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An investigation into the factors influencing hedgehog (*Erinaceus europaeus*) occupancy throughout rural and urban Britain

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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

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"*Unless someone like you*

cares a whole awful lot,

nothing is going to get better.

It's not."

- Dr Seuss, The Lorax (1971)

"*Nature is not a place to visit. It is home*."

- Gary Snyder (1990)

Abstract

Wildlife conservation and management require robust field data in order to formulate appropriate evidence-based management actions. Yet collecting such data can be challenging. For example, monitoring programmes in the UK indicate that populations of West European hedgehogs (*Erinaceus europaeus*) have declined markedly. However, these programmes are potentially associated with a range of limitations that raise questions about the robustness of estimated trends and their usefulness in determining underlying causal factors.

In this study, the efficacy of footprint-tunnels in conjunction with occupancy analysis was examined as a method for monitoring the presence / absence of hedgehogs in both urban and rural landscapes. Overall, 261 sites in England and Wales, and 219 gardens in Reading, Berkshire, were surveyed. Given the limited availability of funding for conservation monitoring in the UK, such that any future monitoring would most likely have to be conducted as a "citizen science" project, surveying was conducted primarily by members of the general public.

False-absence error rates in both landscapes were extremely low (rural: ≤ 0.8%; urban: 0.1 - 0.4%), indicating the technique was very reliable. However, occupancy rates were also low: hedgehogs were only detected at 21% of rural sites and in 32-40% of gardens. Rural hedgehog occupancy was negatively affected by badger (*Meles meles*) sett density and positively influenced by the built environment, although hedgehogs were also absent from 71% of sites without badger setts. Collectively, this indicates that hedgehogs are absent from large areas of the rural landscape.

Garden occupancy was negatively influenced by the presence of badgers, but not significantly. No other within- or outside-garden factors affected hedgehog presence in residential gardens. As such, it is not clear what promotes the use of gardens by hedgehogs in urban areas. However, inter-annual patterns of garden use were very consistent: hedgehogs were and were not detected in 52% and 27% of gardens (N=60) surveyed in two separate years, respectively.

Expanding road networks in countries such as the UK potentially exert two important effects on hedgehog populations: (i) direct mortality and / or (ii) barrier effects to movement. Analysis of the locations of road-killed hedgehogs from Suffolk (Eastern England) indicated that casualties were clustered at all spatial scales and concentrated in urban areas. In both urban and rural landscapes, hedgehogs were more likely to be killed on roads with a speed limit ≤ 30 mph, potentially indicating an association with areas of human habitation. Hedgehog carcasses in urban areas were also positively associated with the presence of parked cars and proximity to road junctions; rural hedgehog carcasses were positively associated with the presence of neighbouring hedgerows / woodland edges. These results suggest that road signs may be one possible means for helping reduce the numbers of road casualties.

Using a panel of microsatellites to investigate hedgehog population structure showed no discrete genetic clusters in Southern England. The results suggest good gene flow between individuals with no absolute barriers to movement.

Deterministic matrix population modelling indicated that current estimates of key demographic parameters in the literature do not generate patterns of decline in hedgehog populations observed in ongoing monitoring programmes. This highlights an urgent need for further research into hedgehog population demographics. Small changes *c.* 5-10% in adult or juvenile survival are likely to enable hedgehog population growth.

In summary, hedgehogs appear to have a negative relationship with badgers and be positively associated with urban areas. Work here highlights several areas of concern for hedgehog conservation and expedited work is needed to address this; however, with successful conservation initiatives the hedgehog population should be able to recover relatively rapidly.

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Chapter One

Introduction

Species' declines, shifts in geographical range and extinction are all natural phenomena and are well documented in the fossil record (Barnosky *et al.* 2011). These changes may happen for a number of reasons; habitat loss, the arrival of a competitor, a change in climatic conditions, a natural disaster or the introduction of a novel disease (Gurevitch and Padilla 2004; Schulte *et al.* 2010; Barnosky *et al.* 2011; Bond and Grasby 2017). In the absence of catastrophic events, extinctions tend to be slow and affect relatively small numbers of species at any one time. Currently, however, species are declining and becoming extinct at an unusually high rate, in line with that of the five previous mass extinction events (Barnosky *et al.* 2011; Wagler 2013), as a direct consequence of human activities (Butchart *et al.* 2010; Pimm *et al.* 2014; Maxwell *et al.* 2016). This pattern is only expected to worsen (Pimm *et al.* 2014; Sutherland *et al.* 2017), particularly with the predicted effects of climate change (Millennium Ecosystem Assessment 2005).

Two of the major activities undertaken by humans which are associated with extensive habitat loss and deterioration are intensive agricultural production and urbanisation. Collectively, both these forms of land alteration are generally associated with negative impacts on global biological diversity (e.g. Egli *et al.* 2018), particularly as humans have tended to colonise areas associated with high natural biodiversity (Luck 2007). Both forms of land use are also expected to increase in area to meet the demands of the growing global human population, but urbanisation in particular (Seto *et al.* 2011).

The negative impacts associated with agricultural and urban areas arise from a broad range of physical and biological changes, some of which differ substantially between the two, while others are contextually similar. For example, agricultural landscapes are affected by soil degradation and compaction (Lees *et al.* 2016) and the widespread application of chemicals to control fungal, plant and invertebrate pests (e.g. Szczepaniec *et al.* 2013) whereas urban areas are associated with the modification of surface albedo and evapotranspiration (Arnfield 2003) and noise and light pollution (e.g. Khan *et al.* 2018). Conversely, both landscapes have been affected by the introduction of non-native species which have given rise to human-wildlife conflicts, although the species involved and the forms of conflicts vary: agricultural areas are predominantly associated with predation on, competition with and disease spread to introduced livestock from non-native species (e.g. Baker *et al.* 2008a; Legge *et al.* 2011; Eklund *et al.* 2017) but also indirect effects such as the facilitation of the spread of other introduced species (Doody *et al.* 2017) and the decline of native species following the release of biological control agents (Lees and Bell 2008); whereas urban areas are associated with the introduction of species for aesthetic reasons (McKinney 2006; 2008) or as companion animals (Baker *et al.* 2010), which may cause nuisance problems (Adams 2016) or predate native species (Crooks and Soulé 1999; van Heezik *et al.* 2010). Both landscape types are also typified by road and rail networks to facilitate the transport of goods and people, but other networks as well such as electrical grids and gas pipelines; all of these can affect native wildlife (e.g. Forman and Alexander 1998; Spellerberg 2002; Forman *et al.* 2003; Bartzke *et al.* 2015).

Conversely, the modification of natural habitats into agricultural or urban landscapes has been beneficial for some species. For example, several mammalian carnivores are more abundant in urban areas than in their natural habitats (Bateman and Fleming 2012), partly as a consequence of the potential to forage on human food waste (e.g. Newsome and van Eeden 2017) but also because people may deliberately feed them (e.g. Baker *et al.* 2000). Similarly, animal densities may be higher in agricultural landscapes as a consequence of habitat modification and the increased availability of prey species (e.g. red fox *Vulpes vulpes*: Webbon *et al.* 2004). For other species, urban areas may act as a refuge habitat where they are able to avoid predators (Lonsinger *et al.* 2017); in such circumstances, however, urban populations may become increasingly isolated because of the difficulties associated with dispersing through surrounding habitats where predator density is high.

Given their pervasive effects on a broad range of taxa, there is increasing emphasis on how to manage agricultural and urban habitats sympathetically to minimise impacts on biodiversity whilst optimising food production, standards of living and economic gain (e.g. Foley *et al.* 2011; Kleijn *et al.* 2011; Balmford *et al.* 2012). At its most basic, the development of effective evidence-based conservation strategies (Sutherland *et al.* 2004) requires a means to monitor changes in the size and distribution of focal populations; these are necessary to both identify when a species may be in decline, but also to measure the effectiveness of any measures implemented to reverse such declines. Obtaining such baseline data can, however, be associated with significant practical challenges related to, for example, the biology of the focal species, the range of contrasting habitats it occupies and the availability of funds.

The challenges associated with surveying wild animals

Biodiversity, conservation, wildlife management and scientific studies all require data on which to base decisions and devise appropriate management actions (Sutherland *et al.* 2004; Lovett *et al.*

2007; Lindenmayer and Likens 2010). Quantification of the distribution and abundance of populations and how these are changing over time in relation to biotic and abiotic factors are, therefore, fundamental to these disciplines (Battersby and Greenwood 2004). However, surveying and monitoring populations poses a wide range of theoretical and logistical problems since species vary in relation to e.g. physical size, patterns of habitat utilization, degree of evasiveness / catchability, periods of activity and density (Witmer 2005). Subsequently many different techniques have had to be developed to overcome these issues.

This is particularly the case for mammals (Harris and Yalden 2004). For example, many species are nocturnal and communicate primarily using chemical scent marks. Such species are therefore most active at a time when human surveyors are not, and they cannot easily be seen or heard; surveying at night also raises additional safety concerns. Similarly, trapping many mammal species is expensive and time-consuming, as well as being associated with significant animal welfare and legal issues. In addition, many species are hunted, culled or persecuted by humans such that they are actively wary of humans. As a consequence of these practical biological constraints, there has been increased interest in the use of "indirect" methods of surveying mammal populations based on, for example, counts of dead animals on roads (Baker *et al.* 2004; Bright *et al.* 2015), refugia (Judge *et al.* 2014) and / or field signs such as feeding remains, footprints (Alibhai *et al.* 2017), faeces (Webbon *et al.* 2004) and fur (Baker *et al.* 2003; Pocock and Jennings 2006; Judge *et al.* 2017) (see also e.g. Wilson and Delahay 2001; Sadlier *et al.* 2004; Long *et al.* 2008).

Such approaches are potentially associated with two major advantages. First, field signs are static and persist over time (e.g. Brown *et al.* 2014) so they can be surveyed during daylight hours and should, theoretically at least, be easier to find with sufficient survey effort than mobile animals. However, care must be taken as they will disappear over time. For example, carcasses on roads may be scavenged and / or destroyed by weather and traffic (Santos *et al.* 2011), such that adequate sampling regimes must be devised (Santos *et al.* 2015). Second, they also increase the potential to use volunteer surveyors to help collect field data.

Advantages and disadvantages of using citizen scientists to survey wild animals

The use of volunteer surveyors ("citizen science") to gather data for scientific studies (Irwin 1995) has become increasingly common (Conrad and Hilchey 2011; Follett and Strezov 2015; Theobold *et al.* 2015; Bonney *et al.* 2016). Such activities engage the public in scientific studies, provide them with an increased understanding of environmental and conservation issues (Battersby and

Greenwood 2004; Bonney *et al.* 2016) and enhance their connection with nature (Devictor *et al.* 2010). As a consequence, citizen-science based approaches have been, and continue to be, positively encouraged by governmental and non-governmental agencies and funding bodies (*sensu* Pocock *et al.* 2015).

Within the fields of wildlife management and conservation, such approaches offer a range of benefits, but also potentially generate problems. From a practical standpoint, citizen scientists are a potentially large labour force that require little or no payment and which enable data collection on a scale and scope that would otherwise be difficult to achieve (Newman *et al.* 2003; Mccaffrey 2005; Toms and Newson 2006; Bell *et al.* 2008). These larger sample sizes increase statistical power in otherwise "noisy" datasets (Isaac *et al.* 2014), thereby enabling more robust conclusions to be drawn whilst helping minimise costs.

The most pressing problem potentially arising from the use of volunteer scientists, however, concerns the quality and consistency of the data submitted (Darwall and Dulvy 1996; Hunter *et al.* 2013). At the most basic level, one of the major potential issues associated with volunteer surveys is site selection. In general terms, statistical analyses of the data emerging from citizen science surveys are predicated on the assumption that data are independent and random; where volunteers are able to self-select their sites, it is probably reasonable to assume that they are more likely to select sites where they know, or have a strong suspicion that, the focal species is present: this would introduce a form of directional bias that may be hard to overcome at the analysis stage. It is however, eminently avoidable at the design stage by randomly selecting sites for volunteers. Such biases are potentially most evident in surveys of urban species where volunteers may be more likely to select their own gardens over other habitats (e.g. Wembridge and Langton 2016). Similar biases may also arise where homeowners can opt to select to survey for focal species or not (e.g. Toms and Newson 2006).

Closely allied with these problems is the focus on methodologies whereby volunteers are asked to report sightings or other evidence of focal species. In these circumstances, the emphasis on positive information results in datasets that consist only of (potentially non-random) locations where a species has been spotted, or thought to have been spotted (see Marks *et al.* (2017) for an extreme example of observer bias). As such, these data will consist of a subset of sites where: (i) the species is known to exist; (ii) the species is present but has not been (a) surveyed, (b) reported or (c) spotted; and (iii) the species is truly absent. Analysing such data is problematic (e.g. Scott *et al.* 2014).

Interpreting field signs themselves can also pose significant challenges. For example, the faeces of many species may be broadly similar (e.g. Costa *et al.* 2017), but the shape and form for an individual species may vary with diet. In addition, tell-tale patterns of placement may vary with density (e.g. Hutchings *et al.* 2002), and the characteristic smell of a given species may be hard to describe reliably. Such differences are known to be associated with significant levels of identification error, even for professional mammalogists (e.g. Davison *et al.* 2002; Reynolds and Short 2003), such that there is increased emphasis on the use of detection dogs to locate faecal remains of specific species (e.g. Long *et al.* 2007; Orkin *et al.* 2016) and / or the use of laboratory methods to identify species genetically (Kohn and Wayne 1997). Both approaches are, however, associated with significant financial costs. In addition, genetic approaches may also be associated with methodological limitations that require careful validation (Gonçalves *et al.* 2014), but have been applied successfully to studies based on faecal and fur samples (Schwartz and Monfort 2008).

Similar problems associated with the accurate identification of species are also evident with the use of footprints. In addition to the difficulties associated with discriminating between the prints of morphologically similar species, the quality of footprints available for examination is also likely to be affected strongly by the sort of medium available. As a result, footprint surveys have often been confined to locations with a suitable medium (e.g. snow, sand) for generating good quality prints (Pulliainen 1981; Stanley and Bart 1991; Kurki *et al.* 1998; Mahon *et al.* 1998; Heinemeyer *et al.* 2008). Alternatively, researchers may place artificial media (usually sand) at specific locations to help generate prints (e.g. Travaini *et al.* 1996; Ray and Zielinski 2008): when used properly, it may then be possible to identify the sex of the individual, or even the individual themselves (e.g. Alibhai *et al.* 2017).

Perhaps the biggest advance in recent years for the non-invasive sampling of wild animals, however, has been the development of remotely activated cameras (Burton *et al.* 2015). At their most basic, these can be used to record the presence / absence of individual focal species; this approach can then be easily applied to multiple species to compile species inventories and / or relative species diversity. Photographs of identifiable individuals (e.g. from pelage characteristics) can also be used in a capture-mark-recapture framework to estimate animal density, and methods are being developed to estimate density for those species were individuals are not individually identifiable (e.g. Rowcliffe *et al.* 2008).

Although remotely activated cameras are increasingly being used in citizen science and other collaborative projects (Swanson *et al.* 2016; Scotson *et al.* 2017; Steenweg *et al.* 2017), their major limitation is cost. One consequence of this has been that conservation biologists have often ended up having to buy relatively cheap products which then generate problems with reliability in the field (Newey *et al.* 2015), and the resultant robustness of conclusions.

Despite the long list of practical problems associated with enrolling citizen scientists to help collect field data, the focus on involving volunteer surveyors is likely to continue given the very real problems associated with funding conservation projects. As such, it is incumbent on researchers to develop programmes with rigorous data collection protocols. These may include: appropriate training of surveyors prior to data collection and / or supervision during field work (Darwall and Dulvy 1996; Newman *et al.* 2003); the simplification of the data collected; or the adoption of protocols where data can be independently verified (e.g. via photographs or genetic analysis).

These issues are currently of interest in helping devise evidence-based strategies for the conservation of hedgehogs (*Erinaceus europaeus*) in the UK.

The West European hedgehog

The West European hedgehog (henceforth referred to as “hedgehog”) is a nocturnal insectivorous mammal found in almost all British lowland habitats but which is scarce or absent from large pine forests, wetland, moorland, mountainsides and above the tree line (Morris and Reeve 2008; Morris 2010). It is a native species and the only member of its family (Erinaceidae) in Britain. Currently, the species is considered common and widespread throughout the UK, inhabiting mainland Britain, Ireland and many smaller islands (Morris and Reeve 2008). It has been introduced to both New Zealand and the Uist Islands in Scotland where it is considered a pest because of its impact on native wildlife (King 1990; Jackson and Green 2000; Jackson 2001; Long 2003).

Hedgehogs are found in a wide range of habitats, including farmland, woodland and urban / suburban areas. The species is non-territorial, with male home ranges overlapping those of several females. Seasonal / annual home ranges as large as 1 km^2 have been recorded (Reeve 1994; Table 1.1), but vary markedly with habitat, sex and the presence / absence of badgers (e.g. Pettett *et al.* 2017a) and sex: Morris (1988) considers distance travelled per night (Table 1.1) as a better indicator of activity.

Table 1.1. Summary of nightly home range size and / or distance travelled by radio–tracked hedgehogs in relation to habitat and sex. Home ranges delineated by 100% minimum convex polygons. Figures in brackets indicate: range (min.-max.); standard deviation (SD); or standard error (SE). For clarity, sample sizes and tracking regimes have not been presented: see references for these details.

Habitat	HR size (ha)		Distance travelled (m)		Reference
	Females	Males	Females	Males	
Urban, UK	0.77 (0.31-2.13)	2.87 (0.94-6.05))	514 (210-1029)	861 (427-1759)	Dowding *et al.* (2010a)
Urban, UK	1.88 (SD: 1.63)		590 (SD: 300)		Molony *et al.* (2006)
Urban, UK	5.0 (SE: 0.7)		380 (SE: 30)		Rondinini and Doncaster (2002)
Mixed farmland, UK	6[1]	27[1]	900[1]	1300[1]	Dowie (1988)
Urban golf course	-	-	1006	1690	Reeve (1994)
Farmland, UK	16.3 (95% CI: 10.4-25.6)		-		Doncaster *et al.* (2001)
Farmland, UK	12.4[2] (SE: 2.7)	21.6[2] (SE: 5.8)			Pettett *et al.* (2017a)
Urban, Switzerland	-	17.3[3] (SE: 3.0)	-	-	Braaker *et al.* (2014)
Coastal Mediterranean	47.1[4] (5.5-102.5)		-		Boitani and Reggiani (1984)
Mixed farmland, Denmark	26[5] (SD: 15)	96[5] (SD: 24)	1187 (SD: 538)	2042 (SD: 860)	Riber (2006)

[1] Figures for home range size are across multiple nights, but author does not state sampling effort. Figures for distance travelled per night are estimated from Figure 1 of Dowie (1988). [2] Details for length of time individual hedgehogs were radio-tracked is outlined in the authors' supplementary information. [3] Individual hedgehogs tracked using GPS tags for 1-6 nights. [4] Home range size calculated for periods of 17-98 days. [5] Home range size calculated for periods of 6-58 days.

In the UK, hedgehogs typically hibernate from December-March, although the hibernation period may start earlier and finish later if prevailing weather conditions are bad. During hibernation, animals are likely to move nest sites several times (Morris 1973; Bearman-Brown pers. comm.). The breeding season extends from April-September, with two peaks of pregnancies: May-July and September (Morris and Reeve 2008). Hedgehogs are promiscuous (Reeve and Morris 1986), and mixed-paternity litters may occur (Moran *et al.* 2009). Typical litter size is 4-5 but may be as large as 7 (Morris and Reeve 2008): with pre-weaning mortality of approximately 20% (Morris 1977). In the UK, it is plausible that hedgehogs could raise two litters per year, but this has only been demonstrated in the Uist Islands where the species is considered invasive (Jackson 2006).

Major sources of mortality for hedgehogs include predation, collisions with vehicles, misadventure (mainly urban landscapes) and death during hibernation. Because of their spiny coats, hedgehogs have relatively few natural predators but which does include foxes (*Vulpes vulpes*), eagle owls (*Bubo bubo*) and occasionally golden eagles (*Aquila chrysaetos*) (Morris and Reeve 2008; Hubert, Julliard, Biagianti and M.-L. Poulle 2011). In the UK, however, the major predators are domestic dogs (*Canis familiaris*) (Reeve and Huijser 1999) and the Eurasian badger (*Meles meles*) (Doncaster 1992, 1994; Micol *et al.* 1994): road traffic accidents are estimated to account for 167,000-335,000 hedgehog deaths annually (Wembridge *et al.* 2016). Large numbers of hedgehogs are also admitted to wildlife rehabilitation hospitals annually: estimates range from 40,000 (Molony *et al.* 2007) to 71,000 (Grogan and Kelly 2013), although these may be under-estimates. At present there are also very few data on the proportion of hedgehogs admitted to hospitals that survive to release, although post-release survival rates can be comparable to those of non-rehabilitated individuals (Molony *et al.* 2006).

The relative importance of these different forms of mortality, and annual mortality rates, are however relatively unknown. However, Kristiansson (1990) reported mean annual mortality rates of 47% and 34% for adults and juveniles, respectively, for rural hedgehogs in southern Sweden; over-winter mortality rates for both adult and juveniles animals (28%) was higher than that during the summer (15% for adults, 3% for juveniles). The main cause of mortality was road traffic. Average life expectancy in this population was approximately 1.2 years.

Similarly, in Rautio *et al.'s* (2016) study in Finland, 77 of 106 (73%) hedgehog carcasses collected had been killed by vehicles. The majority of the remainder had been killed by a pathological condition (21%) or starved (14%): only one individual (1%) was recovered dead from a hibernation nest. In contrast, of 28 animals radio-tagged during September-October in Gloucestershire and Nottinghamshire, six (21%) died before the hibernation period (November–March); four of the remaining 22 animals (18%) died during hibernation (Bearman-Brown pers. comm.)

Although at the time of writing the species is classified as Least Concern by the IUCN (Amori 2016), it is likely to be upgraded to Near Threatened in the near future (Baker pers. comm.). Within the UK, it is thought to have undergone substantial declines in the last 20-30 years (Wilson and Wembridge 2018). As a consequence, it was added to the UK's Biodiversity Action Plan (BAP) and made a species of principal importance in 2007. From an ecosystem context, the decline of hedgehogs is noteworthy as they are a generalist forager feeding on a range of macro-invertebrates, which are themselves a primary food source for numerous mammalian and avian taxa (e.g. Schmidt *et al.* 2005; Greenberg *et al.* 2007). As such, this makes hedgehogs a useful model species for understanding how changes within the rural (and urban) landscape have affected wildlife in the UK.

The following sections discuss evidence for declines in hedgehog populations in the UK and factors likely to be associated with those changes.

Decline of hedgehogs in the UK

Evidence for a decline in hedgehog numbers within the UK is evident from eight different survey and monitoring programmes coordinated principally by the People's Trust for Endangered Species (PTES) or the British Trust for Ornithology (BTO). The results of these schemes are discussed briefly below.

Mammals on Roads survey

The *Mammals on Roads* (MoR) survey is coordinated by the PTES and is based upon sightings of living and dead individuals observed by volunteers undertaking car journeys (transects) of ≥20 miles during July–September inclusive (Roos *et al.* 2012): data are then analysed on a 10x10km basis. Volunteers are asked specifically not to record sightings on motorways or dual carriageways for safety reasons, or in urban areas (PTES 2008); these data therefore reflect trends in the number of hedgehogs killed on rural roads. The survey has been running since 2001.

Inter-annual variation in the number of road-killed hedgehogs recorded is marked (Figure 1.1). Collectively, these data indicate a (crude) decline of approximately 4.5% per annum but with a very steep decline from 2007-2013 inclusive.

However, sample sizes have fallen dramatically over time. In 2001, a total of 2,111 transects (car journeys) from 749 10x10km squares were analysed, but this has dropped to 53 transects in 45 squares in 2017 (Wembridge pers. comm.), a decline of >90% for both transects and squares. This declining pattern of retention of surveyors does potentially raise questions about the robustness of estimates in the latter period (<65 sites have been surveyed each year since 2014: Figure 1.1).

In addition to a declining sample size, further possible limitations associated with this approach include: (i) an absence of information relating to the volume of traffic on roads surveyed, a factor that has been shown to significantly affect the likelihood that animals, including hedgehogs, may attempt to cross roads (Fahrig *et al.* 1995; Clarke *et al.* 1998; Rondinini and Doncaster 2002; Taylor and Goldingay 2004; but see Bright *et al.* 2015); and (ii) problems associated with the influence of road and roadside characteristics on the likelihood of animals being killed (Clevenger *et al.* 2003a; Orłowski 2008). As such, the MoR programme should attempt to incorporate such factors in their data recording programme, although this will be exceedingly challenging. Despite these caveats, the MoR survey provides greater detail than many other current surveys as it generates quantitative information on relative density (number of hedgehogs killed per unit length travelled) rather than just their presence /absence (Roos *et al.* 2012).

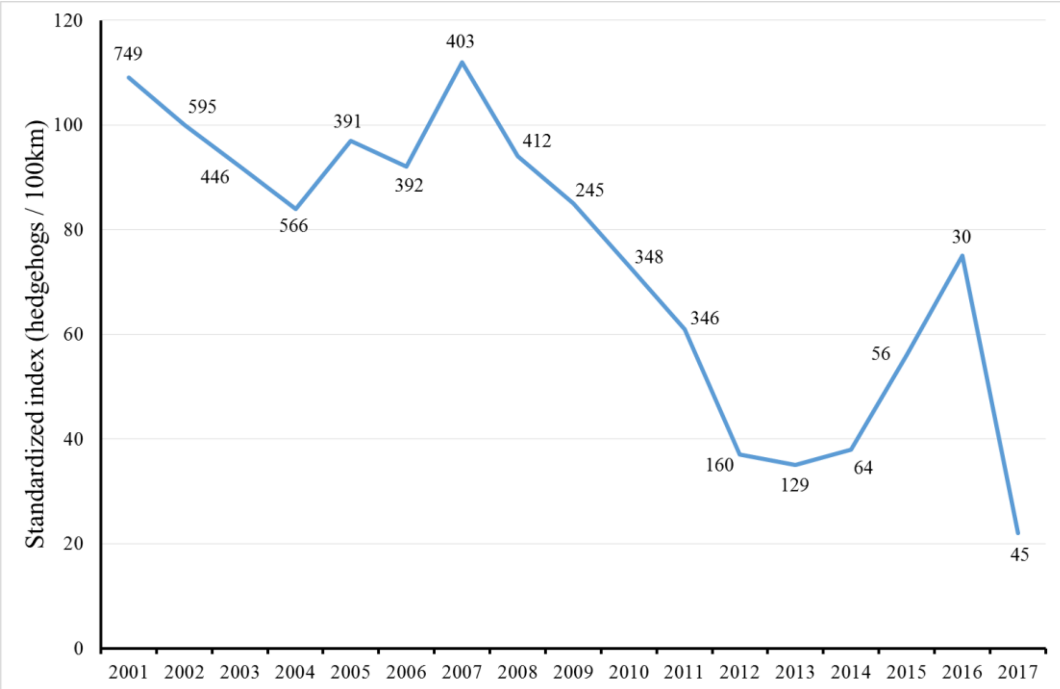

Figure 1.1. Summary of the trend in rural hedgehog numbers as illustrated by the *Mammals on Roads* survey. Data are presented as the standardized number of dead hedgehogs recorded per 100km relative to the baseline year of 2002; data from Wilson and Wembridge (2018). Figures above / below the line indicate the number of 10x10km squares surveyed.

Breeding Bird Survey

The *Breeding Bird Survey* (BBS) coordinated by the BTO, Joint Nature Conservation Committee (JNCC) and Royal Society of the Protection of Birds (RSPB), started in 1994 and relies on volunteers to survey birds in randomly allocated 1km squares throughout the UK. Participants are required to have moderately high levels of skill, and are expected to be able to identify >100 species by sight and / or sound. The voluntary recording of mammal species was added in 1995 (Harris *et al.* 2017). Approximately 3,500 randomly selected sites are surveyed each year, of which > 80% regularly have mammals recorded. Mammal information recorded ranges from field signs to sightings of animals themselves, and can be based on observations by the surveyor during or outside the survey period itself (e.g. the surveyor may visit the site several times over the course of the year) or from information received from a third party (e.g. farmer, gamekeeper). Particular effort is made to ensure that zero returns (i.e. surveyors who did not survey for mammals at all, or who failed to find evidence of a given species) are collated correctly to reduce the number of false negatives (Roos *et al.* 2012).

The manner in which mammal information has been recorded during the BBS has changed over time, potentially affecting its use for determining long-term trends. For example, since 2002 more detailed information has been recorded for hedgehogs at each site in response to the decline observed in other surveys. Provisional analysis of these data has suggested that "local knowledge" is the most common indicator of hedgehog presence (Roos *et al.* 2012). Although numbers of hedgehogs are also recorded, they are rarely seen during the daytime and have only been recorded in 1% of sites during morning bird surveys meaning the data are of only limited use for assessing abundance; overall detection rate is approximately 8.6% when all signs of presence are considered (Roos *et al.* 2012). The random stratified approach to allocating survey squares does mean, however, that a range of habitats within the UK are surveyed annually.

Living with Mammals survey

The *Living with Mammals* (LwM) survey, coordinated by the PTES, focuses on green spaces in the urban environment (e.g. gardens, parks, allotments, playing fields, derelict land). Survey sites are selected by volunteers themselves and must be located within 200m of buildings unless wholly surrounded by towns / cities (e.g. large parks): domestic gardens comprise >70% of the sites selected (Wembridge and Langton 2016). Volunteers are asked to visit each site at least once a week from April–June inclusive.

Inter-annual variation in the number of road-killed hedgehogs recorded in this data set (Figure 1.2) is less pronounced than for the *Mammals on Roads* data (Figure 1.1), potentially reflecting a marked difference between urban and rural hedgehog populations. Collectively, these data indicate a (crude) decline of approximately 2.2% per annum but with a very shallow decline from 2006 onwards.

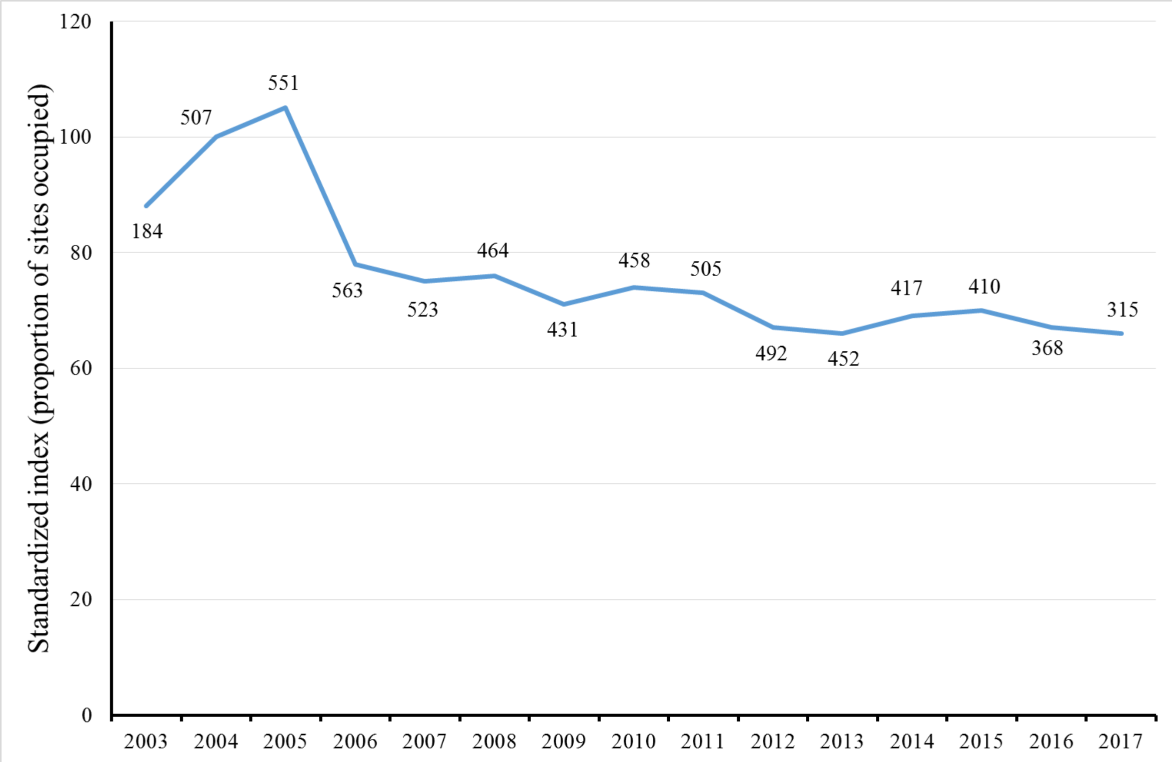

Figure 1.2. Summary of the trend in urban hedgehog numbers as illustrated by the *Living with Mammals* survey. Data are presented as the standardized number of sites where hedgehogs were recorded relative to the baseline year of 2004; data from Wilson and Wembridge (2018). Figures above / below the line indicate the number of sites (e.g. gardens) surveyed.

The highest return rate was observed in 2005 (N=551 sites) but more recently sample sizes have oscillated between 300 and 500. This difference in comparison to the *Mammals on Roads* survey almost certainly reflects a difference in the amount of effort required for volunteers to survey a familiar site close to them (e.g. their garden) compared to recording the numbers of dead hedgehogs seen during a car journey. However, the non-random recruitment of surveyors means it is plausible that there is a substantial sampling bias with these data (i.e. people may be more likely to volunteer if they have hedgehogs in their garden). At present, analysis of these data to help identify factors associated with the presence / absence of hedgehogs (or other species) has been limited (Wembridge and Langton 2016) but is urgently required to help identify characteristics that make gardens "hedgehog friendly" (*sensu* Baker and Harris 2007).

Waterways Breeding Bird Survey

The BTO's *Waterways Breeding Bird Survey* (WBBS) is an annual survey of breeding birds and mammals along waterways (e.g. rivers, canals) that started in 1998 (Baillie *et al.* 2011). Volunteers survey transects of 500m to 5km along waterways recording all birds and mammals seen and heard (Baillie *et al.* 2011). Over recent years, 200–250 transects have been surveyed each year, with an annual turnover of 10-15% of sites. As with the BBS, recording information on mammals is optional and can be based upon observations by the surveyor throughout the year or from information received. Of 2,277 transects completed between 1998-2009, hedgehogs were observed (living animal, dead animal or field sign) on just 115 (5%); additional local knowledge implied that they were present on a further 114 sites (5%) (Roos *et al.* 2012). These data are, however, of limited use for national trends generally given their focus on waterside habitats.

Garden BirdWatch

The BTO's *Garden BirdWatch* (GBW) survey asks volunteers (who pay a fee to join in) to record birds and other wildlife that are actively using their garden each week. Mammal data are often submitted as presence / absence information since surveyors are not specifically required to record information about this taxon; approximately 67% of recorders do, however, submit mammal data (Roos *et al.* 2012). On average, 1,619 gardens have been surveyed annually, approximately 3.7 times the number of participants in the *Living with Mammals* survey. Like the *LwM* survey, the data indicate a relatively stable proportion of gardens occupied by hedgehogs since 2007 (Figure 1.3); again, however, the non-random recruitment of volunteers may be associated with a sampling bias (i.e. "bird-friendly" gardens more likely to be represented).

