philos. Trans. R. Soc. B Biol. Sci. 363, 777–787. https://doi.org/10.1098/rstb.2007.2183

Fischer, C.P., Romero, L.M., 2019. Chronic captivity stress in wild animals is highly species-specific. Conserv. Physiol. 7, 1–38. https://doi.org/10.1093/conphys/coz093

Fischer, G., Tubiello, F.N., van Velthuizen, H., Wiberg, D.A., 2007. Climate change impacts on irrigation water requirements: Effects of mitigation, 1990-2080. Technol. Forecast. Soc. Change 74, 1083–1107. https://doi.org/10.1016/j.techfore.2006.05.021

Flowerdew, J.R., Shore, R.F., Poulton, S.M.C., Sparks, T.H., 2004. Live trapping to monitor small mammals in Britain. Mamm. Rev. 34, 31–50. https://doi.org/10.1046/j.0305-1838.2003.00025.x

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M., 2011. Solutions for a cultivated planet. Nature 478, 337–342. https://doi.org/10.1038/nature10452

Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231.

Foster, S., Ijichi, C., 2017. The association between infrared thermal imagery of core eye temperature, personality, age and housing in cats. Appl. Anim. Behav. Sci. 189, 79–84. https://doi.org/10.1016/j.applanim.2017.01.004

Freilich, J.E., Emlen, J.M., Duda, J.J., Freeman, D.C., Cafaro, P.J., 2003. Ecological effects of ranching: A six-point critique. Bioscience 53, 759. https://doi.org/10.1641/0006-3568(2003)053[0759:eeoras]2.0.co;2

Garcês, A., Pires, I., Pacheco, F., Fernandes, L.S., Soeiro, V., Lóio, S., Prada, J., Cortes, R., Queiroga, F., 2019. Natural and anthropogenic causes of mortality in wild birds in a wildlife rehabilitation centre in Northern Portugal: a ten-year study. Bird Study 66, 484–493. https://doi.org/10.1080/00063657.2020.1726874

Garcês, A., Pires, I., Rodrigues, P., 2020. Teratological effects of pesticides in vertebrates: A review. J. Environ. Sci. Heal. - Part B Pestic. Food Contam. Agric. Wastes 55, 75–89. https://doi.org/10.1080/03601234.2019.1660562

García-Rippolles, C., López-Lopez, P., Urios, V., 2010. First description of migration and wintering of adult egyptian vultures neophron percnopterus tracked by GPS satellite telemetry. Bird Study 57, 261–265. https://doi.org/10.1080/00063650903505762

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11, 97–105. https://doi.org/10.1016/j.baae.2009.12.001

Geiser, F., 2013. Hibernation. Curr. Biol. 23, 188–193. https://doi.org/10.1016/j.cub.2013.01.062

Geiser, F., 2011. Hibernation: Endotherms, in: ELS. John Wiley & Sons, Ltd, Chichester, UK. https://doi.org/10.1002/9780470015902.a0003215.pub2

Geiser, F., Ruf, T., 1995. Hibernation versus daily torpor in mammals and birds: Physiological variables and classification of torpor patterns. Physiol. Zool. 68, 935–966.

Glasby, L., Yarnell, R.W., 2013. Evaluation of the performance and accuracy of Global Positioning System bug transmitters deployed on a small mammal. Eur. J. Wildl. Res. 59, 915–919. https://doi.org/10.1007/s10344-013-0770-3

Glen, A.S., Russell, J.C., Veltman, C.J., Fewster, R.M., 2018. I smell a rat! Estimating effective sweep width for searches using wildlife-detector dogs. Wildl. Res. 45, 500–504. https://doi.org/10.1071/WR18021

Global Invasive Species Database, 2020. Species profile: Erinaceus europaeus [WWW Document]. URL http://www.iucngisd.org/gisd/species.php?sc=176 (accessed 5.11.20).

Goldsworthy, S.D., Giese, M., Gales, R.P., Brothers, N., Hamill, J., 2000. Effects of the Iron baron oil spill on little penguins (Eudyptula minor). II. Post-release survival of rehabilitated oiled birds. Wildl. Res. 27, 573–582. https://doi.org/10.1071/WR99076

Goodwin, C.E.D., Hodgson, D.J., Al-Fulaij, N., Bailey, S., Langton, S., Mcdonald, R.A., 2017. Voluntary recording scheme reveals ongoing decline in the United Kingdom hazel dormouse Muscardinus avellanarius population. Mamm. Rev. 47, 183–197. https://doi.org/10.1111/mam.12091

Goodwin, K.M., Engel, R.E., Weaver, D.K., 2010. Trained dogs outperform human surveyors in the detection of rare Spotted Knapweed (Centaurea stoebe). Invasive Plant Sci. Manag. 3, 113–121. https://doi.org/10.1614/ipsm-d-09-00025.1

Gordon, I.J., 2018. Review: Livestock production increasingly influences wildlife across the globe. Animal 12, S372–S382. https://doi.org/10.1017/S1751731118001349

Goszczyński, J., Jędrzejewska, B., Jędrzejewski, W., 2000. Diet composition of badgers (Meles meles) in a pristine forest and rural habitats of Poland compared to other European populations. J. Zool. 250, 495–505. https://doi.org/10.1017/S0952836900004076

Grafen, A., Hails, R., 2002. Modern Statistics for the Life Sciences. Oxford University Press, Oxford, UK.

Graham, N.A.J., Robinson, J.P.W., Smith, S.E., Govinden, R., Gendron, G., Wilson, S.K., 2020. Changing role of coral reef marine reserves in a warming climate. Nat. Commun. 11, 1–8. https://doi.org/10.1038/s41467-020-15863-z

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L., Owens, I.P.F., 2006. Global distribution and conservation of rare and threatened vertebrates. Nature 444, 93–96. https://doi.org/10.1038/nature05237

Griffith, J.E., Dhand, N.K., Krockenberger, M.B., Higgins, D.P., 2013. A retrospective study of admission trends of koalas to a rehabilitation facility over 30 years. J. Wildl. Dis. 49, 18–28. https://doi.org/10.7589/2012-05-135

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., 2008. Global change and the ecology of cities. Science. 319, 756–760. https://doi.org/10.1126/science.1150195

Grogan, A., 2009. The importance of research in wildlife rehabilitation [WWW Document]. Proc. Br. Wildl. Rehabil. Counc. Conf. URL http://bwrc.org.uk/conference-proceedings/4549145806

Grogan, A., Kelly, A., 2013. A review of RSPCA research into wildlife rehabilitation. Vet. Rec. 172, 211–215. https://doi.org/10.1136/vr.101139

Guerry, A.D., Hunter, M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: An examination of landscape composition and configuration. Conserv. Biol. 16, 745–754. https://doi.org/10.1046/j.1523-1739.2002.00557.x

Gurevitch, J., Padilla, D.K., 2004. Are invasive species a major cause of extinctions? Trends Ecol. Evol. 19, 470–474. https://doi.org/10.1016/j.tree.2004.07.005

Gurnell, J., Bowen, C., 2016. A Study of Hedgehogs in The Regent’s Park Year 3. London, UK.

Gutzwiller, K.J., 1990. Minimizing dog-induced biases in game bird research. Wildl. Soc. Bull. 18, 351–356. https://doi.org/10.2307/3782226

Guy, A.J., Curnoe, D., Banks, P.B., 2014. Welfare based primate rehabilitation as a potential conservation strategy: Does it measure up? Primates 55, 139–147. https://doi.org/10.1007/s10329-013-0386-y

Guy, A.J., Curnoe, D., Banks, P.B., Guy, A.J., Curnoe, Á.D., Curnoe, D., Banks, P.B., 2013. A survey of current mammal rehabilitation and release practices. Biodivers. Conserv. 22, 825–837. https://doi.org/10.1007/s10531-013-0452-1

Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesk, P.A., Corlett, R.T., Norton, B.A., Clemants, S.E., Duncan, R.P., Thompson, K., Schwartz, M.W., Williams, N.S.G., 2009. A global synthesis of plant extinction rates in urban areas. Ecol. Lett. 12, 1165–1173. https://doi.org/10.1111/j.1461-0248.2009.01372.x

Haigh, A., 2011. The Ecology of the European hedgehog (Erinaceus europaeus) in rural Ireland. PhD Thesis, Univ. Coll. Cork.

Haigh, A., Butler, F., O’Riordan, R.M., 2012a. An investigation into the techniques for detecting hedgehogs in a rural landscape. J. Negat. Results Ecol. Evol. Biol. 9, 15–26.

Haigh, A., Butler, F., O’Riordan, R.M., 2009. Habitat use by the European hedgehog (Erinaceus europaeus L., 1758) in an Irish rural landscape. Irish Nat. J. 36–45.

Haigh, A., Kelly, M., Butler, F., O’Riordan, R.M., 2014a. Non-invasive methods of separating hedgehog (Erinaceus europaeus) age classes and an investigation into the age structure of road kill. Acta Theriol. (Warsz). 59, 165–171. https://doi.org/10.1007/s13364-013-0142-0

Haigh, A., O’Riordan, R.M., Butler, F., 2014b. Hedgehog Erinaceus europaeus mortality on Irish roads. Wildlife Biol. 20, 155–160. https://doi.org/10.2981/wlb.12126

Haigh, A., O’Riordan, R.M., Butler, F., 2012b. Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (Erinaceus europaeus). Acta Theriol. (Warsz). 57, 321–331. https://doi.org/10.1007/s13364-012-0080-2

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., De Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS One 12. https://doi.org/10.1371/journal.pone.0185809

Harris, S., 1981. The food of suburban foxes (Vulpes vulpes), with special reference to London. Mamm. Rev. 11, 151–168. https://doi.org/10.1093/acprof:oso/9780198070689.003.0005

Harris, S., Baker, P.J., 2001. Urban Foxes, 2nd ed. Whittet Books, Stowmarket, Suffolk.

Harris, S., Baker, P.J., Soulsbury, C.D., 2010. Eurasian badgers (Meles meles), in: Gehrt, S.D., Riley, S.P.D., Cypher, B.L. (Eds.), Urban Carnivores. John Hopkins University Press., Baltimore, MD, pp. 109–119.

Harris, S., Morris, P.A., Wray, S., Yalden, D.W., 1995. A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans. JNCC, Peterborough, UK.

Harris, S.J., Massimino, D., Balmer, D.E., Eaton, M.A., Noble, D.G., Pearce-Higgins, J.W., Woodcock, P., Gillings, S., 2020. The Breeding Bird Survey 2019, BTO Research Report 726.

Harris, S.J., Massimino, D., Gillings, S., Eaton, S., Noble, M.A., Balmer, D.G., Procter, D., Pearce-Higgins, J.W., Woodcock, P., 2018. The Breeding Bird Survey 2017. BTO Research Report 706. British Trust for Ornithology, Thetford, UK.