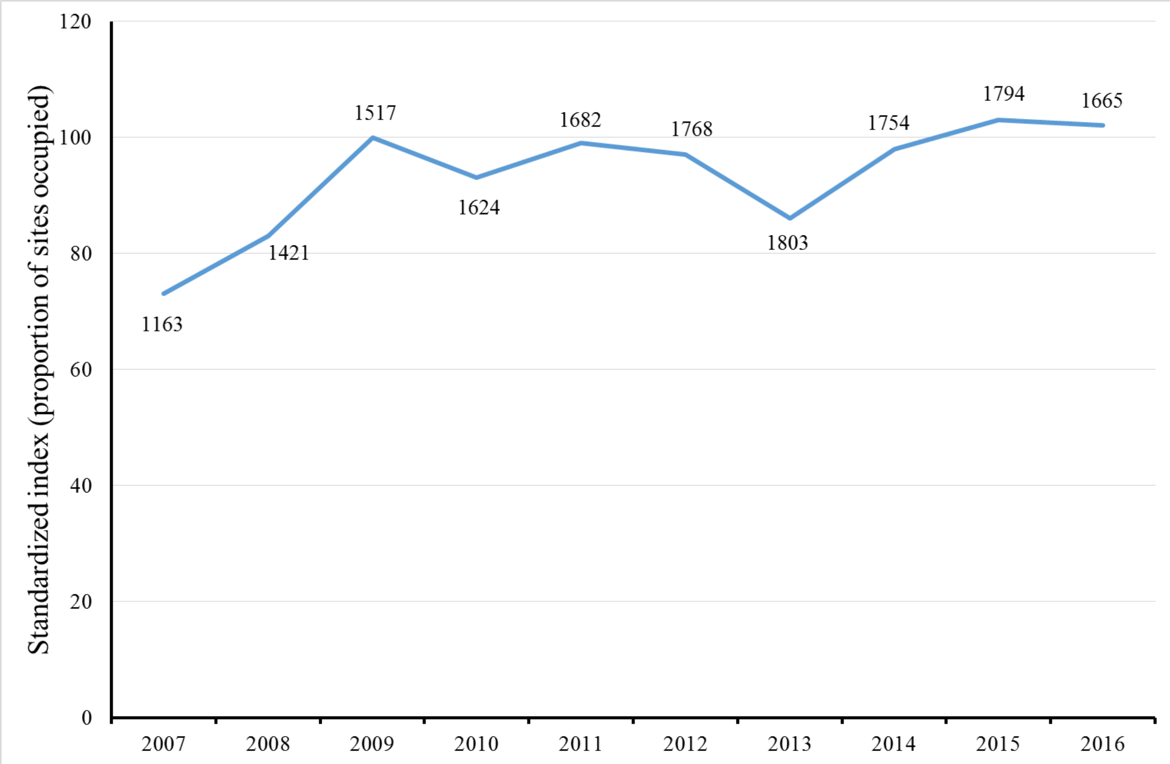

Figure 1.3. Summary of the trend in urban hedgehog numbers as illustrated by the *Garden BirdWatch* survey. Data are presented as the standardized number of gardens where hedgehogs were recorded relative to the baseline year of 2009; data from Wilson and Wembridge (2018). Figures above / below the line indicate the number of gardens surveyed.

National Gamebag Census

The *National Gamebag Census* (NGC), coordinated by Game and Wildlife Conservation Trust (GWCT), contains records for 20 mammal species killed on game estates in the UK since 1961 although records for some estates stretch back much further (Tapper 1992; Aebischer *et al.* 2011; Whitlock *et al.* 2003). It is a voluntary programme for which gamekeepers and land-owners are asked to submit data at the end of each season (Aebischer *et al.* 2011). Although the NGC data represent the longest temporal dataset for mammals in the UK, there are a number of well known issues associated with such data including: (i) a decline in the total amount of keepered-land which can give rise to problems associated with immigration of individuals from surrounding areas (Smallwood 1994; Krauss *et al.* 2003); (ii) geographical variation in the amount of keepered-land (>5% nationally but varying from 1% in Northern Ireland and the Midlands to 15% in eastern Scotland: Whitlock *et al.* 2003); (iii) changes in the amount of e.g. trapping effort exerted by gamekeepers on individual estates (Mcdonald and Harris 1999); (iv) changes in the legal status of methods used to cull different species (e.g. a ban on the use of gin traps in 1958, and the outlawing of self-locking snares in 1991: Whitlock *et al.* 2003); (v) the adoption of measures to limit the killing of non-target species (e.g. the use of baffles to prevent hedgehogs entering tunnel traps intended for stoats (*Mustela erminea*) and weasels (*Mustela nivalis*): Short and Reynolds 2001); and (vi) the non-reporting of species likely to be viewed as controversial by the wider public (e.g. hedgehogs). Despite these caveats, data from the NGC indicate a decline in the numbers of hedgehogs killed in the UK (Figure 1.4).

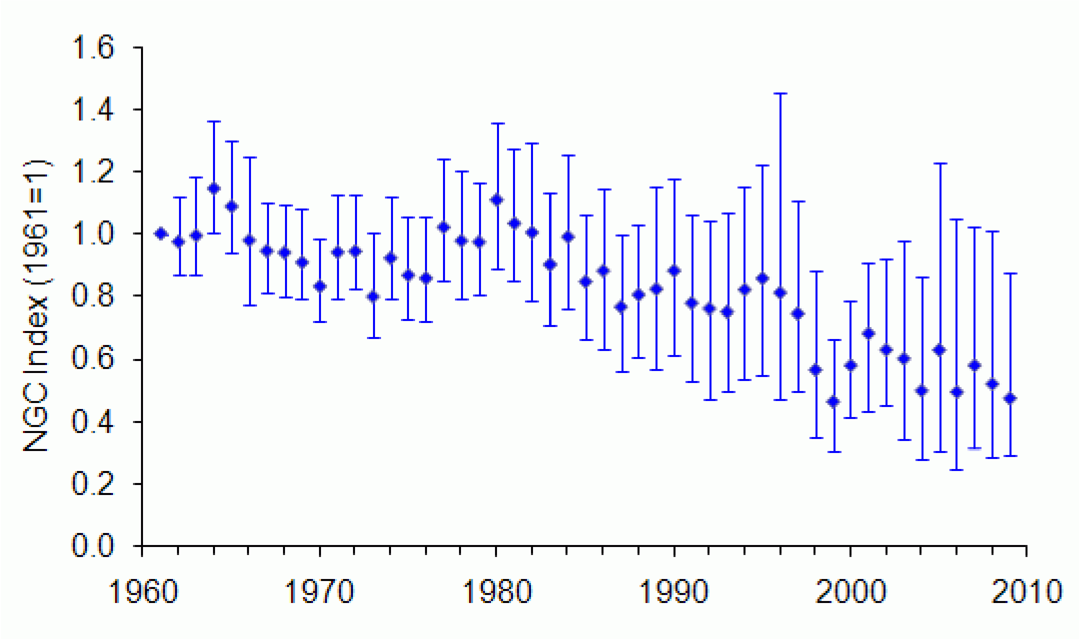

Figure 1.4. Index of gamebag density for hedgehogs in the UK between 1961 and 2009 inclusive. Relative change is standardized to 1961. Error bars are 95% confidence intervals (from www.gwct.org.uk).

Make Your Nature Count

The *Make Your Nature Count* (MYNC) week-long annual survey was launched in 2009 and is run by the Royal Society for the Protection of Birds (RSPB) (Roos *et al.* 2012). Volunteers are primarily asked to record numbers of birds, mammals and other taxa observed during one 1-hour period during the survey week in the early part of June. As the survey is conducted during daylight hours, hedgehogs are rarely recorded although volunteers are also asked to indicate how often (daily, weekly, monthly, less than monthly, never) they encounter different species, including hedgehogs. Hedgehogs were recorded as present in a very high proportion of sites (72-78%). However, as with the biases likely to be evident in both the *LwM* and *GBW* surveys, this is likely to associated with a bias towards 'hedgehog friendly' gardens. The survey does not seem to have continued beyond 2012.

Hog Watch

The *Hog Watch* (HW) survey, coordinated by the PTES and British Hedgehog Preservation Society (BHPS), ran between 2005 and 2007 with data recorded at two different levels. For the first (HWa), people were asked to indicate whether they had observed one or a number of hedgehogs in their garden or any other location (the spatial identifier was postcode level) within the previous 12 months. Respondents were also asked their opinion on how hedgehog numbers had changed over the last five and ten years (don't know, hedgehogs are equally / less / more common now than five / ten years ago). In the second scheme (HWb), respondents completed a more detailed questionnaire asking whether they had seen a hedgehog in their garden, the maximum number seen, whether they had seen a nest (including number and rough age of young) and to supply information on sightings at other locations including a description of the habitat and a grid reference.

Hedgehogs were observed in 66% and 92% of unique locations submitted via the HWa and HWb schemes, respectively. Both figures likely represent over-estimates of the true pattern of occupancy because of the sampling bias inherent in the two surveys (Roos *et al.* 2012); most records were from gardens. The number of nests found with large young was far higher than those found with small young. The vast majority of people either did not respond (73%) or stated that they did not know (6%) how hedgehog numbers had changed in the last five years; of those people (N = 3,955) that did indicate a trend, 37%, 44% and 19% replied that they thought hedgehog numbers had remained the same, declined or increased respectively.

However, despite the potential problems associated with controlling for survey effort in this sort of survey, analysis of the Hog Watch data in comparison with records held in the database of the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/) for the period 1960-1975 suggest that hedgehogs are now present in fewer 10x10km squares in England (Hof and Bright 2016). Most recently, the Hog Watch survey has been subsumed by “The Big Hedgehog Map” project, again coordinated by the PTES, which allows members of the public to submit ad hoc sightings of hedgehogs via a web portal (bighedgehogmap.org).

In summary, a wide range of hedgehog monitoring programmes have been implemented since 2001. Of these, the majority (LwM, GBW, MYNC, HW) have tended to focus primarily on hedgehogs in urban landscapes, and peoples’ gardens in particular. Of the remainder, only the MoR is especially focused on obtaining data for rural hedgehogs populations in the wider countryside. However, all of these surveys are associated with a range of limitations, not least of which are the biases associated with how the raw data are collected. As such, these programmes indicate that hedgehogs are likely to be declining but the rate of decline is not clear.

In addition, very few of the published outputs resulting from these surveys have attempted to address the underlying biotic and abiotic factors associated with the changes in relative abundance / occupancy they purport to show. Those that have (e.g. Hof and Bright 2009; Pettett *et al.* 2017b) have also tended to focus at spatial scales that do not clearly match the scale at which the data were collected. As such, there is a need for a more robust survey protocol where the problems highlighted above can be eliminated.

Potential factors related to a decline in hedgehog numbers in the UK

Four major factors can be recognised that might be expected to have negatively affected hedgehogs in the UK: habitat loss, fragmentation and homogenisation; intra-guild predation; climate change; and anthropogenic mortality.

Habitat loss and homogenisation

Habitat loss is one of the main threats to global biodiversity and the key cause of species loss in terrestrial ecosystems (Brooks *et al.* 2002; Millennium Ecosystem Assessment 2005; Macdonald *et al.* 2007; Giam *et al.* 2010), and can occur directly (e.g. habitat removed to build roads, urban areas or agricultural land) or indirectly through the degradation of habitat quality (e.g. from road emissions such as noise or pollutants; Jaeger *et al.* 2005). Habitat loss affects many taxa but has a disproportionately damaging impact on threatened species (European Environment Agency 2012).

Key causes of habitat loss are the development of intensive agricultural systems (Robinson and Sutherland 2002; Donald and Evans 2006; Kareiva *et al.* 2007; Maron and Fitzsimons 2007; Rounsevell and Reay 2009; Sutcliffe *et al.* 2015) and urbanisation. A major change associated with agricultural intensification has been an increase in field size, often achieved by the removal of hedgerow stock. In the UK, the total length of hedgerows has halved since 1945 (Figure 1.5; Barr and Gillespie 2000), and the density of hedgerows in arable counties may now only be 20-30% that of pastoral counties (Robinson and Sutherland 2002).

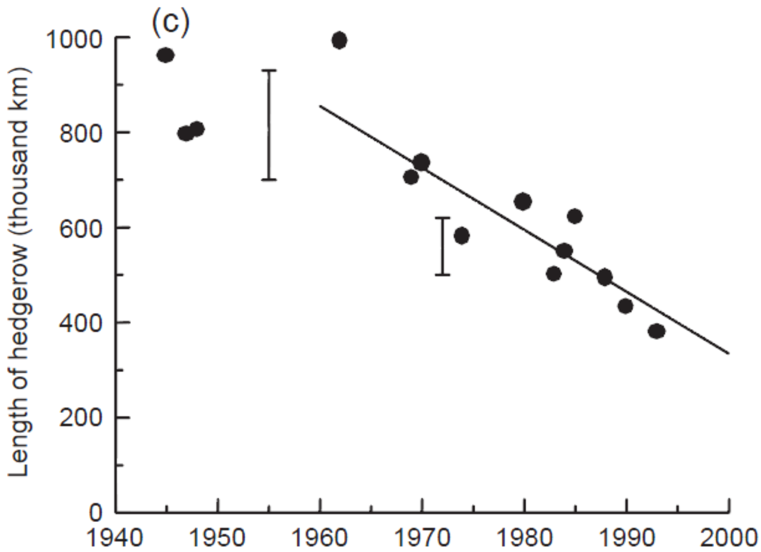

Figure 1.5. Published estimates of hedgerow length in England and Wales: dots indicate (mean) estimates; bars indicate ranges. Slope of regression (1960–98) = -13,000 km year^{-1}, R^2 = 0·74 (from Robinson and Sutherland 2002).

In addition to their destruction / removal, hedgerow management practices have also changed with many now neglected and left to turn into tree-lines or managed intensively, often with flails, a practice intended to keep them tidy but which reduces their ecological benefit (e.g. Barr and Gillespie 2000; Hinsley and Bellamy 2000; Croxton and Sparks 2002; Robinson and Sutherland 2002; Roy and de Blois 2008; Staley *et al.* 2018). For hedgehogs, the loss of hedgerows, including through changes in quality, represents a reduction in both foraging and potential refugia (e.g. Shanahan *et al.* 2007; Hof and Bright 2010; Hof *et al.* 2012) but also increases the likelihood that they may encounter predators as they travel through the landscape.

Although the hedgehog is considered a dietary and habitat generalist (Reeve 1994), it prefers heterogeneous areas which deliver good feeding grounds (e.g. grassland) and sites for resting during the daytime, breeding and hibernating (Morris 2012). At one level, hedgehogs may be considered potentially better able to cope with the loss of linear habitats such as hedgerows since they are fairly mobile, covering distances of >1km (females, 1.5km males) per night (Table 1.1; Reeve 1994), and will forage in non-edge habitats (Hof *et al.* 2012). Indeed, for the majority of their evolutionary life, hedgerows have not been part of the landscape, therefore, are not essential for the survival of hedgehogs.

Hedgehogs also show a tendency toward favouring grassland habitats (e.g. Morris and Morris 1988; Doncaster 1992; Harris *et al.* 1995; Shanahan *et al.* 2007). Although the absolute amount of grassland has remained relatively constant in the UK (Bibby 2009; Rounsevell and Reay 2009), this has been associated with an increase in more intensively managed pasture fields, a decline in the amount of fallow set-aside and temporary grassland (Bibby 2009) and high-densities of livestock, both of which may be detrimental to hedgehogs. In particular, there are pronounced regional differences in the amount of grassland available with more arable farming in the east and pastoral in the west (Robinson and Sutherland 2002). Furthermore, the application of chemical treatments to farmland may have reduced the amount of invertebrate prey available to insectivores such as hedgehogs (Giller *et al.* 1997).

Habitat fragmentation

"Habitat fragmentation" is often used as an umbrella term for many phenomena and used inconsistently (Lindenmayer and Fischer 2007). For the purposes of this discussion, I will use the definition provided by Seiler (2001): "a splitting of contiguous areas into smaller and increasingly dispersed fragments". Habitat fragmentation has the dual effect of isolating sub-populations and diminishing the area that each sub-population can occupy (Figure 1.6); if remnant habitat patches become too small and isolated, then this reduces the number and size of populations that can survive in the area (Seiler 2001). Globally, habitat fragmentation is considered to be a major cause of biodiversity loss (Lindenmayer *et al.* 1999; Parker and Mac Nally 2002).

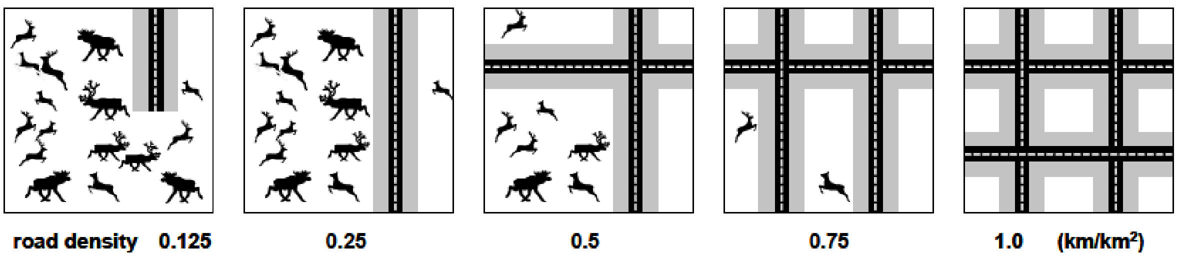

Figure 1.6. Illustration of the process of fragmentation, using roads as an example: white – undisturbed habitat; grey – habitat degradation; black – road (reproduced from Seiler 2001).

Although a distinct phenomenon, habitat fragmentation is closely linked to habitat loss, as some forms of fragmentation can make areas of habitat inaccessible or harder to access. One well studied example is the barrier to movement created by roads (e.g. Seiler 2001; Langevelde and Jaarsma 2004; Jaeger *et al.* 2005; Coffin 2007; Mcgregor *et al.* 2008). Shah (2012) estimated the total road length in GB in 2011 to be 245,000 miles, an increase of 2,100 miles over the previous 10 years; 'A' roads and motorways accounted for 12% and 1% of this length, respectively, but 65% of road traffic. This could potentially lead to the isolation of hedgehog populations (Becher and Griffiths 1998), since they have been shown to avoid crossing major roads (Rondinini and Doncaster 2002).

Although habitat fragmentation is often considered in the context of a linear barrier inhibiting movement, it can also occur when favoured habitats are isolated by distance within a matrix of less suitable habitats (e.g. woodland blocks within agricultural landscapes). For some species, this can be a considerable problem, especially when there are no corridors connecting the habitat fragments (Fahrig and Merriam 1985). Matrix habitats may also become barriers to movement if they contain e.g. high densities of competitors or predators.

Overall, hedgehogs are likely to be affected negatively by habitat fragmentation but, as their name suggests, are positively associated with edge habitats (e.g. Doncaster *et al.* 2001; Shanahan *et al.* 2007; Hof and Bright 2010b; Hof *et al.* 2012). Consequently, some habitat fragmentation may be of benefit (Bright 1993; Collinge 1996), although not all edge habitats would necessarily be beneficial (Becher and Griffiths 1998; Rondinini and Doncaster 2002).

Predation and competition

The main predator of hedgehogs in the UK is the badger (*Meles meles*), which is able to predate even healthy individuals. It is estimated that the UK badger population has almost doubled in the last 20 - 30 years as a consequence of increased legal protection (Harris *et al.* 1995; Wilson *et al.* 1997; Macdonald and Burnham 2011; Judge *et al.* 2014, 2017). The species was given limited protection by the Badgers (Protection Act) 1973 and the Wildlife and Countryside Act 1981. Although these protected the animals themselves from e.g. snaring, gassing, trapping and shooting, they did not protect their setts, posing particular problems with prosecuting offenders caught digging out setts. The passing of the Badgers Act 1991 gave legal protection to badger setts (Wilson 1998). The Protection of Badgers Act 1992 subsequently bought together the various forms of protection encapsulated in these previous laws (Wilson 1998).

The badger is an intra-guild predator of the hedgehog, not only killing them but also competing for the same foods (Doncaster 1992; Morris 2006). Based purely on competition for food, Morris (2006) has postulated that for every extra badger seven fewer hedgehogs can survive in the same area. Similarly, Micol *et al.* (1994) predicted that hedgehogs would be extirpated in all but isolated pockets of the environment in areas where badger sett density exceeded 2.27 setts per 10 km^2; badger density already exceeds this in Wales and the south and west of England (Morris 2006; Judge *et al.* 2014, 2017).

Most recently, Young *et al.* (2006), Parrott *et al.* (2014) and Trewby *et al.* (2014) have all documented increased "abundance" of hedgehogs in areas where badgers have been removed as part of a government strategy to control bovine tuberculosis in cattle. Similarly, Hof and Bright (2009) and Pettett *et al.* (2017b) have reported negative correlations between badgers and hedgehogs at the 10x10 km scale. However, the exact biological mechanism underlying some of these results is not clear. For example, Hubert *et al.* (2011) recorded markedly higher densities of hedgehogs in urban areas than in rural areas, attributing this difference primarily to the higher abundance of badgers in rural areas. Consequently, the results reported by Trewby *et al.* (2014) and others may simply reflect differences in the movement behaviours of hedgehogs rather than actual changes in abundance. This hypothesis is supported by Hof *et al.*'s (2012) observation of "edge refuging behaviour", whereby hedgehogs preferentially forage close to edge cover in areas where badgers are present even though these areas are associated with lower macro-invertebrate availability.

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 (e.g. by using statistical tests) by changes in the mean and / or the variability of its properties and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings, or to persistent anthropogenic changes in the composition of the atmosphere or in land use" (Solomon *et al.* 2007).

Climate change has been studied in relation to a number of taxa in a plethora of publications (Williams *et al.* 2008). It is well documented that climate change threatens ecosystem function and global biodiversity (e.g. McCarty 2001; Williams *et al.* 2008; Mawdsley *et al.* 2009). Thomas *et al.* (2004) estimated that between *c*. 18–35% of species face extinction because of changes associated with climate warming. The best known examples of how climate affects species and ecosystems is that of coral reefs (e.g. Baker *et al.* 2008b; Cinner *et al.* 2012) and the poles (e.g. Meek 2011; Peacock *et al.* 2011), but it affects all ecosystems, including rainforests (Shoo *et al.* 2005; Ledru *et al.* 2009; Quesada *et al.* 2012) and temperate grasslands (Finger *et al.* 2010). There are a number of pathways that a change in climatic conditions can take in affecting community structure and composition. Climate can affect species directly (e.g. increased temperature making the area uninhabitable) or indirectly (e.g. changing food availability).

A changing climate can affect species in many ways including: (i) altering species distributions; (ii) changes to demographic variables e.g. fecundity and / or survival; (iii) reduced or increased population size; (iv) species extirpation; (v) population isolation; and (vi) increased spread of disease (Mawdsley *et al.* 2009). The effects of a changing climate can already be seen in a number of taxa (McCarty 2001); the extent to which species are affected depends on their exposure and sensitivity, the latter represented by a combination of ecology, genetic diversity, physiology, resilience and adaptive capacity (Williams *et al.* 2008). Furthermore, it may not be the overall change that poses a problem, but the rate at which it happens; species need enough time to be able to adapt to the changes (McCarty 2001) and those that are unable to disperse have a greater chance of becoming extinct (Thomas *et al.* 2004).

Climate change increases the occurrence and magnitude of extreme weather such as heavy daily precipitation, temperature extremes (hot and cold), droughts, and increased wind speed (Hughes 2000; IPCC 2012). Such events can cause areas to become uninhabitable due to e.g. flash floods or wildfire (IPCC 2012). This can have severe negative consequences on organisms in the area forcing them to relocate or die. It is highly likely that floods would have adverse effects on hedgehogs and other fossorial species; these could include local extirpation (as was the case with the fringe-tailed garble, *Tatera robusta*: Senzota 1984) or a decrease in abundance (Chamberlain and Leopold 2003). Hedgehogs may be particularly vulnerable during periods of hibernation when they will be unable to retreat rapidly to safety.

Campbell and Smith (2000) predict that grassland in Europe will become wetter; this could benefit hedgehogs as one of their main foods, the earthworm (*Lumbricus terrestris*) (Reeve 1994; Vermeulen *et al.* 2010), likes moisture-rich soils, develop faster and have an increased mass in such an environment (Berry and Jordan 2001). However, if the area is too wet, nesting sites will be reduced. Hedgehogs are able to adapt to a range of climates, as indicated by the range of countries where they exist currently (e.g. Scandinavia, New Zealand, Spain).

Within the UK, hedgehogs are more likely to be affected by climatic conditions that: (a) reduce food availability in summer (e.g. prolonged dry periods that limit the availability of earthworms and beetles: see Macdonald *et al.* (2010) for effects on badgers) such that (i) they enter hibernation with low levels of fat reserves and / or (ii) which reduces juvenile survival; and (b) periods of warm weather during winter which rouses them from hibernation early at a time when there is limited availability of food. The latter could potentially also be an issue in urban habitats due to the "urban heat island effect", which makes them several degrees warmer than surrounding rural areas; such roused individuals may be especially likely to then be handed in to wildlife rehabilitation hospitals. In addition, periodic flooding events may also elevate mortality at a local scale.

Direct anthropogenic mortality

Mortality caused by humans affects many taxa and can occur deliberately (e.g. to control predators: Kinnear *et al.* 2002; Graham *et al.* 2005; Whitehead *et al.* 2008) or accidentally (e.g. bycatch: Berggren *et al.* 2002; or road deaths: Bonnet *et al.* 1999; Hostetler *et al.* 2009; Schaub *et al.* 2010). Historically, hedgehogs were killed by gamekeepers. However, this practice has largely stopped and they are now protected under Schedule 6 of the Wildlife and Countryside Act 1981; Wild Mammals (Protection) Act 1996; Section 41 NERC 2006; UK BAP 2007 and Appendix 3 of the Bern Convention. Accidental trapping does still occur, however (JNCC 2010; Morris 2012). Furthermore, current "best practice" guidelines recommend the use of baffles to make it harder for hedgehogs to enter tunnels set to trap stoats (*Mustela erminea*) and weasels (*Mustela nivalis*), although these will not eliminate hedgehog deaths completely (Short and Reynolds 2001).

Hedgehogs are also exposed to a wide range of anthropogenic hazards including mowers, strimmers, bonfires, cattle grids, drains, ponds, roads, netting (e.g. tennis nets, football nets, garden nets), rubbish (e.g. plastic ring binders, tin cans, discarded rubber bands), swimming pools and heavy machinery (e.g. tractors with flails) (Reeve 1994; Morris 2012). They are also a species that is relatively easy to catch, which means that they are frequently victims of intentional abuse by humans (Grogan pers. comm.). Consequently, hedgehogs are one of the species most commonly admitted to wildlife hospitals (Molony *et al.* 2007; Grogan and Kelly 2013; Barnes and Farnworth 2017; Matthews pers. comm.).

Perhaps the biggest anthropogenic cause of mortality in hedgehogs, however, is collisions with vehicles. As outlined above, 167,000-335,000 hedgehogs are estimated to be killed on roads in Britain each year (Wembridge *et al.* 2016), and traffic mortalities have frequently been reported as the most common cause of death in studies of hedgehog populations (Reeve and Huijser 1999), especially urban populations (Orłowski and Nowak 2004; Rautio *et al.* 2016). Hedgehogs may be especially vulnerable to road traffic, not only because they are small and grey in colour, but because they freeze when threatened; this stationary stance makes it especially difficult for drivers to see them at night.

Hedgehogs are also directly and indirectly exposed to a range of toxins (a poisonous substance produced by an organism; e.g. snake venom, toad "venom" (bufotoxin) and cantharidin: Reeve 1994), toxicants (a poisonous substance not produced by an organism e.g. heavy metals) and chemicals (produced by humans). For example, heavy metals can have various effects on wild animals including stunted growth and death, but can also lead to changes in community composition (Underhill and Angold 2000; Millán *et al.* 2008). Heavy metals readily move through insectivorous food chains and have a tendency to bio-accumulate (Walker *et al.* 2002, 2007). Spurgeon and Hopkin (1996) showed that earthworms also accumulate heavy metals, and are an important pathway for their transfer into predators, which would include hedgehogs.

Poisons may enter organisms directly or indirectly (e.g. via the consumption of carrion). For non-target species the most common pathway is indirectly by eating poisoned prey; this has been known to affect e.g. harbour (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) (Bernt *et al.* 1999), mustelids (Shore *et al.* 1996, 2003; Elmeros *et al.* 2011), and raptors (Giraudoux *et al.* 2006; Thomas *et al.* 2011). In agricultural landscapes, invertebrates are often controlled using chemical compounds: this may act to reduce the amount of ground-dwelling insect and mollusc prey available to hedgehogs, but could also pose a risk of secondary (most likely sub-lethal) poisoning (Morris 2006).

Hedgehogs are also potentially vulnerable to direct and indirect exposure to anti-coagulant rodenticides used to control rats and mice. For example, Dowding *et al.* (2010b) detected first and seconded generation anticoagulant rodenticides (FGARs and SGARs) in hedgehogs from the UK, with almost a quarter (22.5%) containing more than one compound (see also Sánchez-Barbudo *et al.* (2012) for anticoagulant residues detected in Spain). In the UK, hedgehogs may be exposed directly to FGARs and SGARs if they are used inappropriately (e.g. users do not follow the supplier's instructions), but juvenile individuals are also able to enter bait boxes designed specifically to reduce risks to non-target species. In addition, hedgehogs are likely to consume rodents that have been poisoned, but invertebrates entering bait boxes may also pose a risk if they are later consumed by hedgehogs (Alomar *et al.* 2018).

Summary and thesis structure

Overall, the conservation position of the hedgehog in the UK (and elsewhere) is potentially at a critical point. Despite several publications highlighting our general lack of knowledge about many key aspects of hedgehog populations in the mid-1990s (Morris 1993; Harris *et al.* 1995), which were intended to act as a spur to fill these gaps, relatively little progress was made in the subsequent 20 years. During that period, however, evidence from several monitoring programmes has indicated that populations have declined, perhaps by as much as 30-40% (or even more), although the robustness of the data from all of these programmes is equivocal and patterns / rates of decline may vary between urban and rural landscapes.

Conversely, there has been much less attention focussed on identifying the underlying biological and anthropogenic mechanisms associated with this decline, although our knowledge of general hedgehog ecology suggests that there are likely to be several factors. The exception is the negative effects of a burgeoning badger population, although, even for this factor, there are several potential mechanisms (predation, competition, avoidance) that could explain the results presented by various authors thus far.

Most especially, however, there have been no studies of management actions to help reverse declines. In part, this is associated with the lack of a clear understanding of why hedgehogs are declining. The work presented in this thesis aims to help fill some of the knowledge gaps highlighted in this chapter, as well as investigating the utility of alternative methods for monitoring hedgehog populations and which are not affected by the limitations associated with current approaches. These data form part of an integrated set of studies coordinated by the People's Trust for Endangered Species and British Hedgehog Preservation Society in conjunction with research partners such as Nottingham Trent University, the University of Oxford and the University of Reading, to provide the evidence necessary for making informed decisions on how best to improve the status of hedgehogs in this country.

The work completed for this thesis is presented in six chapters, followed by a concluding Discussion. With the exception of *Chapter Seven*, each is intended to be submitted as a paper to a peer-reviewed journal. For this reason, the style of presentation varies slightly from chapter to chapter and there is a degree of repetition between some sections of these chapters. An overview of the objectives of each chapter are given below.

Chapter Two

As outlined in this Introduction, there is an urgent need for the development of a field survey method that can be used to reliably monitor hedgehog populations, avoiding the limitations associated with current monitoring programmes. Footprint tunnels have been identified as a potentially suitable technique for monitoring hedgehog populations (Harris and Yalden 2004), having been used previously in at least one scientific study (Huijser and Bergers 2000). Since this time, a new analytical method (occupancy analysis: MacKenzie *et al.* 2006) has also been developed from which it is possible to estimate the false-absence error rate (the rate associated with failing to detect a species at a site where it is actually present). Therefore, in this chapter, data are presented from a pilot project to test the reliability of footprint tunnels as a method for surveying hedgehogs at sites in the rural landscape. The specific objectives of this study were to:

(i) Evaluate the use of footprint tunnels as a survey method for rural sites, with specific emphasis on:
   a) Whether the survey technique could be used reliably by volunteer surveyors, and
   b) Whether patterns of occupancy varied within sites at different times of the year.

Chapter Three

Having successfully demonstrated that footprint tunnels are a reliable field method for surveying rural hedgehog populations, these were then used as the basis for a national survey of hedgehogs in England and Wales. This involved the recruitment of a range of volunteers throughout these countries. Sites surveyed had previously been surveyed for badger sett density by Judge *et al.* (2014, 2017). The objectives of this study were to:

(i) Quantify current levels of occupancy of hedgehogs in the rural landscape based upon the survey of randomly selected sites, and
(ii) Quantify the influence of both relative badger density and habitat availability on patterns of hedgehog occupancy.

The data generated in this national survey were also used to form a baseline against which future changes in occupancy could be measured.

Chapter Four

Surveying hedgehogs in urban landscapes poses a different set of challenges to surveying populations in rural areas. Most especially, hedgehogs appear to preferentially use residential gardens, especially back gardens, over other habitats (Dowding *et al*. 2010): these cannot be easily observed from publicly accessible areas and are privately owned, so that access is difficult. In addition, each garden is relatively small (~190m^2: Davies *et al.* 2009), such that any effective conservation action will require the coordinated involvement of many householders. One of the first steps in implementing such actions is, however, identifying the factors which make a garden "hedgehog friendly"; these could potentially be factors within the garden itself (e.g. microhabitat availability, wildlife gardening practices) but also outside the garden (e.g. proximity to natural or semi-natural habitats) as well. The aims of this Chapter were:

(i) To evaluate the use of footprint tunnels as a survey method for urban gardens sites, with specific emphasis on whether the survey technique could be used reliably by volunteer surveyors, and

(ii) To use occupancy analysis to identify the within-garden and outside-garden factors associated with the presence-absence of hedgehogs in private residential gardens.

This study was conducted in Reading over two separate years. Consequently, it was possible to also consider:

(iii) How patterns of occupancy of hedgehogs in gardens varied on an inter-annual basis.

Chapter Five

Road and roadside characteristics have been shown to influence the likelihood of animals being killed and recent estimates on the numbers of hedgehogs killed annually indicate that a significant proportion of the population could be affected (Wembridge *et al.* 2016). However, it is unclear as to what road and roadside characteristics may be associated with them being killed by motor vehicles. The potential influence of such factors also has implications for using counts of dead hedgehogs as a robust method for monitoring changes in hedgehog populations, the only method used currently for assessing changes in rural hedgehog populations in the UK, and for devising appropriate strategies to help mitigate the effects of roads. Therefore, in this chapter, data on the positioning of hedgehog casualties reported during a hedgehog awareness campaign run by the Suffolk Wildlife Trust were used to:

(i) Identify whether hedgehog casualties were clustered spatially, as this could potentially enable some forms of mitigation (e.g. road signage) to be used to help reduce collision rates, and

(ii) Identify whether road and / or roadside characteristics appeared to increase the risk of collision by comparing these factors at those sites where dead hedgehogs were reported in comparison with a random set of locations determined using Google Street View. Data were analysed for both urban and rural landscapes.

Chapter Six

In addition to direct mortality effects, roads may act as barriers to the movements of hedgehogs, potentially leading to the isolation of populations (Becher and Griffiths 1998). Although hedgehogs have been shown to avoid crossing A-roads and motorways (Rondinini and Doncaster 2002), these are associated with bridges and footpaths which may enable hedgehog populations to remain connected. In addition, mitigation measures put in to help other species get across motorways (e.g. badger tunnels) may or may not also increase connectivity. In this study, genetic samples were collected from hedgehogs in a region spanning from Bristol to Slough (West - East) and Southampton to Cirencester (South - North) to investigate:

(i) Whether there was any evidence for isolation of hedgehog populations and, if so, whether this appeared to be related to (a) road structure, (b) other habitat features (e.g. rivers) and / or (c) badger abundance

Chapter Seven

Although hedgehog numbers appear to be declining throughout the UK, the rate of decline is uncertain because of the limitations associated with the surveying methods. One alternative approach to estimate the rate of decline is to use age-structured matrices to model population growth rates. In this chapter, a basic age-structured Leslie matrix population model was constructed from data extracted from published literature to:

(i) Estimate the current population growth rate,
(ii) Identify the relative importance of different demographic parameters on the population growth rate, and
(iii) Identify any gaps in knowledge about current hedgehog population demographics.

General Discussion

The final chapter summarises the results presented in the thesis in the context of the future conservation of hedgehogs in the UK. This includes a set of recommendations for future research that build upon the current work.

Chapter two

Currently, three programmes are being used to monitor rural hedgehog populations in the UK: the People's Trust for Endangered Species *Mammals on Roads* survey; the British Trust for Ornithology's *Breeding Bird Survey*; and the Game and Wildlife Conservation Trust's *National Gamebag Census*. All of these are potentially associated with significant problems (Chapter One). Consequently, a new field method is required which overcomes these limitations, whilst at the same time allowing the underlying factors associated with any observed changes to be quantified. Footprint tunnels have previously been used in studies of wild hedgehogs to document their relative abundance in the vicinity of roads (Huijser and Bergers 2000). Since that study, new analytical methods such as occupancy analysis (MacKenzie *et al.* 2006) have been developed which potentially extend the utility of footprint tunnels as a method for monitoring hedgehog populations. In this chapter, I conducted a pilot study to investigate the effectiveness of footprint tunnels as a method for surveying hedgehog occupancy in rural landscapes.

The manuscript presented in this chapter has been published in the journal *Mammal Review*.
Yarnell, R.W., Pacheco, M., Williams, B., 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. Mammal Rev*. 44, 234-238.

With a slightly altered version aimed at ecological consultants published in *In Practice*:
Yarnell, R.W., Williams, B., Thomas, E., Baker, P. (2015) Hedgehogs in tunnels: Footprint tracking tunnels as a method for detecting hedgehog populations. *In Practice*. 88, 38-41.

My contribution to the work

I surveyed *c.* 14% of the sites and conducted the analysis with input from Richard Yarnell. I co-wrote the manuscript with Richard Yarnell and Philip Baker.

A step forward: using occupancy analysis to validate the use of footprint-tunnels as a method for monitoring an elusive mammal species, the hedgehog

Keywords: *citizen science, field sign surveys, footprint tracking tunnels, occupancy modelling, population monitoring, Erinaceidae*

Abstract

Indirect survey methods are often used in mammal studies but are susceptible to biases caused by failing to detect species where they are present. Occupancy analysis is an analytical technique which enables non-detection rates to be estimated and which can be used to develop and refine novel survey methods. In this study, I investigated footprint-tunnels as a volunteer-appropriate method for monitoring hedgehog (*Erinaceus europaeus*) occupancy. The survey protocol had a very low non-detection rate and could reasonably be used to detect occupancy changes of 25% with 95% power in a national survey.

Introduction

Accurate estimates of population size, or reliable surrogate measures, are essential for effective wildlife management and conservation. However, as many mammal species are difficult to observe directly, indirect techniques based upon field signs have been used widely (Wilson and Delahay 2001). Yet indirect methods can be associated with significant problems (e.g. a lack of evidence that they correlate with animal density, failing to detect a species when it is present), which can lead to erroneous conclusions and inappropriate management actions.

One approach for overcoming the problem of non-detection is occupancy analysis, a maximum-likelihood based method which uses repeated surveys to generate site-specific detection records from which the non-detection error rate can be estimated (MacKenzie *et al.* 2006). This therefore enables novel survey methods to be developed and refined so that error rates are minimised. In this communication, I describe the results of a study examining the use of footprint-tunnels (Huijser and Bergers 2000) in combination with occupancy analysis as a method for monitoring western European hedgehogs (*Erinaceus europaeus*), a species currently of conservation concern in the UK (Battersby 2005) and elsewhere.

Methods

One-hundred and eleven sites were surveyed between April 2011-September 2013 inclusive (Figure 2.1). Surveys were conducted by local mammal groups and by university students supervised by the authors. Sites (e.g. farms, golf courses) were selected randomly (i.e. not based upon prior knowledge of hedgehog status) based on landowner permissions and commuting distance. Ten tunnels (Figure 2.2) were deployed at each site placed parallel to linear features (hedgerows, fences) as hedgehogs frequently follow these when travelling (Hof *et al.* 2012); tunnels were placed >100m apart, with no more than two tunnels in the same field. Tunnels were checked every morning for five continuous days at each site: food bait (tinned sausages) was replaced if necessary. Footprint papers were replaced if they were damaged or had recorded hedgehog or non-target animal footprints; all papers were returned for verification.

Data were analysed using PRESENCE v5.7 (Hines 2006). Each night was treated as a repeat survey; sites were classified as occupied if ≥1 tunnels recorded hedgehog footprints on any night. Tunnels were not considered independent as hedgehogs could have visited >1 tunnel each night. Data were analysed annually and after pooling across all three years; as some sites had been surveyed more than once, only the most recent information within the respective time period was used. Initial analyses compared models based upon constant versus variable ("survey-specific") daily detection rates; the latter was used to investigate whether hedgehogs habituated to the tunnels over time. The optimal model was selected using minimum Akaike's Information Criterion (AIC) values and used to estimate the number of days required to determine absence at a site at 0.80 and 0.90 confidence levels (McArdle 1990).

The effects of three categories of covariates on occupancy were investigated using subsets of the data: (i) season (spring: April-May; summer: June-July; autumn: August-September; N=111 sites); (ii) habitat (N=87); and (iii) habitat and the presence-absence of badgers (*Meles meles*) (N=73). The former relates to optimising survey timing, whereas both habitat structure and badger presence have been shown to influence hedgehog presence (Young *et al.* 2006; Hubert *et al.* 2011). Land cover types representing UK Biodiversity Action Plan Broad Habitats were obtained from Land cover 2007 vector data (Centre for Ecology and Hydrology 2012) and aggregated into five categories: urban, woodland, grasslands, arable and "other". Habitat availability was quantified as the proportional area of each class within a circle of radius 500m centred on each site; this radius was selected to encapsulate the likely home range size of hedgehogs in these sites. As sample sizes were moderate, individual occupancy models included a maximum of two habitat classes. Badger presence was estimated from field signs, observations during nocturnal spotlight counts and from conversations with landowners. As the data were often over-dispersed, adjustments were made to the variance inflation factor ($\hat{c}$) and models were ranked by quasi-AIC (QAIC) values (Anderson and Burnham 2002). Models with ΔQAIC values >2 or which did not converge were excluded as having little or no support (Burnham and Anderson 2002), except where models with constant and variable detection daily detection rates were compared; in this case, models with ΔQAIC values > 2 were included for illustrative purposes.

The suitability of the survey protocol for future monitoring purposes was assessed by estimating the number of sites needed to detect a change (α=0.05) in occupancy between two surveys given an actual decline (50%, 25%, 10%) with four different levels of replication (2, 3, 4 and 5 days) at a given level of power (0.80, 0.90, 0.95). Estimates of occupancy and detection were derived from the 111 sites surveyed. Simulations were used to verify the performance of each study design; each scenario was run 5000 times and power was calculated as the proportion of simulations in which a significant difference was detected. All analyses were conducted using R code provided by Guillera-Arroita and Lahoz-Monfort (2012).

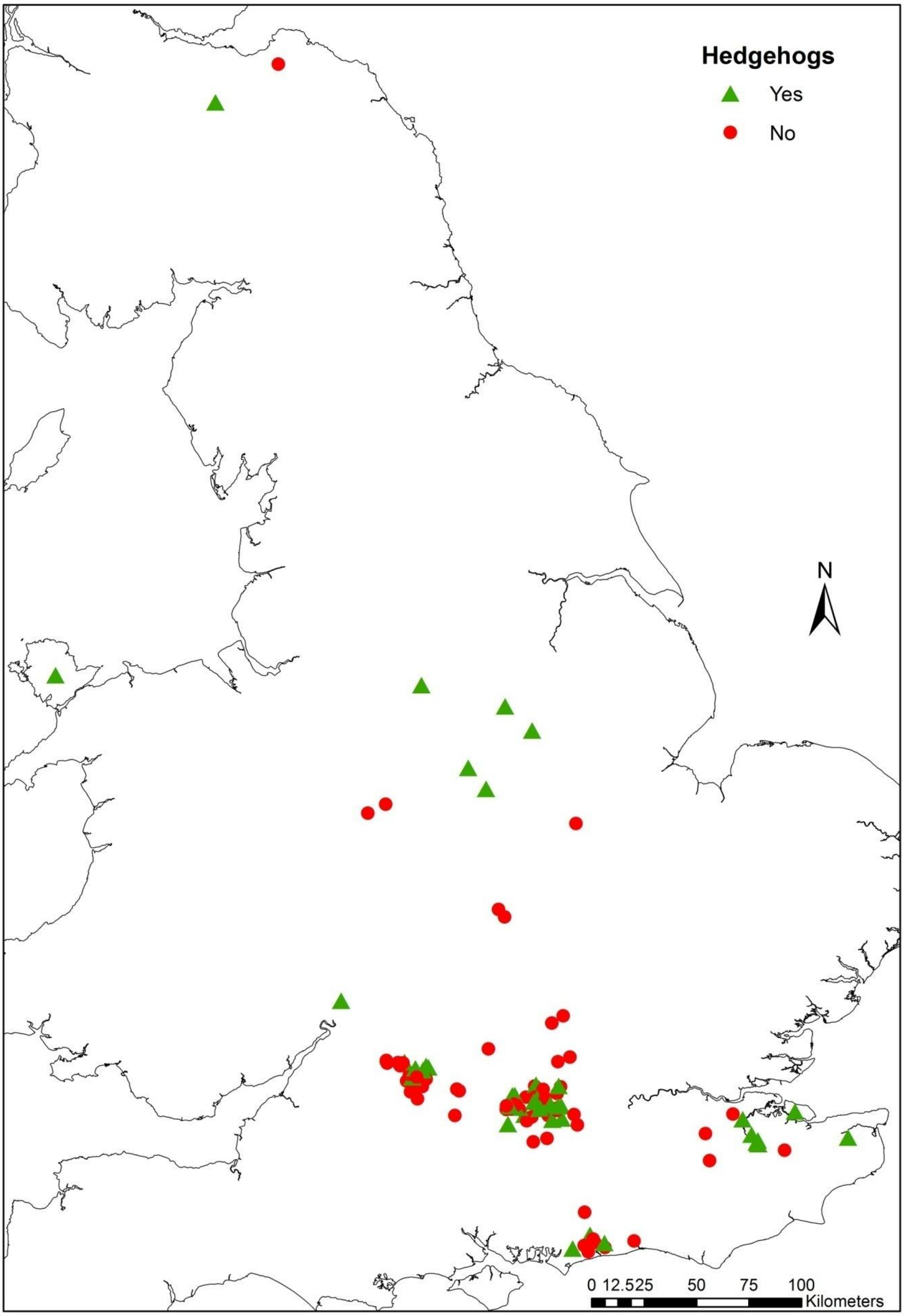

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Figure 2.1. Distribution of sites surveyed (N=111) showing which sites detected hedgehog presence (▲) and absence (●).

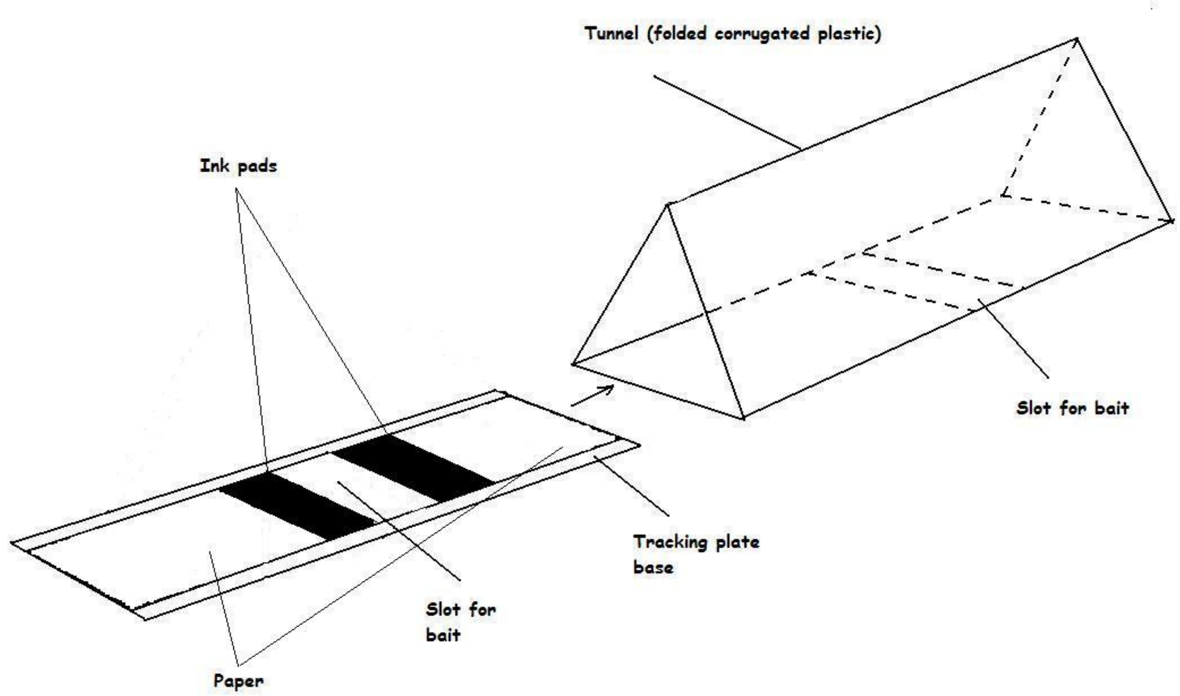

Figure 2.2. Design of the footprint-tunnels used in this study. Tunnels were constructed from corrugated plastic (Correx®).

Results

Occupancy models with a constant detection rate performed better than those with a variable detection rate (Table 2.2). All further analyses were, therefore, conducted using constant daily detection models.

Collectively, naïve occupancy was 0.392 with a daily detection probability of 0.593 (Table 2.2). The absolute difference in naïve and estimated occupancy rates based on the pooled data was 0.5%, with the number of survey replicates required to determine species absence ranging up to 3.6 (Table 2.2). Therefore, five days was sufficient to be confident that the absence of footprints at a site reflected a true absence.

Neither season (Table 2.3a) nor habitat (Table 2.3b) covariates alone improved model fit above that based solely on a constant daily detection rate. However, there was a significant negative relationship between badgers and hedgehogs (Table 2.3c), with hedgehogs twice as likely to be present on sites without badgers (Ψ = 0.506 ±SE 0.095) compared to those where badgers were present (Ψ = 0.247 ±SE 0.065).

Given the sample sizes typically achieved in volunteer-based mammal surveys in the UK (N < 1000: Battersby 2005), power analyses indicated that the survey protocol would be suitable for detecting changes in occupancy in the order of 25% (Table 2.1). Substantially larger sample sizes would be required to detect changes of smaller magnitudes.

Table 2.1. Results of power analysis showing the number of sites required to detect a significant change in occupancy for a given survey effort to different levels of statistical power.

% change in occupancy	Survey effort (no. of days surveyed)	No. of sites required to achieve stated level of statistical power		
		0.80	**0.90**	**0.95**
10	2	4250	5690	7036
25		640	856	1059
50		140	188	232
10	3	2820	3775	4668
25		429	574	710
50		95	127	157
10	4	2537	3396	4200
25		387	519	641
50		86	115	142
10	5	2453	3283	4060
25		375	502	621
50		84	112	138

Table 2.2. Summary of occupancy (Ψ) models based upon constant (2 parameters) versus variable daily detection rates (6 parameters); naïve and estimated occupancy rates are given only for constant detection rate models. Number of surveys required at two levels of confidence that non-detection shows absence of hedgehogs.

Year	No. of sites	Daily Detection rate (P)	QAIC	ΔQAIC	AICwgt	Estimated (naïve) Ψ	Detection rate P (±SE)	No. of surveys needed (±SE)	
								80% confidence	95% Confidence
2011	26	Constant	55.11	0.00	0.937	0.385 (0.385)	0.820 (0.055)	1.0 (0.6 - 1.4)	1.7 (1.1 - 2.5)
		Variable	60.51	5.40	0.063				
2012	62	Constant	117.30	0.00	0.961	0.476 (0.468)	0.556 (0.043)	1.9 (1.6 - 2.5)	3.6 (2.9 - 4.6)
		Variable	123.68	6.38	0.039				
2013	32	Constant	92.33	0.00	0.971	0.315 (0.315)	0.615 (0.071)	1.7 (1.2 – 2.5)	3.1 (2.2 – 4.6)
		Variable	99.35	7.02	0.029				
All years	111	Constant	159.95	0.00	0.944	0.392 (0.387)	0.593 (0.035)	1.8 (1.5 – 2.2)	3.3 (2.8 – 4.1)
		Variable	165.58	5.63	0.056				

Table 2.3. Summary of constant detection rate models comparing the effects of (a) season (N=111 sites), (b) habitat composition only (N=87 sites) and (c) habitat composition and the presence / absence of badgers (N=73 sites) on hedgehog occupancy. Models with ΔQAIC values >2 were excluded.

Analyses	Covariates	QAIC	ΔQAIC	AIC Wgt	No. parameters	-2 log likelihood
(a) Season	-	165.73	0.00	1.00	2	436.67
(b) Habitat	-	126.95	0.00	0.55	2	319.66
	ARABLE	128.70	1.75	0.23	3	319.01
	URBAN	128.71	1.76	0.22	3	319.05
(c) Habitat and badgers	BADGER	112.91	0.00	0.36	3	256.59
	-	112.98	0.07	0.35	2	261.54
	ARABLE+BADGER	114.60	1.69	0.15	4	255.83
	GRASS+BADGER	114.87	1.96	0.14	4	256.49

Discussion

As hedgehog populations in Britain may be declining rapidly (Wembridge 2011), there is an urgent need for a method that can be used to monitor changes in hedgehog occupancy, abundance and distribution, which can identify factors associated with their decline and which overcomes some of the limitations associated with other methods currently being used (Battersby 2005; Hof and Bright 2009; Roos *et al.* 2012) such as e.g. low detection rates (Poulton and Reeve 2010), the non-random selection of sites (Toms and Newson 2006) and road avoidance behaviours (Rondinini and Doncaster 2002). The footprint-tunnels used in this study meet this need. Most importantly, naïve versus estimated occupancy rates were very similar (38.7% versus 39.2% respectively) indicating a very small non-detection rate. These results provide strong evidence that the survey methodology reliably detected hedgehogs at sites where they were present. In addition, footprint-tunnels can be used in a wide range of habitats and at a spatial scale which is likely to reflect different management practices within the wider landscape (e.g. individual farms). They are also suitable for use by volunteer surveyors: tunnels can be placed optimally within each site in known positions, thereby eliminating the need to search for potentially sparse field signs; they can be checked during the day; and the resultant footprints can be retained for verification. Furthermore, the absence of a seasonal effect on detection success and the potential for reducing the amount of survey time required from five days to four further increases the technique's utility. The use of volunteers is likely to significantly reduce costs whilst simultaneously increasing statistical power and engaging stakeholders (Battersby 2005; Toms and Newson 2006).

Although most sites surveyed were from southern England, the overall occupancy rate recorded in this study was similar to or lower than indices reported in other studies (36-45% in urban areas, 30% for farms, 47-57% of roads surveyed: Hof and Bright 2009; Roos *et al.* 2012). Collectively, these data indicate that hedgehogs appear to be more heterogeneously distributed than they were historically. Similarly acknowledging the limited sample size, only the presence-absence of badgers significantly affected hedgehog occupancy: this is consistent with other studies which have indicated a negative relationship between the two species (Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012). Given the sample sizes achieved in other volunteer-based mammal surveys in the UK (Battersby 2005), this technique would be appropriate for detecting *c*. 25% changes in hedgehog occupancy with a high degree of statistical power.

In summary, I have field-tested an indirect survey method for monitoring hedgehogs using the framework of occupancy analysis to specifically address the potential problem of non-detection. This represents a powerful approach for validating indirect methods in mammal surveys, something that is often problematic but which is also, on occasion, ignored.

Acknowledgements

I thank Ian Stephens for designing the footprint-tunnel, Gurutzeta Guillera-Aroita for advice on power analysis and all students and volunteers who conducted surveys. The study was funded by The People's Trust for Endangered Species and the British Hedgehog Preservation Society and conducted in accordance with UK legislative requirements.

Chapter three

Given the success of the pilot study which demonstrated that footprint tunnels in conjunction with occupancy analysis was a robust field method for determining the presence / absence of hedgehogs in rural habitats, the technique was then applied to a national survey of hedgehogs in England and Wales. Given badger presence had been shown to significantly influence hedgehog occupancy in the pilot study (similar negative associations having also been reported in other studies: e.g. Young *et al.* 2006; Parrott *et al.* 2014; Trewby *et al.* 2014), I took the opportunity to integrate the hedgehog survey into a recently completed study of badger sett density in these countries (Judge *et al.* 2014). As in the pilot study, members of the general public were enlisted to undertake field surveys.

The manuscript presented in this chapter has been published in the journal *Scientific Reports*.

Williams, B., Baker, P., Thomas, E., Wilson, G., Judge, J., Yarnell, R.W. (2018) 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.

My contribution to the work

I executed the project design and co-administered it with Emily Thomas. I conducted all analysis with input from Richard Yarnell. I co-wrote the manuscript with Richard Yarnell and Philip Baker.

Reduced occupancy of hedgehogs (*Erinaceus europaeus*) in rural England and Wales: the influence of habitat and an asymmetric intra-guild predator

Keywords: *badgers, citizen science, field sign surveys, footprint tracking tunnels, population monitoring, insectivore, Meles meles, intra-guild competition*

Abstract

Agricultural landscapes have become increasingly intensively managed resulting in population declines across a broad range of taxa, including insectivores such as the hedgehog (*Erinaceus europaeus*). Hedgehog declines have also been attributed to an increase in the abundance of badgers (*Meles meles*), an intra-guild predator. The status of hedgehogs across the rural landscape at large spatial scales is, however, unknown. In this study, I used footprint tracking tunnels to conduct the first national survey of rural hedgehog populations in England and Wales. Single and two-species occupancy modelling was used to quantify hedgehog occupancy in relation to habitat and predator covariates. Hedgehog occupancy was low (22% nationally), and significantly negatively related to badger sett density and positively related to the built environment. Hedgehogs were also absent from 71% of sites that had no badger setts, indicating that large areas of the rural landscape are not occupied by hedgehogs. Our results provide the first field based national survey of hedgehogs, providing a robust baseline for future monitoring. Furthermore, the combined effects of increasing badger abundance and intensive agriculture may have provided a perfect storm for hedgehogs in rural Britain, leading to considerably low levels of occupancy over large spatial scales.

Introduction

Quantification of the distribution and abundance of populations in relation to biotic and abiotic factors, and how these are changing over time, are fundamental to the development of sound wildlife management strategies (Battersby and Greenwood 2004). The conservation status of the West European hedgehog (*Erinaceus europaeus*) throughout the United Kingdom is currently uncertain, although monitoring programmes based upon questionnaire surveys, timed observations in known habitats and counts of dead animals on roads indicate that numbers have declined markedly over the last two decades (e.g. Wembridge 2011; Roos *et al.* 2012; Hof and Bright 2016; Wembridge and Langton 2016). In addition, a range of ecological and anthropogenic factors can be recognised which would be expected to have potentially negatively impacted hedgehog populations.

Habitat loss is one of the main threats to global biodiversity and the key cause of species loss in terrestrial ecosystems (Brooks *et al.* 2002; Millennium Ecosystem Assessment 2005; Giam *et al.* 2010), and has been driven principally by the increased intensity of agricultural production (Robinson and Sutherland 2002; Donald and Evans 2006; Maron and Fitzsimons 2007; Rounsevell and Reay 2009; Hayhow *et al.* 2016). Within the UK, agricultural landscapes have changed significantly since the early 1900s, becoming more intensively managed and homogenised through practices such as the removal of hedgerows to create larger fields (Robinson and Sutherland 2002; Cornulier *et al.* 2011), the widespread application of molluscicides, insecticides and other pesticides (Robinson and Sutherland 2002; Hayhow *et al.* 2016) and increased mechanisation. In the UK, one of the hedgehog's preferred habitats, grassland, has declined in area since the 1950s (Wilkins 2000). Such changes are known to have resulted in detrimental impacts on a range of taxa (Krebs *et al.* 1999; Donald *et al.* 2001; Robinson and Sutherland 2002; Hayhow *et al.* 2016) and are likely to have negatively affected hedgehog populations by: reducing habitat heterogeneity (Morris 2012); affecting dispersal behaviour (Moorhouse *et al.* 2014); reducing invertebrate prey abundance (Giller *et al.* 1997) and distribution (Hof and Bright 2010a; 2010b); and also possibly via the bioaccumulation of toxic compounds (e.g. Dowding *et al.* 2010b).

In addition, rural landscapes are further fragmented by road networks which could potentially act as a significant source of mortality and a barrier to movement (Becher and Griffiths 1998; Huijser and Bergers 2000). For example, Rondinini and Doncaster (2002) identified that hedgehogs appeared to avoid crossing major roads, most likely as a response to the risk associated with crossing an increased number of lanes of traffic and / or the increased volume of traffic (but see Sadleir and Linklater 2016). Since 1970, the total length of motorways (the major road type in the UK) has increased from 1,000 km to >3,500 km (Department for Transport 2016). Such avoidance and / or barrier effects could lead to the isolation of hedgehog populations, potentially making them more vulnerable.

Within the UK, hedgehogs have few natural predators (Morris and Reeve 2008), but numbers of their principal predator, the Eurasian badger (*Meles meles*), have approximately doubled in the last 25 years following increased legal protection (Judge *et al.* 2014, 2017). A range of studies in the UK

(Young *et al.* 2006; Parrott *et al.* 2014; Trewby *et al.* 2014; Yarnell *et al.* 2014) and elsewhere (Hubert *et al.* 2011) have documented a negative relationship between hedgehog density / occupancy and badgers, although the mechanism behind this relationship is not fully understood. As an intra-guild predator of hedgehogs, badgers could potentially negatively affect hedgehog populations via direct predation and / or through increased competition for food resources; alternatively hedgehogs may preferentially occupy "refuge" habitats where badgers are rare or absent (Hubert *et al.* 2011; Pettett *et al.* 2017a; Pettett *et al.* 2017b). Historically, Micol *et al.* (1994) estimated that where badger main sett density exceeded 0.23 setts per km^2, hedgehogs would be extirpated from all but isolated pockets; this main sett density has now been surpassed across much of England and Wales (Judge *et al.* 2014).

The relative importance of the factors outlined above in affecting the current distribution and abundance of hedgehogs is, however, not known. This has, in part, been due to the absence of a reliable technique for surveying rural hedgehogs at the appropriate spatial scale (Roos *et al.* 2012). For example, anthropogenic management practices are likely to vary within the rural landscape at the scale of individual properties such as farms and amenity sites, whereas approaches such as counts of road traffic casualties are typically conducted at much larger scales spanning multiple properties. Consequently, Yarnell *et al.* (2014) successfully developed and tested a survey method based upon the use of footprint tunnels to record the presence / absence of hedgehogs. In this study, I utilise that method to conduct the first national scale survey of rural hedgehog populations to: (i) measure levels of occupancy across rural England and Wales; and (ii) quantify the effects of habitat availability and predator abundance on patterns of occupancy. These data can then (iii) be used as a baseline against which future changes can be measured.

Methods

Sites (1km Ordnance Survey grid squares) were surveyed between April-October inclusive in 2014-2015 (Figure 3.1). Sites were selected randomly from 1km squares surveyed as part of a prior national survey of badger setts in November 2011-March 2013 (Judge *et al.* 2014), stratified by land class (Bunce *et al.* 1981). As the focus of both surveys was on rural populations, squares had been excluded if they contained >50% urban area.

Surveys were conducted by volunteers and university students supervised by the authors. Surveyors were asked to survey an area of approximately 500m x 500m near the centre of their allocated square(s) and which was owned / managed by one person or organisation. Volunteers were provided with all field equipment and a comprehensive manual detailing the background to the project, survey methodology, health and safety information, data recording sheets and example hedgehog footprint sheets. No prior knowledge of hedgehog status at any site was known and all knowledge of badger activity at sites was withheld from surveyors.

Ten footprint tunnels were deployed at each site placed parallel to linear features (e.g. woodland edges, hedgerows, fences) as hedgehogs frequently follow these when travelling (Hof *et al.* 2012). Tunnels were placed >100m apart, with no more than two tunnels in the same field (Yarnell *et al.* 2014). Tunnels were checked daily for five continuous days: food bait (commercially available dry hedgehog food) was replaced if necessary and footprint papers were replaced if they were damaged or had recorded hedgehog or non-target animal footprints. All footprint papers were returned for verification by the authors.

Factors affecting hedgehog occupancy

Single-species single-season occupancy models were first used to examine hedgehog presence / absence in relation to habitat availability, habitat complexity and relative badger density. Occupancy models use repeated detection / non-detection data of a species over a series of surveys to estimate its occurrence and relationship with covariates whilst allowing for imperfect detection (MacKenzie *et al.* 2006). Each survey night was treated as a repeat survey; tunnels were not considered independent as individual hedgehogs could have visited > 1 tunnel each night. Sites were therefore classified as occupied if ≥ 1 tunnel recorded hedgehog footprints on any night. Data were analysed after pooling across both years. Naïve occupancy is defined as the proportion of sites surveyed where hedgehogs were detected; true occupancy is the proportion of sites estimated to be occupied after taking the false-absence error rate into account. Analyses were conducted using PRESENCE v12.6 (Hines 2006).

Habitat variables that were expected to directly or indirectly influence hedgehog occupancy and / or detection at different scales were included in occupancy models. Larger-scale effects were investigated by incorporating individual and merged land classes ($1km^2$ resolution: Bunce *et al.* 1981; Tables 3.1 and 3.2); these represent broad habitat types and general patterns of land use within survey squares. Finer-scale effects were investigated using the areal availability of four land cover types aggregated from UK Biodiversity Action Plan Broad Habitats as hedgehog abundance is known to vary markedly between habitats (e.g. Micol *et al.* 1994; Hubert *et al.* 2011; Reeve 1994): BUILT (built, urban and suburban habitats combined); WOODLAND (broadleaved and coniferous woodland combined); GRASSLAND (all grassland habitats combined); and ARABLE. Habitat availability ($25m^2$ resolution from Land cover 2007 maps: Centre for Ecology and Hydrology 2012) was calculated as the proportion of the 1km grid square area; data were arcsine square root transformed for analysis.

Table 3.1. Summary of the covariates used in the single-season single-species occupancy models (MacKenzie *et al.* 2006) and data format for each. Land classes are described in Table 3.2.

Variable name	Description	Variable type
LANDCLASS	All seven land classes	Binary for each land class
LCARABLE	Land classes 1, 2 and 3 merged	Binary
LCPASTORAL	Land classes 4 and 5 merged	Binary
LCUPLANDS	Land classes 6 and 7 merged	Binary
ARABLE	Proportional area of arable habitat in the survey square	Arcsine square root transformed
GRASSLAND	Proportional area of grassland habitat in the survey square	Arcsine square root transformed
BUILT	Proportional area of built habitat in the survey square	Arcsine square root transformed
WOODLAND	Proportional area of woodland habitat in the survey square	Arcsine square root transformed
SETTS	Number of badger setts in the survey square	Z-scores
ALLROADS	Total length (km) of roads in the survey square	Z-scores
MOTORWAY	Length (km) of motorways, dual carriageways and 'A' roads in the survey square	Z-scores
ARODAS	Length (km) of dual carriageways and 'A' roads in the survey square	Z-scores
BROADS	Length (km) of 'B' roads in the survey square	Z-scores
MINORROADS	Length (km) of all minor (e.g. residential) roads in the survey square	Z-scores
HABITATS	Number of different habitat types in the survey square	Z-scores

In addition, as hedgehogs have been shown to avoid crossing major roads (Rondinini and Doncaster 2002), and hedgehog presence may be influenced by road density (Poel *et al.* 2015), I incorporated five measures of road "availability": the total length of all roads in the survey square (ALLROADS); the total length of motorways (MOTORWAY: in rural areas in the UK these typically have 6 lanes of traffic, a speed limit of 70 mph and a central median); the total length of 'A' roads and dual carriageways (AROADS: these typically have 2 or 4 lanes of traffic, with a speed limit of 60 or 70 mph; dual carriageways also have a central median); the total length of 'B' roads (BROADS: these are typically single lane roads with no central median and a speed limit of 40-60 mph); and minor roads (MINORROADS: typically these are associated with villages and built up areas with a speed limit of 30 mph). Lengths were determined from the OS Meridian™ 2 data set in ArcMap 10.1; data were converted to z-scores for analysis as recommended by (Donovan and Hines 2007).

Habit complexity (HABITATS) was defined as the number of different habitat types excluding roads (maximum = 23) in the survey square. Data were obtained from Land cover 2007 maps (Centre for Ecology and Hydrology 2012).

The number of badger setts (main, subsidiary, annex and outlier) in each survey square (SETTS) was used as a measure of relative badger abundance (Judge *et al.* 2014). Badger surveys were conducted by trained surveyors employed by the National Wildlife Management Centre (Judge *et al.* 2014). Sites were surveyed on foot looking for refugia (setts). Both sides of all field boundaries were surveyed, and any badger runs radiating from boundaries into the middle of fields were followed if there was a possibility they would lead to a badger sett (e.g. to a small copse). Woodland and other rough terrain was surveyed using transects; particularly difficult terrain was walked by teams of surveyors walking parallel transects in visual contact with one another.

As sample sizes were moderate, individual occupancy models included a maximum of two covariates for occupancy and one for detection. In addition, preliminary analyses of potential associations between the number of badger setts (SETTS) and areal habitat availability indicated a significant correlation with the area of GRASSLAND (Pearson's Correlation Coefficient, $r = 0.164$, $df = 260$, $P = 0.008$) but not any other habitat type. Consequently, these two variables were not modelled together as explanatory covariates of occupancy or detection, but both were permitted in models using each for either occupancy or detection (i.e. a model including both GRASSLAND plus SETTS for occupancy was excluded, but a model with SETT as a covariate for occupancy and GRASSLAND as a covariate for detection was included).

The goodness of fit for the most global model was assessed using a bootstrap method (1,000 replications) resulting in a variance inflation factor of $\hat{c} = 1.67$, and standard errors were inflated by a factor of $\sqrt{\hat{c}} = 1.29$. As data were over-dispersed, adjustments were made to the variance inflation factor ($\hat{c}$) and models were ranked by quasi-AIC (ΔQAIC) values (Burnham and Anderson 2002). Models with ΔQAIC values >2 were regarded as having little or no support (Burnham and Anderson 2002). Models that did not converge were excluded.

Further investigation of the relationship with badgers

As the number of badger setts significantly affected hedgehog occupancy (see *Results*), a two-species occupancy model was used to estimate a Species Interaction Factor (SIF) between hedgehog and badger occupancy (Mackenzie *et al.* 2004; MacKenzie *et al.* 2006); this is a ratio of the likelihood of the two species co-occurring compared to a hypothesis of independence. A value <1 indicates avoidance (i.e. the two species co-occur less frequently than would be expected if they were distributed independently) whereas a value >1 indicates aggregation (i.e. the two species co-occur more frequently than would be expected if they were distributed independently; (e.g. Luiselli 2006; Bailey *et al.* 2009). As two-species occupancy models tend not to converge when covariates are added, they were omitted (Richmond *et al.* 2010).

To investigate whether the relationship between badger sett density and hedgehog presence / absence has changed since that reported by Micol *et al.* (1994), a polynomial regression analysis was used to estimate the badger sett density at which naïve hedgehog occupancy would be zero. Regression analysis was performed in Minitab 16.1.1. All figures are mean (±SE) unless otherwise stated.