Harris, S.J., Massimino, S., Newson, S.E., Eaton, M.A., Marchant, J.H., Balmer, D.E., Noble, D.G., Gillings, S., Procter, D., Pearce-Higgins, J.W., 2016. The Breeding Bird Survey 2015, BTO Research Report 687. Thetford, UK.

Hartig, F., 2017. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models [WWW Document]. URL https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, P.B., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science. 348, 336–340. https://doi.org/10.1126/science.aaa1788

Havaei-Ahary, B., 2019. Road Traffic Estimates: Great Britain 2018. London.

Hayhow, D.B., Ausden, M.A., Bradbury, R.B., Burnell, D., Copeland, A. l., Crick, H.Q.P., Eaton, M.A., Frost, T., Grice, P.V., Hall, C., Harris, S.J., Morecroft, M.D., Noble, D.G., Pearce-Higgins, J.W., Watts, O., William, J.M., 2017. The State of the UK's Birds 2017. Sandy, Bedfordshire.

Hayhow, D.B., Burns, F., Eaton, M.A., Al Fulaij, N., August, T.A., Babey, L., Bacon, L., Bingham, C., Boswell, J., Boughey, K.L., Brereton, T., Brookman, E., Brooks, D.R., Bullock, D.J., Burke, O., Collis, M., Corbet, L., Cornish, N., De Massimi, S., Densham, J., Dunn, E., Elliott, S., Gent, T., Godber, J., Hamilton, S., Havery, S., Hawkins, S., Henney, J., Holmes, K., Hutchinson, N., Isaac, N.J.B., Johns, D., Macadam, C.R., Mathews, F., Nicolet, P., Noble, D.G., Outhwaite, C.L., Powney, G.D., Richardson, P., Roy, D.B., Sims, D., Smart, S., Stevenson, K., Stroud, R.A., Walker, K.J., Webb, J.R., Webb, T.J., Wynde, R., Gregory, R.D., 2019. State of Nature 2019. The State of Nature Partnership.

Helton, W.S. (ed), 2009. Canine ergonomics: The Science of Working Dogs, CRC Press. CRC Press, Boca Raton, FL:

Hill, D.A., Greenaway, F., 2005. Effectiveness of an acoustic lure for surveying bats in British woodlands. Mamm. Rev. 35, 116–122. https://doi.org/10.1111/j.1365-2907.2005.00058.x

Hoegh-Guldberg, O., 2011. Coral reef ecosystems and anthropogenic climate change. Reg. Environ. Chang. 11, 215–227. https://doi.org/10.1007/s10113-010-0189-2

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., Roberts, C., 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x

Hof, A.R., 2009. A Study of the Current Status of the Hedgehog (Erinaceus europaeus), and its Decline in Great Britain Since 1960. PhD Thesis. Royal Holloway, University of London.

Hof, A.R., Allen, A.M., Bright, P.W., 2019. Investigating the role of the Eurasian badger (Meles meles) in the nationwide distribution of the Western European hedgehog (Erinaceus europaeus) in England. Animals 9. https://doi.org/10.3390/ani9100759

Hof, A.R., Bright, P.W., 2016. Quantifying the long-term decline of the West European hedgehog in England by subsampling citizen-science datasets. Eur. J. Wildl. Res. 62, 407–413. https://doi.org/10.1007/s10344-016-1013-1

Hof, A.R., Bright, P.W., 2012. Factors affecting hedgehog presence on farmland as assessed by a questionnaire survey. Acta Theriol. (Warsz). 57, 79–88. https://doi.org/10.1007/s13364-011-0044-y

Hof, A.R., Bright, P.W., 2010a. The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields. Agric. Ecosyst. Environ. 139, 280–283. https://doi.org/10.1016/j.agee.2010.08.014

Hof, A.R., Bright, P.W., 2010b. The value of agri-environment schemes for macro-invertebrate feeders: Hedgehogs on arable farms in Britain. Anim. Conserv. 13, 467–473. https://doi.org/10.1111/j.1469-1795.2010.00359.x

Hof, A.R., Bright, P.W., 2009. The value of green-spaces in built-up areas for - western hedgehogs. Lutra 52, 69–82.

Hof, A.R., Snellenberg, J., Bright, P.W., 2012. Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. Anim. Behav. 83, 1099–1106. https://doi.org/10.1016/j.anbehav.2012.01.042

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Vié, J.C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Ortiz, A.L.A., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G., W., Burfield, I.J., Burton, J.A., Capper, D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M., Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Cortez Fernandez, C.F., Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C., Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D.L., Gerlach, J., Gower, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.M., Hughes, B., Hussain, S.A., Icochea M., J., Inger, R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M., Kuzmin, S.L., La Marca, E., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison, R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.. K., McIvor, A., Moehlman, P.D., Molur, S., Alonso, A.M., Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., De Mitcheson, Y.S., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith, A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsytsulina, K., Tweddle, D., Ubeda, C., Valenti, S.V., Van Dijk, P.P., Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., Da Fonseca, G.A.B., Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A., Stuart, S.N., 2010. The impact of conservation on the status of the world’s vertebrates. Science. 330, 1503–1509.

https://doi.org/10.1126/science.1194442

Holsbeek, L., Rodts, J., Muyldermans, S., 1999. Hedgehog and other animal traffic victims in Belgium: Results of a countrywide survey. Lutra 42, 111–119.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavourel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J., Wardle, D.., 2005. Effects of biodiversity on ecosystem functioning: A concensus of current knowledge. Eol. Monogr. 75, 3–35. https://doi.org/10.1890/04-0922

Hopkins, J.J., Kirby, K.J., 2007. Ecological change in British broadleaved woodland since 1947. Ibis (Lond. 1859). 149, 29–40. https://doi.org/10.1111/j.1474-919X.2007.00703.x

Howell, H.J., Mothes, C.C., Clements, S.L., Catania, S.V., Rothermel, B.B., Searcy, C.A., 2019. Amphibian responses to livestock use of wetlands: New empirical data and a global review. Ecol. Appl. 29, 1–15. https://doi.org/10.1002/eap.1976

Hubert, P., Julliard, R., Biagianti, S., Poulle, M.L., 2011. Ecological factors driving the higher hedgehog (Erinaceus europeaus) density in an urban area compared to the adjacent rural area. Landsc. Urban Plan. 103, 34–43. https://doi.org/10.1016/j.landurbplan.2011.05.010

Huijser, M.P., 2000. Life on the edge: Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape. PhD Thesis. Wagieningen University, Wagingen, The Netherlands.

Huijser, M.P., Bergers, P.J.M., 2000. The effect of roads and traffic on hedgehog (Erinaceus europaeus) populations. Biol. Conserv. 95, 6–9. https://doi.org/10.17487/rfc3104

Huijser, M.P., Bergers, P.J.M., de Vries, J.G., 1998. Hedgehog traffic victims: How to quantify effects on the population level and the prospects for mitigation, in: Evink, G.L., Garrett, P., Zeigler, D., Berry, J. (Eds.), Proceedings of the International Conference on Wildlife Ecology and Transportation. Tallahassee, pp. 171–180.

Hunter, C.M., Caswell, H., Runge, M.C., Regehr, E.V., Amstrup, S.C., Stirling, I., 2010. Climate change threatens polar bear populations: A stochastic demographic analysis. Ecology 91, 2883–2897. https://doi.org/10.1890/09-1641.1

Imhoff, M.L., Zhang, P., Wolfe, R.E., Bounoua, L., 2010. Remote sensing of the urban heat island effect across biomes in the continental USA. Remote Sens. Environ. 114, 504–513.

https://doi.org/10.1016/j.rse.2009.10.008

Inouye, D.W., Barr, B., Armitage, K.B., Inouye, B.D., 2000. Climate change is affecting altitudinal migrants and hibernating species. Proc. Natl. Acad. Sci. U. S. A. 97, 1630–1633. https://doi.org/10.1073/pnas.97.4.1630

IPCC, 2012. Glossary of Terms, in: Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M.D., Mach, K.J., Plattner, G.-K., Allen, S.K., Tignor, M., Midgley, P.M. (Eds.), Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change (IPCC). Cambridge, UK, pp. 555–564.

Jackson, D.B., 2007. Factors affecting the abundance of introduced hedgehogs (Erinaceus europaeus) to the Hebridean island of South Uist in the absence of natural predators and implications for nesting birds. J. Zool. 271, 210–217. https://doi.org/10.1111/j.1469-7998.2006.00204.x

Jackson, D.B., Green, R.E., 2000. The importance of the introduced hedgehog (Erinaceus europaeus) as a predator of the eggs of waders (Charadrii) on machair in South Uist, Scotland. Biol. Conserv. 93, 333–348. https://doi.org/10.1016/S0006-3207(99)00135-4

Jamieson, L.T., Baxter, G.S., Murray, P.J., 2018. You are not my handler! impact of changing handlers on dogs’ behaviours and detection performance. Animals 8, 176. https://doi.org/10.3390/ani8100176

Jamieson, L.T.J., Baxter, G.S., Murray, P.J., 2017. Identifying suitable detection dogs. Appl. Anim. Behav. Sci. 195, 1–7. https://doi.org/10.1016/j.applanim.2017.06.010

Jaspers, V.L.B., Voorspoels, S., Covaci, A., Eens, M., 2006. Can predatory bird feathers be used as a non-destructive biomonitoring tool of organic pollutants? Biol. Lett. 2, 283–285. https://doi.org/10.1098/rsbl.2006.0450

Jensen, A.B., 2004. Overwintering of European hedgehogs Erinaceus europaeus in a Danish rural area. Acta Theriol. (Warsz). 49, 145–155. https://doi.org/10.1007/BF03192516

Johnson, D.D.P., Jetz, W., Macdonald, D.W., 2002. Environmental correlates of badger social spacing across Europe. J. Biogeogr. 29, 411–425. https://doi.org/10.1046/j.1365-2699.2002.00680.x

Jones, S.A., Chapman, S., 2019. The ethics and welfare implications of keeping Western European hedgehogs (Erinaceus europaeus) in captivity. J. Appl. Anim. Welf. Sci. 00, 1–17. https://doi.org/10.1080/10888705.2019.1672553

Judge, J., Wilson, G.J., Macarthur, R., Delahay, R.J., McDonald, R.A., 2014. Density and abundance of badger social groups in England and Wales in 2011-2013. Sci. Rep. 4, 3809. https://doi.org/10.1038/srep03809

Judge, J., Wilson, G.J., Macarthur, R., McDonald, R.A., Delahay, R.J., 2017. Abundance of badgers (Meles meles) in England and Wales. Sci. Rep. 7, 276. https://doi.org/10.1038/s41598-017-00378-3

Kaplan, E.L., Meier, P., 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53, 457. https://doi.org/10.2307/2281868

Karp, D., 2020. Detecting small and cryptic animals by combining thermography and a wildlife detection dog. Sci. Rep. 10, 14–17. https://doi.org/10.1038/s41598-020-61594-y

Keller, T.J., Trusso, S., Gregg, I.D., Williams, L., 2019. Using Infrared technology to locate and monitor American woodcock nests, in: Proceedings of the American Woodcock Symposium. pp. 256–262. https://doi.org/10.24926/aws.0133

Kelly, A., Goodwin, S., Grogan, A., Mathews, F., 2008. Post-release survival of hand-reared pipistrelle bats (Pipistrellus spp). Anim. Welf. 17, 375–382.