Results

Site characteristics

Overall, 261 sites were surveyed; 83 in 2014 and 178 in 2015. Eighteen sites were surveyed in Wales and 243 in England (Figure 3.1) covering all seven land class groups (Table 3.2). Badger setts were found at 163 (62%) sites. The number of badger setts per survey square ranged from 0-16 (mean: 2.0 ± 0.2 setts km^{-2}); the number of habitats present at each site ranged from 0-11 (5.2 ± 0.1). The most commonly occurring habitat type was GRASSLAND (253 sites; 97%), followed by ARABLE (243 sites; 93%), WOODLAND (219 sites; 84%) and BUILT (148 sites; 57%). On average, ARABLE, GRASSLAND, WOODLAND and BUILT habitats covered 45% ± 2%, 36% ± 2%, 11% ± 1% and 5% ± 1% of each survey square, respectively. The total length of roads per survey square ranged from 0.00-6.78km (mean: 1.71 ± 0.09km): the majority of roads were classified as minor (MINORROADS: 1.34 ± 0.07km), followed by A-roads (AROADS: 0.20 ± 0.03km) and, B-roads (BROADS: 0.14 ± 0.02km); MOTORWAY accounted for the lowest density (0.02 ± 0.01km).

No badger setts or hedgehogs were detected at 70 (27%) sites; badger setts were detected at 163 (62%) sites and hedgehogs at 55 (21%) sites. Badgers and hedgehogs were both found at 27 (10%) sites with only badgers or hedgehogs being detected at 136 (52%) and 28 (11%) sites respectively.

Table 3.2. Descriptions of the seven land class groups used (from Judge *et al.* 2014) in the current study, and a summary of the number of sites surveyed, the number of sites where hedgehogs were detected (naïve occupancy), the number of sites where badger setts were detected and relative badger sett density.

Land class	Subclass	Description	% area of England and Wales	No. (%) of sites surveyed	No. (%) of sites where hedgehogs were detected	No. (%) of sites where badger setts were detected	Mean (± SD) badger sett density
Arable	1	Open, gentle slopes, varied agriculture, often wooded or built-up	9.6%	33 (13%)	4 (12.12%)	28 (84.85%)	3.36 ± 3.64
	2	Flat, arable and intensive agriculture, often cereals and grass mixtures	31.7%	106 (41%)	28 (26.42%)	60 (56.60%)	1.52 ± 2.15
	3	Lowlands with variable land use, mainly arable and intensive agriculture	2.3%	8 (3%)	2 (25.00%)	2 (25.00%)	0.25 ± 0.46
Pastoral	4	Undulating country, gently rolling enclosed country mainly fertile pastures. Some coastal areas mainly pasture with varied morphology and vegetation.	21.0%	58 (22%)	7 (12.07%)	43 (74.14%)	3.02 ± 3.59
	5	Heterogeneous land-use, includes flat plains, valley bottoms and undulating lowlands with mixed agriculture including pastoral and arable	17.8%	37 (14%)	10 (27.03%)	24 (64.86%)	1.57 ± 2.02
Marginal upland		Rounded hills and slopes, wide range of vegetation types including moorland and improvable permanent pasture	14.7%	12 (5%)	4 (33.33%)	5 (41.67%)	1.25 ± 1.90
Upland		Mountainous, with moorlands, afforestation and bogs	3.0%	7 (3%)	0 (0.00%)	2 (25.57%)	0.43 ± 0.79

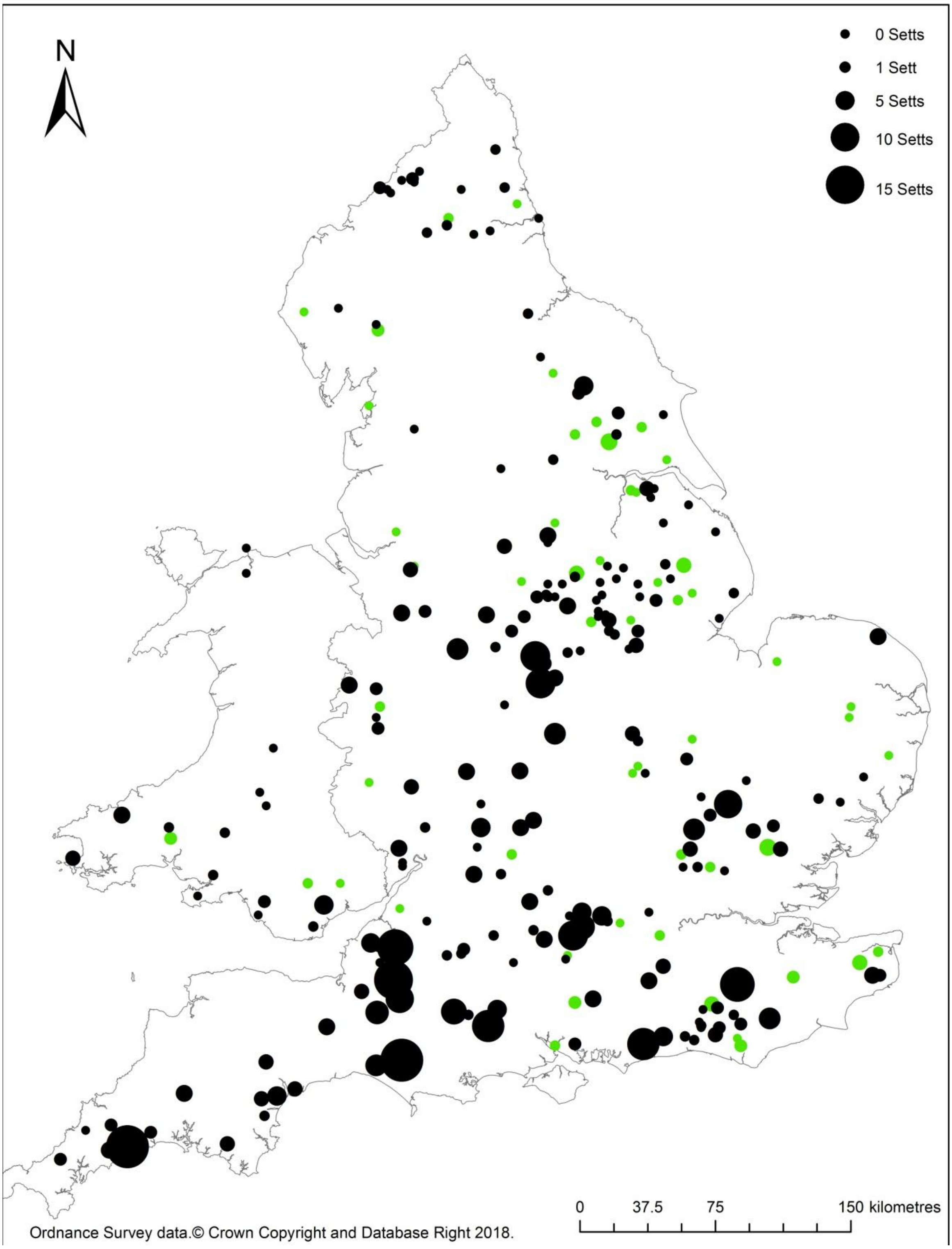

Figure 3.1. Pattern of hedgehog occupancy on sites surveyed in England and Wales in relation to relative badger density. ● = hedgehog detected, ● = no hedgehog detected. The size of the circle indicates the number of badger setts at each site.

Patterns of occupancy

Hedgehogs were detected in only 55 sites, indicating an overall naïve occupancy rate of 21.1%. Within land classes, naïve occupancy rates varied from 0.0% to 33.3%, although sample sizes were small in some categories; for those land classes where >30 sites were surveyed, naïve occupancy rates varied from 12.1% to 27.0% (Table 3.2). Comparable figures for merged land class groupings were: arable 23.1% (N=147); pastoral 17.9% (N=95); and uplands 21.1% (N=19). Accounting for the area of each land class in England and Wales, this gives an overall occupancy rate across England and Wales of 22.3%.

The best fitting models for hedgehog occupancy included relative badger abundance (SETTS) and two measures of urbanisation (BUILT and ALLROADS), with detection influenced by the proportional area of GRASSLAND and the number of different habitats (HABITAT) (Table 3.3). These covariates made up the best five fitting models, with a combined QAIC weight of 0.61; all five models contained SETTS as a covariate of occupancy. In the highest ranked model, relative badger abundance was significantly negatively associated with hedgehog occupancy (β = -1.14, 95% CI = -0.3, -1.97: Figure 3.2), whereas the total length of all roads had a significant positive relationship (β = 0.41, 95% CI = 0.04, 0.78: Figure 3.3). There was also some support for hedgehog occupancy being positively related to the proportion of BUILT area at a site (β = 1.90, 95% CI = -0.04, 3.84) in the third highest ranked model, although this was not significant. GRASSLAND was positively associated with hedgehog detection (β = 1.25, 95% CI = -0.09, 2.59) in the top ranked model, and a negative relationship with number of habitats also gained support in two of the top 5 ranked models (β = -0.32, 95% CI = -0.70, 0.05), although these were not significant.

Table 3.3. Summary of single-species occupancy models ran on the complete data set (N = 261 sites). The top ranked models (ΔQAIC < 2.0) are shaded. Variables are listed in Table 3.1. Ψ: occupancy; P: detection.

Model	QAIC	ΔQAIC	AICwgt	Model likelihood	No. of par.
Ψ(SETTS+ALLROADS),P(GRASSLAND)	364.04	0.00	0.1816	1.0000	5
Ψ(SETTS+ALLROADS),P(HABITATS)	364.71	0.67	0.1299	0.7153	5
Ψ(SETTS+BUILT),P(GRASSLAND)	364.84	0.80	0.1218	0.6703	5
Ψ(SETTS+ALLROADS),P(.)	365.46	1.42	0.0893	0.4916	4
Ψ(SETTS+BUILT),P(HABITATS)	365.49	1.45	0.0880	0.4843	5
Ψ(SETTS+BUILT),P(.)	366.26	2.22	0.0599	0.3296	4
Ψ(SETTS),P(GRASSLAND)	366.46	2.42	0.0542	0.2982	4
Ψ(SETTS),P(HABITATS)	367.21	3.17	0.0372	0.2049	4
Ψ(SETTS),P(AROADS)	367.80	3.76	0.0277	0.1526	4
Ψ(SETTS+WOODLAND), P(GRASSLAND)	367.92	3.88	0.0261	0.1437	5
Ψ(SETTS),P(.)	367.92	3.88	0.0261	0.1437	3
Ψ(SETTS),P(ARABLE)	368.47	4.43	0.0198	0.1092	4
Ψ(SETTS),P(LCUPLANDS)	368.58	4.54	0.0188	0.1033	4
Ψ(SETTS),P(BUILT)	368.59	4.55	0.0187	0.1028	4
Ψ(SETTS),P(MOTORWAY)	369.09	5.05	0.0145	0.0801	4
Ψ(SETTS),P(LCPASTORAL)	369.29	5.25	0.0132	0.0724	4
Ψ(SETTS),P(BROADS)	369.44	5.40	0.0122	0.0672	4
Ψ(SETTS),P(WOODLAND)	369.67	5.63	0.0109	0.0599	4
Ψ(SETTS),P(SETTS)	369.85	5.81	0.0099	0.0547	4
Ψ(SETTS),P(ALLROADS)	369.87	5.83	0.0098	0.0542	4
Ψ(SETTS),P(MINORROADS)	369.89	5.85	0.0097	0.0537	4
Ψ(SETTS),P(LCARABLE)	369.89	5.85	0.0097	0.0537	4
Ψ(BUILT),P(GRASSLAND)	373.25	9.21	0.0018	0.0100	4
Ψ(ALLROADS),P(GRASSLAND)	373.25	9.21	0.0018	0.0100	4
Ψ(ALLROADS),P(.)	374.61	10.57	0.0009	0.0051	3
Ψ(BUILT),P(.)	374.62	10.58	0.0009	0.0050	3
Ψ(MINORROADS),P(GRASSLAND)	374.65	10.61	0.0009	0.0050	4
Ψ(BROADS),P(GRASSLAND)	374.67	10.63	0.0009	0.0049	4
Ψ(.),P(GRASSLAND)	375.53	11.49	0.0006	0.0032	3
Ψ(WOODLAND),P(GRASSLAND)	376.01	11.97	0.0005	0.0025	4
Ψ(SETTS),P(LANDCLASS)	376.26	12.22	0.0004	0.0022	10
Ψ(.),P(.)	376.9	12.86	0.0003	0.0016	2
Ψ(LCPASTORAL),P(GRASSLAND)	376.95	12.91	0.0003	0.0016	4
Ψ(LCARABLE),P(GRASSLAND)	376.99	12.95	0.0003	0.0015	4
Ψ(ARABLE),P(GRASSLAND)	377.2	13.16	0.0003	0.0014	4
Ψ(AROADS),P(GRASSLAND)	377.28	13.24	0.0002	0.0013	4
Ψ(HABITATS),P(GRASSLAND)	377.37	13.33	0.0002	0.0013	4
Ψ(MOTORWAY),P(GRASSLAND)	377.44	13.40	0.0002	0.0012	4
Ψ(LCUPLANDS),P(GRASSLAND)	377.53	13.49	0.0002	0.0012	4
Ψ(HABITATS),P(.)	378.74	14.70	0.0001	0.0006	3
Ψ(.),P(*variable detection*)	381.84	17.80	0.0000	0.0001	6
Ψ(LANDCLASS),P(GRASSLAND)	382.43	18.39	0.0000	0.0001	10

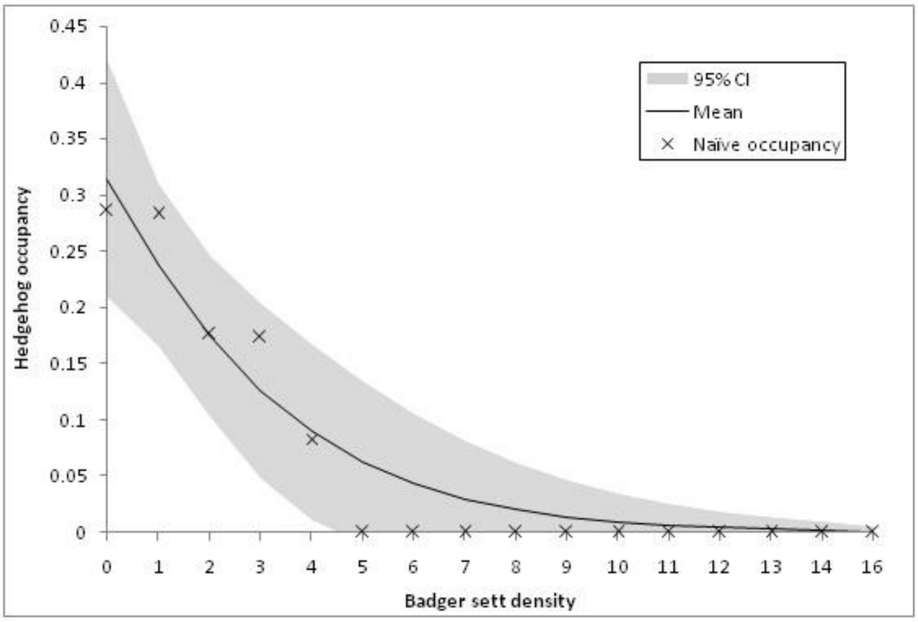

Figure 3.2. Relationship between total badger sett density (SETTS) and hedgehog occupancy in England and Wales 2014-15. Black line indicates the mean number of sites occupied; shaded area indicates 95% confidence interval; naïve occupancy rates are indicated by x. The probability of hedgehog occupancy was based on an occupancy model with sett density added as a covariate, and constant detection.

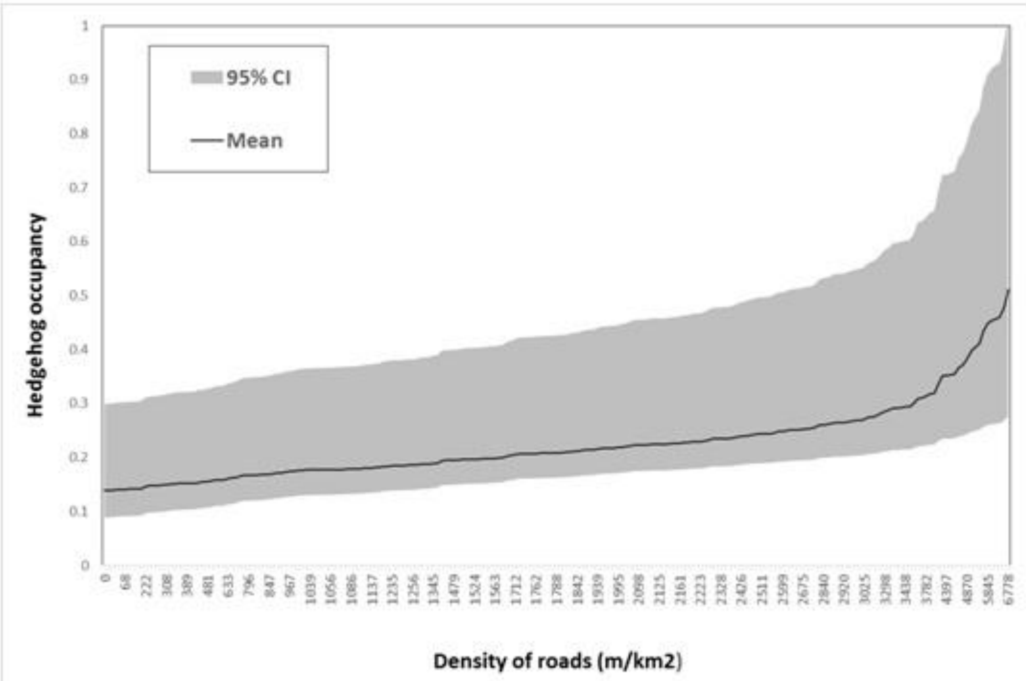

Figure 3.3. Relationship between hedgehog occupancy and road density (m km^{-2}) in England and Wales in 2014-15. Probability of hedgehog occupancy was based on an occupancy model with the length of all roads added as a covariate, and constant detection.

Further investigation of the relationship with badgers

The two-species occupancy models showed the probability (mean ± SE) that hedgehogs would be present at a site: (a) regardless of the presence of badgers was 21.1% ± 3.2%; (b) given that it was occupied by badgers was 17.8% ± 3.6%; and (c) given that it was not occupied by badgers was 31.0% ± 7.0%. The probability of detecting hedgehogs rose from 59.3% ± 6.2% when no badgers were present to 62.2% ± 4.1% when badgers were present. The Species Interaction Factor was 0.670 ± 0.126, indicating that hedgehogs were significantly less likely to co-occur with badgers than would be expected under an independence hypothesis (i.e. hedgehogs show avoidance of badgers; 95% CI: 0.503, 0.891).

The predicted sett density above which the probability of a site being occupied by hedgehogs becomes zero was 5.21 setts km^{-2} (95% CI: 4.07, 6.35) or 3.29 main setts km^{-2} (95% CI: 2.17, 4.40 (Figure 3.4).

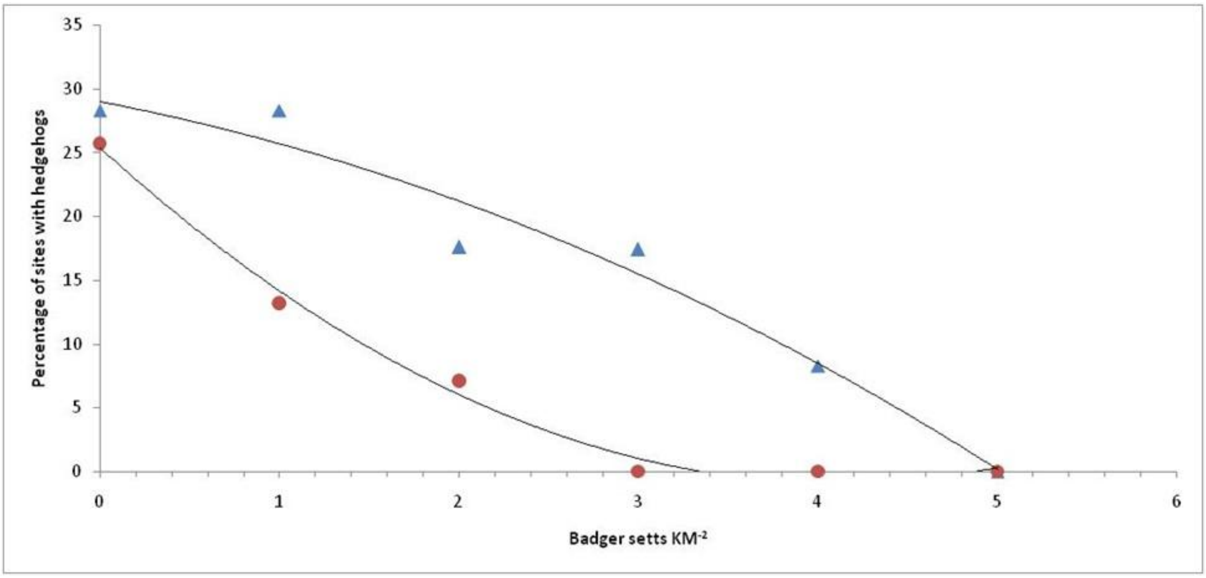

Figure 3.4. Relationship between hedgehog occupancy and density of badger setts. The percentage of sites where hedgehogs were detected regressed against density of all badger setts (▲ $F_{1,4}$ = 60.12, $P < 0.001$; $y = -0.626x^2 - 2.628x + 28.96$, $R^2 = 0.961$) and main setts only (● $F_{1,3}$ = 28.06, P = 0.01; $y = 1.551x^2 - 12.76x + 25.35$, $R^2 = 0.992$).

Discussion

Agricultural landscapes have become more intensively managed and homogenised resulting in population declines across a range of taxa (Krebs *et al.* 1999; Hayhow *et al.* 2016). In the UK, the hedgehog, a generalist insectivore, may be one such species (Roos *et al.* 2012; Wembridge and Langton 2016). Hedgehogs select habitats with high prey availability (Pettett *et al.* 2017a), and which provide secure resting, breeding and hibernating sites safe from predators (Hof *et al.* 2012). However, the current rural landscape is often lacking such habitats (e.g. Wilkins 2000; Robinson and Sutherland 2002; Cornulier *et al.* 2011), leading some to the suggestion that the wider British landscape has become "unsuitable" for hedgehog populations (Pettett *et al.* 2017b). However, there is a lack of empirical data regarding historical hedgehog abundance and distribution at the landscape scale, making inferences on the magnitude of population change difficult.

One reason for this lack of information has been the practical problems associated with surveying hedgehog populations within rural habitats (Yarnell *et al.* 2014). Although hedgehog populations have been relatively well studied in urban areas (e.g. Molony *et al.* 2006; Dowding *et al.* 2010a; Williams *et al.* 2015; Hof and Bright 2016; Williams *et al.* 2018b: Chapter Four), studies in rural landscapes have typically been conducted either at a local level (e.g. Hof and Bright 2010a; Haigh *et al.* 2012; Glasby and Yarnell 2013; Pettett *et al.* 2017a; 2017b), such that their results may not be representative of larger geographic scales, or at a large-spatial scale that makes it difficult to clearly identify underlying biological and / or anthropogenic influences (e.g. Pettett *et al.* 2017c). Therefore, the data presented in the current study represent the first national scale estimate of hedgehog occupancy across rural England and Wales; as such, these can be used as a baseline against which any future changes can be measured.

Hedgehogs were widely distributed across England and Wales, being found in all but one land class (upland): this is not surprising as hedgehogs are known to be absent above the tree line (Morris and Reeve 2008). Occupancy rates were, however, low across all other land classes as well, ranging from 12-33%. I contend that this is the first unbiased estimate of occupancy at a landscape scale, since the selection of study sites was random, with each land class being surveyed in proportion to its coverage. Consequently, it is to be expected that this study would provide a lower estimate of occupancy (22.3% across all land classes) compared to Yarnell et al. (2014) (39.2%) who used exactly the same methodology, but where sites were biased towards pasture and amenity grasslands situated close to urban areas, which hedgehogs seem to prefer (Micol *et al.* 1994a).

The occupancy estimate recorded here is also lower than in other studies conducted at smaller scales and using different methods: 26% of amenity grasslands in villages (Parrott *et al.* 2014); 36–45% of gardens in urban areas, 30-55% of farms and 47–57% of roads (Baker and Harris 2007; Hof and Bright 2012; Roos *et al.* 2012; Williams *et al.* 2018b). This apparently patchy distribution of rural hedgehog populations may suggest that some populations are isolated and fragmented (Becher and Griffiths 1998). Consequently, there is an urgent need to investigate patterns of gene flow between populations of hedgehogs in relation to potential physical obstacles such as major roads, but also in relation to less visible biological obstacles such as predator / competitor populations (see below).

I was not able to detect any significant influence of the areal availability of rural habitat types on hedgehog occupancy, nor any effect of habitat complexity, although this may have, in part, been constrained by the low number of sites where hedgehogs were recorded. This study did, however, detect a positive relationship between hedgehogs and both the proportional area of built habitat and total road density. This is consistent with previous radio-tracking studies that have demonstrated that hedgehogs prefer to occupy areas associated with human habitation rather than the wider countryside, as these may be associated with e.g. reduced badger abundance, increased food availability and / or novel refugia (Doncaster 1992; Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012; Pettett *et al.* 2017b). Similarly, Poel *et al.* (2015) found a significant positive correlation between hedgehog presence / absence and road density in the Netherlands (but see Huijser and Bergers 2000); this is likely, in part, to reflect a similar association with areas of human habitation, as road density will increase with increasing housing coverage.

The major explanatory variable in the occupancy models, however, was relative badger density, quantified as the total number of all sett types present in survey squares (Judge *et al.* 2014). I elected to use this variable rather than the number of main setts alone (which is typically used to estimate the number of badger social groups (Judge *et al.* 2014, 2017) as it is arguably likely to better represent the intensity of use of the survey site by badgers (e.g. where main setts were not present within the 1km survey square itself, the sites itself is still likely to be used by these neighbouring groups).

Badgers are the main predator of hedgehogs but also competitors for food resources, and an increasing number of studies have shown a negative association between the two species in terms of density (Trewby *et al.* 2014), occupancy (Yarnell *et al.* 2014), and also spatial separation at the local scale (e.g. Young *et al.* 2006; Hubert *et al.* 2011; Hof and Bright 2012; Hof *et al.* 2012; Pettett *et* *al.* 2017b), although Haigh *et al.* (2012b) reported hedgehog and badger co-occurrence locally in Ireland. The two different occupancy models (i.e. single-species and two-species) presented here support these studies, showing a negative relationship between hedgehog occupancy and badger sett density. However, this relationship appears complex.

For example, of those 55 sites where hedgehogs were present, badgers were also present on 49.1% of these sites. This demonstrates that badgers and hedgehogs can, and do, coexist at the $1km^2$ scale (Haigh *et al.* 2012a), as must have happened historically prior to the recent decline in hedgehog numbers. The extent to which the ranging patterns of the two species overlap in space and / or time is, however, not known, although this does not appear to be a simple case of hedgehogs "hiding" in built environments, as footprint tunnels were placed in rural habitats. Consequently, there is the need for studies focussed on the behaviour of sympatric hedgehogs and badgers to investigate how the two species can live alongside one another, and what factors promote this co-existence.

However, the probability of hedgehog occupancy did decline as the number of badger setts increased: naïve occupancy was 28.6% where badgers were not present, but only 16.6% where they were present. As outlined above, it is plausible that an increase in sett numbers does reflect an increased level of badger activity / intensity, although the continually changing and highly variable nature of badger social groups and densities makes it imposable to directly relate sett density to badger density (e.g. Ostler and Roper 1998; Delahay *et al.* 2013; Macdonald *et al.* 2009). Despite these caveats, the sett density predicted here where hedgehogs would no longer occupy an area (5.21 setts km^{-2} or 3.29 main setts / km^2) is far greater than that reported by Micol *et al.* (1994) (≥ 0.227 main setts km^{-2}). This will in part be down to methodological differences as Micol *et al.*'s (1994) prediction was based on hedgehog abundance whereas I have been limited to hedgehog presence / absence. Micol *et al.* (1994) also acknowledged that hedgehogs would still be present in isolated areas whereas our prediction is for complete extirpation.

In the context of the current distribution and abundance of badgers in the UK following their increased legal protection since 1992, the threshold density estimated by Micol *et al.* (1994) has already been surpassed for much of England and Wales (the exception is Land Class 7; Judge *et al.* 2014). This raises significant concerns for the future of hedgehogs in rural environments in the UK, although I predict that badger main sett density would have to increase more than six fold from that reported by Judge *et al.* (2014) for badgers to completely extirpate hedgehogs from England and Wales: for comparison, the density of main setts increased by approximately 24% between 1988 and

1997 (Gavin Wilson *et al.* 1997), and by 88% between 1988 and 2013 (Judge *et al.* 2014). Furthermore, given the absence of information concerning the biological mechanism(s) by which this negative association arises, it is reasonable to suppose that changes in badger numbers alone might not necessarily be the only factor affecting future changes in hedgehog populations. For example, hedgehogs may be able to persist in areas not used extensively by badgers, as predicted by intra-guild predation theory (Holt and Polis 1997).

Whilst badgers are clearly negatively associated with hedgehog occupancy, over a quarter (26.8%) of the sites surveyed in this study had no badgers or hedgehogs present; in addition, the two-species occupancy modelling estimated that the probability that hedgehogs would be present at a site given that it is not occupied by badgers was still only 31.0%. These figures would seem to indicate that a large proportion of rural England and Wales is unsuitable for both species. Given the similarity in diets of the two species (Shepherdson *et al.* 1990; Reeve 1994), one plausible explanation for this result might be the reduced availability of macro-invertebrate prey in relation to factors such as agricultural intensification and climate change. In addition, this might also suggest that hedgehog occupancy would still be low even if badger numbers were reduced, for example during culling programs designed to reduce the incidence of bovine tuberculosis in cattle (Bourne *et al*. 2007).

In summary, much of the blame for hedgehog decline in the UK has focussed upon the impacts of badgers as both a competitor but especially as a predator (e.g. Trewby *et al.* 2014). Although our findings support the negative relationship between the two species, the results of this study suggest that this relationship is likely to be complex, involving elements of predation, competition and avoidance; in the context of the latter, areas associated with human habitation appear to mitigate against some of the negative effect of badgers. At the same time, however, rates of hedgehog occupancy were low even in the absence of badgers, and badgers themselves were absent from 47.9% of sites surveyed. Collectively, this suggests that intensive management of rural areas is negatively impacting both these generalist terrestrial insectivores. Future work must, therefore, focus on identifying the exact biological mechanism(s) by which badgers negatively impact hedgehogs, and how these impacts can be managed effectively to promote the co-existence of these species.

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Chapter Four

The data presented in Chapters Two and Three relate to identifying rates of occupancy and factors affecting occupancy in rural landscapes. However, there is increasing evidence that hedgehogs are now increasingly likely to be found in urban landscapes (Young *et al.* 2006; Hubert *et al.* 2011; Parrott *et al.* 2014; Trewby *et al.* 2014; van de Poel *et al.* 2015). As with those methods currently used to monitor hedgehog population trends in rural landscapes, approaches to monitor hedgehogs in urban landscapes are also potentially associated with a range of limitations. Given the effectiveness of footprint tunnels as a survey method for rural hedgehog populations using volunteer surveyors, I undertook a similar survey in Reading, Berkshire, to investigate their potential utility as a future method for monitoring urban hedgehogs in the UK.

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My contribution to the work

I was responsible for the design of the project, in discussion with Philip Baker. All analysis were mine. Data were collected by volunteers, supervised by Nittan Mann. The manuscript was co-written by me and Philip Baker with input from Richard Yarnell.

A prickly problem: developing a volunteer-friendly tool for monitoring populations of a terrestrial urban mammal, the West European hedgehog (*Erinaceus europaeus*)

Keywords: *badgers, citizen science, field sign surveys, footprint tracking tunnels, population monitoring, insectivore, Meles meles, urban ecology, garden conservation*

Abstract

Across Europe, hedgehogs (*Erinaceus europaeus*) appear to be in decline in both urban and rural landscapes. Current methods used to monitor urban populations are, however, associated with several potential limitations. In this study, I conducted hedgehog footprint-tunnel surveys in 219 residential gardens across Reading, UK, between May-September in 2013 and / or 2014; gardens were surveyed for five continuous days. Single-species occupancy models were used to investigate factors influencing hedgehog occupancy and two-species occupancy models were used to estimate species interaction factors (SIF) between hedgehogs and (a) badgers (*Meles meles*) and (b) foxes (*Vulpes vulpes*). The five-day survey protocol was associated with a false-absence error rate of 0.1-0.4%, indicating that it was a reliable method for determining hedgehog presence; conversely, 34.7% of householders were not able to correctly predict hedgehog presence or absence. Hedgehogs were widely distributed across Reading, but detected in only 32-40% of gardens. None of the within-garden or outside-garden factors significantly affected hedgehog occupancy in the single-species models, but the two-species models indicated that badgers (SIF = 0.471 ± 0.188), but not foxes (SIF = 0.954 ± 0.048), negatively affected the presence of hedgehogs in gardens, although not significantly. Overall, footprint-tunnels represent a viable field method for monitoring urban hedgehog populations, however, other approaches are required to identify factors that make gardens "hedgehog friendly".

Introduction

Urbanisation is one of the most significant forms of habitat modification undertaken by humans, typically resulting in marked changes in e.g. animal behaviour, reproductive output, community composition and nutrient cycling (Marzluff *et al.* 2008; Gaston 2010; Douglas *et al.* 2011; Niemelä 2011; Forman 2014). In many instances, the construction of urban areas leads to species' declines or extirpations, although some "urban adapters" may thrive in such modified landscapes (Blair 1996; Kettel *et al.* 2017). Indeed, for some species, urban areas may represent a refuge habitat in which they may be able to escape some of the biotic and abiotic pressures present in other habitats and / or which offer new opportunities to be exploited (Bateman and Fleming 2012).

The West European hedgehog (*Erinaceus europaeus*) is a medium-sized (<1.2kg) insectivorous mammal found from Spain and Italy north to Scandinavia (Morris and Reeve 2008). In many parts of its range the species is thought to be in decline (Huijser and Bergers 2000; Poel *et al.* 2015); in the UK, data from several monitoring schemes indicate that populations have declined markedly since the 1950s (Harris *et al.* 1995; Battersby 2005; Wembridge 2011; Roos *et al.* 2012) leading to its designation as a species of conservation concern in 2007 (JNCC 2010). Possible reasons for this decline include: changes associated with agricultural intensification such as the loss of hedgerows, increased field sizes and reductions in the availability of invertebrate prey (Krebs *et al.* 1999; Hof and Bright 2010; Haigh 2012a; Hof and Bright 2012; Hof *et al.* 2012; Moorhouse *et al.* 2014); the increased abundance of Eurasian badgers (*Meles meles*) (Judge *et al.* 2014, 2017), an intra-guild predator (Doncaster 1994); an increase in the density of road networks and associated traffic (Becher and Griffiths 1998; Rondinini and Doncaster 2002); and climate mediated effects on food availability and over-winter hibernation. Conversely, other studies (e.g. Williams *et al.* 2018a: Chapter Three; Foster and Soluk, 2004; Young *et al.*, 2006; Hubert *et al.*, 2011; Parrott, Etherington and Dendy, 2014; Trewby *et al.*, 2014; Poel *et al.*2015) have indicated an increased tendency for hedgehogs to be found within, or associated with, areas dominated by human habitation, including towns and cities (Hof and Bright 2009).

From a conservation perspective, urban areas pose a number of challenges. Potentially the biggest problem, but simultaneously the biggest opportunity, is that the major habitat present is residential gardens. Although gardens collectively cover a large area (21-27% of UK cities: Loram *et al.* 2007; Davies *et al.* 2009), each one is typically small (~190m^2: Davies *et al.*, 2009), privately-owned, and has to deliver a range of functions (Cameron *et al.* 2012). As such, garden-based conservation strategies have to persuade large numbers of householders to put aside areas of their property for the benefit of wildlife (Goddard *et al.* 2010), although such actions are not always successful (Gaston *et al.* 2005; Matteson and Langellotto 2011). Identifying factors within a garden that can help promote focal species is, therefore, a priority.