Kelly, A., Scrivens, R., Grogan, A., 2010. Post-release survival of orphaned wild-born polecats Mustela putorius reared in captivity at a wildlife rehabilitation centre in England. Endanger. Species Res. 12, 107–115. https://doi.org/10.3354/esr00299

Khaldi, M., Ribas, A., Barech, G., Hugot, J.P., Benyettou, M., Albane, L., Arrizabalaga, A., Nicolas, V., 2016. Molecular evidence supports recent anthropogenic introduction of the Algerian hedgehog Atelerix algirus in Spain, Balearic and Canary islands from North Africa. Mammalia 80, 313–320. https://doi.org/10.1515/mammalia-2014-0180

Kharouba, H.M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E., Wolkovich, E.M., 2018. Global shifts in the phenological synchrony of species interactions over recent decades. Proc. Natl. Acad. Sci. U. S. A. 115, 5211–5216. https://doi.org/10.1073/pnas.1714511115

Kirkwood, J.K., 2003. Introduction: Wildlife casualties and the veterinary surgeon, in: BSAVA Manual of Wildlife Casualties. BSAVA, Gloucester, pp. 1–4.

Kirkwood, J.K., 1992. Wild animal welfare, in: Ryder, R.D. (Ed.), Animal Welfare and the Environment. Gerald Duckworth and Co Ltd, London, UK, pp. 139–154.

Kirkwood, J.K., Best, R., 1998. Treatment and rehabilitation of wildlife casualties: Legal and ethical aspects. In Pract. 20, 214–216. https://doi.org/10.1136/inpract.20.4.214

Kirkwood, J.K., Sainsbury, A.W., 1996. Ethics of interventions for the welfare of free-living wild animals. Anim. Welf. 5, 235–243.

Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E.D., Clough, Y., Díaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovács, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2012. On the relationship between farmland biodiversity and land-use intensity in Europe. Proc. R. Soc. B Biol. Sci. 276, 903–909. https://doi.org/10.1098/rspb.2008.1509

Kristiansson, H., 1990. Population variables and causes of mortality in a hedgehog (Erinaceus europaeus) population in Southern Sweden. J. Zool. 220, 391–404.

Kristiansson, H., 1984. Ecology of a Hedgehog (Erinaceus europaeus) Population in Southern Sweden. PhD Thesis. University of Lund, Sweden.

Kuhn, C.E., Johnson, D.S., Ream, R.R., Gelatt, T.S., 2009. Advances in the tracking of marine species: Using GPS locations to evaluate satellite track data and a continuous-time movement model. Mar. Ecol. Prog. Ser. 393, 97–109. https://doi.org/10.3354/meps08229

Lal, R., 2001. Soil degradation by erosion. L. Degrad. Dev. 12, 519–539. https://doi.org/10.1002/ldr.472

Lane, J.E., 2012. Evolutionary Ecology of Mammalian Hibernation Phenology, in: Ruf, T., Bieber, C., Arnold, W., Millesi, E. (Eds.), Living in a Seasonal World. Springer, Berlin, Germany, pp. 51–61. https://doi.org/10.1007/978-3-642-28678-0

Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie, J.O., Dobson, F.S., 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature 489, 554–557. https://doi.org/10.1038/nature11335

Lane, J.M., McDonald, R.A., 2010. Welfare and "best practice" in field studies of wildlife, in: Hubrecht, R.C., Kirkwood, J. (Eds.), The UFAW Handbook on the Care and Management of

Laboratory and Other Research Animals. John Wiley & Sons, Ltd, London, UK, pp. 92–106.

Langbein, J., Hutchings, M.R., Harris, S., Stoate, C., Tapper, S.C., Wray, S., 1999. Techniques for assessing the abundance of Brown Hares Lepus europaeus. Mamm. Rev. 29, 93–116. https://doi.org/10.1046/j.1365-2907.1999.00040.x

Langton, T., Beckett, C., Foster, J., 2001. Great Crested Newt Conservation Handbook, Froglife.

Lapini, L., 1999. Atelerix algirus, in: Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Kryštufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralík, V., Zima, J. (Eds.), The Atlas of European Mammals. Academic Press, London UK.

Laycock, H.F., Moran, D., Smart, J.C.R., Raffaelli, D.G., White, P.C.L., 2011. Evaluating the effectiveness and efficiency of biodiversity conservation spending. Ecol. Econ. 70, 1789–1796. https://doi.org/10.1016/j.ecolecon.2011.05.002

Lee, J.R., Raymond, B., Bracegirdle, T.J., Chadès, I., Fuller, R.A., Shaw, J.D., 2017. Climate change drives expansion of Antarctic ice-free habitat. Nature 547, 49–54. https://doi.org/10.1038/nature22996

Leigh, K.A., Dominick, M., 2015. An assessment of the effects of habitat structure on the scat finding performance of a wildlife detection dog. Methods Ecol. Evol. 6, 745–752. https://doi.org/10.1111/2041-210X.12374

Leighton, K., Grogan, A., 2011. Factors affecting the likelihood of release of injured and orphaned woodpigeons (Columba palumbus). Anim. Welf. 20, 523–534.

Lesiński, G., Sikora, A., Olszewski, A., 2011. Bat casualties on a road crossing a mosaic landscape. Eur. J. Wildl. Res. 57, 217–223. https://doi.org/10.1007/s10344-010-0414-9

Lewis, J.C., Sallee, K.L., Golightly, R.T., 1999. Introduction and range expansion of non-native red foxes (Vulpes vulpes) in California. Am. Midl. Nat. 142, 372–381.

Lifson, N., Gordon, G.B., McClintock, R., 1955. Measurement of total carbon dioxide production by means of D2O18 1. J. Appl. Physiol. 7, 704–710. https://doi.org/https://doi.org/10.1152/jappl.1955.7.6.704

Lifson, N., McClintock, R., 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. J. Theor. Biol. 12, 46–74. https://doi.org/10.1016/0022-5193(66)90185-8

Long, J.L., 2003. Introduced Mammals of the World: Their History, Distribution and Influence. CSIRO Publishing, Victoria, Australia.

Long, R.A., Donovan, T.M., Mackay, P., Zielinski, W.J., Buzas, J.S., 2007. Effectiveness of scat detection dogs for detecting forest carnivores. J. Wildl. Manage. 71, 2007–2017. https://doi.org/10.2193/2006-230

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2, 191–198. https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2

Lord, R.D., Vilches, A.M., Maiztegui, J.I., Soldini, C.A., 1970. The tracking board: A relative census technique for studying rodents. J. Mammal. 51, 2828–823.

Lovegrove, R., 2007. Silent Fields: The Long Decline of a Nation's Wildlife. Oxford University Press, UK, Oxford, UK.

Loyd, K.A.T., Hernandez, S.M., Carroll, J.P., Abernathy, K.J., Marshall, G.J., 2013. Quantifying free-roaming domestic cat predation using animal-borne video cameras. Biol. Conserv. 160, 183–189. https://doi.org/10.1016/j.biocon.2013.01.008

Loyd, K.A.T., Hernandez, S.M., McRuer, D.L., 2017. The role of domestic cats in the admission of injured wildlife at rehabilitation and rescue centers. Wildl. Soc. Bull. 41, 55–61. https://doi.org/10.1002/wsb.737

Luck, G.W., 2007. A review of the relationships between human population density and biodiversity. Biol. Rev. 82, 607–645. https://doi.org/10.1111/j.1469-185X.2007.00028.x

Lunney, D., Gresser, S.M., Mahon, P.S., Matthews, A., 2004. Post-fire survival and reproduction of rehabilitated and unburnt koalas. Biol. Conserv. 120, 567–575. https://doi.org/10.1016/j.biocon.2004.03.029

Macdonald, D.W., Burnham, D., 2011. State of Britain's Mammals, 2011. People's Trust for Endangered Species, London.

Macdonald, D.W., Newman, C., 2002. Population dynamics of badgers (Meles meles) in Oxfordshire, UK: Numbers, density and cohort life histories, and a possible role of climate change in population growth. J. Zool. 256, 121–138. https://doi.org/10.1017/s0952836902000158

MacDonald, D.W., Tattersall, F.H., Service, K.M., Firbank, L.G., Feber, R.E., 2007. Mammals, agri-environment schemes and set-aside - What are the putative benefits? Mamm. Rev. 37, 259–277. https://doi.org/10.1111/j.1365-2907.2007.00100.x

Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: A multilayered relationship. Trends Ecol. Evol. 27, 19–25. https://doi.org/10.1016/j.tree.2011.08.006

Manly, B.F.L., McDonald, L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2007. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Springer Netherlands, Netherlands.

Martay, B., Brewer, M.J., Elston, D.A., Bell, J.R., Harrington, R., Brereton, T.M., Barlow, K.E., Botham, M.S., Pearce-Higgins, J.W., 2017. Impacts of climate change on national biodiversity population trends. Ecography (Cop.). 40, 1139–1151. https://doi.org/10.1111/ecog.02411

Martin, A.R., Da Silva, V.M.F., 1998. Tracking aquatic vertebrates in dense tropical forest using VHF telemetry. Mar. Technol. Soc. J. 32, 82–88.

Martínez, J.A., Martínez, J.E., Mañosa, S., Zuberogoitia, I., Calvo, J.F., 2006. How to manage human-induced mortality in the Eagle Owl Bubo bubo. Bird Conserv. Int. 16, 265–278. https://doi.org/10.1017/S0959270906000402

Martínez, J.C., Rosique, A.I., Royo, M.S., 2014. Causes of admission and final dispositions of hedgehogs admitted to three wildlife rehabilitation centers in eastern Spain. Hystrix 25, 107–110. https://doi.org/10.4404/hystrix-25.2-10248

Marzluff, John M, Knick, S.T., Millspaugh, Joshua J, 2001. High-Tech Behavioral Ecology: Modeling the Distribution of Animal Activities to Better Understand Wildlife Space Use and Resource Selection, in: Millspaugh, J.J., Marzluff, J.M. (Eds.), Radio Tracking and Animal Populations. Academic Press, London, UK, pp. 309–326. https://doi.org/10.1016/B978-012497781-5/50006-2

Mathews, F., Kubasiewicz, L.M., Gurnell, J., Harrower, C.A., McDonald, R.A., Shore, R.F., 2018. A Review of the Population and Conservation Status of British Mammals. A report by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough, UK.