Monitoring wildlife populations in urban areas is also typically reliant on engaging substantial numbers of urban residents because of the fact that wild animals cannot be observed easily from publicly accessible areas. Previous studies aimed at monitoring hedgehog populations in urban areas in the UK have relied extensively on questionnaire surveys where participants are typically asked whether they believe hedgehogs are present in their garden and / or sightings of hedgehogs in gardens or other urban habitats (Baker and Harris 2007; Hof and Bright 2009; Toms and Newson 2006). Although the use of volunteers can help reduce costs whilst simultaneously increasing statistical power and helping communities engage with conservation issues (Toms and Newson 2006; Silvertown 2009; Schmeller *et al.* 2009; Mackechnie *et al.* 2011; Wright *et al.* 2014), citizen science based approaches can be associated with limitations which reduce their reliability as a mechanism for guiding management actions (e.g. Perkins *et al.* 2013). For example, strategies used to recruit volunteers can generate biased samples (e.g. participants may be more likely to submit positive records: *sensu* Scott *et al.* 2014), participants may vary in their ability to identify different species (Dickinson *et al.* 2010) and species such as hedgehogs may exhibit behavioural patterns that make them elusive (Dowding *et al.* 2010a) such that householders may not always be aware that the focal species is present in their garden (Williams *et al.* 2014). The latter would lead to an increased frequency of "false absences" (i.e. failing to record a species when it is present). Consequently, there is the need for a method which can be used by householders to record hedgehog presence reliably.

One potentially suitable method is footprint-tunnels (Williams *et al.*, 2018a: Chapter Three; Huijser and Bergers, 2000; Yarnell *et al.*, 2014); these are designed to document hedgehog presence by using food bait to lure individuals across an ink pad so their distinctive footprints are recorded. The major advantages of this approach are that: (i) they are cheap (unit price for the current study was approximately £5); (ii) they can record hedgehog activity remotely throughout the 24h cycle; (iii) footprint papers can be returned to researchers for verification; and (iv) they can be used easily by volunteers. For example, the use of these tunnels has been illustrated on several UK television programmes and, as a result, individual householders are known to have purchased and successfully used their own simply out of personal interest. In addition, this method can be easily incorporated into an occupancy analysis framework (MacKenzie *et al.* 2006; Yarnell *et al.* 2014), a maximum likelihood technique used specifically to estimate presence / absence whilst accounting for imperfect detection. Such models can also incorporate covariates to identify factors affecting a species' distribution (MacKenzie *et al.* 2006); these could then be used as the basis for advice to householders about making their gardens more hedgehog friendly.

Therefore, in this study, I conducted a survey of residential gardens in Reading, UK using footprint-tunnels deployed by volunteer householders according to a standardised protocol with the specific objectives of: (i) identifying a suitable survey protocol as a method for the future monitoring of hedgehogs in urban landscapes; and (ii) identifying factors associated with the presence / absence of hedgehogs in residential gardens.

Methods

The study was conducted in Reading, UK (51°, 27’ N: 0°, 58’ W) during May-September 2013-2014 inclusive. Reading is a large town which straddles the River Thames and covers an area of approximately 55km^2; the human population is approximately 230,000 people (Figure 4.1). There are four major residential sectors within the town surrounding the town’s central commercial district: Caversham (North), Woodley (East), Earley (South) and Tilehurst (West). Individual gardens were surveyed in one or both years.

To ensure coverage across the town as a whole, and to engage volunteers who were likely to have and not have hedgehogs in their gardens, a pseudo-random recruitment protocol was used. Within each 1-km Ordnance Survey grid square (n = 55), two 500m x 500m quadrants were selected at random: leaflets were then delivered to *c*. 50 houses in the centre of each of these quadrants. Leaflets specifically requested that householders volunteer to take part in the study regardless of whether they thought hedgehogs did or did not visit their garden, but that they thought hedgehogs could potentially access their garden via holes under fences or gates and / or via gaps in boundaries.

Gardens were surveyed using triangular footprint-tunnels constructed from corrugated plastic (Correx®) measuring 1,200 mm in length, 210 mm wide and 180 mm high (Yarnell *et al.* 2014). The base contained a removable insert onto which a piece of A4 paper (297 x 210 mm) was attached at each end. A petri dish was placed at the centre of the base insert to house the food bait (commercially available dry Spikes® hedgehog food). Ink made from carbon powder mixed with vegetable oil was applied to two strips of masking tape between the food and each piece of paper.

Approximately 20-30 gardens were surveyed at any one time, with equipment recycled between volunteers so that successive batches (groups of gardens surveyed over the same five night period) were investigated. Surveyors from each of the four major residential sectors were included in each batch to ensure that any spatial differences in detection rates were not confounded with the time of surveying. Volunteers in close proximity to one another were allocated to separate batches for surveying to increase independence and ensure that any spatial differences in detection rates were not confounded with the time of surveying.

Each householder was given one footprint-tunnel to mimic the likely pattern of surveying achievable by persons who may opt to purchase their own. Householders were instructed to place the tunnel in their rear garden in a position where they thought hedgehogs would be likely to encounter it (e.g. parallel to fences at points where animals could enter the garden). Surveys were conducted in rear gardens as hedgehogs are known to avoid front gardens (Dowding *et al.* 2010b). Each garden was surveyed for five continuous days, with the tunnel checked every morning. If footprints (of any species) were present and / or if the food bait had been taken, the paper and / or bait were replaced respectively. All footprint papers were returned for verification by the authors. Each night was treated as a repeat survey and gardens were classified as occupied (hedgehog-positive gardens) if hedgehog footprints were recorded on any of the five nights.

Chi-squared tests were used to quantify: (a) the consistency of hedgehog presence / absence in gardens between years for that subset of gardens surveyed in both 2013 and 2014 (N = 60); and (b) the relationship between the householders' predictions that hedgehogs would / would not be detected and the actual pattern of detection (N = 147 gardens surveyed in 2014).

Footprint-tunnels as a monitoring tool

Data on the five-day pattern of presence-absence of hedgehogs in each garden were analysed using occupancy analysis (MacKenzie *et al.* 2006). I assessed the goodness of fit for the most global modal using a bootstrap method (100 replications) resulting in a variance inflation factor of $\hat{c}$ = 2.08. Therefore, Akaike's Information Criterion (AIC) values were modified by the variance inflation factor ($\hat{c}$) to give quasi-AIC (QAIC) values for use in subsequent model selection procedures (Anderson and Burnham 2002): Models with ΔQAIC values >2 or which did not converge were excluded as having little or no support (Burnham and Anderson 2002); standard errors were inflated by a factor of $\sqrt{\hat{c}}$ = 1.44.

Initial analyses compared two baseline models independently of any covariates and which assumed that daily detection rates were (i) constant or (ii) variable; the optimal model was selected based on the minimum QAIC value. Models were constructed separately for: houses surveyed in (a) 2013 and (b) 2014; and (c) using the last available data from each household (i.e. data from 2013 for houses surveyed only in 2013 and 2014 for those surveyed in both years or in 2014 only: hereafter "pooled" data). Data were analysed using PRESENCE v12.7 (Hines 2006). Naïve occupancy rate is defined as the proportion of gardens surveyed where hedgehogs were detected (the latter are hereafter termed “hedgehog-positive gardens”); the true occupancy rate is estimated by accounting for false-absences.

The suitability of the survey protocol for the future monitoring of hedgehogs in residential gardens in the UK was assessed by estimating the number of sites needed to detect ($\alpha = 0.05$) 50%, 25% and 10% changes in occupancy between two surveys with 2-5 days of surveying per garden at 0.80, 0.90 and 0.95 levels of power. Estimates of occupancy and detection were derived from the pooled data. Analyses were conducted using R (Anonymous 2008) using code provided by Guillera-Arroita and Lahoz-Monfort (2012): power was calculated as the proportion of 5,000 simulations in which a significant difference was detected.

Factors affecting hedgehog occupancy

Factors within gardens that could potentially affect the presence of hedgehogs were quantified using a questionnaire survey of participants. Questionnaires requested information on: house type (HOUSETYPE: detached, semi-detached, other), as this is related to the size of the garden (Loram *et al.* 2008) and, to some extent, access down the side of the house; the percentage areal cover of lawn (BACKLAWN), flowerbeds (BACKFLOWER) and shrubs (BACKSHRUB) in the rear garden; whether the rear garden contained a pond / other water feature (WATER), a compost heap (COMPOST) or log pile (LOGS); whether householders thought hedgehogs could access their back garden from their front garden (FRONT2BACK); if foxes (*Vulpes vulpes*) (FOX) and / or badgers (BADGER) visited their garden (at least yearly); whether any supplementary food from feeding either foxes, hedgehogs, badgers and / or birds on the ground was available at least once a month (FOOD); and whether they used slug pellets (SLUGPELLET), weed killer (WEEDKILLER), rat or mouse poison (POISON) or chemical fertilisers (FERTLISER). Percentage coverage was converted to standardised Z values as recommended by Donovan and Hines (2007). POISON and FERTILISER were subsequently omitted from all analyses as too few householders stated that they used these compounds.

Models also included parameters summarising the garden’s location within the town (DISTRICT: i.e. which of the four major residential sectors it was located in) and four metrics for habitats outside the garden: the distance to the edge of the town (EDGE), nearest allotment gardens (ALLOTMENT), amenity grassland (e.g. park, sports field, school playing field: AMENITY) and woodland

(WOODLAND). Distances were determined using ArcMap v10.1 based on Ordnance Survey 1:10,000 maps checked against Google Maps satellite layer (Google Maps 2015).

Models included no more than one covariate for occupancy and detection due to limited sample sizes; models were fitted with a constant daily detection rate, as this was shown to better fit the data than models with variable daily detection rates (see Results). Model fit was assessed using the bootstrap procedure in PRESENCE (Mackenzie and Bailey 2004). This is a Monte-Carlo type simulation process in which the detection and occupancy rates identified by the original model are used to randomly assign sites as occupied or unoccupied for each of 100 simulations: a Pearson chi-squared statistic is then generated for each run and compared to the original observed χ^2 value; the model is considered to fit the data well if the observed value falls within the range calculated across the simulation process. The significance of individual covariates was determined by whether the corresponding 95% confidence interval crossed zero or not.

Associations with predators

Fishers exact tests and two-species occupancy models were used to estimate a species interaction factor (SIF) to investigate the likelihood of hedgehogs co-occurring in gardens with badgers or foxes (Mackenzie *et al.* 2004; MacKenzie *et al.* 2006). The SIF is a ratio of the likelihood of the species co-occurring compared to a hypothesis of independence: a value <1 indicates avoidance (i.e. the two species co-occur less frequently than would be expected if they were distributed independently) whereas a value >1 indicates aggregation (i.e. the two species co-occur more frequently than would be expected if they were distributed independently) (e.g. Luiselli 2006; Bailey *et al.* 2009). As two-species occupancy models tend not to converge when covariates are added, they were left out of the models (Richmond *et al.* 2010).

Results

Overall, 219 gardens were surveyed: 51 in 2013 only, 108 in 2014 only and 60 in both years (Figure 4.1). Naïve occupancy rates for those gardens surveyed in 2013 and 2014 were 31.5% (N=111) and 39.9% (N=168), respectively (Table 4.1). The pattern of detection of hedgehogs in gardens surveyed in both years (N=60) was highly consistent (χ^2_1 =17.631, P <0.001) with 31 households (51.7%) failing to record hedgehogs in either year, 16 (26.7%) recording hedgehogs in both years and 5 (8.3%) and 8 (13.3%) households recording hedgehogs only in the first or second year of the study respectively.

There was a significant association between predicted patterns of occupancy in gardens based on householders' perceptions and the actual detection of hedgehogs in gardens ($\chi^2_1 = 14.529$, $P < 0.001$). Overall, 52 (35.4%) and 44 (29.9%) householders correctly predicted the absence and presence of hedgehogs, respectively. However, hedgehogs were recorded in 19 (12.9%) gardens where householders thought they were absent, and were not recorded in 32 (21.8%) gardens where householders thought they were present. Collectively, these data indicate an error rate of 34.7%.

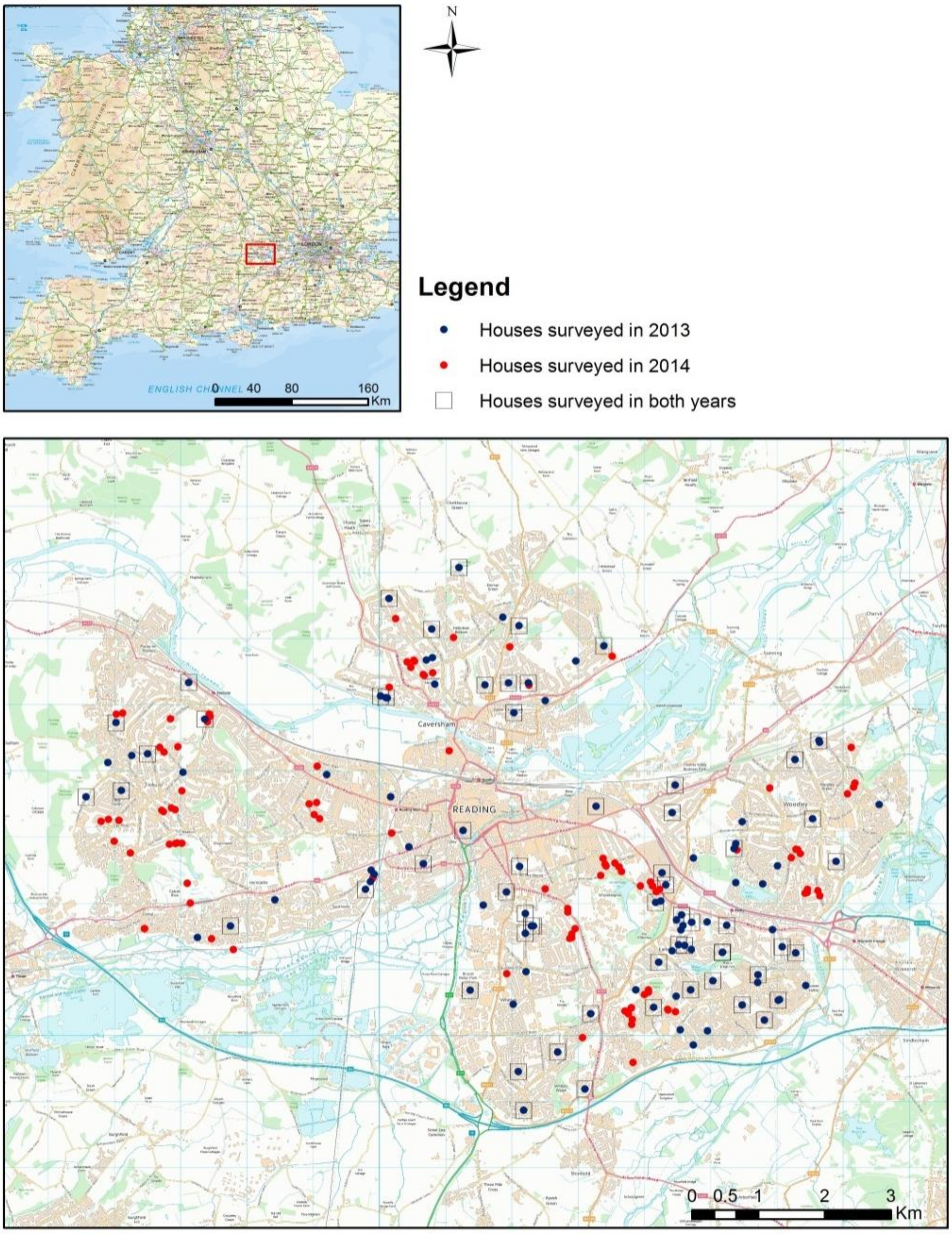

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Figure 4.1. Distribution of gardens surveyed for hedgehogs in Reading, UK, in 2013 and / or 2014.

Table 4.1. Summary of models to estimate the probability of occupancy (Ψ (± SE)) of hedgehogs in residential gardens in Reading based upon constant (two parameters) versus variable daily detection rates (six parameters). Results are given for houses surveyed in 2013 (N=111) and 2014 (N=168). Naïve occupancy is the proportion of sites surveyed where hedgehogs were detected; estimated occupancy is the proportion of gardens estimated to have hedgehogs after correcting for false-absences; estimated occupancy rates are given only for constant detection rate models. Detection rate indicates the probability of detecting hedgehogs in gardens where they were present on any given day of the 5-day survey period. The number of surveys needed is the number of visits required on consecutive nights to be 80% and 95% confident that non-detection reflects the true absence of hedgehogs. Since the number of surveys needed is derived from a sample estimate of detection, the confidence intervals around the number of sites needed were calculated from the SEs derived from the detection estimates (McArdle 1990). ΔQAIC is the difference in QAIC value between each model and the current top-ranked model (that with the lowest QAIC). AIC weight is a measure of support for each model being the 'best' model.

Year	**Model**	**QAIC**	**ΔQAIC**	**AIC weight**	**Model likelihood**	**Naïve Ψ**	**Estimated Ψ (± SE)**	**Detection rate (± SE)**	**No. of surveys needed (±1.96 SE)**	
									80 % confidence interval	**95% confidence interval**
2013	Constant	121.36	0.00	0.9755	1.0000	0.315	0.316 (0.077)	0.684 (0.062)	1.4 (1.0-2.0)	2.6 (1.8-3.6)
	Variable	128.73	7.37	0.0245	0.0251					
2014	Constant	210.62	0.00	0.9097	1.0000	0.399	0.403 (0.069)	0.603 (0.050)	1.7 (1.3-2.3)	3.2 (2.5-4.3)
	Variable	215.24	4.62	0.0903	0.0993					
Pooled	Constant	228.43	0.00	0.9419	1.0000	0.370	0.373 (0.063)	0.615 (0.048)	1.7 (1.3-2.2)	3.1 (2.4-4.1)
	Variable	234.00	5.57	0.0581	0.0617					

Footprint-tunnels as a monitoring tool

On average, hedgehogs were detected in approximately 60-65% of hedgehog-positive gardens on a night-by-night basis (Figure 4.2a). There was an apparent difference in the cumulative pattern of detection of hedgehogs between the two years, with >90% of positive gardens identified after two days of surveying in 2013 but only after four days in 2014 (Figure 4.2b). Similarly, a higher proportion of hedgehog-positive gardens were visited on all five nights in 2013, whereas a higher proportion of hedgehog-positive gardens were visited on just one night in 2014 (Figure 4.2c). Collectively, hedgehogs were recorded on 21.6% and 24.3% of tunnel-nights in 2013 (N=555 tunnel-nights) and 2014 (N=840) respectively; comparable figures considering hedgehog-positive gardens only were 68.6% (N=175 tunnel-nights) and 60.9% (N=335) (Figure 4.2c). On average, hedgehog-positive gardens were visited on 3.2 nights.

Despite these differences, however, occupancy models with a constant daily detection rate performed better than those with survey-specific detection rates for both years (Table 4.1). Power analyses indicated that approximately 3.1 nights of surveying were required to be 95% confident of detecting hedgehogs (Table 4.1). Consequently, differences between the naïve and estimated occupancy rates were very small: false-absence error rates were 0.1% in 2013 and 0.4% in 2014.

Sample sizes required to detect different levels of change to different levels of statistical power are outlined in Table 4.2. In comparison with those sample sizes achieved in different field studies of terrestrial mammals in the UK (Table 4.3), this survey protocol would be suitable for detecting changes in the order of 25% with 95% power at a national level (N=668 gardens).

Factors affecting hedgehog occupancy

Overall, 151 (68.9%) participants returned their questionnaire. Of these, 132 (60.3% of all householders) were complete and used for the occupancy analysis. Only two models had ΔQAIC values < 2 (Table 4.4). However, based on 95% confidence intervals, none of the variables considered significantly affected hedgehog occupancy; although, two did affect hedgehog detection (FOOD, FRONT2BACK) .

Table 4.2. Results of power analysis showing the number of residential gardens that would need to be surveyed to detect a significant percentage change in site occupancy by hedgehogs in relation to survey effort (no. of days each garden was surveyed) and different levels of statistical power.

% change in occupancy	Survey effort (no. of days surveyed)	No. of sites required to achieve stated level of statistical power		
		0.80	0.90	0.95
10	2	4190	5609	6937
25		631	845	1044
50		138	185	229
10	3	2954	3954	4890
25		449	601	743
50		99	133	164
10	4	2716	3636	4496
25		414	554	685
50		92	123	152
10	5	2647	3544	4383
25		404	540	668
50		90	120	148

Associations with predators

Of the 151 gardens for which data were available from the questionnaire survey, hedgehogs, badgers and foxes visited 64 (42.4%), 36 (23.8%) and 51 (33.7%) gardens respectively. Collectively, foxes and / or badgers visited 76 (50.3%) gardens, whereas 39 (25.8%) gardens were not visited by any of these three species.

There was no significant difference in the relative numbers of gardens where hedgehogs were detected in relation to the presence / absence of badgers (Fisher's exact test: P = 0.123) or foxes (P = 0.605). Hedgehogs were detected in 46.1% of gardens where badgers were absent (N=115) and 30.5% of gardens where badgers were present (N=36); comparable figures for gardens visited by foxes were 44.0% (N=100) and 39.2% (N=51) respectively. However, the SIF between badgers and hedgehogs was 0.471 ± 0.188 indicating that hedgehogs were less likely to co-occur with badgers than would be expected under an independence hypothesis, although this was not significant (95% CI: -1.538, 0.030). The SIF between foxes and hedgehogs was 0.954 ± 0.048 indicating that hedgehogs co-occur with foxes as would be expected under an independence hypothesis.

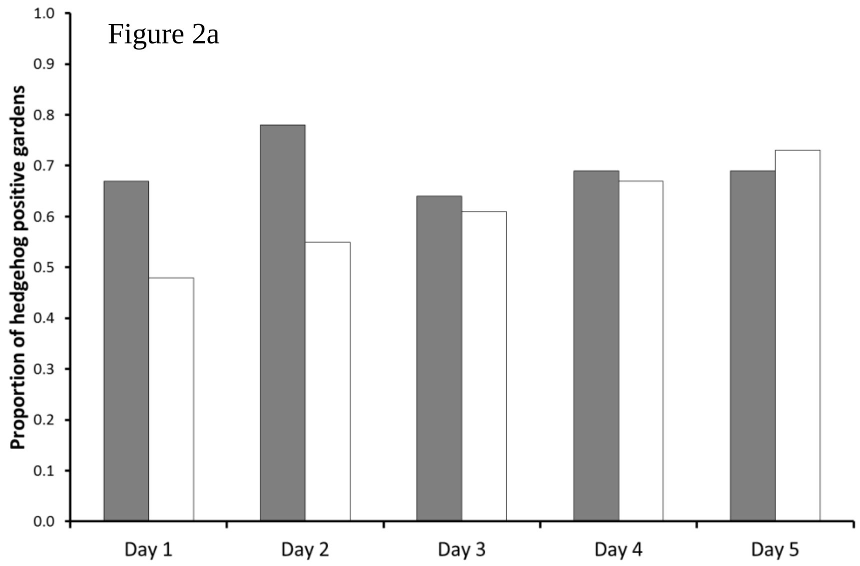
Table 4.3. Summary of sample sizes achieved in selected terrestrial mammal and bird surveys in the UK, with particular emphasis on studies relating to hedgehogs.

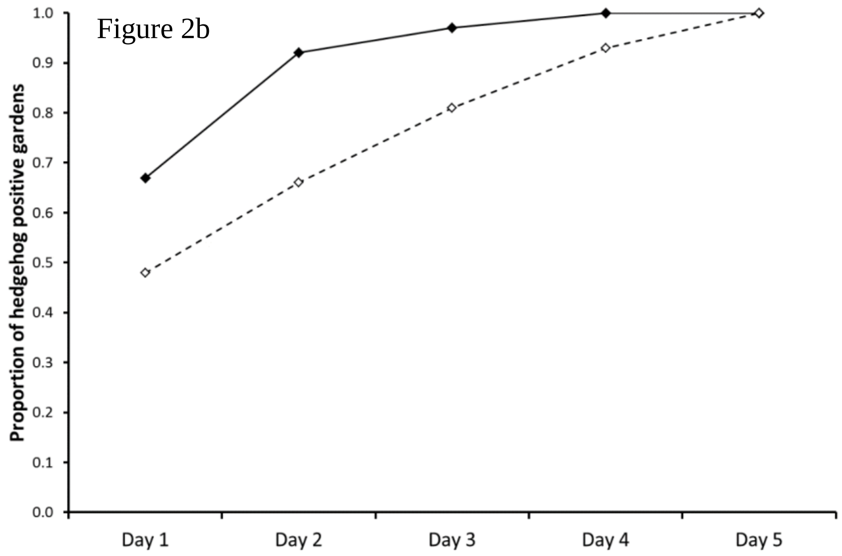
Species / Survey	**Location**[1]	**Habitat**	**Method**[2]	**Surveyor type(s)**[3]	**Sample size**[4]	**Reference**
Badger (*Meles meles*)	GB	Rural	Sett counts in 1-km squares	P, V	2455 (w)	Cresswell *et al.* (1989)
	GB	Rural	Sett counts in 1-km squares	P, V	2578 (w)	Wilson *et al.* (1997)
	E and W	Rural	Sett counts in 1-km squares	P	1614 (w)	Judge *et al.* (2014)
Brown hare (*Lepus europaeus)*	GB	Rural	Sightings in 1-km squares	P, V	751 (w)	Hutchings and Harris (1996)
Hedgehog (*Erinaceus europaeus*)	UK	Urban	Sightings or field signs as part of PTES *Living with Mammals* survey	V	450-750 (y)	Roos *et al.* (2012)
	UK	Urban	Presence/absence in BTO *Garden BirdWatch* scheme	V	1925 (y)	Toms and Newson (2006)
	UK	Rural	Sightings of live or dead animals as part of PTES *Mammals on Roads* survey	V	>2,000 (y)[5]	Roos *et al.* (2012)
	GB	Both	Sightings as part of the PTES/BHPS *Hogwatch* programme	V	>16,000 (y)[5]	Roos *et al.* (2012)
	GB	Rural	Footprint-tunnels	S, V	111 (w)	Yarnell *et al.* (2014)
	GB	Rural	Footprint-tunnels	S, V	261 (w)	Williams *et al.* (2018a)
Red fox (*Vulpes vulpes*)	GB	Rural	Faecal counts in 1-km squares	V, P, S	444 (w)	Webbon *et al.* (2004)
	GB	Rural	Faecal counts in 1-km squares	V, P, S	160 (y)	Baker, Harris and Webbon (2002)
	GB	Urban	Sightings	V	17,477 (y)	Scott *et al.* (2014)
RSPB *Make your nature count* survey	UK	Both	Sightings	V	30,000 (y)[5]	Roos *et al.* (2012)
BTO *Breeding Bird Survey*	UK	Both	Sightings and field signs in 1-km squares	V	1791 (y)	Battersby (2005)
Winter Mammal Monitoring	GB	Rural	Sightings and field signs in 1-km squares	V	323-880 (y)	Battersby (2005)

[1] E = England; GB = Great Britain; UK = United Kingdom; W = Wales. [2] BHPS = British Hedgehog Preservation Society; BTO = British Trust for Ornithology; PTES = People's Trust for Endangered Species. [3] P = paid surveyor; S = student at UK university; V = volunteer; [4] Sample size is given for: w = whole project; y = yearly. [5] Where appropriate, maximum sample sizes in one year of a multi-year study have been indicated.

Table 4.4. Summary of occupancy models investigating factors associated with the presence / absence of hedgehogs in residential gardens (N = 134) in Reading, UK. Models were selected on the basis of Quasi-Akaike's Information Criterion (QAIC) values; top ranked models (ΔQAIC < 2) are shaded. Models with ΔQAIC values > 2 or which did not converge were excluded as having little or no support (Burnham and Anderson 2002). Variables are described in the text.

Model	QAIC	ΔQAIC	AIC wgt	Model	No. of par.
Ψ (BADGER),p(FOOD)	258.97	0.00	0.3469	1.0000	4
Ψ(.),p(FOOD)	259.56	0.59	0.2583	0.7445	3
Ψ(BADGER),p(FRONT2BACK)	262.08	3.11	0.0733	0.2112	4
Ψ(.),p(FRONT2BACK)	262.63	3.66	0.0556	0.1604	3
Ψ(BADGER),p(FOX)	264.46	5.49	0.0223	0.0642	4
Ψ(.),p(FOX)	264.98	6.01	0.0172	0.0495	3
Ψ(BADGER),p(.)	265.04	6.07	0.0167	0.0481	3
Ψ(COMPOST),p(.)	265.17	6.20	0.0156	0.0450	3
Ψ(.),p(.)	265.59	6.62	0.0127	0.0365	2
Ψ(FRONT2BACK),p(.)	265.80	6.83	0.0114	0.0329	3
Ψ(LOGS),p(.)	266.40	7.43	0.0084	0.0244	3
Ψ(.),p(ALLOTMENT)	266.49	7.52	0.0081	0.0233	3
Ψ(.),p(COMPOST)	266.51	7.54	0.0080	0.0231	3
Ψ(FOX),p(.)	266.70	7.73	0.0073	0.0210	3
Ψ(.),p(BACKFLOWER)	266.80	7.83	0.0069	0.0199	3
Ψ(HOUSETYPE),p(.)	266.81	7.84	0.0069	0.0198	3
Ψ(.),p(AMENITY)	266.84	7.87	0.0068	0.0195	3
Ψ(BACKLAWN),p(.)	267.04	8.07	0.0061	0.0177	3
Ψ(AMENITY),p(.)	267.05	8.08	0.0061	0.0176	3
Ψ(.),p(HOUSETYPE)	267.13	8.16	0.0059	0.0169	3
Ψ(.),p(LOGS)	267.22	8.25	0.0056	0.0162	3
Ψ(.),p(BADGER)	267.25	8.28	0.0055	0.0159	3
Ψ(WEEDKILLER),p(.)	267.28	8.31	0.0054	0.0157	3
Ψ(.),p(SLUGPELLET)	267.33	8.36	0.0053	0.0153	3
Ψ(.),p(EDGE)	267.38	8.41	0.0052	0.0149	3
Ψ(FOOD),p(.)	267.38	8.41	0.0052	0.0149	3
Ψ(.),p(WOODLAND)	267.39	8.42	0.0052	0.0148	3
Ψ(.),p(WATER)	267.41	8.44	0.0051	0.0147	3
Ψ(ALLOTMENT),p(.)	267.46	8.49	0.0050	0.0143	3
Ψ(BACKSHRUB),p(.)	267.49	8.52	0.0049	0.0141	3
Ψ(SLUGPELLET),p(.)	267.50	8.53	0.0049	0.0141	3
Ψ(EDGE),p(.)	267.52	8.55	0.0048	0.0139	3
Ψ(BACKFLOWER),p(.)	267.54	8.57	0.0048	0.0138	3
Ψ(.),p(WEEDKILLER)	267.58	8.61	0.0047	0.0135	3
Ψ(.),p(BACKSHRUB)	267.58	8.61	0.0047	0.0135	3
Ψ(.),p(BACKLAWN)	267.58	8.61	0.0047	0.0135	3
Ψ(WOODLAND),p(.)	267.58	8.61	0.0047	0.0135	3
Ψ(.),p(DISTRICT)	267.59	8.62	0.0047	0.0134	3
Ψ(WATER),p(.)	267.59	8.62	0.0047	0.0134	3
Ψ(DISTRICT),p(.)	267.59	8.62	0.0047	0.0134	3





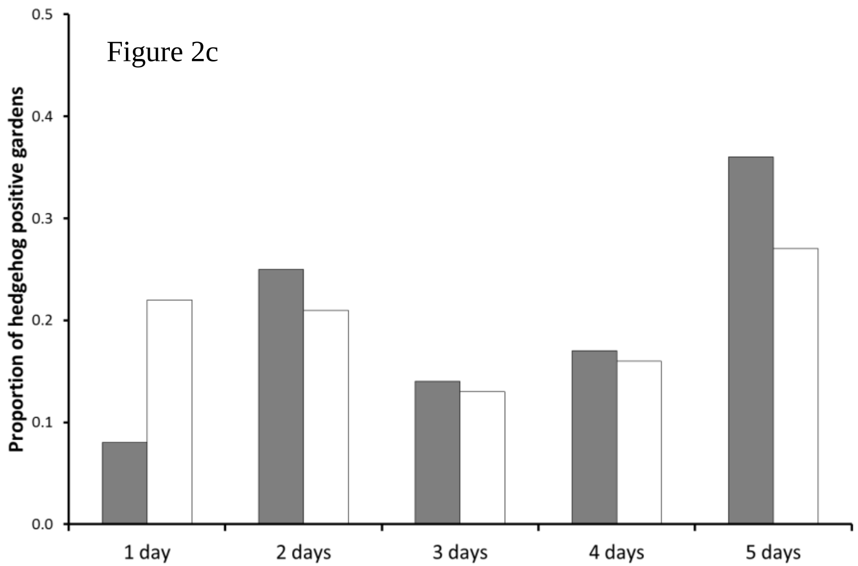


Figure 4.2. Summary of: (a) the proportion of hedgehog-positive gardens where hedgehogs were detected each day; (b) the cumulative pattern of detection of hedgehogs in hedgehog-positive gardens; and (c) the number of days where hedgehogs were detected in each hedgehog-positive garden. Shaded columns / solid lines and open columns / dotted lines denote hedgehog-positive gardens surveyed in 2013 (N=36) and 2014 (N=67) respectively.

Discussion

Previous studies aimed at documenting the use of gardens by hedgehogs in the UK have focussed on questionnaire surveys (Baker and Harris 2007) and timed or anecdotal observations (Toms and Newson 2006; Hof and Bright 2009; Hof and Bright 2016; Wembridge and Langton 2016). The current study suggests that such approaches may be problematic. In this study, 34.7% of 147 householders failed to correctly predict the presence or absence of hedgehogs across the 5-day sampling period. Similarly, in their footprint-tunnel study in Gloucestershire, UK, Williams *et al.* (2014) reported that hedgehogs were only recorded in 35% and 38% of gardens where the householder had reported seeing (N=23) or not seeing (N=24) hedgehogs previously. Although houses were studied for only five days in each study, and householders may be basing their perceptions on longer time frames, both studies suggest that a large proportion of householders may be unaware of the pattern of use of their gardens by hedgehogs.

Footprint-tunnels do, however, appear to offer a clear solution to this problem; the 5-day sampling period used in this study was associated with a false-absence error rate of just 0.1-0.4%. In addition, the technique is self-evidently one that can be easily applied by members of the general public, as they collected all the data used in the current analyses. Based on the current study, the 5-day sampling protocol used would be capable of detecting changes in the order of 25% with 95% power with moderate levels of citizen participation (N=668 gardens). In actuality, given the hedgehog's wide appeal to members of the public, it is not unreasonable to assume that much larger sample sizes would be achievable. For example, the *Hogwatch* survey (Hof and Bright 2016) received information from > 16,000 people; such high levels of participation suggest that much smaller changes in urban hedgehog numbers could be detected using this methodology. However, it is worth noting that hedgehog-positive gardens in Reading were visited on almost twice as many nights (mean of 3.2) as those in Gloucestershire (1.7 nights: Williams *et al.* 2014); the reason for this disparity is not clear, but such variations would affect the methodology's statistical power.

Factors affecting the use of gardens by hedgehogs

Hedgehogs were found in 32–40% of gardens in Reading across the two years of the study, a figure very similar to the 36% reported by Williams *et al.* (2014) in Gloucestershire. Therefore, although hedgehogs appear to be widely distributed within individual urban areas (hedgehogs were detected in all four residential sectors within Reading, with no significant differences in occupancy), they appear to be utilising only a minority of gardens. The occupancy rates identified in this study are likely to be maximum levels, since the recruitment protocol was, if anything, likely to engage people with hedgehogs in their garden (even though I specifically asked for volunteers not to base their involvement on an any prior knowledge of hedgehogs in their garden). Therefore, true, unbiased, occupancy rates are likely to be lower, raising concern for the long term stability of urban hedgehog populations.