Mathews, F., Swindells, M., Goodhead, R., August, T.A., Hardman, P., Linton, D.M., Hosken, D.J., 2013. Effectiveness of search dogs compared with human observers in locating bat carcasses at wind-turbine sites: a blinded randomized trial. Wildl. Soc. Bull. 37, 34–40. https://doi.org/10.1002/wsb.256

Matsushita, K., Yamane, F., Asano, K., 2016. Linkage between crop diversity and agro-ecosystem resilience: Nonmonotonic agricultural response under alternate regimes. Ecol. Econ. 126, 23–31. https://doi.org/10.1016/j.ecolecon.2016.03.006

Mawdsley, J.R., O'Malley, R., Ojima, D.S., 2009. A review of climate-change adaptation strategies for wildlife management and biodiversity conservation. Conserv. Biol. 23, 1080–1089. https://doi.org/10.1111/j.1523-1739.2009.01264.x

Maxwell, S.L., Fuller, R.A., Brooks, T.M., Watson, J.E.M., 2016. Biodiversity: The ravages of guns, nets and bulldozers. Nature 536, 143–145. https://doi.org/10.1038/536143a

Mayer, W. V., 1957. A method for determining the activity of burrowing mammals. J. Mammology 38, 531.

Mayle, B.A., Peace, A.J., Gill, R.M.A., 1999. How Many Deer? A Field Guide to Estimating Deer Population Size. Forestry Commission, Edinburgh, UK. https://doi.org/10.1038/250530e0

McCarthy, D.P., Donald, P.F., Scharlemann, J.P.W., Buchanan, G.M., Balmford, A., Green, J.M.H., Bennun, L.A., Burgess, N.D., Fishpool, L.D.C., Garnett, S.T., Leonard, D.L., Maloney, R.F., Morling, P., Schaefer, H.M., Symes, A., Wiedenfeld, D.A., Butchart, S.H.M., 2012. Financial costs of meeting global biodiversity conservation targets: Current spending and unmet needs. Science. 338, 946–949. https://doi.org/10.1126/science.1229803

McCarty, J.P., 2001. Ecological consequences of recent climate change. Conserv. Biol. 15, 320–331. https://doi.org/10.1046/j.1523-1739.2001.015002320.x

McClean, S.A., Rumble, M.A., King, R.M., Baker, W.L., 1998. Evaluation of Resource Selection Methods with Different Definitions of Availability. J. Wildl. Manage. 62, 793. https://doi.org/10.2307/3802356

McDonald, R.A., Harris, S., 1999. The use of trapping records to monitor populations of stoats Mustela erminea and weasels M. nivalis: The importance of trapping effort. J. Appl. Ecol. 36, 679–688. https://doi.org/10.1046/j.1365-2664.1999.00433.x

McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127, 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

Mcruer, D.L., Gray, L.C., Horne, L.A., Clark, E.E., 2017. Free-roaming cat interactions with wildlife admitted to a wildlife hospital. J. Wildl. Manage. 81, 163–173. https://doi.org/10.1002/jwmg.21181

Meek, W.R., Burman, P.J., Sparks, T.H., Nowakowski, M., Burman, N.J., 2012. The use of Barn Owl Tyto alba pellets to assess population change in small mammals. Bird Study 59, 166–174. https://doi.org/10.1080/00063657.2012.656076

Micol, T., Doncaster, C.P., Mackinlay, L.A., 1994. Correlates of local variation in the abundance of hedgehogs Erinaceus europaeus. J. Anim. Ecol. 63, 851–860. https://doi.org/10.2307/5262

Middleton, A.D., 1935. The food of a badger (Meles meles). J. Anim. Ecol. 4, 567–580.

Mikkola, H., Tornberg, R., 2014. Sex-specific diet analysis of the Eurasian Eagle Owl in Finland. Ornis Fenn. 91, 195–200.

Millennium Ecosystem Assessment (MEA), 2005. Millennium ecosystem assessment: ecosystems and human well-being. Island Press, Washington, DC.

Miller, E.A. (ed), 2012. Minimum Standards for Wildlife Rehabilitation, 4th ed. National Wildlife Rehabilitators Association, St. Cloud, MN.

Molina-López, R.A., Casal, J., Darwich, L., 2011. Causes of morbidity in wild raptor populations admitted at a wildlife rehabilitation centre in Spain from 1995-2007: A long term retrospective study. PLoS One 6. https://doi.org/10.1371/journal.pone.0024603

Molina-López, R.A., Mañosa, S., Torres-Riera, A., Pomarol, M., Darwich, L., 2017. Morbidity, outcomes and cost-benefit analysis of wildlife rehabilitation in Catalonia (Spain). J. Wildl. Rehabil. 38, 17–30.

Molony, S.E., Baker, P.J., Garland, L., Cuthill, I.C., Harris, S., 2007. Factors that can be used to predict release rates for wildlife casualties. Anim. Welf. 16, 361–367.

Molony, S.E., Dowding, C.V., Baker, P.J., Cuthill, I.C., Harris, S., 2006. The effect of translocation and temporary captivity on wildlife rehabilitation success: An experimental study using European hedgehogs (Erinaceus europaeus). Biol. Conserv. 130, 530–537. https://doi.org/10.1016/j.biocon.2006.01.015

Monadjem, A., Botha, A., Murn, C., 2013. Survival of the African white-backed vulture Gyps africanus in north-eastern South Africa. Afr. J. Ecol. 51, 87–93. https://doi.org/10.1111/aje.12009

Monclús, R., Rödel, H.G., Palme, R., Von Holst, D., De Miguel, J., 2006. Non-invasive measurement of the physiological stress response of wild rabbits to the odour of a predator. Chemoecology 16, 25–29. https://doi.org/10.1007/s00049-005-0324-6

Montesdeoca, N., Calabuig, P., Corbera, J.A., Oros, J., 2017. A long-term retrospective study on rehabilitation of seabirds in Gran Canaria Island, Spain (2003-2013). PLoS One 12, 1–17. https://doi.org/10.1371/journal.pone.0177366

Moore, N.W., 1962. The heaths of Dorset and their conservation. J. Ecol. 50, 367–391.

Moorhouse, T.P., Palmer, S.C.F., Travis, J.M.J., Macdonald, D.W., 2014. Hugging the hedges: Might agri-environment manipulations affect landscape permeability for hedgehogs? Biol. Conserv. 176, 109–116. https://doi.org/10.1016/j.biocon.2014.05.015

Morner, T., 2002. Health monitoring and conservation of wildlife in Sweden and Northern Europe. Ann. N. Y. Acad. Sci. 969, 34–38.

Morris, P.A., 2018. Hedgehog. HarperCollins, London.

Morris, P.A., 2014. Hedgehogs, 4th ed. Whittet Books, Stansted, UK.

Morris, P.A., 1998. Hedgehog rehabilitation in perspective. Vet. Rec. 143, 633–636.

Morris, P.A., 1997. Released, rehabilitated hedgehogs: A follow-up study in Jersey. Anim. Welf. 6, 317–327.

Morris, P.A., 1988. A study of home range and movements in the hedgehog (Erinaceus europaeus). J. Zool. 214, 433–449. https://doi.org/10.1111/j.1469-7998.1988.tb03751.x

Morris, P.A., 1986. Nightly movements of hedgehogs (Erinaceus-europaeus) in forest edge habitat. Mammalia 50, 395–398. https://doi.org/10.1515/mamm.1986.50.3.391

Morris, P.A., 1984. An estimate of the minimum body weight necessary for hedgehogs (Erinaceus europaeus) to survive hibernation. J. Zool. 203, 291–294.

Morris, P.A., 1973. Winter nests of the hedgehog (Erinaceus europaeus L.). Oecologia 11, 299–313.

Morris, P.A., Reeve, N.J., 2008. Hedgehog Erinaceus europaeus, in: Harris, S., Yalden, D.W.

(Eds.), Mammals of the British Isles: Handbook. The Mammal Society, Southampton, pp. 241–249.

Morris, P.A., Warwick, H., 1994. A study of rehabilitated juvenile hedgehogs after release into the wild. Anim. Welf. 3, 163–177.

Müller, F., 2018. Langzeit-monitoring der Strassenverkehrsopfer beim Igel (Erinaceus europaeus L.) zur Indikation von Populationsdichte veränderungen entlang zweier Teststrecken im Landkreis Fulda. Beiträge zur Naturkd. Osthessen 54, 21–26.

Mullineaux, E., 2014. Veterinary treatment and rehabilitation of indigenous wildlife. J. Small Anim. Pract. 55, 293–300. https://doi.org/10.1111/jsap.12213

Mullineaux, E., Kidner, P., 2011. Managing public demand for badger rehabilitation in an area of England with endemic tuberculosis. Vet. Microbiol. 151, 205–208. https://doi.org/10.1016/j.vetmic.2011.02.045

Murray, J.K., Browne, W.J., Roberts, M.A., Whitmarsh, A., Gruffydd-Jones, T.J., 2010. Number and ownership profiles of cats and dogs in the UK. Vet. Rec. 166, 163–168. https://doi.org/10.1136/vr.b4712

Mwebi, O., Nguta, E., Onduso, V., Nyakundi, B., Jiang, X.L., Kioko, E., 2019. Small mammal diversity of Mt. Kenya based on carnivore fecal and surface bone remains. Zool. Res. 40, 61–69. https://doi.org/10.24272/j.issn.2095-8137.2018.055

Nagy, K.A., 2001. Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. Nutr. Abstr. Rev. Ser. B 71, 21R-31R.

National Research Council, 1992. Conserving Biodiversity: A Research Agenda for Development Agencies. The National Academies Press, Washington, DC. https://doi.org/10.17226/1925

Natural England, 2013. Entry Level Stewardship, 4th ed. Defra, Peterborough, UK.

Nelli, L., Langbein, J., Watson, P., Putman, R., 2018. Mapping risk: Quantifying and predicting the risk of deer-vehicle collisions on major roads in England. Mamm. Biol. 91, 71–78. https://doi.org/10.1016/j.mambio.2018.03.013

Neumann, S.L., 2010. Animal welfare volunteers: Who are they and why do they do what they do? Anthrozoos 23, 351–364. https://doi.org/10.2752/175303710X12750451259372

Newman, S.H., Ziccardi, M.H., Berkner, A.B., Holcomb, J., Clumpner, C., Mazet, J.A.K., 2003. A historical account of oiled wildlife care in California. Mar. Ornithol. 31, 59–64.

Newport, J., Shorthouse, D.J., Manning, A.D., 2014. The effects of light and noise from urban development on biodiversity: Implications for protected areas in Australia. Ecol. Manag. Restor. 15, 204–214. https://doi.org/10.1111/emr.12120

Nielsen, T.P., Jackson, G., Bull, C.M., 2016. A nose for lizards; can a detection dog locate the endangered pygmy bluetongue lizard (Tiliqua adelaidensis)? Trans. R. Soc. South Aust. 140, 234–243. https://doi.org/10.1080/03721426.2016.1218698

Nkem, J.N., de Bruyn, L.L., King, K., 2020. The effect of increasing topsoil disturbance and abundance under grazing and cropping regimes on Vertisols in north-west New South Wales, Australia. Insects 11, 1–17. https://doi.org/10.3390/insects11040237

Nolan, C., Overpeck, J.T., Allen, J.R.M., Anderson, P.M., Betancourt, J.L., Binney, H.A., Brewer, S., Bush, M.B., Chase, B.M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M.E., Gosling, W.D., Haberle, S., Hotchkiss, S.C., Huntley, B., Ivory, S.J., Kershaw, A.P., Kim, S.H., Latorre, C., Leydet, M., Lezine, A.M., Liu, K.B., Liu, Y., Lozhkin, A.V., McGlone, M.S., Marchant, R.A., Momohara, A., Moreno, P.I., Muller, S., Otto-Bliesner, B.L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P.E., Tipton, J., Vincens, A., Weng, C., Xu, Q., Zheng, Z., Jackson, S.T., 2018. Past and future global transformation of terrestrial ecosystems under climate change. Science. 361, 920–923. https://doi.org/10.1126/science.aan5360

Nottingham, C.M., Glen, A.S., Stanley, M.C., 2019. Snacks in the city: The diet of hedgehogs in Auckland urban forest fragments. N. Z. J. Ecol. 43. https://doi.org/10.20417/nzjecol.43.24

O’Connor, S., Park, K.J., Goulson, D., 2012. Humans versus dogs; A comparison of methods for the detection of bumble bee nests. J. Apic. Res. 51, 204–211. https://doi.org/10.3896/IBRA.1.51.2.09

Office for National Statistics, 2017. Total number of households by region and country of the UK, 1996 to 2017 [WWW Document]. URL https://www.ons.gov.uk/peoplepopulationandcommunity/birthsdeathsandmarriages/families/adhocs/005374totalnumberofhouseholdsbyregionandcountryoftheuk1996to2015 (accessed 1.6.20).

Oliver, T.H., Isaac, N.J.B., August, T.A., Woodcock, B.A., Roy, D.B., Bullock, J.M., 2015. Declining resilience of ecosystem functions under biodiversity loss. Nat. Commun. 6, 1–8.

https://doi.org/10.1038/ncomms10122

Öllerer, K., Varga, A., Kirby, K., Demeter, L., Biró, M., Bölöni, J., Molnár, Z., 2019. Beyond the obvious impact of domestic livestock grazing on temperate forest vegetation – A global review. Biol. Conserv. 237, 209–219. https://doi.org/10.1016/j.biocon.2019.07.007

Otto, S.B., Berlow, E.L., Rank, N.E., Smiley, J., Brose, U., 2008. Predator diversity and identity drive interaction strength and trophic cascades in a food web. Ecology 89, 888.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parris, K., 2011. Impact of agriculture on water pollution in OECD countries: Recent trends and future prospects. Int. J. Water Resour. Dev. 27, 33–52. https://doi.org/10.1080/07900627.2010.531898

Parrott, D., Etherington, T.R., Dendy, J., 2014. A geographically extensive survey of hedgehogs (Erinaceus europaeus) in England. Eur. J. Wildl. Res. 60, 399–403. https://doi.org/10.1007/s10344-014-0795-2

Parrott, D., Prickett, A., Pietravalle, S., Etherington, T.R., Fletcher, M., 2012. Estimates of regional population densities of badger Meles meles, fox Vulpes vulpes and hare Lepus europaeus using walked distance sampling. Eur. J. Wildl. Res. 58, 23–33. https://doi.org/10.1007/s10344-011-0536-8

Paula, J., Leal, M.C., Silva, M.J., Mascarenhas, R., Costa, H., Mascarenhas, M., 2011. Dogs as a tool to improve bird-strike mortality estimates at wind farms. J. Nat. Conserv. 19, 202–208. https://doi.org/10.1016/j.jnc.2011.01.002

Pearce-Higgins, J.W., Baillie, S.R., Boughey, K., Bourn, N.A.D., Foppen, R.P.B., Gillings, S., Gregory, R.D., Hunt, T., Jiguet, F., Lehikoinen, A., Musgrove, A.J., Robinson, R.A., Roy, D.B., Siriwardena, G.M., Walker, K.J., Wilson, J.D., 2018. Overcoming the challenges of public data archiving for citizen science biodiversity recording and monitoring schemes. J. Appl. Ecol. 55, 2544–2551. https://doi.org/10.1111/1365-2664.13180

Peterson, J.T., Dunham, J., 2003. Combining inferences from models of capture efficiency, detectability, and suitable habitat to classify landscapes for conservation of threatened bull trout. Conserv. Biol. 17, 1070–1077. https://doi.org/10.1046/j.1523-1739.2003.01579.x

Pettett, C.E., 2015. Factors affecting hedgehog distribution and habitat selection in the rural landscapes. PhD Thesis. University of Oxford, Oxford, UK.

Pettett, C.E., Johnson, P.J., Moorhouse, T.P., Hambly, C., Speakman, J.R., Macdonald, D.W., 2017a. Daily energy expenditure in the face of predation: Hedgehog energetics in rural landscapes. J. Exp. Biol. 220, 460–468. https://doi.org/10.1242/jeb.150359

Pettett, C.E., Johnson, P.J., Moorhouse, T.P., Macdonald, D.W., 2018. National predictors of hedgehog Erinaceus europaeus distribution and decline in Britain. Mamm. Rev. 48, 1–6. https://doi.org/10.1111/mam.12107

Pettett, C.E., Moorhouse, T.P., Johnson, P.J., Macdonald, D.W., 2017b. Factors affecting hedgehog (Erinaceus europaeus) attraction to rural villages in arable landscapes. Eur. J. Wildl. Res. 63, 54. https://doi.org/10.1007/s10344-017-1113-6

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of Intra-guild Predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297–330.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., Curtis, P.D., 1989. Survival analysis in telemetry studies: The staggered entry design. J. Wildl. Manage. 53, 7–15.

Poulton, S.M.C., Reeve, N.J., 2010. A pilot study of a method to monitor hedgehogs (Erinaceus europaeus). Mammal Notes Autumn, 1–4.

Putman, R.J., 1995. Ethical considerations and animal welfare in ecological field studies. Biodivers. Conserv. 4, 903–915. https://doi.org/10.1007/BF00056197

Pyke, G.H., Szabo, J.K., 2018. What can we learn from untapped wildlife rescue databases? The masked lapwing as a case study. Pacific Conserv. Biol. 24, 148–156. https://doi.org/10.1071/PC18003

Pyke, G.H., Szabo, J.K., 2017. Conservation and the four Rs, which are rescue, rehabilitation, release, and research. Conserv. Biol. 32, 50–59. https://doi.org/10.1111/cobi.12937

R Core Team, 2016. R: A language and environment for statistical computing [WWW Document]. URL www.r-project.org/

Randall, N.J., Blitvich, B.J., Blanchong, J.A., 2012. Efficacy of wildlife rehabilitation centers in surveillance and monitoring of pathogen activity: A case study with west Nile virus. J. Wildl. Dis. 48, 646–653. https://doi.org/10.7589/0090-3558-48.3.646

Rasmussen, S.L., Berg, T.B., Dabelsteen, T., Jones, O.R., 2019a. The ecology of suburban juvenile European hedgehogs (Erinaceus europaeus) in Denmark. Ecol. Evol. 9, 13174–13187. https://doi.org/10.1002/ece3.5764

Rasmussen, S.L., Larsen, J., Van Wijk, R.E., Jones, O.R., Berg, T.B., Angen, O., Larsen, A.R., 2019b. European hedgehogs (Erinaceus europaeus) as a natural reservoir of methicillin-resistant Staphylococcus aureus carrying mecC in Denmark. PLoS One 14, 1–13. https://doi.org/10.1371/journal.pone.0222031

Rast, W., Barthel, L.M.F., Berger, A., 2019. Music festival makes hedgehogs move: How individuals cope behaviorally in response to human-induced stressors. Animals 9, 455. https://doi.org/10.3390/ani9070455

Rautio, A., Isomursu, M., Valtonen, A., Hirvelä-Koski, V., Kunnasranta, M., 2016. Mortality, diseases and diet of European hedgehogs (Erinaceus europaeus) in an urban environment in Finland. Mammal Res. 61, 161–169. https://doi.org/10.1007/s13364-015-0256-7

Rautio, A., Valtonen, A., Auttila, M., Kunnasranta, M., 2014. Nesting patterns of European hedgehogs (Erinaceus europaeus) under northern conditions. Acta Theriol. (Warsz). 59, 173–181.

Rautio, A., Valtonen, A., Kunnasranta, M., 2013. The effects of sex and season on home range in European Hedgehogs at the northern edge of the species range. Ann. Zool. Fennici 50, 107–123. https://doi.org/10.5735/086.050.0110

Recio, M.R., Mathieu, R., Seddon, P.J., 2011. Design of a GPS backpack to track European hedgehogs Erinaceus europaeus. Eur. J. Wildl. Res. 57, 1175–1178. https://doi.org/10.1007/s10344-011-0530-1

Redpath, S., Clarke, R., Madders, M., Thirgood, S.J., 2001. Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. Condor 103, 184–188. https://doi.org/10.1650/0010-5422(2001)103

Reeve, N.J., 1998. The survival and welfare of hedgehogs (Erinaceus europaeus) after release back into the wild. Anim. Welf. 7, 189–202.

Reeve, N.J., 1994. Hedgehogs. T & AD Poyser Ltd., London, UK.

Reeve, N.J., Bowen, C., Gurnell, J., 2019. An improved identification marking method for hedgehogs. Mammal Commun. 5, 1–5.

Reeve, N.J., Huijser, M.P., 1999. Mortality factors affecting wild hedgehogs: a study of records from wildlife rescue centres. Lutra 42, 7–24.

Reeve, N.J., Morris, P.A., 1985. Construction and use of summer nests by the hedgehog. Mammalia 49, 187–194.

Riber, A., 2006. Habitat use and behaviour of European hedgehog Erinaceus europaeus in a Danish rural area. Acta Theriol. (Warsz). 51, 363–371. https://doi.org/10.1007/BF03195183

Robertson, C.P.., Harris, S., 1995. The behaviour after release of captive-reared fox cubs. Anim. Welf. 4, 295–306.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157–176. https://doi.org/10.1046/j.1365-2664.2002.00695.x

Robinson, T.P., Wint, G.R.., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D’Aietti, L., Hay, S.I., Gilbert, M., 2014. Mapping the global distribution of livestock. PLoS One 9. https://doi.org/10.1371/journal.pone.0096084

Rodríguez, A., Rodríguez, B., Lucas, M.P., 2012. Trends in numbers of petrels attracted to artificial lights suggest population declines in Tenerife, Canary Islands. Ibis (Lond. 1859). 154, 167–172. https://doi.org/10.1111/j.1474-919X.2011.01175.x

Rondinini, C., Doncaster, C.P., 2002. Roads as barriers to movement for hedgehogs. Funct. Ecol. 16, 504–509. https://doi.org/10.1046/j.1365-2435.2002.00651.x

Roos, S., Johnston, A., Noble, D.G., 2012. UK Hedgehog Datasets and their Potential for Long-Term Monitoring. British Trust for Ornithology, Thetford, UK.