Alternatively, this does indicate that urban areas might be capable of holding much higher densities of hedgehogs than they do currently, if those factors that make gardens “hedgehog-friendly” could be identified. However, none of the within-garden or outside-garden habitat factors incorporated into single-species occupancy models significantly affected hedgehog occupancy (see also Williams *et al.* 2014): the presence of badgers was the only factor included in the two highest-ranked models, but this was not significant.

There are several potential explanations for these results. For example, it may be that the factors included in these models did not reflect the characteristics actually selected for by hedgehogs. However, this is unlikely. The variables selected represent a range of important biotic processes (the availability of food and shelter, predation risk, inter-specific competition, habitat connectivity and distance to more natural habitats), some of which have been shown to affect rural and urban hedgehogs in other studies (Young *et al.* 2006; Hubert *et al.* 2011; Parrott *et al.* 2014; Trewby *et al.* 2014; Poel *et al.* 2015).

Alternatively, this lack of difference may reflect the fact that back gardens represent multi-functional space (Cameron *et al.* 2012), such that ground-level microhabitats likely to be important to hedgehogs are often overtly similar at the neighbourhood level (Loram *et al.* 2008) with a strong emphasis on cultivated lawns, (non-native) flower borders (Smith *et al.* 2006) and features such as sheds, decking and patios. One factor that does affect garden structure and habitat richness, however, is garden size (Loram *et al.* 2008), with larger gardens typically containing a broader range of micro-habitats. This pattern is, in turn, evident between house types, with larger gardens historically being associated with detached houses and the smallest gardens with terraced houses, although this pattern is changing; the increased emphasis on high-density, low-cost housing throughout the UK means that garden size is becoming more similar across a broad range of house types. Within this study, however, occupancy was not affected by house type nor by the residential sector where the garden was located, suggesting that garden size per se does not affect their suitability for hedgehogs.

However, footprint-tunnels are associated with one significant limitation in the context of discriminating between gardens. As they are baited with relatively small amounts of food bait in an attempt to minimise their impact on normal patterns of hedgehog movement, they are likely to be visited by animals regardless of whether the tunnel is positioned within a garden where the animal spends a great deal of its time foraging versus one where the animal may simply be travelling. Consequently, tunnel visits may not always reflect "good" gardens. Therefore, future studies will require other field methods, such as radio- or GPS-tracking (e.g. Glasby and Yarnell 2013), to identify characteristics associated with the differential use of individual gardens.

Despite this limitation, the two-species occupancy modelling did identify that the use of gardens by hedgehogs is potentially influenced by the presence of badgers, although this result was not significant; the presence of foxes had no observable effect. Both badgers and foxes represent potential predators and competitors of hedgehogs (Pettett *et al.* 2018) and declines in the abundance of both badgers (due to culling to manage bovine tuberculosis) and foxes (due to an outbreak of sarcoptic mange) have been associated with increases in hedgehogs in rural (Trewby *et al.* 2014) and urban (Harris and Baker 2000) habitats, respectively. Similarly, Pettett *et al.* (2018) reported a negative relationship between hedgehogs and both badgers and foxes based on sightings of animals killed on roads. As such, hedgehogs might be expected to avoid using gardens frequented by these larger species.

Evidence for this is, however, equivocal. For example, Ward *et al.* (1997) documented only a short-term avoidance (5-30 minutes) of badger odour by hedgehogs. Furthermore, urban areas contain large amounts of natural foods and food supplied deliberately by humans, often targeted at focal species such as badgers, foxes and / or hedgehogs (e.g. Baker *et al.* 2000; Bateman and Fleming 2012). These anthropogenic foods may, therefore, act to reduce competition by increasing the volume of food available, but also minimise the risk of predation since predators are likely to be well-fed and foods supplied by householders require minimal foraging effort compared to breaking through the defences of a curled hedgehog. In addition, conservation NGOs also recommend that householders supply food for hedgehogs in covered feeding stations for protection but which also avoid the food being stolen by other species. Supplying food in this way could lead to spatial convergence and temporal divergence of hedgehog foraging patterns relative to those of the other two species, thereby favouring co-existence. As such, reported "increases" in hedgehogs in relation to declines in badgers or foxes may well represent increases in abundance, but also changes in avoidance-related movement patterns; identifying which mechanism(s) are involved would require studies focussing on both simultaneous patterns of movement and population demographics.

In summary, this study has demonstrated that footprint-tunnels represent an effective "citizen science" technique for monitoring urban hedgehog populations and which overcome the potential problems associated with sightings-based techniques. In addition, they are cheap (the £5 cost mentioned could be further reduced by getting householders to build a similar design using materials they are likely to have lying around) and the data collected can be easily verified, either by returning or photographing footprint papers. The data presented here, and elsewhere, suggest that hedgehogs can typically be found throughout the urban landscape, but may only be utilising a minority (≤40%) of gardens: although this is low, it does imply that substantive improvements could be made. Therefore, more detailed studies are urgently required to identify those within- and outside-garden factors that influence garden use by hedgehogs.

Acknowledgements

I would like to thank the many Reading householders who participated in this study and Karl Schroepfer, Scott Hudson, Sarah Murton and Sarah Putnam who helped with surveying. The project was conducted in collaboration with the People's Trust for Endangered Species and the British Hedgehog Preservation Society.

Chapter Five

The work presented in the previous three chapters focussed on the development of footprint tunnels as a method for the future monitoring of populations in rural and urban habitats. In contrast to the effort expended by non-governmental organisations and associated partners over the last 20 years to monitor changes in relative abundance, much less attention has focussed on identifying the root causes of the decline in hedgehog numbers in the UK and how these could be reversed.

The UK road network has grown markedly in recent decades, and is set to increase further in the foreseeable future. Previous work has indicated that roads may affect hedgehogs in several ways (e.g. Huijser and Bergers 2000; Rondinini and Doncaster 2002), but perhaps the most obvious is through direct mortality associated with collisions with vehicles. Despite a range of studies examining the numbers of hedgehogs killed on roads (e.g. Sleeman *et al.* 1985; Huijser *et al.* 1998; Holsbeek *et al.* 1999; Ludgate and Kelly 2013), highlighting its susceptibility to vehicles, less attention has focussed on how to relate this information towards developing strategies to reduce the numbers of hedgehogs killed. Therefore, in this study, the spatial distribution of road-killed hedgehogs in Suffolk, England, and the road and roadside characteristics associated with the position of hedgehog carcasses, were quantified in order to help identify possible future mitigation strategies.

The manuscript presented in this chapter will, in due course, be submitted for peer review in a scientific journal, possibly *Landscape Ecology.*

My contribution to the work

I designed the project in discussion with Philip Baker. All analysis was my own. Hedgehog road kill location data was supplied by Simone Bullion / Suffolk Wildlife Trust; data on road and roadside characteristics was collected by myself. The manuscript was co-written by me and Philip Baker.

Factors affecting the position of road-killed hedgehogs (*Erinaceus europaeus*): implications for mitigation and monitoring?

Keywords: *Citizen science; Hedgehog; Wildlife-vehicle collisions; Roads; Vehicles; Mitigation*

Abstract

Populations of the West European hedgehog (*Erinaceus europaeus*) appear to have declined markedly in the UK in recent decades, perhaps by as much as 40%. There are a number of potential reasons for this decline, but the species is also frequently killed by collisions with vehicles, such that reducing casualty rates could potentially represent one measure to help start to reverse this decline. In this study, data from a one year project run by the Suffolk Wildlife Trust (England) were used to determine (i) whether hedgehog casualties were spatially clustered and (ii) what (a) road and (b) roadside factors were associated with the presence / absence of hedgehog carcasses.

Network K-function analysis indicated hedgehog casualties were clustered at all spatial scales. Overall, 66% of carcasses (N=1407) were reported from urban areas; a habitat that typically covers >6% of total land cover in the UK.

There were similarities, but also differences, in the factors that significantly affected the presence / absence of carcasses on roads in urban versus rural landscapes. These data potentially indicate: (i) hedgehogs are more likely to be killed in areas associated with human habitation; (ii) hazards associated with driving which divert the driver's attention away from the road surface and (iii) the tendency for hedgehogs to move along linear features can increase the likelihood of hedgehogs being killed.

The distribution of hedgehog carcasses suggest that road signage could potentially be used to reduce the number of animals killed. However, before such mitigation measures are considered additional data on the inter-annual stability of road-kill "hotspots" and the relative importance of traffic as a cause of mortality are required. Additionally, studies investigating the ability of drivers to spot hedgehogs on the road and the effectiveness of signage in reducing casualty numbers would also be merited.

Introduction

Roads impose a wide range of direct and indirect impacts on wildlife, including: habitat loss and degradation; the creation of barriers to movement; noise, light and chemical pollution; and direct mortality through wildlife-vehicle-collisions (WVCs) (Forman and Alexander 1998; Spellerberg 2002; Forman *et al.* 2003; Benítez-lópez *et al.* 2010; Kociolek *et al.* 2011; Rytwinski and Fahrig 2012; Van der Ree *et al.* 2015). Surveys of animals killed on roads indicate that a broad range of species are affected (e.g. Clevenger *et al.* 2003; Grilo *et al.* 2009; Carvalho and Mira 2011; Červinka *et al.* 2015), although not all populations are affected negatively by this traffic-related mortality (Rytwinski and Fahrig 2012, 2015; but see Jackson and Fahrig 2011; Van der Ree *et al.* 2015). In addition, collisions with larger-bodied species also cause vehicle damage as well as posing a risk of injury or death to humans (Conover *et al.* 1995; Niemi *et al.* 2017). Mitigation measures aimed at reducing the numbers of collisions are, therefore, likely to lead to financial gains (Huijser *et al.* 2009) as well as conservation benefits.

However, the implementation of many mitigation measures (e.g. bridges, overpasses, underpasses, culverts, fences) are based on the premise that animals cross roads (or can be guided to cross roads) at defined points in the landscape. As these measures are often expensive to implement, they are often targeted at charismatic megafauna, species of high conservation concern and / or those that pose a risk to human drivers (see case studies in Van der Ree *et al.* 2015). But such approaches are not practical for smaller-bodied species which are likely to cross roads at multiple points in the wider landscape. In these instances, it is more realistic to consider the use of warning signs as a means to help reduce the number of wildlife fatalities (Huijser *et al.* 2015). Even this approach, however, is typically dependent on casualties being clustered so that particular stretches of roads can be targeted.

The West-European hedgehog (*Erinaceus europaeus*) is known, or suspected, to be affected by roads in several different ways. For example, Huijser and Bergers (2000) estimated that hedgehog density was reduced by approximately 30% in the vicinity of roads in the Netherlands and Rondinini and Doncaster (2002) observed that animals avoided crossing major roads; both of these processes are likely to result in the increased isolation of hedgehog populations (Becher and Griffiths 1998; Braaker *et al.* 2017). WVCs can also represent a significant cause of mortality within populations e.g. 73% of the carcasses collected by Rautio *et al.* (2016) had been killed by vehicles. Currently, it is estimated that approximately 167,000-335,000 hedgehogs are killed on the roads annually in the UK (Wembridge *et al.* 2016).

Within the UK, evidence from several monitoring programmes suggest that the species has declined markedly in the last 20-30 years (Hof and Bright 2016; Wembridge and Langton 2016; Wilson and Wembridge 2018), prompting its addition to the country's Biodiversity Action Plan and designation as a species of principal importance in 2007. This decline is likely to be the result of a combination of factors including: agricultural intensification (Robinson and Sutherland 2002; Hof and Bright 2010a,b), an increase in badger (*Meles meles*) numbers(Hof *et al.* 2012; Judge *et al.* 2014, 2017; Parrott *et al.* 2014), an intra-guild predator; and an increase in the size of the road network (33% increase in total road length since 1951: Office for National Statistics 2018). Furthermore, one of these monitoring programmes (the *Mammals on Roads* survey coordinated by the People's Trust for Endangered Species) is itself based upon counts of dead hedgehogs on roads by volunteer surveyors. Specifically, people are asked to record the number of casualties observed in journeys of ≥20 miles but excluding urban areas and motorways or dual carriageways for safety reasons; data are then analysed on a 10 x 10km basis.

The robustness of this survey methodology is, however, equivocal. In addition to the fact that journey routes are decided by surveyors rather than being assigned randomly, road and roadside characteristics could also potentially influence the likelihood that hedgehogs are killed; this would result in transects (journey routes) not being "true repeats" of one another. In citizen science surveys, such problems with non-randomness can be reduced by having large sample sizes, including receiving repeated information from the same site (Toms *et al.* 1999). However, if mortality risk is influenced by road / roadside characteristics, then even repeat information from the same route may not be directly comparable because of intra- and inter-annual changes associated with e.g. housing construction, field rotations, improved safety measures and / or verge maintenance.

The aims of this study were, therefore, to: (i) identify whether hedgehogs casualties are clustered in space or not; and (ii) identify the factors associated with the presence / absence of hedgehog carcasses on roads.

Methods

Sightings of dead hedgehogs on roads were reported to Suffolk Wildlife Trust by members of the general public in 2014 as part of a campaign to obtain baseline data on the distribution of hedgehogs in the county. The survey was advertised widely in the local media, and leaflets were distributed throughout the towns asking for sightings of both live and dead animals. Respondents were able to submit their sightings via the Trust's website: information was requested on the date and position of any sightings. Based on the respondent's description of the location, carcass position was estimated; any obviously erroneous data points were omitted. Only road-killed hedgehogs were used in the current analyses.

Are hedgehog casualties clustered?

Multi-distance spatial analysis was performed using SANET 4.1 Standalone (Okabe *et al.* 2006). SANET analyses data on a network (e.g. roads, rivers) to determine if it is distributed randomly, clustered or dispersed (described by Okabe and Yamada (2001) as an extension of Ripley (1976)). This procedure works by comparing two sets of points, one representing the reported carcasses and the other representing what would be expected if animals occurred with complete spatial randomness (CSR) along the network. Network K-function provides all point-to-point analysis across a range of spatial scales rather than just nearest-neighbour analysis. 10^4 permutations of 1,409 random data points (i.e. the same number as the total number of hedgehog carcasses reported: see *Results*) were used to generate a confidence envelope at each inclusion distance for comparison with the observed data: observed values which fall above the confidence envelope are taken to indicate clustering; values below the confidence envelope indicate dispersion from complete spatial randomness (Spooner *et al.* 2004). All road types were merged to create one network layer and was processed to ensure that all lines (roads) were properly connected before analysis in SANET using the Global Auto K-Function Method. The resultant output data were exported to R 3.4.3 (R Core Development Team 2018) to graphically illustrate the results.

Factors affecting carcass position

Binary logistic regression was used to compare the road and roadside characteristics associated with the presence of carcasses compared to those of randomly selected locations. For analysis, 149 (10.6%) records of dead hedgehogs were selected at random in ArcMap 10.1 (see Figure 5.1). For each of these 'real' locations, a 'model' position was created randomly on a road within a 500m radius of the real location; this distance was selected to represent the maximum distance that the real hedgehog could have travelled but still have been within its home range (Reeve 1994). Of the 149 real hedgehog carcasses, 91 (61%) were classified as urban and 58 (39%) as rural. In comparison, 85 (57%) and 64 (43%) model locations were classified as urban and rural, respectively.

Data on the habitat and road characteristics associated with each real and fake location were collected using Google Maps and Google Street View (Google 2018); data from 45 (15%) data points were checked independently by a second person (D. Bennett) to ensure accuracy and consistency. Variables recorded relating to the road itself were: LANDSCAPE (urban or rural); ROADTYPE (A-road, B-road or C-road / Unclassified); the total number of lanes (LANES: one lane only versus two or more lanes); speed limit (SPEED: ≤30 mph versus >30mph); whether there were or were not streetlamps (LIGHTS) or a raised kerb (KERB) present; whether cars were parked on the road or not (PARKED); and whether there was a bend (BEND) or junction (JUNCTION) with 75 feet (Table 5.1).

Variables recorded which related to roadside characteristics were: whether the surrounding area either side of the road was flat with the road surface or not (TOPOGRAPHY); and whether each of six linear features (woodland / hedgerow (GREENEDGE), fence / wall, embankment, footpath, grass verge, water) were present or not on either side of the road. In addition, the presence / absence of each of five different habitat types (woodland / scrub, housing / built environment, amenity grassland, arable fields, pastoral fields) was recorded. This was done as a two-stage process. First the dominant habitat on each side of the road was determined based on the area covered. Second, the dominant habitats identified were then summed across both sides of the road. Consequently, each neighbouring habitat was classified as either: not the dominant habitat on either side of the road; the dominant habitat on one side of the road only; or the dominant habitat on both sides of the road.

Because of the inherent differences in road and roadside characteristics associated with urban versus rural landscapes, separate models were constructed for each. Initial starting models included all main effects (except PASTORAL which had to be excluded from the urban model) and were simplified using a backwards stepwise elimination procedure ($\alpha < 0.05$): interaction terms were not included because of the relatively small sample size. Probability thresholds were adjusted to maximize the model's ability to assign cases into dichotomous classes and increase overall prediction success. Final model fit was assessed using Cox and Snell's and Nagelkerke's R^2 values, Hosmer-Lemeshow goodness-of-fit tests and sensitivity, specificity and overall classification indices. All analyses were conducted using SPSS version 18 (SPSS Inc. 2009).

Table 5.1: Summary of the variables used in the binary logistic regression analyses to identify factors associated with the presence-absence of hedgehog carcasses on roads in Suffolk.

Variable	Description	LEVELS
LANDSCAPE	Was the hedgehog killed in a rural habitat	• Rural • Suburban / urban
ROADTYPE	The category of road the hedgehog was killed on	• A-road • B-road • C-road / unclassified
LANES	The total number of lanes on the road in both directions (e.g. a road with one lane in each direction was classified as a two lane road)	• One lane • Two or more lanes
SPEED	The speed limit of the road on which the hedgehog was killed	• ≤30 mph • >30 mph
LIGHTS	Were street lights present?	• Not present on either side • Present on at least one side
KERB	Was there a raised kerb present?	• Yes • No
TOPOGRAPHY	The topography of the road relative to the surrounding area	• Surrounding area was flat with the road on both sides • Surrounding area was either lower or higher than the road on both sides
PARKED	Are cars parked on the road at night	• Yes • No
BEND	Was there a bend within 75 feet of the hedgehog?	• Yes • No
JUNCTION	Was there a junction within 75 feet of the hedgehog?	• Yes • No
Roadside habitats: • WOOD • BUILT • AMENITY • ARABLE • PASTORAL	What was the main habitat type on either side of the road of the hedgehog	All coded: • 0 - Not present • 1 - Present on one side only • 2 - Present on both sides
Parallel: • GREENEDGE (e.g. woodland, hedgerow) • FENCEWALL • EMBANKMENT • FOOTPATH • GRASSVERGE • WATER	What features were running parallel to the road (on either side)?	All coded: • 0 - Not present • 1 - Present

Results

In total, 1,407 records of dead hedgehogs on roads were received (Figure 5.1); of these, 922 (66%) and 485 (34%) were of hedgehogs in urban and rural areas, respectively. The number of casualties reported peaked in May, with the fewest records received in the winter months when hedgehogs are hibernating (Figure 5.2).

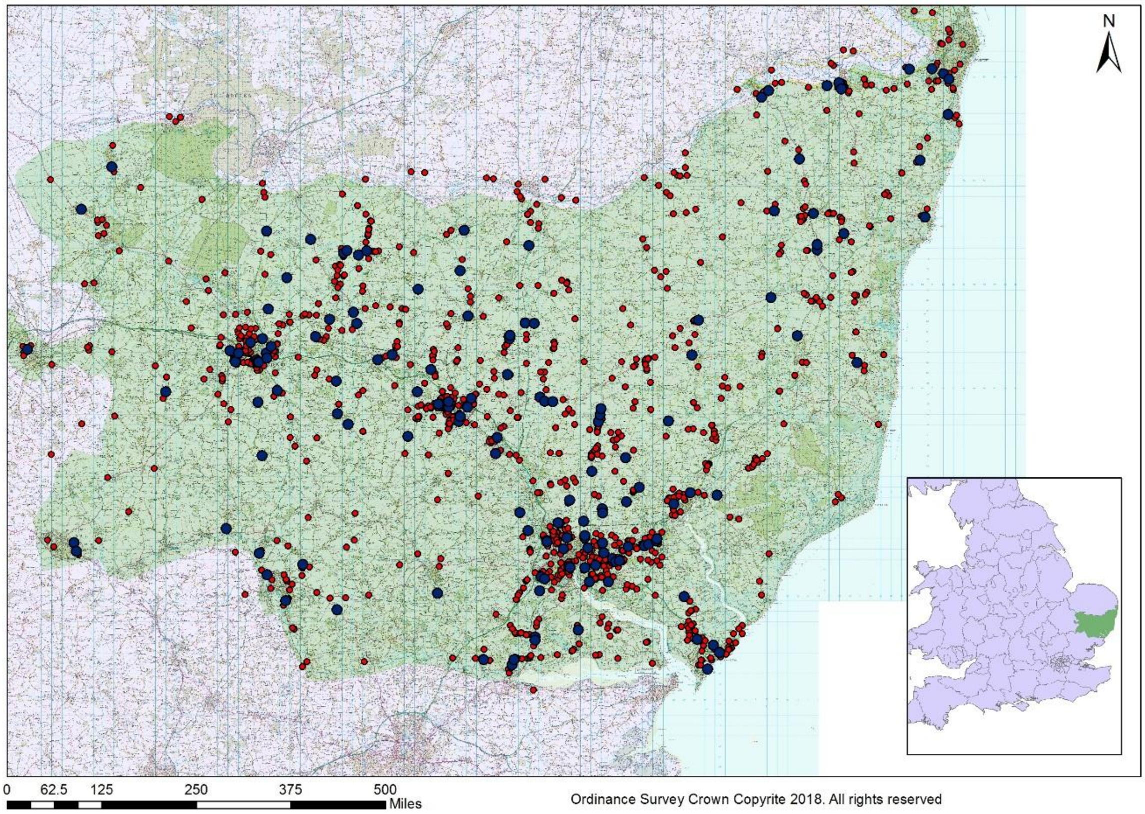


Figure 5.1. Distribution of hedgehogs reported dead on roads in Suffolk in 2014. Symbols denote those animals that were (blue) and were not (red) included in the binary logistic regression analysis to determine factors affecting carcass position.

Are hedgehog casualties clustered?

Hedgehog casualties were clustered over all spatial scales (Figure 5.3). The majority of clustering was associated with areas of human habitation (Figure 5.1).

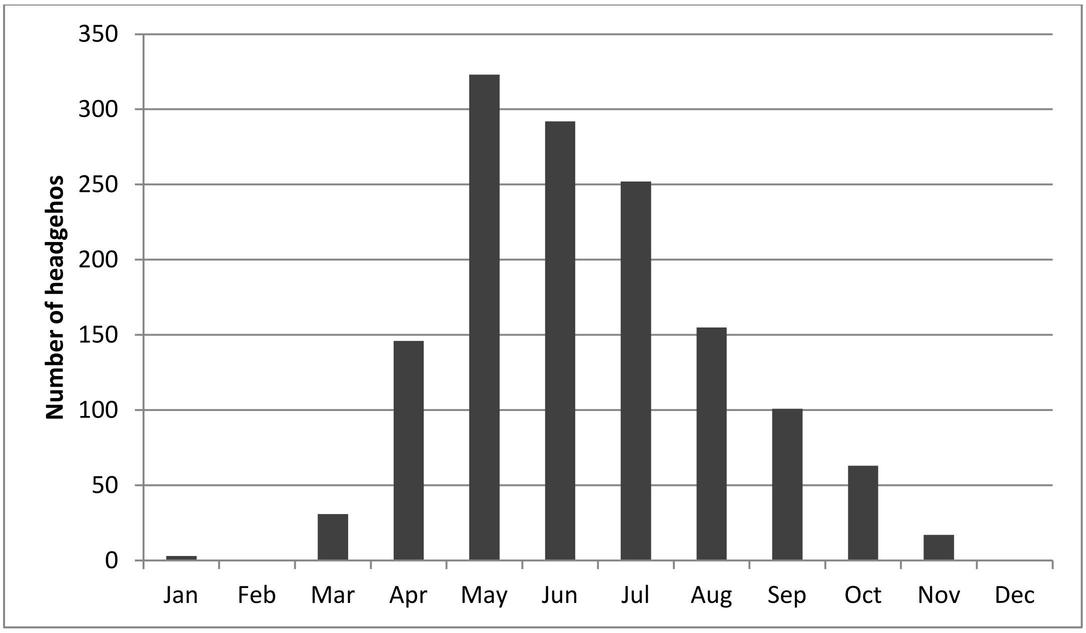


Figure 5.2. The numbers of hedgehogs reported dead on roads each month in Suffolk in 2014.

Factors affecting carcass position

The position of hedgehog carcasses in urban areas was significantly affected by the speed limit, the number of lanes and the presence / absence of woodland / hedgerow running parallel to the road (Table 5.2). Hedgehogs were less likely to be killed on roads with a speed limit >30 mph (Figure 5.4a), on roads with two or more lanes of traffic (Figure 5.4b) and where GREENEDGE habitats were absent (Figure 5.4c). Model fit metrics were generally good but with low sensitivity (41.7%), indicating that the model was not as able to predict factors associated with the presence of hedgehog carcasses in this type of landscape.

Table 5.2. Summary of the binary logistic regression investigating factors associated with the presence of hedgehog carcasses on urban roads. Reference levels for variables are indicated in parentheses. Model summary statistics were: Hosmer-Lemeshow goodness-of-fit test: X^2_2 = 0.444, P=0.801; Cox and Snell R^2 = 0.084; Nagelkerke R^2 = 0.112; specificity = 81.2%; sensitivity = 41.7%; overall classification = 60.2%. Cut-off threshold used was 0.5.

Variable	**B**	**S.E.**	**Wald**	**df**	**Sig.**	**Exp(B)**	**95% C.I. for EXP(B)**	
							Lower	**Upper**
SPEED(≤30 mph)			4.518	1	0.034			
>30 mph	-1.532	0.721	4.518	1	0.034	0.216	0.053	0.888
LANES(One lane)			6.565	1	0.010			
> one lane	1.593	0.622	6.565	1	0.010	4.917	1.454	16.625
GREENEDGE(Present)			6.428	1	0.011			
Absent	-0.859	0.339	6.428	1	0.011	0.424	0.218	0.823
Constant	-0.769	0.597	1.658	1	0.198	0.464		

In rural areas, the position of hedgehog carcasses was significantly affected by road type, speed limit, the presence / absence of parked cars and proximity to a road junction (Table 5.3). Hedgehogs were less likely to be killed on C / Unclassified roads (Figure 5.5a) and on roads with a speed limit >30 mph (Figure 5.5b), but more likely to have been killed where parked cars were present (Figure 5.5c) and in close proximity (within 75 feet) of a junction (Figure 5.5d). Model fit metrics were excellent with very high specificity (75.0%) and sensitivity (42.4%) indices.

Table 5.3. Summary of the binary logistic regression investigating factors associated with the presence of hedgehog carcasses on rural roads. Reference levels for variables are indicated in parentheses. Model summary statistics were: Hosmer-Lemeshow goodness-of-fit test: X^2_6 = 0.383, P=0.699; Cox and Snell R^2 = 0.267; Nagelkerke R^2 = 0.356; specificity = 75.0%; sensitivity = 72.4%; overall classification = 73.8%. Cut-off threshold used was 0.4.

Variable	B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I. for EXP(B)	
							Lower	Upper
ROADTYPE(A-road)			8.097	2	0.017			
B-road	-0.304	0.608	0.250	1	0.617	0.738	0.224	2.428
C / Unclassified road	-1.529	0.571	7.168	1	0.007	0.217	0.071	0.664
SPEED(≤30 mph)			4.363	1	0.037			
> 30mph	-1.096	0.525	4.363	1	0.037	0.334	0.119	0.935
PARKED(Yes)			14.095	1	<0.001			
No	-3.139	0.836	14.095	1	<0.001	0.043	0.008	0.223
JUNCTION(Yes)			5.394	1	0.020			
No	-1.314	0.566	5.394	1	0.020	0.269	0.089	0.815
Constant	5.346	1.246	18.407	1	<0.001	209.825		

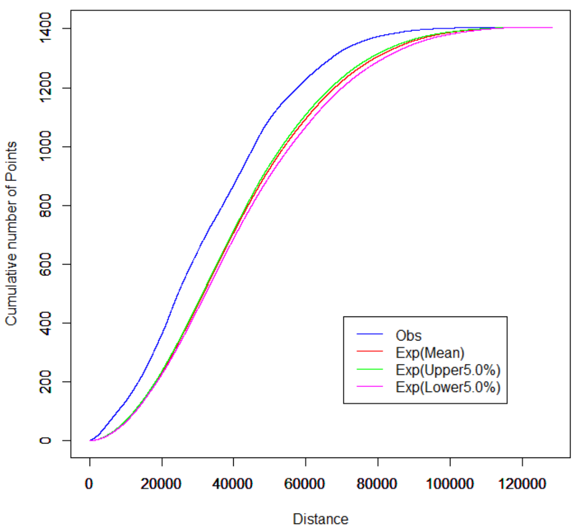


Figure 5.3. Observed K-function (blue line) for hedgehog casualties in Suffolk with expected confidence envelope (green and pink lines) based on complete spatial randomness. Observed data were significantly more clustered at all spatial scales. Distance on x-axis in metres.

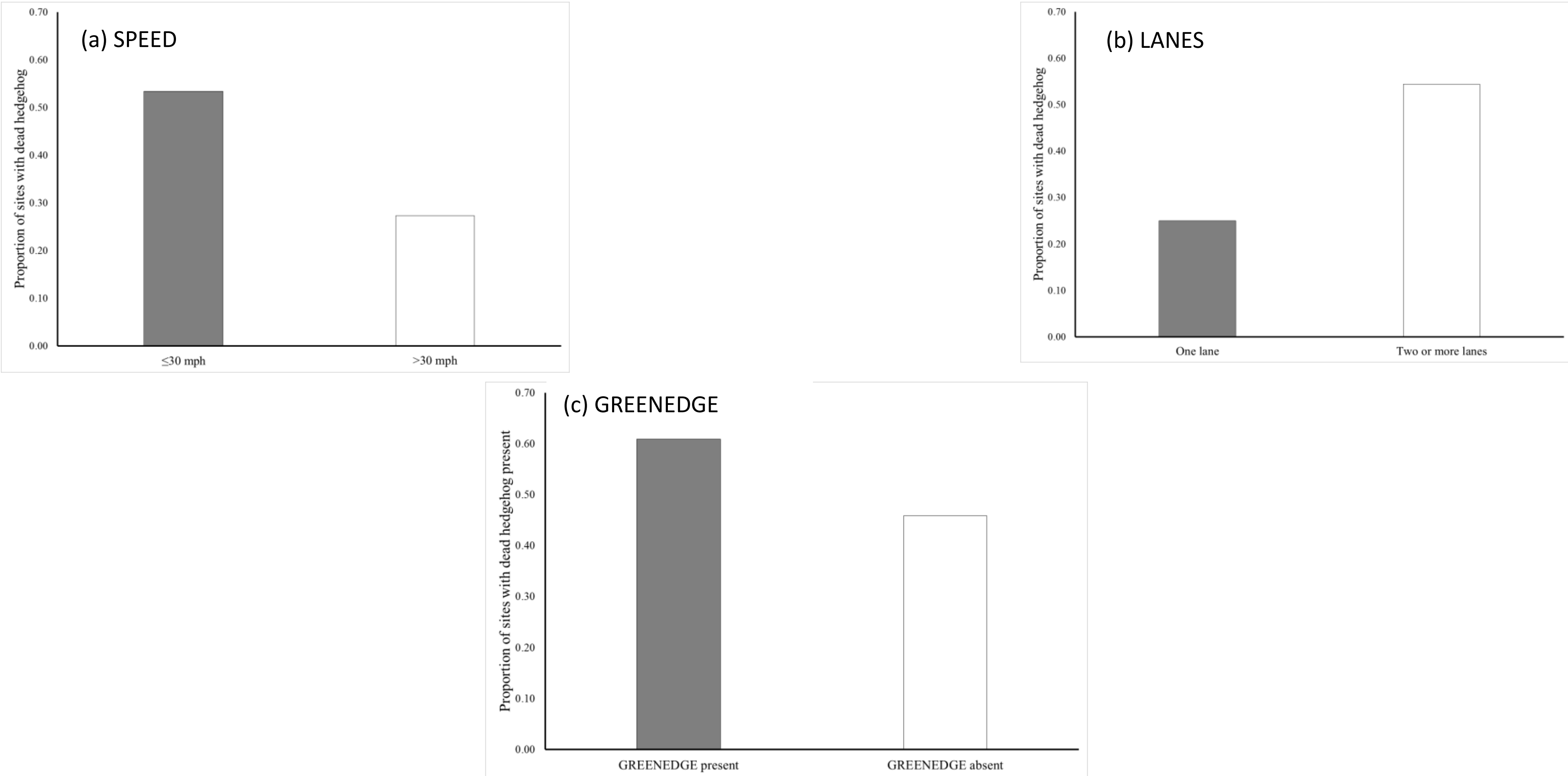


Figure 5.4. Proportion of urban sites where dead hedgehogs were located in relation to: (a) posted speed limit; (b) the total number of lanes of traffic; and (c) the presence / absence of GREENEDGE (e.g. hedgerows, woodland edges) habitats running parallel to the road. Proportions derived from the comparison of 91 locations where dead hedgehogs were recorded and 85 simulated random points on roads in urban areas. Reference levels are indicated by the shaded column.

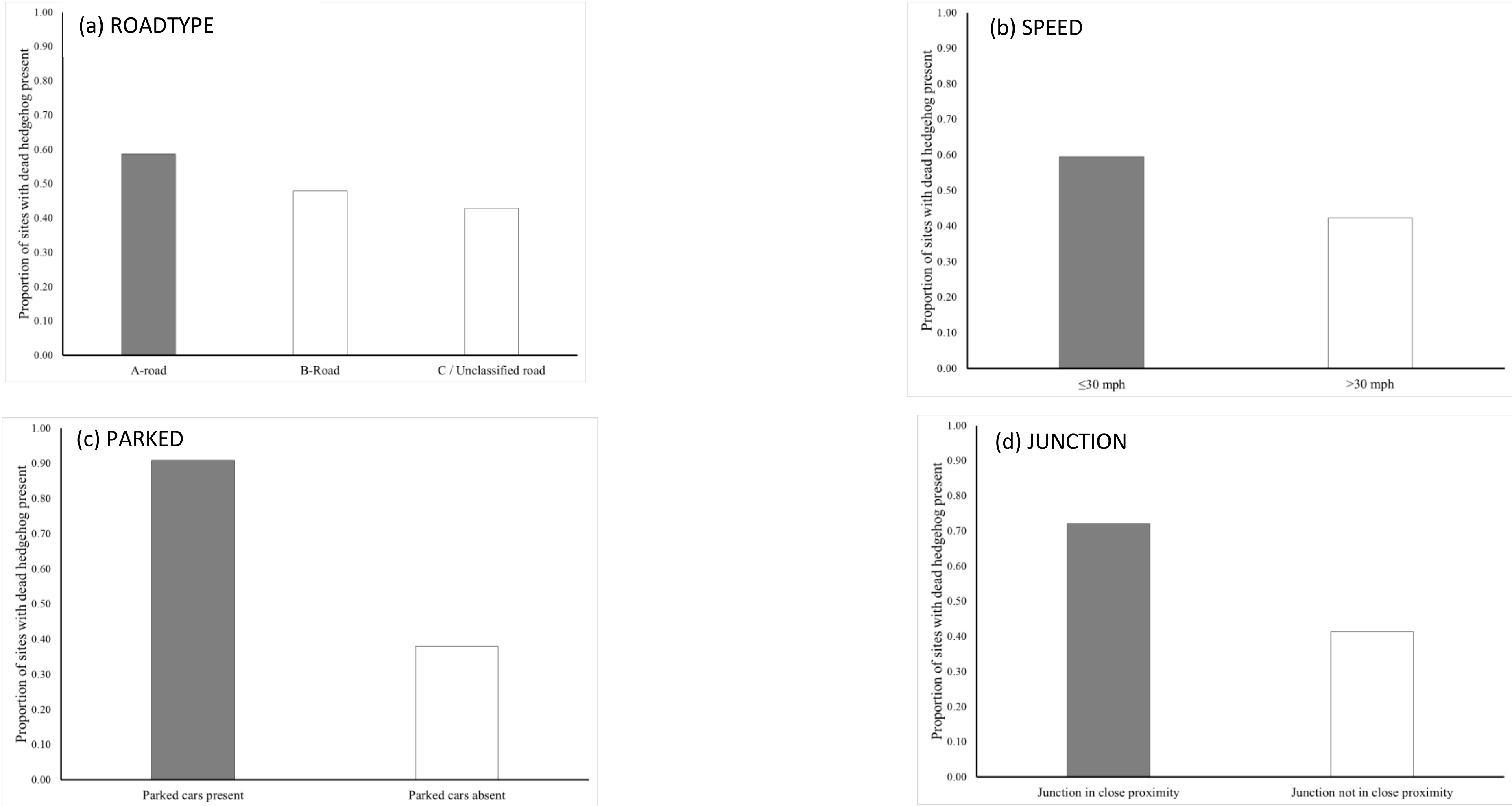


Figure 5.5. Proportion of rural sites where dead hedgehogs were located in relation to: (a) road type; (b) posted speed limit; (c) the presence / absence of parked cars; and (d) proximity to the nearest junction. Proportions derived from the comparison of 58 locations where dead hedgehogs were recorded and 64 simulated random points on roads in urban areas. Reference levels are indicated by the shaded column.