Roper, T.J., 2010. Badger. HarperCollins, London.

Ropert-Coudert, Y., Wilson, R.P., 2005. Trends and perspectives in animal-attached remote sensing. Front. Ecol. Environ. 3, 437–444. https://doi.org/10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2

RSPCA, 2013. RSPCA wildlife rehabilitation protocol: hedgehogs. RSPCA, Southwater, UK.

Ruf, T., Geiser, F., 2015. Daily torpor and hibernation in birds and mammals. Biol. Rev. 90, 891–926. https://doi.org/10.1111/brv.12137

Sabol, B.M., Hudson, M.K., 1995. Technique Using Thermal Infrared-Imaging for Estimating Populations of Gray Bats. J. Mammal. 76, 1242–1248.

Sainsbury, A.W., Cunningham, A.A., Morris, P.A., Kirkwood, J.K., Macgregor, S.K., 1996. Health and welfare of rehabilitated juvenile hedgehogs (Erinaceus europaeus) before and after release into the wild. Vet. Rec. 138, 61–5. https://doi.org/10.1136/vr.138.3.61

Sala, O.E., Iii, F.C., Armesto, J.J., Berlow, E., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Robert, B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2017. Global biodiversity scenarios for the year 2100. Science. 287, 1770–1775.

Saldanha, I.F., Lawson, B., Goharriz, H., Rodriguez-Ramos Fernandez, J., John, S.K., Fooks, A.R., Cunningham, A.A., Johnson, N., Horton, D.L., 2019. Extension of the known distribution of a novel clade C betacoronavirus in a wildlife host. Epidemiol. Infect. 147, 1–8. https://doi.org/10.1017/S0950268819000207

Sánchez-Barbudo, I.S., Camarero, P.R., Mateo, R., 2012. Primary and secondary poisoning by anticoagulant rodenticides of non-target animals in Spain. Sci. Total Environ. 420, 280–288. https://doi.org/10.1016/j.scitotenv.2012.01.028

Sangster, L., Blake, D.P., Robinson, G., Hopkins, T.C., Sa, R.C.C., Cunningham, A.A., Chalmers, R.M., Lawson, B., 2016. Detection and molecular characterisation of Cryptosporidium parvum in British European hedgehogs (Erinaceus europaeus). Vet. Parasitol. 217, 39–44. https://doi.org/10.1016/j.vetpar.2015.12.006

Santilli, F., Galardi, L., 2016. Effect of habitat structure and type of farming on European hare (Lepus europaeus) abundance. Hystrix 27, 1–3. https://doi.org/10.4404/hystrix-27.2-11974

Sapolsky, R.M., Romero, L.M., Munck, A.U., 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr. Rev. 21, 55–89. https://doi.org/10.1210/er.21.1.55

Schaus, J., Uzal, A., Gentle, L.K., Baker, P.J., Bearman-Brown, L.E., Bullion, S., Gazzard, A., Lockwood, H., North, A., Reader, T., Scott, D.M., Sutherland, C.S., Yarnell, R.W., 2020. Application of the Random Encounter Model in citizen science projects to monitor animal densities. Remote Sens. Ecol. Conserv. 10.1002/rse2.153. https://doi.org/10.1002/rse2.153

Schenk, A.N., Souza, M.J., 2014. Major anthropogenic causes for and outcomes of wild animal presentation to a wildlife clinic in East Tennessee, USA, 2000-2011. PLoS One 9, 1–3. https://doi.org/10.1371/journal.pone.0093517

Schindler, D.W., Lee, P.G., 2010. Comprehensive conservation planning to protect biodiversity and ecosystem services in Canadian boreal regions under a warming climate and increasing exploitation. Biol. Conserv. 143, 1571–1586. https://doi.org/10.1016/j.biocon.2010.04.003

Schipper, J., Chanson, J.S., Chiozza, F., Cox, N.A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A.S.L., Stuart, S.N., Temple, H.J., Baillie, J., Boitani, L., Lacher, T.E., Mittermeier, R.A., Smith, A.T., Absolon, D., Aguiar, J.M., Amori, G., Bakkour, N., Baldi, R., Berridge, R.J., Bielby, J., Black, P.A., Blanc, J.J., Brooks, T.M., Burton, J.A., Butynski, T.M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J.G., Da Fonseca, G.A.B., Derocher, A.E., Dublin, H.T., Duckworth, J.W., Emmons, L., Emslie, R.H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D.L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J.F., Good, T.C., Hammerson, G., Hammond, P.S., Happold, D., Happold, M., Hare, J., Harris, R.B., Hawkins, C.E., Haywood, M., Heaney, L.R., Hedges, S., Helgen, K.M., Hilton-Taylor, C., Hussain, S.A., Ishii, N., Jefferson, T.A., Jenkins, R.K.B., Johnston, C.H., Keith, M., Kingdon, J., Knox, D.H., Kovacs, K.M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L.F., Macavoy, Z., Mace, G.M., Mallon, D.P., Masi, M., McKnight, M.W., Medellín, R.A., Medici, P., Mills, G., Moehlman, P.D., Molur, S., Mora, A., Nowell, K., Oates, J.F., Olech, W., Oliver, W.R.L., Oprea, M., Patterson, B.D., Perrin, W.F., Polidoro, B.A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R.R., Reilly, S.B., Reynolds, J.E., Rondinini, C., Rosell-Ambal, R.G., Rulli, M., Rylands, A.B., Savini, S., Schank, C.J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., De Silva, N., Smith, D.E., Srinivasulu, C., Stephenson, P.J., Van Strien, N., Talukdar, B.K., Taylor, B.L., Timmins, R., Tirira, D.G., Tognelli, M.F., Tsytsulina, K., Veiga, L.M., Vié, J.C., Williamson, E.A., Wyatt, S.A., Xie, Y., Young, B.E., 2008. The status of the world's land and marine mammals: Diversity, threat, and knowledge. Science. 322, 225–230. https://doi.org/10.1126/science.1165115

Schulte, P., Alegret, L., Arenillas, I., Arz, J.A., Barton, P.J., Bown, P.R., Bralower, T.J., Christeson, G.L., Claeys, P., Cockell, C.S., Collins, G.S., Deutsch, A., Goldin, T.J., Goto, K., Grajales-Nishimura, J.M., Grieve, R.A.F., Gulick, S.P.S., Johnson, K.R., Kiessling, W., Koeberl, C., Kring, D.A., MacLeod, K.G., Matsui, T., Melosh, J., Montanari, A., Morgan, J.V., Neal, C.R., Nichols, D.J., Norris, R.D., Pierazzo, E., Ravizza, G., Rebolledo-Vieyra, M., Reimold, W.U., Robin, E., Salge, T., Speijer, R.P., Sweet, A.R., Urrutia-Fucugauchi, J., Vajda, V., Whalen, M.T., Willumsen, P.S., 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. Science. 327, 1214–1218. https://doi.org/10.1126/science.1177265

Schwartz, J.W., Hopkins, M.E., Hopkins, S.L., 2016. Group Prerelease Training Yields Positive Rehabilitation Outcomes Among Juvenile Mantled Howlers (Alouatta palliata). Int. J. Primatol. 37, 260–280. https://doi.org/10.1007/s10764-016-9900-6

Scott, D.M., Berg, M.J., Tolhurst, B.A., Chauvenet, A.L.M., Smith, G.C., Neaves, K., Lochhead, J., Baker, P.J., 2014. Changes in the distribution of red foxes (Vulpes vulpes) in urban areas in Great Britain: Findings and limitations of a media-driven nationwide survey. PLoS One 9, e99059. https://doi.org/10.1371/journal.pone.0099059

Seiler, A., Helldin, J.-O., Seiler, C., 2004. Road mortality in Swedish mammals: results of a drivers' questionnaire. Wildlife Biol. 10, 225–233. https://doi.org/10.2981/wlb.2004.028

Senapathi, D., Nicoll, M.A.C., Teplitsky, C., Jones, C.G., Norris, K., 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. Proc. R. Soc. B Biol. Sci. 278, 3184–3190. https://doi.org/10.1098/rspb.2011.0212

Sergio, F., Marchesi, L., Pedrini, P., 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. J. Anim. Ecol. 72, 232–245. https://doi.org/10.1046/j.1365-2656.2003.00693.x

Seto, K.C., Fragkias, M., Guneralp, B., Reilly, M.K., 2011. A meta-analysis of global urban land expansion. PLoS One 6, e23777. https://doi.org/10.1371/ journal.pone.0023777

Sikes, R.S., Gannon, W.L., 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. 92, 235–253. https://doi.org/10.1644/10-mamm-f-355.1

Silpa, M.A.C., Thornton, S.M., Cooper, T., Hedley, J., 2015. Prevalence of presenting conditions in grey seal pups (Halichoerus grypus) admitted for rehabilitation. Vet. Sci. 2, 1–11. https://doi.org/10.3390/vetsci2010001

Sinclair, A.R.E., Pech, R.P., 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75, 164–173.

Smigaj, M., Gaulton, R., Barr, S.L., Suárez, J.C., 2015. UAV-Borne thermal imaging for forest health monitoring: Detection Of disease-induced canopy temperature increase. Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci. - ISPRS Arch. 40, 349–354. https://doi.org/10.5194/isprsarchives-XL-3-W3-349-2015

Smith, C., 2008. London: Garden City? London Wildlife Trust, London, UK.

Smith, D.A., Ralls, K., Cypher, B.L., Maldonado, J.E., 2005. Assessment of scat-detection dog surveys to determine kit fox distribution. Wildl. Soc. Bull. 33, 897–904. https://doi.org/10.2193/0091-7648(2005)33[897:aosdst]2.0.co;2

Smith, T.S., Amstrup, S.C., Kirschhoffer, B.J., York, G., 2020. Efficacy of aerial forward-looking infrared surveys for detecting polar bear maternal dens. PLoS One 15, 1–10. https://doi.org/10.1371/journal.pone.0222744

Soorae, P.S., 2013. Global Re-introduction Perspectives: 2013; Further case studies from around the globe. IUCN/SSC Reintroduction Specialist Group, Gland, Switzerland.

Stanley, M.C., Beggs, J.R., Bassett, I.E., Burns, B.R., Dirks, K.N., Jones, D.N., Linklater, W.L., Macinnis-Ng, C., Simcock, R., Souter-Brown, G., Trowsdale, S.A., Gaston, K.J., 2015. Emerging threats in urban ecosystems: A horizon scanning exercise. Front. Ecol. Environ. 13, 553–560. https://doi.org/10.1890/150229

Stanton, R.L., Morrissey, C.A., Clark, R.G., 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: A review. Agric. Ecosyst. Environ. 254, 244–254. https://doi.org/10.1016/j.agee.2017.11.028

Staples, J.F., 2014. Metabolic suppression in mammalian hibernation: The role of mitochondria. J. Exp. Biol. 217, 2032–2036. https://doi.org/10.1242/jeb.092973

Statista, 2020. United Kingdom: Degree of urbanisation from 2009 to 2019 [WWW Document]. URL https://www.statista.com/statistics/270369/urbanization-in-the-united-kingdom/

Stevenson, D.J., Ravenscoft, K.R., Zappalorti, R.T., Ravenscroft, M.D., Weigley, S.W., Jenkins, C.L., 2010. Using a wildlife detector dog for locating Eastern Indigo snakes (Drymarchon couperi). Herpetol. Rev. 41, 2006.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., Snoo, G.R. d., de Snoo, G.R., Rakosy, L., Ramwell, C., 2009. Ecological impacts of early 21st century agricultural change in Europe - A review. J. Environ. Manage. 91, 22–46. https://doi.org/10.1016/j.jenvman.2009.07.005

Stocker, L., 2005. Practical Wildlife Care. Blackwell Publishing Ltd, Oxford.

Storm, D.J., Samuel, M.D., Van Deelen, T.R., Malcolm, K.D., Rolley, R.E., Frost, N.A., Bates, D.P., Richards, B.J., 2011. Comparison of visual-based helicopter and fixed-wing forward-looking infrared surveys for counting white-tailed deer Odocoileus virginianus . Wildlife Biol. 17, 431–440. https://doi.org/10.2981/10-062

Stroh, P.A., Leach, S.J., August, T.A., Walker, K.J., Pearman, D.A., Rumsey, F.J., Harrower, C.A., Fay, M.F., Martin, J.P., Pankhurst, T., Preston, C.D., Taylor, I., 2014. A Vascular Plant Red List for England. Botanical Society of Britain and Ireland, Bristol.

Sutherland, W.J. (Ed.), 2013. Ecological Census Techniques: A Handbook, 2nd ed. Cambridge University Press, Cambridge, UK.

Sutherland, W.J., Armstrong-Brown, S., Armsworth, P.R., Brereton, T., Brickland, J., Campbell, C.D., Chamberlain, D.E., Cooke, A.I., Dulvy, N.K., Dusic, N.R., Fitton, M., Freckleton, R.P., Godfray, H.C.J., Grout, N., Harvey, H.J., Hedley, C., Hopkins, J.J., Kift, N.B., Kirby, J., Kunin, W.E., Macdonald, D.W., Marker, B., Naura, M., Neale, A.R., Oliver, T., Osborn, D., Pullin, A.S., Shardlow, M.E.A., Showler, D.A., Smith, P.L., Smithers, R.J., Solandt, J.L., Spencer, J., Spray, C.J., Thomas, C.D., Thompson, J., Webb, S.E., Yalden, D.W., Watkinson, A.R., 2006. The identification of 100 ecological questions of high policy relevance in the UK. J. Appl. Ecol. 43, 617–627. https://doi.org/10.1111/j.1365-2664.2006.01188.x

Tähti, H., Soivio, A., 1977. Respiratory and circulatory differences between induced and spontaneous arousals in hibernating hedgehogs (Erinaceus europaeus L .). Ann. Zool. Fennici 14, 198–203.

Tapper, S.S., 1992. Game Heritage: An Ecological Review from Shooting and Gamekeeping Records. Game Conservancy Ltd, Fordingbridge, Hampshire, UK.

Taylor-Brown, A., Booth, R., Gillett, A., Mealy, E., Ogbourne, S.M., Polkinghorne, A., Conroy, G.C., 2019. The impact of human activities on Australian wildlife. PLoS One 14, 1–28. https://doi.org/10.1371/journal.pone.0206958

Tejera, G., Rodríguez, B., Armas, C., Rodríguez, A., 2018. Wildlife-vehicle collisions in lanzarote biosphere reserve, Canary Islands. PLoS One 13, e0192731.

https://doi.org/10.1371/journal.pone.0192731

Telfer, S., Lambin, X., Birtles, R., Beldomenico, P., Burthe, S., Paterson, S., Begon, M., 2010. Species interactions in a parasite community drive infection risk in a wildlife population. Science. 330, 243–246. https://doi.org/10.1126/science.1190333.Species

The Mammal Society, 2020. Red List for Britain's Mammals [WWW Document]. URL https://www.mammal.org.uk/science-research/red-list/ (accessed 7.30.20).

Thebault, E., Loreau, M., 2003. Food-web constraints on biodiversity–ecosystem functioning relationships. Proc. Natl. Acad. Sci. 100, 14949–14954.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Letter to nature: Extinction risk from climate change. Nature 427, 145–148.

Thomas, E., Wilson, E., 2018. Guidance for Surveying Hedgehogs. Hedgehog Street, London, UK.

Thomas, M.J., Peterson, M.L., Friedenberg, N., van Eenennaam, J.P., Johnson, J.R., Hoover, J.J., Klimley, A.P., 2013. Stranding of spawning run green sturgeon in the Sacramento river: Post-rescue movements and potential population-level effects. North Am. J. Fish. Manag. 33, 287–297. https://doi.org/10.1080/02755947.2012.758201

Thomas, M.L., Baker, L., Beattie, J.R., Baker, A.M., 2020. Determining the efficacy of camera traps, live capture traps, and detection dogs for locating cryptic small mammal species. Ecol. Evol. 10, 1054–1068. https://doi.org/10.1002/ece3.5972

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U. S. A. 108, 20260–20264. https://doi.org/10.1073/pnas.1116437108

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science. 292, 281–284. https://doi.org/10.1126/science.1057544

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, L., Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, H.D., Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch, T.L., Höft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., Loh, J., Lojenga, R.K., Malsch, K., Marques, A., Morgan, D.H.W., Mumby, P.J., Newbold, T., Noonan-Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, T., Rondinini, C., Santini, L., Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., Teh, L.S.L., Van Kolck, J., Visconti, P., Ye, Y., 2014. A mid-term analysis of progress toward international biodiversity targets. Science. 346, 241–244. https://doi.org/10.1126/science.1257484

Trewby, I.D., Wilson, G.J., Delahay, R.J., Walker, N., Young, R.P., Davison, J., Cheeseman, C., Robertson, P.A., Gorman, M.L., Mcdonald, R.A., 2008. Experimental evidence of competitive release in sympatric carnivores. Biol. Lett. 4, 170–172. https://doi.org/10.1098/rsbl.2007.0516

Trewby, I.D., Young, R.P., McDonald, R.A., Wilson, G.J., Davison, J., Walker, N., Robertson, P.A., Doncaster, C.P., Delahay, R.J., 2014. Impacts of removing badgers on localised counts of hedgehogs. PLoS One 9, 2–5. https://doi.org/10.1371/journal.pone.0095477

Tribe, A., Brown, P.R., 2000. The role of wildlife rescue groups in the care and rehabilitation of Australian fauna. Hum. Dimens. Wildl. 5, 69–85. https://doi.org/10.1080/10871200009359180

Trocini, S., Pacioni, C., Warren, K., Butcher, J., Robertson, I., 2008. Wildlife disease passive surveillance: The potential role of wildlife rehabilitation centres, in: Proceedings of the National Wildlife Rehabilitation Conference. pp. 1–5.

Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151, 53–59. https://doi.org/10.1016/j.biocon.2012.01.068

Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis. J. Appl. Ecol. 51, 746–755. https://doi.org/10.1111/1365-2664.12219

Turbill, C., Bieber, C., Ruf, T., 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. Proc. R. Soc. B Biol. Sci. 278, 3355–3363. https://doi.org/10.1098/rspb.2011.0190

Tyrrell, C.L., Christy, M.T., Rodda, G.H., Yackel Adams, A.A., Ellingson, A.R., Savidge, J.A., Dean-Bradley, K., Bischof, R., 2009. Evaluation of trap capture in a geographically closed population of brown treesnakes on Guam. J. Appl. Ecol. 46, 128–135. https://doi.org/10.1111/j.1365-2664.2008.01591.x

UK National Ecosystem Assessment, 2014. UK National Ecosystem Assessment Follow on: Synthesis iof the Key Findings. UNEP-WCMC, LWEC, UK.

United Nations, 2019. World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420), Demographic Research. New York. https://doi.org/10.4054/demres.2005.12.9

Urban, M.C., 2015. Accelerating extinction risk from climate change. Science. 348, 571–573. https://doi.org/10.1126/science.aaa4984 This

Uzal, A., Walls, S., Stillman, R.A., Diaz, A., 2013. Sika deer distribution and habitat selection: The influence of the availability and distribution of food, cover, and threats. Eur. J. Wildl. Res. 59, 563–572. https://doi.org/10.1007/s10344-013-0705-z

Van de Poel, J.L., Dekker, J., Langevelde, F.V., 2015. Dutch hedgehogs Erinaceus europaeus are nowadays mainly found in urban areas, possibly due to the negative effects of badgers Meles meles. Wildlife Biol. 21, 51–55. https://doi.org/10.2981/wlb.00072

van Eeden, L.M., Crowther, M.S., Dickman, C.R., Macdonald, D.W., Ripple, W.J., Ritchie, E.G., Newsome, T.M., 2018a. Managing conflict between large carnivores and livestock. Conserv. Biol. 32, 26–34. https://doi.org/10.1111/cobi.12959

van Eeden, L.M., Eklund, A., Miller, J.R.B., López-Bao, J.V., Chapron, G., Cejtin, M.R., Crowther, M.S., Dickman, C.R., Frank, J., Krofel, M., Macdonald, D.W., McManus, J., Meyer, T.K., Middleton, A.D., Newsome, T.M., Ripple, W.J., Ritchie, E.G., Schmitz, O.J., Stoner, K.J., Tourani, M., Treves, A., 2018b. Carnivore conservation needs evidence-based livestock protection. PLoS Biol. 16, 1–8. https://doi.org/10.1371/journal.pbio.2005577 van Heezik, Y., Freeman, C., Porter, S., Dickinson, K.J.M., 2013. Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. Ecosystems 16, 1442–1454. https://doi.org/10.1007/s10021-013-9694-8

van Moll, G.C.M., 2005. Distribution of the badger (Meles meles L.) in the Netherlands, changes between 1995 and 2001. Lutra 48, 3–34.

Vanwalleghem, T., Gómez, J.A., Infante Amate, J., González de Molina, M., Vanderlinden, K., Guzmán, G., Laguna, A., Giráldez, J.V., 2017. Impact of historical land use and soil management change on soil erosion and agricultural sustainability during the Anthropocene. Anthropocene 17, 13–29. https://doi.org/10.1016/j.ancene.2017.01.002

Veach, V., Moilanen, A., Di Minin, E., 2017. Threats from urban expansion, agricultural transformation and forest loss on global conservation priority areas. PLoS One 12, 1–14. https://doi.org/10.1371/journal.pone.0188397

Vickery, J.A., Feber, R.E., Fuller, R.J., 2009. Arable field margins managed for biodiversity conservation: A review of food resource provision for farmland birds. Agric. Ecosyst. Environ. 133, 1–13. https://doi.org/10.1016/j.agee.2009.05.012

Villard, M.A., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conserv. Biol. 13, 774–783. https://doi.org/10.1046/j.1523-1739.1999.98059.x

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science. 277, 494–499.