Discussion

Relying on casually reported hedgehog carcasses as in this study could potentially be affected by differences in sampling and / or reporting effort, particularly between urban versus rural landscapes. However, this does not seem to be the case. Overall, the temporal pattern of hedgehog carcasses reported closely matched those reported in other studies (e.g. Haigh *et al.* 2014): the peak in numbers reported in May-July reflects the main breading season when males will be searching for females to mate with, as well as some newly emergent offspring.

Similarly, hedgehog casualties were significantly clustered at all spatial scales, but appeared to be especially associated with urban / suburban areas: 66% of carcasses were recorded in urban / suburban areas even though urban areas in the UK as a whole account for only 6% of total land cover (Rae 2017); this figure is likely to be even lower in Suffolk. This pattern is consistent with the Haigh *et al.* (2014) study, in which carcasses were clustered close to towns, but where selected roads had been searched systematically rather than relying on *ad hoc* sightings as in the present study. In addition, several studies have also reported that hedgehogs are increasingly associated with areas of human habitation (Young *et al.* 2006; Hubert *et al.* 2011; Trewby *et al.* 2014; van de Poel *et al.* 2015). Consequently, the distribution of hedgehog carcasses used in this study appears to reflect both the species' biology, as well as the pattern expected from other studies.

Hedgehog-vehicle collisions in both urban and rural areas appeared more likely to occur on roads with a speed limit of 30mph or less. This is perhaps surprising given that more major roads with higher speed limits do occur in both landscapes. However, this pattern is consistent with the fact that hedgehogs may be less likely to cross major roads (Rondinini and Doncaster 2002), and that speed limits are often reduced in areas of residential housing for human safety. The latter could also explain the observation that rural casualties were significantly more likely to have been reported on A-roads; although these typically have a maximum speed limit of 60 mph, this is often reduced to 20-30 mph in and around villages. Collectively, these results support the idea that areas of human habitation are increasingly favoured by hedgehogs in the UK (Young *et al.* 2006; Trewby *et al.* 2014) and elsewhere (Hubert *et al.* 2011; van de Poel *et al.* 2015).

In addition to speed, hedgehog carcasses in rural areas were also positively associated with the presence of parked cars and proximity to road junctions (see also Haigh *et al.* 2014). Both of these factors are potential hazards that require the driver's attention to be focussed away from the road surface. As such, these sorts of hazards would decrease the likelihood that drivers would be likely to spot hedgehogs on the road and avoid hitting them (this is, of course, made additionally difficult by the species' small size, grey colouration and tendency to freeze). There are also a number of other factors which could divert driver attention in the same way, but which could not be investigated in this sort of study: e.g. prevailing weather conditions, oncoming traffic, pedestrians and driver attention. Quantifying the importance of these factors poses significant challenges, however, as most are very transient in nature. One possible solution may be the use of video-recordings similar to that currently used in the UK hazard perception test that new drivers have to take.

Alternatively, the increased risk close to junctions could be associated with an increased tendency for hedgehogs to cross roads close to these locations. Hedgehogs are considered to be "edge foragers". Consequently, they are likely to follow linear habitats as they move through the landscape. Combined with their tendency to avoid crossing roads, this means that if they were travelling parallel to a road and then encounter a road junction they are faced with the decision of either: (i) turning around and retracing their original trajectory; (ii) turning 90° and following the other road; or (iii) crossing one of the two roads they have encountered (Figure 5.6). As the animal has already exploited the habitat behind them, there is an increased likelihood that they may choose to cross a road.

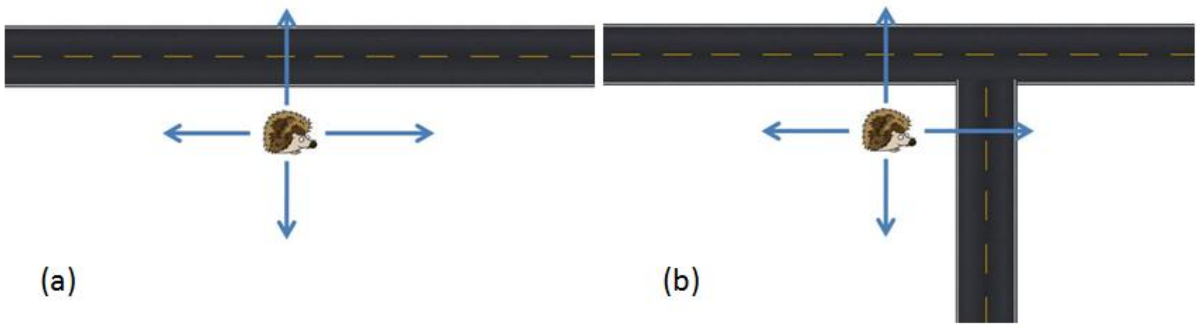


Figure 5.6. Diagram illustrating the possible options available to a hedgehog (a) when following a road and (b) encountering a junction.

The positive association between GREENEDGE habitats (e.g. hedgerows, woodland edges) and the presence of hedgehog carcasses in urban habitats could also be related to how hedgehogs move through the urban environment. Although relatively rare in urban areas, these are the sorts of linear features hedgehogs would be expected to follow as they move through the landscape. However, these sorts of habitats, if very close to the road edge, would obscure the animals from view until they are actually on the road itself.

Overall, this study indicates that hedgehog traffic casualties, although widely distributed in the landscape, tend to be clustered and that carcasses are also commonly associated with features associated with areas of human habitation. This would suggest, provisionally at least, that one possible measure that could be used to help reduce the numbers of casualties would be the use of road signage. In this case, such signage would need to be used to alert drivers to the risk that hedgehogs may be attempting to cross the road, rather than trying to reduce speed, as most casualties are associated with areas where speed limits are already at their lowest. In addition, the provision of street lighting did not seem to have a significant effect on the presence / absence of carcasses, although it was not possible in this study to discriminate between the position of streetlights and the position of carcases on the road (i.e. lights on one side of the road may mean that hedgehogs are more likely to be killed on the unlit side). This requires further investigation.

Further studies also need to address several other key issues. First, although the current study identified that carcasses were clustered, the data were only available for one year. Because of the costs associated with installing and maintaining roads signs, data needs to be collected over several years to ascertain whether such “hotspots” are stable over time. At present, anecdotal data suggests that there are likely to be some roads where large numbers of animals are killed year on year (Baker pers. comm.).

Second, given the goal of any mitigation would be to reduce the numbers of casualties to help reverse population declines, it is important to understand the role of traffic-related mortality within the overall dynamics of hedgehog populations (e.g. Kristiansson 1990; Rautio *et al.* 2016). For example, the absolute numbers of hedgehogs killed does not necessarily represent their relative importance in terms of overall mortality. Hubert *et al.* (2011) indicated that urban hedgehog density may be eight times greater than that seen in rural areas. Consequently, casualty numbers could vary eight-fold even if their relative importance in overall population demographics was identical. This necessitates intensive studies of both urban and rural populations such that observations of the absolute numbers of hedgehogs killed can be quantified at a population level.

Third, studies need to consider the effectiveness of road signs in helping reduce casualties, as other studies have shown them to be ineffective (e.g. Dique *et al.* 2003). This would require a comprehensive experimental study, ideally after the two issues outlined above have been addressed. However, given the potential rate of decline of hedgehog populations in the UK, it is perhaps prudent to consider undertaking such studies now as these other issues would require studies over several years.

Finally, the results of the present study do indicate that some factors, most notably speed but also potentially proximity to areas of human habitation, do significantly impact the likelihood of hedgehogs being killed on roads. Consequently, these factors need to be considered in the analysis of long-term monitoring data such as the *Mammals on Roads* survey since they indicate that transect trajectory can influence the numbers of animals killed.

Acknowledgements

I would like to thank everyone who submitted hedgehog sightings; the Suffolk Wildlife Trust for kindly providing access to the data and David Bennett for assisting with data collection on road and road-side characteristics to help ensure its validity.

Chapter Six

Hedgehogs are commonly killed on roads (e.g. Sleeman *et al.* 1985; Huijser *et al.* 1998; Holsbeek *et al.* 1999; Ludgate and Kelly 2013; see also *Chapter Five*) and appear to avoid crossing major roads (Rondinini and Doncaster 2002). Consequently, it has been widely speculated that roads may act as a barrier to movement leading to the increased fragmentation and isolation of populations and lowering patterns of gene flow (Becher and Griffiths 1998). However, there are currently few data on the extent to which roads, or other barriers, affect hedgehog populations. In this chapter, the effects of landscape composition on the genetic structure of hedgehog populations is examined.

The manuscript presented in this chapter will ultimately be submitted for publication in a peer-reviewed scientific journal. However, the analyses of these data have proved challenging, such that the results presented in this thesis should be considered preliminary.

My contribution to the work.

I designed the project in discussion with Philip Baker. All analysis was my own with advice from Mafalda Costa. The manuscript was written by me with input from Philip Baker and comments from Isa-Rita Russo and Mafalda Costa.

Genetic diversity, population structure and landscape connectivity of hedgehogs (*Erinaceus europaeus*) in a rural landscape

Keywords: *Fragmentation, Gene flow, Mantel tests, Isolation by distance, Isolation by barrier, Isolation by resistance, heterozygote deficiency, wildlife translocations*

Abstract

Globally, habitat modification and fragmentation are exerting pressures on a broad range of taxa. To help understand how species are responding to this and what, if any, mitigation measures are needed necessitates a better understanding of how landscape composition affects wildlife populations. The aims of this study were to: (i) assess the genetic diversity of hedgehogs (*Erinaceus europaeus*) in Southern England; (ii) estimate the number of genetic clusters within the study area; and (iii) conduct preliminary analysis to identify features affecting gene flow.

Genetic heterozygosity was low, but was comparable to other populations within Europe. No discrete genetic clusters were identified indicating an absence of barrier effects associated with natural (e.g. rivers) and anthropogenic (e.g. motorways) features. However, gene flow appeared to be promoted by motorways, and hindered by the built environment. There is no clear explanation for the former, but the latter is consistent with observations from previous studies.

Introduction

Globally, vertebrate populations are declining with approximately 25% of mammal populations considered threatened with extinction (Schipper *et al.* 2008; WWF 2016). Recent changes in agricultural practices have greatly modified landscapes across Europe and the UK (Robinson and Sutherland 2002; Donald and Evans 2006; Maron and Fitzsimons 2007; Rounsevell and Reay 2009). Intensive agricultural production is associated with a range of deleterious activities, but is also accompanied by the increased fragmentation of habitats either by the removal of linear habitats such as hedgerows (Robinson and Sutherland 2002); the creation of less suitable matrix habitats and the increased construction of transport networks. Habitat fragmentation can both create and isolate sub-populations and reduces the size of remaining patches of natural and semi-natural habitats, thereby diminishing the area each sub-population can occupy (Seiler 2001). As such, modified and fragmented landscapes are major threats to global biodiversity across a broad range of taxa (e.g. Fahrig 2003; DeClerck *et al.* 2010; Pardini *et al.* 2010; Sodhi *et al.* 2010; Tabarelli *et al.* 2010; Haddad *et al.* 2015; Wilson *et al.* 2016).

Landscape connectivity is the interaction between species' movement and landscape structure (Taylor *et al.* 1993) and which therefore influences patterns of dispersal and gene flow. Barriers to connectivity may include physical obstacles such as roads, rivers and mountains (e.g. Cozzi *et al.* 2013; Caplat *et al.* 2016; Linnell *et al.* 2016; Trouwborst *et al.* 2016), but also homogenised simplified habitats. The latter acts as a barrier as unfavourable or poor-quality habitat may not provide sufficient food or cover against predators, especially when the distance between suitable habitat patches is greater than can be traversed in one go (Arnold *et al.* 1993; Rösch *et al.* 2013). As such, understanding how habitat fragmentation and connectivity affect movement and dispersal is fundamental for the development of effective conservation strategies (Lawton 1993).

The discipline of landscape genetics combines knowledge of landscape ecology with population genetics and is a valuable tool in assessing the relationship between landscape composition and the genetic structure of populations (Richardson *et al.* 2016). Small, isolated populations with little to no connectivity with neighbouring populations would be expected to exhibit lower levels of gene flow than larger, well-connected populations (Slatkin 1987). This may then, in turn, lead to reduced genetic diversity and a lower effective population size as a consequence of genetic drift and / or Allee effects (Frankham 1996; Stephens *et al.* 1999; Courchamp *et al.* 2008). Such populations are at risk of inbreeding depression and the accumulation of deleterious mutations; consequently, they have reduced evolutionary potential to adapt to environmental change, leading to an increased risk of extirpation (Lande 1995; Frankham 1996; Saccheri *et al.* 1998; Charlesworth and Charlesworth 2000; Frankham 2005).

The West European hedgehog (*Erinaceus europaeus*) is found throughout Western Europe, including the UK, Ireland and Scandinavia (Santucci *et al.* 1998). The species is thought to be in decline across the UK (Wilson and Wembridge 2018), potentially as the result of a decline in the changing availability of invertebrate prey in rural landscapes (Hof and Bright 2010a, b) in combination with the increased abundance of an intra-guild predator, the Eurasian badger (*Meles meles*) (Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012; Judge *et al.* 2014, 2017; Parrott *et al.* 2014; Trewby *et al*. 2014; van de Poel *et al.* 2015), but also potentially because of increased fragmentation arising from the loss of hedgerows (Moorhouse *et al.* 2014) and the growth of the national road network (Rondinini and Doncaster 2002). Additional natural barriers may include mountains and rivers (see Braaker *et al.* 2017).

Although habitat fragmentation has often been postulated to have an effect on hedgehog populations, based in part on the large numbers of animals seen dead on roads (e.g. Huijser *et al.* 1998; Holsbeek *et al.* 1999; Haigh *et al.* 2014; Wembridge *et al.* 2001), there are currently few data on whether these effects exist and, if they do, their magnitude (Becher and Griffiths 1998; but see Braaker *et al.* 2017). For example, even major motorways in the UK are frequently bisected by features (e.g. minor roads, footbridges) that could facilitate hedgehog dispersal movements. In addition, many are also fitted with badger tunnels to allow the movement of this species; theoretically, hedgehogs may be able to use these, but evidence suggests that they are likely to avoid them because of the risk of predation (Petrovan pers. comm.). In fact, most genetic studies involving *E. europaeus* focussed on historical movements / colonisation events (e.g. Bolfíková *et al.* 2013) or the potential hybridisation zone with *Erinaceus roumanicus* and *Erinaceus concolor* (Seddon *et al.* 2001; Bolfíková and Hulva 2012).

Analysis of the effects of landscape structure on population genetics typically utilises three main approaches: isolation by distance (IBD); isolation by barrier (IBB); and / or isolation by resistance (IBR) (e.g. Ruiz-Gonzalez *et al.* 2015). These different approaches are based on the premise that gene flow is a function of: the Euclidean distance between individuals (IBD); the distance on opposite sides of a barrier (IBB); or resistance throughout the landscape (IBR). Most recently, studies have tended to focus on IBR approaches, with resistance maps created as a “whole” (i.e. all landscape features considered collectively e.g. Braaker *et al.* 2017). While this can make intuitive sense, such maps are usually based on "expert" opinion because the number of possible combinations of individual features is prohibitive (Wade *et al.* 2015; see Zeller *et al.* (2012) for a review). Consequently, features that are having an impact may be missed or are classified incorrectly. An alternative approach is to investigate each feature separately and use the results to build up the “resistance model”, although this can be time-consuming given the number of different analysis that need to be conducted. However, it has the advantage of retaining focus on the feature(s) exerting the largest influence on gene flow. Furthermore, this approach is able to identify the degree of resistance each feature is imposing (Marrotte *et al.* 2014).

In this study, genetic samples collected from hedgehogs in Southern England either side of a potential barrier to movement (six-lane motorway) were used to: (i) assess overall genetic diversity; (ii) estimate the number of genetic clusters within the study area; and (iii) identify whether any landscape features appeared to be negatively impacting patterns of gene flow.

Methods

Study area

Hedgehog samples were collected from a region of approximately 7,000 km^2 in Southern England stretching from Bristol in the west to Slough in the east and Southampton in the south to Cirencester in the north (Figure 6.1). This is a predominantly rural landscape, dominated by a combination of arable and pastoral farming, but which also contains a range of villages, towns and several major urban areas, the largest being Bristol, Reading, Swindon, Bath, Newbury and Basingstoke. The study area is relatively flat with no mountainous terrain. This area was selected as it is split by the M4 motorway running east to west; this was the major focus of this study. As with most of the UK, there is an extensive network of rivers, the most expansive is the River Thames, which is over 50m wide in Reading.

Sample collection

Samples were collected from the tissue of dead animals (predominantly road-killed individuals and animals which had died after being submitted to wildlife rehabilitation hospitals) and buccal swabs from live animals (predominantly animals in wildlife hospitals, but also some individuals caged-trapped under licence from Natural England: 20130866-0-0-0-2, 20131240-0-0-0-1). Swabs were taken with Regular Tip 4N6FLOQSwabs™ (Thermo Fisher Scientific); these are individually packaged and have a break-off head to ensure maximum sterilisation and separation of samples. Road-kill samples were collected opportunistically (i.e. when reported by members of the public). Tissue samples were stored in 100% ethanol; swabs were stored in air tight 1.5ml micro-tubes, as recommended by the manufacturer. All samples were stored individually and kept at -20^{o}C until DNA extraction took place.

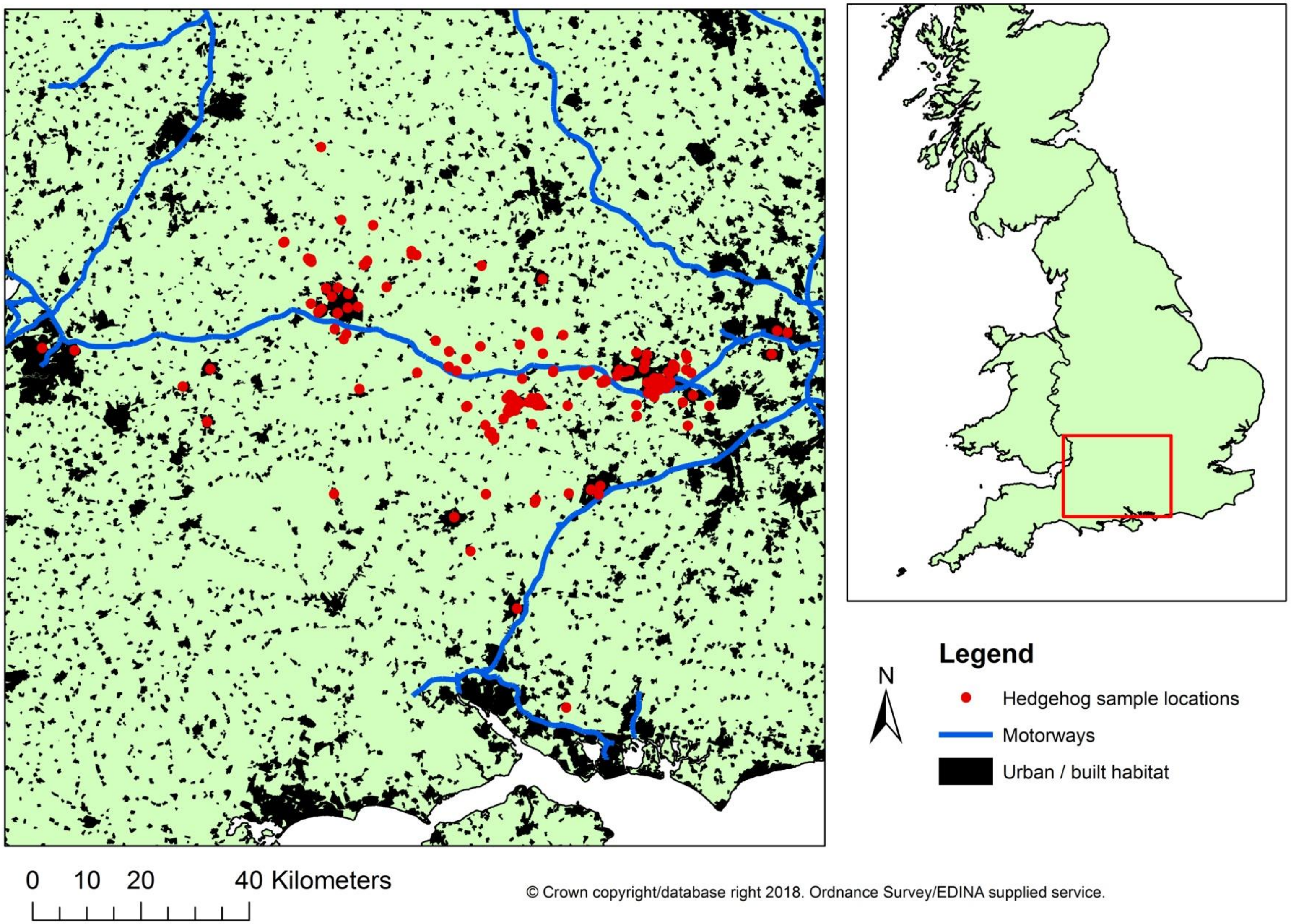


Figure 6.1. Map of the study area showing the distribution of hedgehog samples with reference to motorways and built / urban areas.

DNA extraction and microsatellite genotyping

Genomic DNA was extracted using the DNeasy Blood and Tissue kit (Qiagen) following the manufacturer's instructions. Initially, eleven primers (EEU1, EEU2, EEU3, EEU4, EEU5, EEU6, EEU12, EEU36, EEU37, EEU43, EEU54) were used as developed by Becher and Griffiths (1997) and Henderson *et al.* (2000).

Polymerase chain reactions (PCRs) were conducted to select and amplify each locus to enable fragment analysis. PCR products were labelled with 6-FAM or HEX M13 tag oligonucleotides as described by Costa *et al.* (2012). PCR reactions of 10 µl contained 2 µl of DNA extract, 1X PCR Buffer (Invitrogen), 3 mM $MgCl_2$, 0.2 mM of each dNTP (Promega), 0.5 µM of each primer plus 0.5 µM of labelled M13 tag oligonucleotide, 0.5 µg / µl BSA (New England Biolabs), and 0.75 U of GoTaq® G2 Flexi DNA Polymerase (Promega) (Invitrogen). Singleplex PCR's were conducted using the Veriti 96-well Thermal Cycler (Applied Biosystems). The PCR protocol preformed was: initial denaturation cycle of 95^{o}C for 2 minutes, followed by 35 cycles of 94^{o}C for 45 seconds, annealing temperature (Ta) for 1 minute, and 72^{o}C for 45 seconds finished with a final extension of 72^{o}C for 20 minutes. Ta was 60^{o}C for all primers, except EEU43 and EEU54 where it was 50^{o}C.

Fragment analysis was conducted by the Medical Research Council Protein Phosphorylation and Ubiquitylation Unit DNA Sequencing and Services (www.dnaseq.co.uk) with an ABI 3730 sequencer using Gene-Scan™ 400 HD ROX™ size standard (Applied Biosystems). Subsequent data were analysed using Gene Marker v1.91 (Soft Genetics; Hulce *et al.* 2011). Genotyping was validated by re-amplification and re-analysis of *c.* 32% of the samples (tissue and swab) for each locus.

Microsatellite genetic diversity

For each locus, microsatellite variation was assessed using the following metrics: the number of alleles per locus (N_A); the number of alleles per locus with a frequency greater than 5% (N_A95); the number of effective alleles per locus (N_E); observed (H_O) and unbiased expected (UH_E) heterozygosity and inbreeding coefficient (F_{IS}). These were derived using GENALEX v6.5 (Peakall and Smouse 2012), FSTAT v2.9.3 (Goudet 1995) and R v3.4.3 (R Core Development Team 2018) using the package GSTUDIO (Dyer 2016). Deviation from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were assessed using Gene Pop v4 (Rousset 2008). The presence of null alleles was checked for using MICROCHECKER v 2.2.3 (Van Oosterhout *et al.* 2004).

Population structure

STRUCTURE v2.3.4 (Pritchard *et al.* 2000; Falush *et al.* 2003) was used to estimate the likely number of genetic clusters (*K*) present in the study area. Ten independent runs were conducted using the admixture and correlated allele frequency models with 10^5 burn-in runs followed by 10^6 Markov chain Monte Carlo (MCMC) iterations. In addition, Snapclust within the package ADEGENET (Jombart 2008) was used in R to assign samples to populations. In brief, Snapclust is a maximum likelihood approach to genetic clustering which uses a two-step approach; first, a 'good' initial starting point is found using a distance-based approach; second, likelihood optimization is undertaken using the expectation-maximization algorithm.

ADEGENET was also used to identify the optimal number of populations in the data using the Akaike information criterion (AIC), AIC corrected for small sample size (AICc), Bayesian information criterion (BIC), and Kullback–Leibler information criterion (KIC) values. The package ADE4 (Dray and Dufour 2007) was used to conduct a principal components analysis (PCA) and ADEGENET was used to visualise the results.

Landscape influence on gene flow

To investigate which habitat / landscape feature(s) influenced gene flow within the hedgehog population, ten resistance maps (resistance in : out of the feature: 1:2, 1:5, 1:10, 1:50 1:100, 2:1, 5:1, 10:1, 50:1 100:1) were created for each of nine landscape features: minor roads, 'B' roads, 'A' roads, motorways, railway lines, rivers, lakes, woodland and built / urban areas. Data were obtained from the OS Meridian™ 2 data set (Ordinance Survey 2016). Initially, features were processed in ArcMap 10.1 (ESRI 2012) to select and export the area of interest. The resultant 'layers' were processed in R to create resistance maps using the package RASTER (Hijmans 2017).

GDISTANCE (van Etten 2017) was used to create a point-to-point least cost path (LCP) matrix for each resistance map (N = 90). Mantel tests were ran, using the package VEGAN (Oksanen *et al.* 2018), comparing the resultant matrices with the Euclidean genetic distance between points. The most important feature studied influencing gene flow was identified by the strongest correlation between the matrices; subsequently a partial Mantel test was run on the remaining features controlling for the major feature identified. Results were exported to Excel and processed in GGPLOT2 (Wickham 2009) for visual representation.

Results

A total of 289 hedgehog samples were obtained from tissue (N = 240) and buccal swabs (N = 49). One locus (EEU36) was found to be monomorphic and was subsequently dropped from further analyses; all other loci were polymorphic. A subset of 199 samples that had complete location and loci data available was used for all analysis.

Measures of genetic diversity are presented in Table 6.1. The number of alleles per locus ranged from 4 to 11 (average 8.7). Expected heterozygosity ranged from 0.314 to 0.831, with a significant deficit in 6 out of the 10 loci. The inbreeding coefficient F_{IS} was positive, but not significant, for the overall population after Bonferroni correction. F_{IS} was not significant for any loci, nor was linkage disequilibrium identified among any loci after Bonferroni correction. A significant departure from HWE was detected ($P < 0.05$), after Bonferroni correction, for two loci (EEU2 and EEU54H).

Table 6.1. Microsatellite genetic diversity for 199 hedgehog samples from Southern England. $\boldsymbol{N_A}$ = number of alleles per locus; $\boldsymbol{N_A95}$ = the number of alleles per locus with a frequency greater than 5%; $\boldsymbol{N_E}$ = number of effective alleles per locus; $\boldsymbol{H_O}$ = observed heterozygosity (* denotes significant departure from Hardy-Weinberg equilibrium; values in bold denote significant heterozygote deficit); $\boldsymbol{UH_E}$ = unbiased expected heterozygosity; $\boldsymbol{F_{IS}}$ = inbreeding coefficient; ***Null*** = the presence of null alleles (values in bold indicate significant level). **SE** = standard error. All significance values after Bonferroni correction at $P < 0.05$.

Locus ID	N_A	N_A95	N_E	H_O	UH_E	F_{IS}	*Null*
EEU1	8	3	2.633	**0.543**	0.622	0.128	**Yes**
EEU2	10	6	4.545	**0.724***	0.782	0.075	Yes
EEU3	10	4	3.584	0.673	0.723	0.069	No
EEU4	10	6	5.840	**0.744**	0.831	0.105	Yes
EEU5	8	5	4.252	**0.688**	0.767	0.102	Yes
EEU6	10	4	4.201	0.719	0.764	0.059	No
EEU12H	4	2	1.818	0.452	0.451	- 0.002	No
EEU37H	8	2	1.455	0.271	0.314	0.135	**Yes**
EEU43H	11	5	3.965	**0.673**	0.750	0.102	Yes
EEU54H	8	3	2.754	**0.543***	0.639	0.150	**Yes**
All	87	40	3.505	0.603	0.664	0.092	-
SE	-	-	-	0.048	0.052	-	-

Population structure

Analyses using STRUCTURE did not indicate the presence of any discrete hedgehog populations / genetic clusters within the study area. Similarly, analysis of Snapclust using KIC and BIC (Figures 6.2c and 6.2d respectively) also indicated a single population. However, both AIC (Figure 6.2a) and AICc (Figure 6.2b) indicated the presence of five and three populations, respectively. Given the discrepancy in the Snapclust results, a principal components analysis was conducted; this showed that no discrete populations could be identified (Figures 6.2e-f), again indicating only a single population in the study site. Finally, the proposed populations from the AICc results (K = 3) were plotted on a map for visual inspection: individuals from all potential sub-populations were highly integrated with one another, again indicating the absence of any discrete populations (Figure 6.3).

Landscape influence on gene flow

IBD analysis indicated a significant (P = 0.010) positive correlation (i.e. samples further away were more likely to be dissimilar than samples closer together: Figure 6.4). The results of the resistance Mantel tests indicated that motorways aided gene flow, with the strongest correlation ($r = 0.162$, $P < 0.001$) for resistance of 1 in the feature and 100 outside (Figure 6.5a). The partial Mantel test, controlling for the aforementioned motorway resistance, showed built / urban habitat to restrict gene flow with the strongest correlation ($r = 0.139$, $P = 0.002$) for resistance of 100 in the feature and 1 outside (Figure 6.5b).

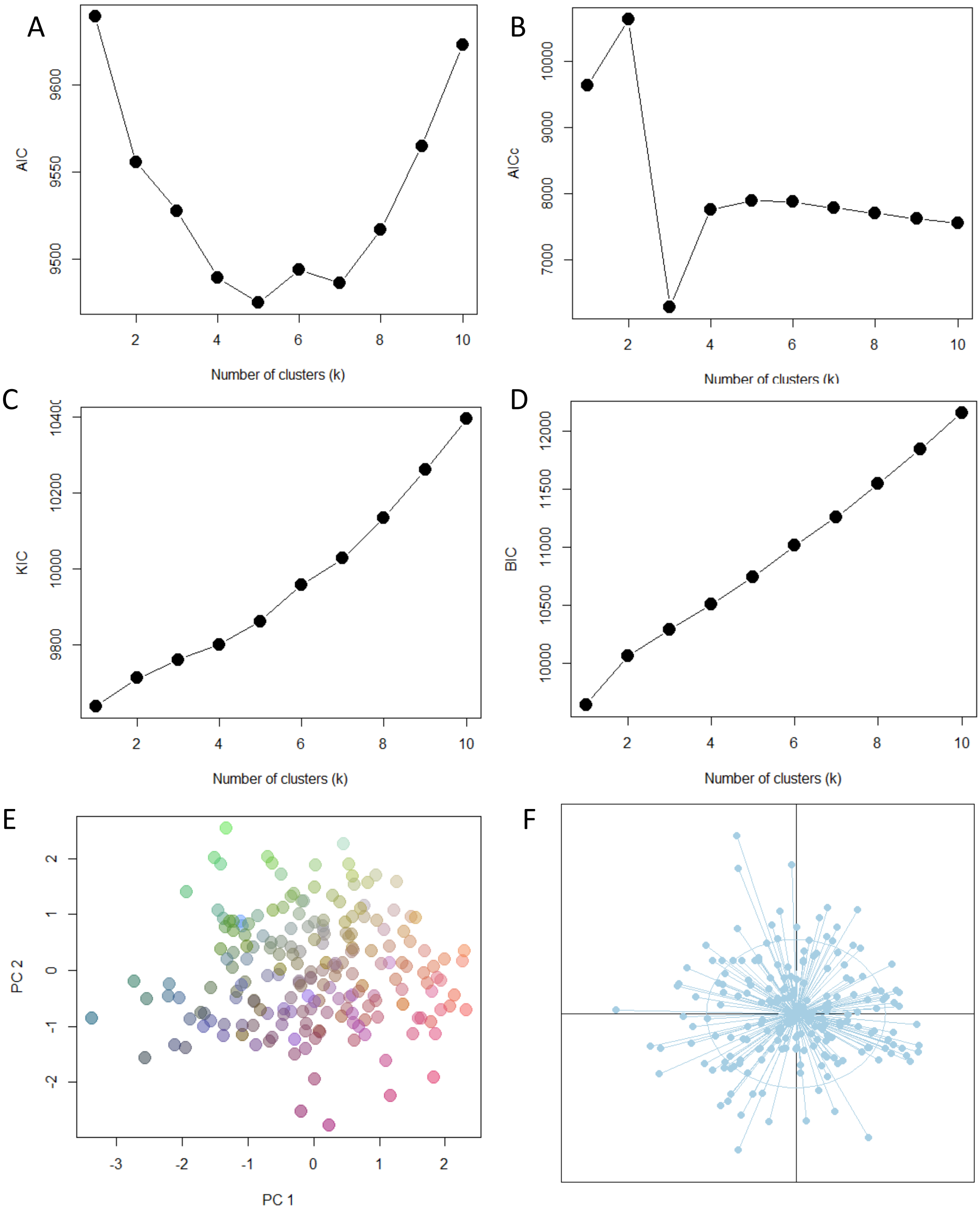


Figure 6.2. Graphical representation of genetic clustering analysis on hedgehogs from Southern England: (a) AIC, (b) AICc, (b) KIC, and (d) BIC analyses for identifying the likely number of populations in the study site in Southern England. Data were analysed using ADEGENET. (e) Colour plot and (f) scatter plot of the principal component analysis conducted in ADE4.