Vogelnest, L., 2008. Chapter 1 . Veterinary considerations for the rescue , treatment , rehabilitation and release of wildlife, in: Vogelnest, L., Woods, R. (Eds.), Medicine of Australian Mammals. CSIRO Publishing, Collingwood, Australia.

Volpov, B.L., Hoskins, A.J., Battaile, B.C., Viviant, M., Wheatley, K.E., Marshall, G., Abernathy, K., Arnould, J.P.Y., 2015. Identification of prey captures in Australian fur seals (Arctocephalus pusillus doriferus) using head-mounted accelerometers: Field validation with animal-borne video cameras. PLoS One 10, 1–19. https://doi.org/10.1371/journal.pone.0128789

Vynne, C., Skalski, J.R., Machado, R.B., Groom, M.J., Jacamo, A.T.A., Marinho-Filho, J., Neto, M.B.R., Pomilla, C., Silveira, L., Smith, H., Wasser, S.K., 2011. Effectiveness of Scat-

Detection Dogs in Determining Species Presence in a Tropical Savanna Landscape. Conserv. Biol. 25, 154–162. https://doi.org/10.1111/j.1523-1739.2010.01581.x

Wagler, R., 2013. Incorporating the current sixth great mass extinction theme into evolution education, science education, and environmental education research and standards. Evol. Educ. Outreach 6, 1–5. https://doi.org/10.1186/1936-6434-6-9

Walhovd, H., 1990. Records of young hedgehogs (Erinaceus europaeus L.) in a private garden. Zeitschrift für Säugetierkd. 55, 289–297.

Walhovd, H., 1979. Partial arousals from hibernation in hedgehogs in outdoor hibernacula. Oecologia 153, 141–153.

Wan, X., Jiang, G., Yan, C., He, F., Wen, R., Gu, J., Li, X., Ma, J., Stenseth, N.C., Zhang, Z., 2019. Historical records reveal the distinctive associations of human disturbance and extreme climate change with local extinction of mammals. Proc. Natl. Acad. Sci. U. S. A. 116, 19001–19008. https://doi.org/10.1073/pnas.1818019116

Ward, J.F., MacDonald, D.W., Doncaster, C.P., 1997. Responses of foraging hedgehogs to badger odour. Anim. Behav. 53, 709–720. https://doi.org/10.1006/anbe.1996.0307

Warren, M.L., Burr, B.M., Walsh, S.J., Bart, H.L., Cashner, R.C., Etnier, D.A., Freeman, B.J., Kuhajda, B.R., Mayden, R.L., Robison, H.W., Ross, S.T., Starnes, W.C., 2000. Diversity, Distribution, and Conservation Status of the Native Freshwater Fishes of the Southern United States. Fisheries 25, 7–31. https://doi.org/10.1577/1548-8446(2000)025<0007:ddacso>2.0.co;2

Warwick, H., 1987. Population ecology of the hedgehogs (Erinaceus europeaus) of north Ronaldsey, Orkney. Masters Thesis. Leicester Polytechnic, Leicester, UK.

Warwick, H., Morris, P.A., Walker, D., 2006. Survival and weight changes of hedgehogs (Erinaceus europaeus) translocated from the Hebrides to Mainland Scotland. Lutra 49, 89–102.

Wassenaar, L.I., Hobson, K.A., 2000. Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. Ecol. Appl. 10, 911–916. https://doi.org/10.1890/1051-0761(2000)010[0911:SCAHIR]2.0.CO;2

Wasser, S.K., Hayward, L.S., Hartman, J., Booth, R.K., Broms, K., Berg, J., Seely, E., Lewis, L., Smith, H., 2012. Using detection dogs to conduct simultaneous surveys of northern spotted (Strix occidentalis caurina) and barred owls (Strix varia). PLoS One 7, e42892. https://doi.org/10.1371/journal.pone.0042892

Waters, J., O'Connor, S., Park, K.J., Goulson, D., 2011. Testing a detection dog to locate bumblebee colonies and estimate nest density. Apidologie 42, 200–205. https://doi.org/10.1051/apido/2010056

Wembridge, D., 2015. State of Britain's Hedgehogs, 2015. People's Trust for Endangered Species, London, UK.

Wembridge, D., 2011. State of Britain's Hedgehogs, 2011. People's Trust for Endangered Species, London, UK.

Wembridge, D., Langton, S., 2016. Living with mammals: An urban study. Br. Wildl. 27, 188–195.

Wembridge, D., Newman, M.R., Bright, P.W., Morris, P.A., 2016. An estimate of the annual number of hedgehog (Erinaceus europaeus) road casualties in Great Britain. Mammal Commun. 2, 8–14.

Whalen, J.K., Parmelee, R.W., Edwards, C.A., 1998. Population dynamics of earthworm communities in corn agroecosystems receiving organic or inorganic fertilizer amendments. Biol. Fertil. Soils 27, 400–407. https://doi.org/10.1007/s003740050450

Wiethoelter, A.K., Beltrán-Alcrudo, D., Kock, R., Mor, S.M., 2015. Global trends in infectious diseases at the wildlife-livestock interface. Proc. Natl. Acad. Sci. U. S. A. 112, 9662–9667. https://doi.org/10.1073/pnas.1422741112

Wikenros, C., Balogh, G., Sand, H., Nicholson, K.L., Månsson, J., 2016. Mobility of moose—comparing the effects of wolf predation risk, reproductive status, and seasonality. Ecol. Evol. 6, 8870–8880. https://doi.org/10.1002/ece3.2598

Williams, B.M., Baker, P.J., Thomas, E., Wilson, G.J., Judge, J., Yarnell, R.W., 2018a. Reduced occupancy of hedgehogs (Erinaceus europaeus) in rural England and Wales: The influence of habitat and an asymmetric intra-guild predator. Sci. Rep. 8, 12156. https://doi.org/10.1038/s41598-018-30130-4

Williams, B.M., Mann, N., Neumann, J.L., Yarnell, R.W., Baker, P.J., 2018b. A prickly problem: Developing a volunteer-friendly tool for monitoring populations of a terrestrial urban mammal, the West European hedgehog (Erinaceus europaeus). Urban Ecosyst. 21, 1075–1086. https://doi.org/10.1007/s11252-018-0795-1

Williams, D., Adeyeye, N., Visser, E., 2017. Ophthalmological abnormalities in wild European hedgehogs (Erinaceus europaeus): a survey of 300 animals. Open Vet. J. 7, 261–267. https://doi.org/10.4314/ovj.v7i3.10

Wilmers, C.C., Nickel, B., Bryce, C.M., Smith, J.A., Wheat, R.E., Yovovich, V., Hebblewhite, M., 2015. The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. Ecology 96, 1741–1753. https://doi.org/10.1890/14-1401.1

Wilson, E., Wembridge, D., 2018. State of Britain's Hedgehogs, 2018. People's Trust for Endangered Species, London, UK.

Wilson, G., Harris, S., McLaren, G., 1997. Changes in the British badger population, 1988 to 1997. People's Trust for Endangered Species, London, UK.

Wilson, G.J., Delahay, R.J., 2001. Using Field Signs and Observation. Wildl. Res. 28, 151–164.

Wimberger, K., Downs, C.T., 2010. Annual intake trends of a large urban animal rehabilitation centre in South Africa: A case study. Anim. Welf. 501–513.

Wimberger, K., Downs, C.T., Boyes, R.S., 2010. A survey of wildlife rehabilitation in South Africa: Is there a need for improved management? Anim. Welf. 19, 481–499.

Woinarski, J.C.Z., Burbidge, A.A., Harrison, P.L., 2015. Ongoing unraveling of a continental fauna: Decline and extinction of Australian mammals since European settlement. Proc. Natl. Acad. Sci. 112, 4531–4540. https://doi.org/10.1073/pnas.1417301112

Worm, B., Duffy, J.E., 2003. Biodiversity, productivity and stability in real food webs. Trends Ecol. Evol. 18, 628–632. https://doi.org/10.1016/j.tree.2003.09.003

Wright, J., 2016. A Natural History of the Hedgerow and Ditches, Dykes and Dry Stone Walls. Profile Books Ltd., London, UK.

Wright, P.G.R., Coomber, F.G., Bellamy, C.C., Perkins, S.E., Mathews, F., 2020. Predicting hedgehog mortality risks on British roads using habitat suitability modelling. PeerJ 2020, 1–22. https://doi.org/10.7717/peerj.8154

Yabsley, M.J., 2020. The role of wildlife rehabilitation in wildlife disease research and surveillance, in: Hernandez, S.M., Barron, H.W., Miller, E.A., Aguilar, R.F., Yabsley, M.J.

(Eds.), Medical Management of Wildlife Species :A Guide for Practitioners. Wiley Blackwell, London, UK, pp. 159–165.

Yalden, D.W., 1976. The food of the hedgehog in England. Acta Theriol. (Warsz). 21, 401–424.

Yarnell, K., Hall, C., Billett, E., 2013. An assessment of the aversive nature of an animal management procedure (clipping) using behavioral and physiological measures. Physiol. Behav. 118, 32–39. https://doi.org/10.1016/j.physbeh.2013.05.013

Yarnell, R.W., Pacheco, M., Williams, B.M., Neumann, J.L., Rymer, D.J., Baker, P.J., 2014. Using occupancy analysis to validate the use of footprint tunnels as a method for monitoring the hedgehog Erinaceus europaeus. Mamm. Rev. 44, 234–238. https://doi.org/10.1111/mam.12026

Yarnell, R.W., Surgey, J., Grogan, A., Thompson, R., Davies, K., Kimbrough, C., Scott, D.M., 2019. Should rehabilitated hedgehogs be released in winter? A comparison of survival, nest use and weight change in wild and rescued animals. Eur. J. Wildl. Res. 65, 6. https://doi.org/10.1007/s10344-018-1244-4

Yasuhiko, N., 2004. New steps in bio-logging science. Mem. Natl. Inst. Polar Res. Spec. issue 58, 50–57.

Young, R.P., Davison, J., Trewby, I.D., Wilson, G.J., Delahay, R.J., Doncaster, C.P., 2006. Abundance of hedgehogs (Erinaceus europaeus) in relation to the density and distribution of badgers (Meles meles). J. Zool. 269, 349–356. https://doi.org/10.1111/j.1469-7998.2006.00078.x

Zabel, F., Delzeit, R., Schneider, J.M., Seppelt, R., Mauser, W., Václavík, T., 2019. Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. Nat. Commun. 10, 1–10. https://doi.org/10.1038/s41467-019-10775-z

Zhiping, C., Yuhui, Q., Baoqing, W., Qin, X., 2006. Influence of agricultural intensification on the earthworm community in arable farmland in the North China Plain. Eur. J. Soil Biol. 42, 362–366. https://doi.org/10.1016/j.ejsobi.2006.07.014

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer Science & Business Media, London, UK.