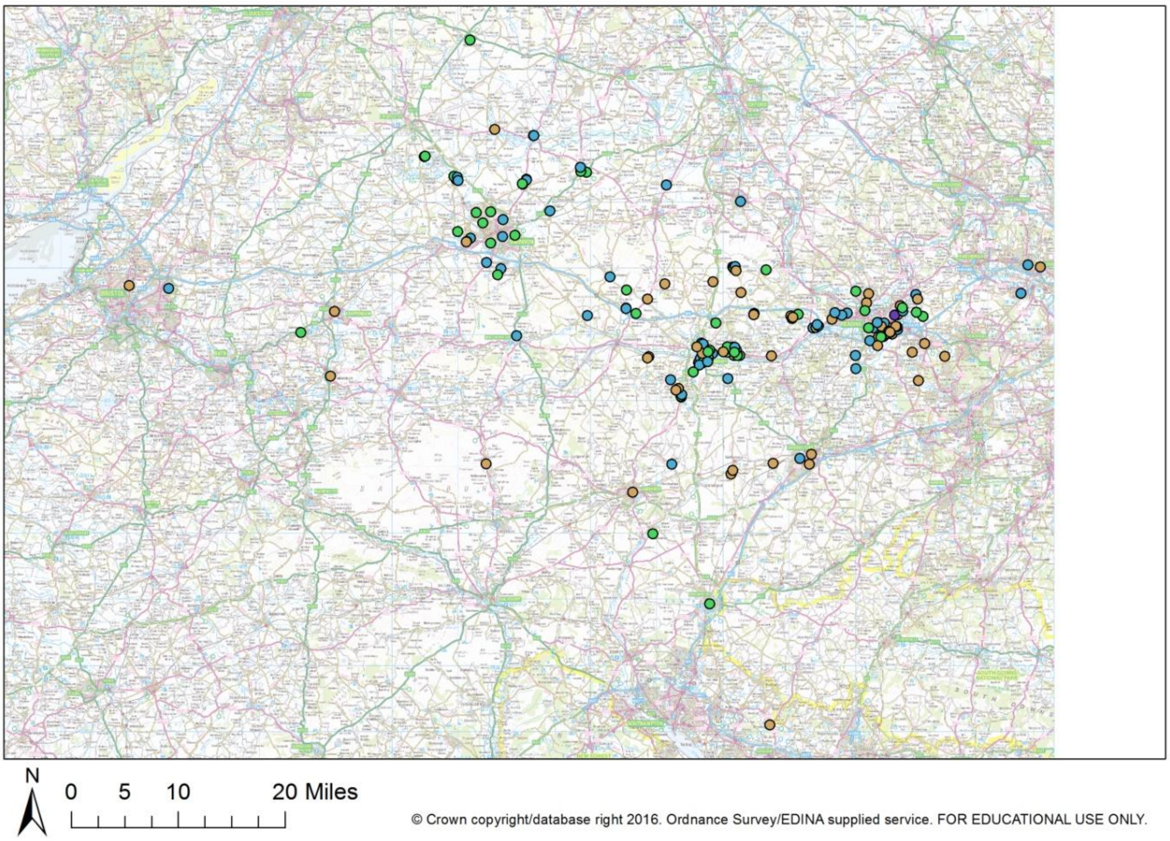


Figure 6.3. Distribution of the 199 hedgehogs samples analysed in Southern England. Colours indicate the provisional assignment of each animal to one of three potential sub-populations as determined in ADEGENET using Snapclust.

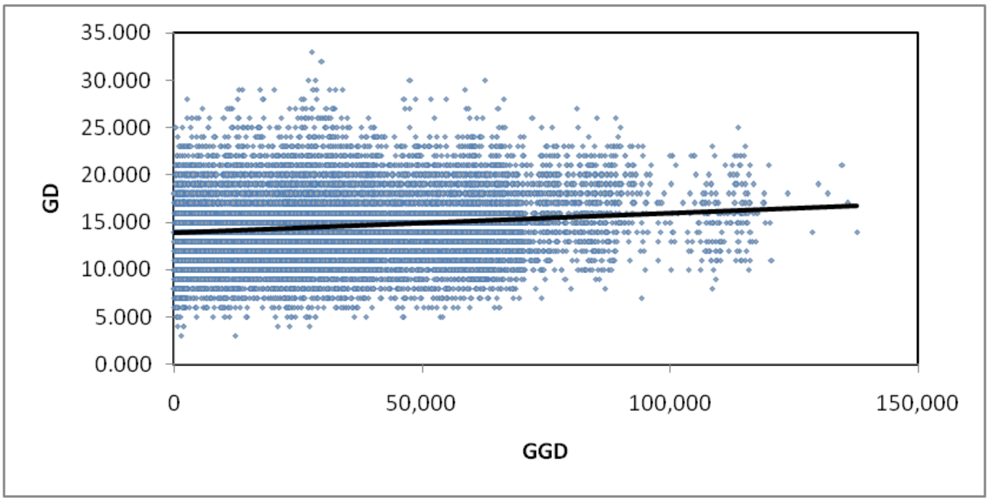


Figure 6.4. Results of a Mantel test between geographic (GGD) distance (m) and genetic (GD) distance for the population of hedgehogs in Southern England. Diamonds represent each sample; solid line is the fitted trend line ($R^2 = 0.018$).

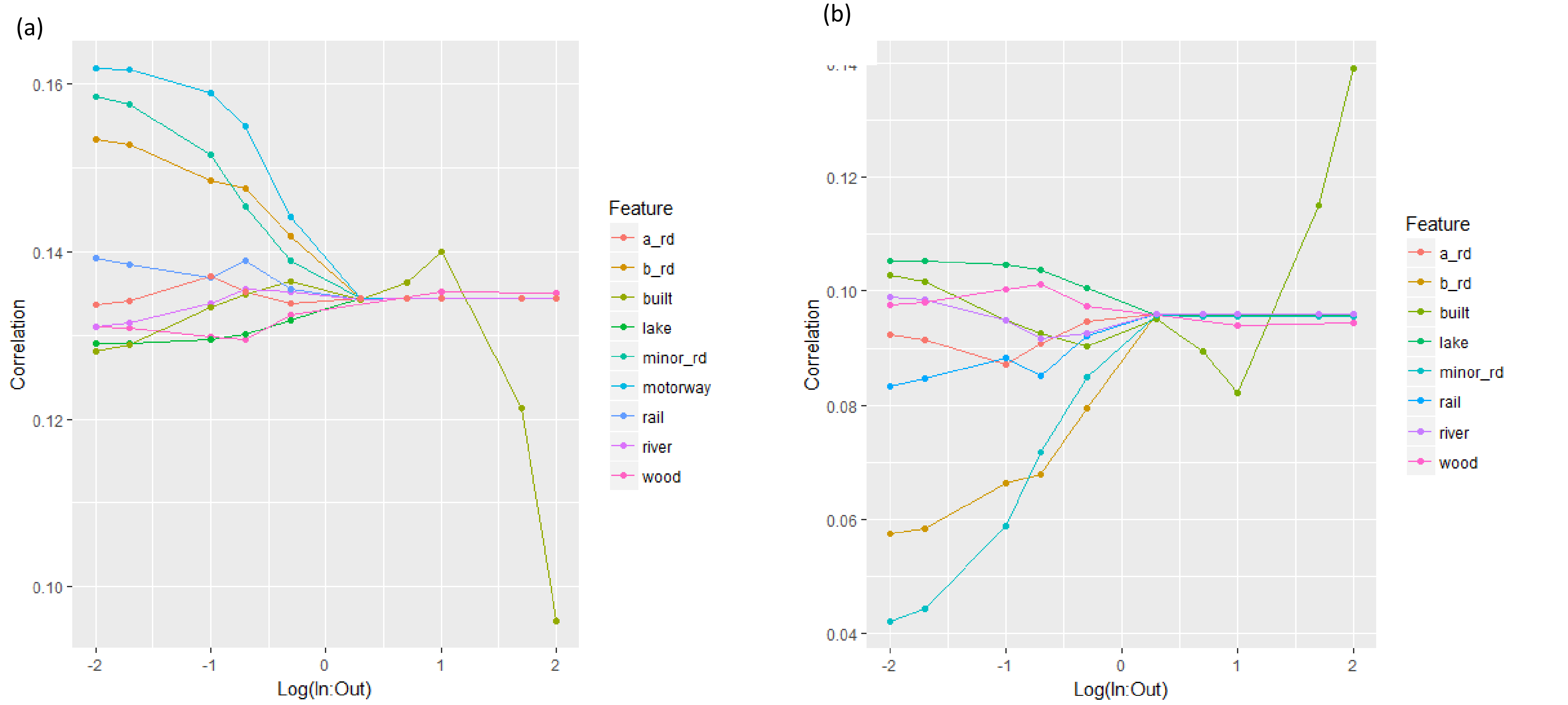


Figure 6.5. Graphical representation of the results of (a) the overall Mantel test and (b) the partial Mantel test controlling for the effect of motorways with resistance of 1 in and 100 outside feature. Landscape features: *minor_rd* = minor roads; *b_rd* = 'B' roads; *a_rd* = 'A' roads; *motorway* = motorways; *rail* = railway lines; *river* = rivers; *lake* = lakes; *wood* = woodland / forest; *built* = built / urban areas. Points on the left of the graph represent low In and high Out feature resistance; the higher a point on the graph the stronger the correlation between Euclidean genetic distance and LCP matrices.

$$y - axis = \text{correlation between Euclidean genetic distance and LCP matrices} \qquad x - axis = \log\left(\frac{\text{Inside feature resistance}}{\text{Outside feature resistance}}\right)$$

Discussion

The data collected and analysed in this study indicate a significant heterozygote deficit for 6 out of the 10 loci tested. There are several possible, nonexclusive, reasons for this. First, null alleles (the presence of which was detected in 7 out of 10 loci) appear to be relatively common in both *E. europaeus* (Bolfíková and Hulva 2012; Bolfíková *et al.* 2013; Braaker *et al.*2017) and *E. roumanicus* (Bolfíková *et al.* 2017) and may be the result of the high homozygote frequency in the data. While null alleles have been shown to slightly decrease the accurate assignment of individuals to genetic clusters, the number of loci has been shown to be more influential. Consequently, all loci were used in the current analyses; the average number of alleles per locus detected (8.7) is within the range reported in other studies (4.6 - 13.4: Braaker 2017; Bolfíková and Hulva 2012 respectively).

Second, decreased heterozygosity may also arise from inbreeding. However, the species appears to be promiscuous, with multiple-paternity litters having been detected (Moran *et al.* 2009), and the increased presence of males in samples of road-killed individuals is also indicative of the fact that they appear to travel widely (at least at a local level) in search of mates. These factors would act to limit inbreeding. In this study, F_{IS} was not significant for any locus, and the F_{IS}, N_A, H_O and H_E values recorded are comparable to other studies of *E. europaeus* throughout Europe and New Zealand (Becher and Griffiths 1998; Henderson *et al.* 2000; Bolfíková and Hulva 2012; Bolfíková *et al.* 2013; Braaker *et al.*2017), and for *E. roumanicus* in central Europe and the Balkans (Bolfíková 2017).

Lastly, overall heterozygosity in a population may decline if that population is comprised of two or more subpopulations each with independent allele frequencies (the Wahlund effect). This might have been expected in this study given the large geographical area sampled and the presence of potential barriers to gene flow. However, no subpopulations were detected. Overall, therefore, further investigations into the heterozygote deficit observed are warranted.

Population structure

The absence of any structure in this data set is somewhat surprising given that this has been recorded in other studies (Becher and Griffiths 1998, Braaker *et al.* 2017: but see Bolfíková and Hulva 2012) and that hedgehogs are perceived to have low dispersal rates (e.g. Reeve 1994), although there are very few data on patterns of dispersal in this species. However, the study site itself did not appear to contain any major natural barriers: those rivers present were within the size range that hedgehogs would potentially be able to cross (Morris 2006). In addition, the M4 motorway, which bisected the study area is itself intersected by approximately seven major (A road) and 43 minor (B or C roads) between Slough and Bristol. All of these roads potentially represent sites where hedgehogs may be able to disperse across the motorway.

Alternatively, given that the motorway itself was only constructed in the 1960s, it may simply be that populations have not been separated long enough to detect any effect. This does, however, seem unrealistic given that Braaker *et al.* (2017) were able to detect an effect of a 4-lane highway in Zurich, Switzerland.

One further potentially confounding factor that also requires further investigation is the role of wildlife rehabilitators in moving hedgehogs. Hedgehogs are commonly admitted to wildlife hospitals in the UK, with estimates ranging from 40,000-70,000 admissions annually (Molony *et al.* 2007; Grogan and Kelly 2013) although the actual number may be much higher. Although wildlife rehabilitators typically work under the general guideline that animals should preferentially be released at the point where they were found, provisional analysis of data collated from wildlife hospitals indicate that this often does not happen with hedgehogs (Bearman-Brown pers. comm.), and that they are likely to be released elsewhere; this is especially likely to be true for hedgehogs because of the large numbers of orphaned juveniles that are received and hand-reared. In fact, one of the hospitals that contributed to the current study was itself involved in a collaboration with a farm on the other side of the M4 motorway. As such, these sorts of facilitated movements could help overcome the barrier effects of major roads, if such effects exist. The numbers of hedgehogs admitted to wildlife hospitals and their release protocols, therefore, require further investigation.

Impact of landscape structure on gene flow

Motorways would generally be expected to act as a barrier to movement (Rondinini and Doncaster 2002; Braaker *et al.* 2014, 2017) but in this study appeared to positively affect gene flow. The reason for this is unclear and difficult to explain.

However, once the effects of motorways were controlled for, the built / urban environment appeared to restrict gene flow; no other landscape features appeared to exert any effect. This is consistent with the observations of a wide range of studies that hedgehogs are increasingly favouring areas of human habitation (Young *et al.*2006; Hubert *et al.* 2011; Hof *et al.* 2012; Judge *et al.* 2014, 2017; Parrott *et al.* 2014; Trewby *et al*. 2014; van de Poel *et al.* 2015; Pettett *et al.* 2017a), these possibly acting as a refuge habitat to escape threats present in agricultural habitats, including the presence of badgers. If this is the case, this could suggest that populations of hedgehogs in villages, towns and cities may become more isolated from one another in the future. As such, further studies investigating patterns of dispersal in agricultural landscapes are urgently required.

In summary, there was no evidence of habitat fragmentation leading to the genetic structuring of the hedgehog population in Southern England. This could be due to the fact that, although motorways are perceived by humans to be major obstacles to hedgehog dispersal, this may not actually be the case. Studies of hedgehog behaviour in the vicinity of motorways and observations of potential crossing points (including badger tunnels) would provide valuable information in this context. There was some evidence in support of the idea that areas of human habitation may be acting as a refuge habitat for hedgehogs but that dispersal between these is problematic; studies of dispersal behaviour in agricultural landscapes are therefore warranted. In addition, investigations into the release protocols of wildlife rehabilitation hospitals are also merited, as these might be moving large numbers of hedgehogs around the countryside.

Acknowledgements

I thank Gill Lucraft for supplying many hedgehog carcasses and assisting with testing various buccal swabs and all the people who reported sightings of dead hedgehogs. I am grateful to Rodney Dyer, Mike Bruford and Isa-Rita Russo for advice on analysis; Mafalda Costa for assistance with laboratory and analytical techniques and Mafalda and Isa-Rita for providing comments on earlier versions of this chapter

Chapter Seven

Throughout the preceding chapters, reference has been made consistently to the fact that hedgehog populations in the UK appear to be declining. Regardless of the underlying reasons, this decline is dependent on changes in fecundity and survival rates. Such demographic data can be incorporated into matrix models to help identify metrics that can inform the development of conservation strategies. In this chapter, population modelling using parameter values extracted from the literature is used to illustrate our current understanding of hedgehog population demography.

My contribution to the work

I was responsible for the design of the project, in discussion with Philip Baker. All analyses were mine.

Population modelling of West European Hedgehogs (*Erinaceus europaeus*): sensitivity and uncertainty

Keywords: *Leslie-matrix, population demographics, sensitivity analysis*

Abstract

The management and conservation of animal populations requires an understanding of their population demographics, how these change over time and the factors associated with these changes. Age-structured matrix population models are one method to aid understanding and may be used to help set priorities for future work. Here, such models were used to help assess the quality and accuracy of data currently available on hedgehogs (*Erinaceus europaeus*) and determine which demographic variables were most influential on their population growth. The results indicate a lack of data in the literature and those that are available do not appear to correlate with the current population trends of ongoing monitoring programmes. Additional research is, therefore, required to update our knowledge of basic demographic data to enable the effective conservation of hedgehog populations.

Introduction

The management and conservation of animal populations requires an understanding of their population demographics, how these may be changing over time and the factors associated with these changes. The preceding chapters in this thesis have highlighted that hedgehogs appear to be declining in the UK, although the magnitude of this decline is uncertain. In part, this uncertainty is related to possible limitations associated with the field methods used to collect these data and how these data have been analysed. In addition, a number of factors that would be expected to negatively affect hedgehog populations can be identified (see *Chapter One*), but the relative importance of these is not known; in particular, there is no understanding of how these factors may affect key demographic parameters. Consequently, it is important to consider other possible approaches that may be useful in helping fill these knowledge gaps.

Age-structured matrix population models have been used widely in wildlife management and conservation (e.g. Zeigler *et al.* 2013; Martínez and Martín 2017; Finch *et al.* 2018), in part because they offer a range of advantages over conventional field-based studies. First, simple matrix models require relatively little information (age-specific mortality and fecundity rates, and population age structure) such that it is potentially possible to construct these models based on information already available in the published literature. Second, once constructed, such models enable a range of key metrics to be estimated (e.g. population growth rate, stable age structure). Third, perturbation or sensitivity analysis allows specific parameters to be identified that may have a greater or lesser effect on rates of growth of the population; these would be the targets for enhancing (e.g. conservation) or reducing (e.g. pest control) target populations. Fourth, simple deterministic models can be easily extended to incorporate variability and stochasticity in parameter estimates, thereby enabling e.g. population viability analyses to be undertaken (Caswell 2001). Perhaps the biggest advantages of these models, however, are that they (a) enable analyses to be conducted over much quicker time-scales than would be possible in the field and (b) they enable future projections of how populations may be expected to change under certain conditions.

The utility of such modelling exercises are, however, dependent on the quality of the data incorporated into that model. Nevertheless, identifying where data are "missing" can, in itself, be an important conclusion. Second, projections of future population growth based on current demographic parameters assume that these are likely to represent future conditions: at the most extreme, deterministic models assume these are constant, whereas stochastic models allow for a degree of variability. But in the most extreme cases, future changes, and the resultant effects on demographic parameters may be difficult to predict (e.g. Wittmer *et al.* 2013). Consequently, it has been suggested that future projections should only be used over relatively short time-scales ("transient analysis": Ezard *et al.* 2010).

The aims of the current study were to construct a Leslie matrix population model based upon parameters extracted from the published literature to: (a) determine whether, based on currently available demographic data, the mainland UK hedgehog population would be expected to be increasing, stable or decreasing; and (b) quantify the sensitivity of the estimated population growth rate to changes in adult fecundity, juvenile survival and / or adult survival rates. The results of these initial analyses did not, however, match the results observed in the recent monitoring programmes coordinated by the PTES and the BTO. Therefore, these data were subjected to two further investigations. First, stochastic modelling was undertaken, whereby the parameter values in the deterministic model with the lowest growth rate identified in (a) were not fixed. Second, fecundity and survival rates were systematically varied to investigate the degree to which published demographic parameters would need to have changed in order for the population growth rate to mirror that observed from the *Living with Mammals* survey.

Methods

Published literature was searched for data on fecundity (*F*), sex ratio (*SR*), juvenile survival (*JS*), adult survival (*AS*) and life expectancy (*LE*) estimates of *Erinaceus europaeus* in any habitat throughout its entire geographical range, excluding New Zealand. Additionally, estimates of total population size for mainland UK were collated. Relatively little information was available for any of the key parameters (see *Results*), so a "base" model was constructed as follows. Maximum life expectancy was taken as 3 years (after Kristiannson 1990). Consequently, the base model considered four age classes (juvenile age class modelled as Year 0), with no adults surviving beyond 3 years old (Equation 7.1).

Equation 7.1. Summary of the structure of the Leslie matrix model used in this study. *N* represents the number of individuals in each of the four age classes, *JS* is juvenile survival, *AS* is adult survival, *JF* is juvenile fecundity (which was kept at 0) and *AF* is adult fecundity.

$$\begin{bmatrix} N0 \\ N1 \\ N2 \\ N3 \end{bmatrix} = \begin{bmatrix} JF & AF & AF & AF \\ JS & 0 & 0 & 0 \\ 0 & AS & 0 & 0 \\ 0 & 0 & AS & 0 \end{bmatrix} \times \begin{bmatrix} N0 \\ N1 \\ N2 \\ N3 \end{bmatrix}$$

Whilst three different estimates of population sex ratio were identified from the literature, it is likely that the reported bias towards males is due to their greater movement through the landscape and, therefore, increased chance of being detected (e.g. caught in a trap), rather than an underlying difference in the sex ratio composition of these populations. Indeed, the long term study by Kristiansson (1990) reports a sex ratio of 1:1. Similar (unpublished) data from a long term study in Jersey also show an even sex ratio (Reeve pers. comm.). Therefore, the population sex ratio was modelled as 1:1.

Analyses were conducted in Excel. Overall, 12 models were constructed, each incorporating combinations of adult survival, juvenile survival and adult fecundity. Two measures of adult survival (low = 0.56; high = 0.70) and three measures of juvenile survival (low = 0.350; medium = 0.640; high = 0.735) were modelled: in each model, adult survival in the second and third age classes was kept constant; as outlined above, adult survival in age class three was set to zero. Two measures of adult fecundity (low = 2.85, high = 3.7) were incorporated; these were kept constant for all adult age classes. Models reflected a broad range of conditions from worst (JS = 0.350, AS = 0.56, AF = 2.85) to the best (JS = 0.735, AS = 0.70, AF = 3.7).

Each model was projected 20 years into the future. Initially, deterministic models were constructed with standard deviations around the demographic variables omitted to retain focus on the central variable value, and due to a lack of available data. Given the uncertainty around the current population level of hedgehogs in the UK, the focus of this exercise was the population growth rate (λ). The average λ was taken for each fixed model once it had stabilised and ranked relative to the other models. The starting population was assumed to contain 75% juveniles of the initial population; adult age classes were equal, sharing the remaining 25% of the initial population. This distribution was based upon the stable age structure for the best fitting model (DM5: see *Results*) and was imposed to ensure a quicker stabilisation rate of the population growth trajectory.

Significance analysis

To determine the relative importance of different demographic parameters, a significance analysis was conducted. The significance of each variable was defined as the average change in population growth rate (λ) per unit change in the variable. To assess this, all values in the model were kept constant at a "base" level, with the exception of the parameter being investigated. Base parameter values were: life expectancy (LE) = 3 years; adult fecundity (AF) = 2.80; adult survival (AS) = 0.53; juvenile survival (JS) = 0.66. For the significance analysis, parameters were varied as follows: life expectancy ranged from 2-7 years in one year increments; adult fecundity ranged from 1-6 in increments of 0.25; and adult and juvenile survival ranged from 0.1 - 0.9 in increments of 0.1. Each model was projected for 20 years.

Stochastic modelling

As none of the population growth rates of the 12 deterministic models indicated a declining population (see *Results*), stochastic modelling was undertaken to see whether variations around the fecundity and survival rates used in the deterministic models might result in a declining trajectory (i.e. could inter-annual variations in fecundity and survival rates, as might be expected in a natural population, result in a population growth rate <1 as has been observed in the majority of monitoring programmes in the UK).

For this, all deterministic models (LM1 - LM12) were converted into stochastic models under two scenarios: one where the standard deviations around the mean estimate was 10% of the mean value; and one where the standard deviations around the mean estimate was 20% of the mean value. All models were projected 20 years with 10^3 repeats.

Comparison with the Living with Mammals survey

In addition to being able to project future patterns of population growth based upon current demographic variables, it is also possible to investigate how contemporary patterns of growth compare to those arising from matrix models based upon "old" data. For example, the data used in the above analysis typically originated from studies published prior to 2005 (see *Results*); this represents the approximate start point for the *Mammals on Roads (MoR)* and the *Living with Mammals (LwM)* monitoring programs coordinated by the People's Trust for Endangered Species (PTES). Therefore, if the population growth rates for both the deterministic matrix model and these field-based surveys are broadly similar, this may be indicative of the fact that those demographic data currently available, although approximately 20 years or more old, are potentially still realistic estimates.

Consequently, the population growth rates of the 12 deterministic models described were initially compared to the average growth rate (λ) from the generalized additive model (GAM) used to analyse the *Living with Mammals* survey data from 2003 - 2017 (Wembridge pers. comm.). These data are based on the recorded presence / absence of hedgehogs at sites (typically urban gardens) selected by volunteer surveyors.

However, the projected population growth rate from these models were not a good fit for the *LwM* data (see *Results*). An exploratory analysis was therefore undertaken to investigate how much these survival and fecundity parameters would need to change in order to more closely match the trend observed in the PTES's monitoring data. For this, starting base variables were taken as those reported by Kristiannson (1990): expectancy (*LE*) = 3 years; adult fecundity (*AF*) = 2.80; adult survival (*AS*) = 0.53; juvenile survival (*JS*) = 0.66. Initially, variables were kept constant, changing only one value at a time; subsequent analyses varied all values simultaneously to find good combination matches.

Results

There was a paucity of information on all demographic parameters in the published literature. Collectively, estimates for adult survival, juvenile survival, fecundity and sex ratio were derived from four studies each (9 studies in total: Table 7.1); life expectancies were cited in just two studies. Of the nine studies overall, only three provided information for hedgehog populations in mainland UK (Table 7.1). Estimates for the total number of hedgehogs in the UK were highly variable, reflecting the paucity of information on hedgehog density in this country (Harris *et al.* 1995). The most recent estimates ranged from 1.5 million in the mid-1990s (Harris *et al.* 1995) to 0.7 - 12.0 million at the present time (Croft *et al.* 2017; Table 7.2), although the latter authors suggest that numbers are more likely to be closer to the lower bound of the 95% confidence interval.

Table 7.1. Values for annual adult (AS) and juvenile (JS) survival rates (%), fecundity (FR: offspring per female), sex ratio (SR: males:females) and life expectancy (LE: years) of hedgehogs extracted from a search of published literature.

Source	**Country**	**AS (%)**	**JS (%)**	**FR**	**SR (♂:♀)**	**LE (years)**
Kristiansson (1990)	Sweden	53	66	2.8	1:1	-
Kristiansson (1981)	Sweden	-	-	5.2	-	2.1
Morris (1977)	England	-	80[1]	3.72 - 4.37	-	1.9
Jackson (2006)	Scotland	-	-	2.85	1:1	-
Haigh *et al.* (2012)	Ireland	-	-	-	3:1	-
Hof and Bright (2010a)	England	80[2]	-	-	-	-
Morris (1991)	England	70	30-40	-	-	-
(Hoeck 1987)	Germany	60-80	20-30	-	-	-
(Jackson 2007)	Scotland	-	-	-	1.8:1	-

[1]Only reported up to one month old, therefore, likely to be far higher than over the whole year;

[2] Only reported during summer, therefore, likely to be higher than over the whole year.

Table 7.2. Published population estimates for hedgehogs in mainland Britain.

Source	**Time period**	**Population estimate**
Burton (1969)	1950s	>30,000,000
Morris (1993)	1993	~ 2,000,000
Harris *et al.*(1995)	1995	1,500,000
Croft *et al.*(2017)	2017	731,546 - 11,979,363

All 12 deterministic models had a population growth rate >1 (Table 7.3), indicating that, based on the parameter values available in the published literature, hedgehog populations would be increasing. This is at odds with those data from e.g. the PTES's *Living with Mammals* and *Mammals on Roads* monitoring programmes.

Table 7.3. Summary of the population growth rate (λ) arising from the age-structured deterministic model and the percentage of runs that show a decline with the 20% standard deviation (*D*) stochastic model for combinations of adult fecundity (*AF*), adult survival (*AS*) and juvenile (*JS*) extracted from the published literature. See text for details.

Model	***AF***	***AS***	***JS***	**λ**	***D* (%)**
LM1	3.7	70	73.5	2.001	0.0
LM2	3.7	70	64	1.889	0.0
LM3	3.7	70	35	1.481	0.1
LM4	3.7	56	73.5	1.932	0.0
LM5	3.7	56	64	1.821	0.0
LM6	3.7	56	35	1.417	0.4
LM7	2.85	70	73.5	1.797	0.0
LM8	2.85	70	64	1.699	0.0
LM9	2.85	70	35	1.338	1.0
LM10	2.85	56	73.5	1.730	0.0
LM11	2.85	56	64	1.632	0.1
LM12	2.85	56	35	1.276	2.7

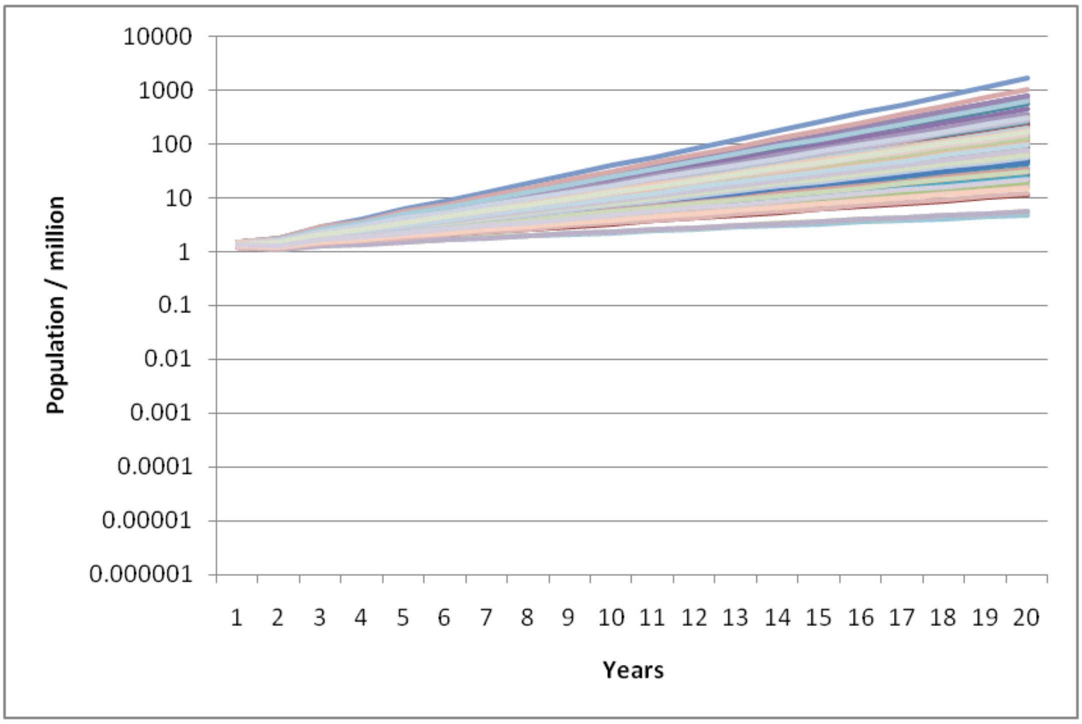
Significance analysis

Significance analysis showed that every 10% change in adult survival and juvenile survival rates changed λ by an average of 5.0% and 13.7%, respectively. Each additional year of life expectancy and each additional offspring born increased the population growth rate by 5.5% and 22.0% respectively (Figure 7.1).

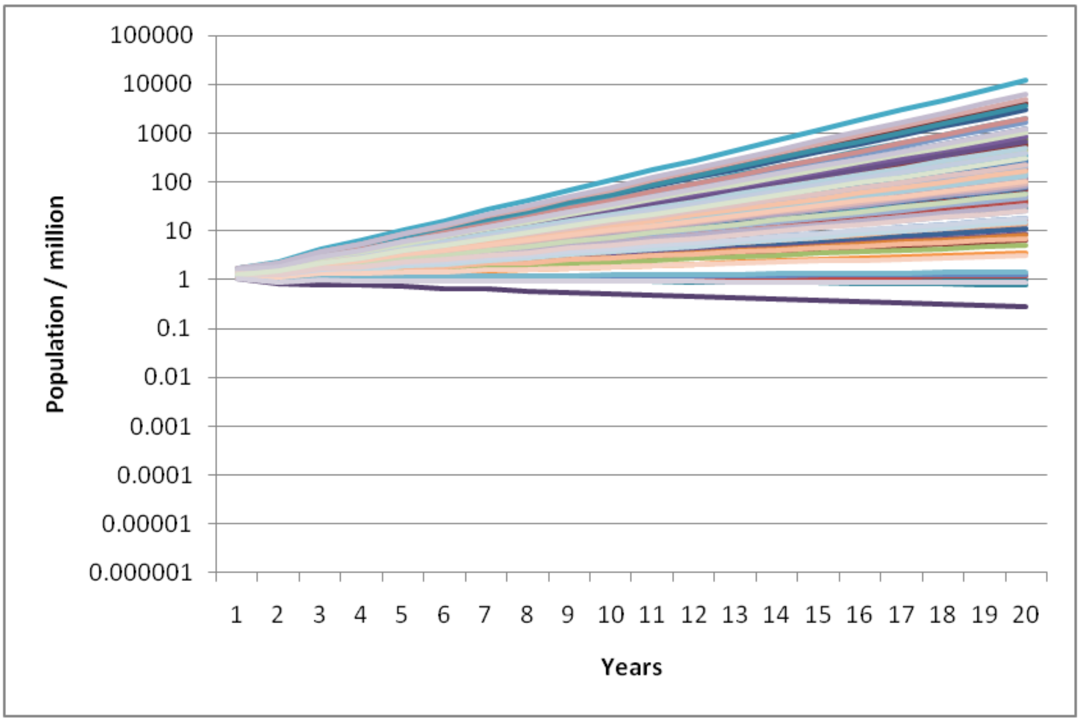
Figure 7.1. Classification of the demographic variables modelled showing: life expectancy (*LE*), adult fecundity (*AF*), adult survival (*AS*) and juvenile survival (*JS*). Uncertainty is a subjective measure of the reliability of each parameter based on a personal opinion derived from the author's assessment of how the data were collected and analysed. Sensitivity is the average change in λ per unit change of the variable as described in text.

Stochastic modelling

Stochastic modelling did not alter the general pattern of projected positive population growth; when the standard deviation was set to 10% of the mean values no negative growth was observed (Figure 7.2a). However, some negative growth was evident in some models when fecundity and survival rates were allowed to vary by a standard deviation of 20% of the mean values (Table 7.3, Figure 7.2b).



(a) Standard deviation set to 10% of mean values.



(b) Standard deviation set to 20% of mean values.

Figure 7.2. Projected pattern of population growth from stochastic modelling of LM12. In each case, initial mean estimates were: fecundity = 2.85; juvenile survival = 0.35; and adult survival = 0.56. In (a) standard deviation set to 10% of mean values. In (b) standard deviation set to 20% of mean values. For visual representation only 100 runs are shown.

Comparison with the Living with Mammals survey data

The *Living with Mammals* survey indicates an average population growth rate of 0.973 over the 15 year period studied (Figure 7.3). None of the population models based on literature data (Table 7.3) were a good fit with *LwM* data; indeed all showed population growth rather than decline. Adjusting the demographic parameters to "force" the population growth rate to match that observed with the *LwM* data indicated that this could be achieved in several ways (Table 7.4). Anecdotal observations (e.g. litters of hoglets found by members of the public, observations of litters associated with radio tagged females) suggest that female fecundity is not likely to have changed substantially. The more plausible explanation, therefore, is a reduction in juvenile and / or adult survival compared to that observed by Kristiansson (1990). Models DM4 - DM6 indicate this could be achieved by reductions in juvenile survival in the order of 40-60% combined with reductions in adult survival of <40%.

Figure 7.3. Results of the general additive model (solid line) used to analyse the PTES's *Living with Mammals* survey data for 2003 - 2017. Crosses are estimated annual means; dashed lines indicate 95% confidence limits. Adapted from Wilson and Wembridge (2018).

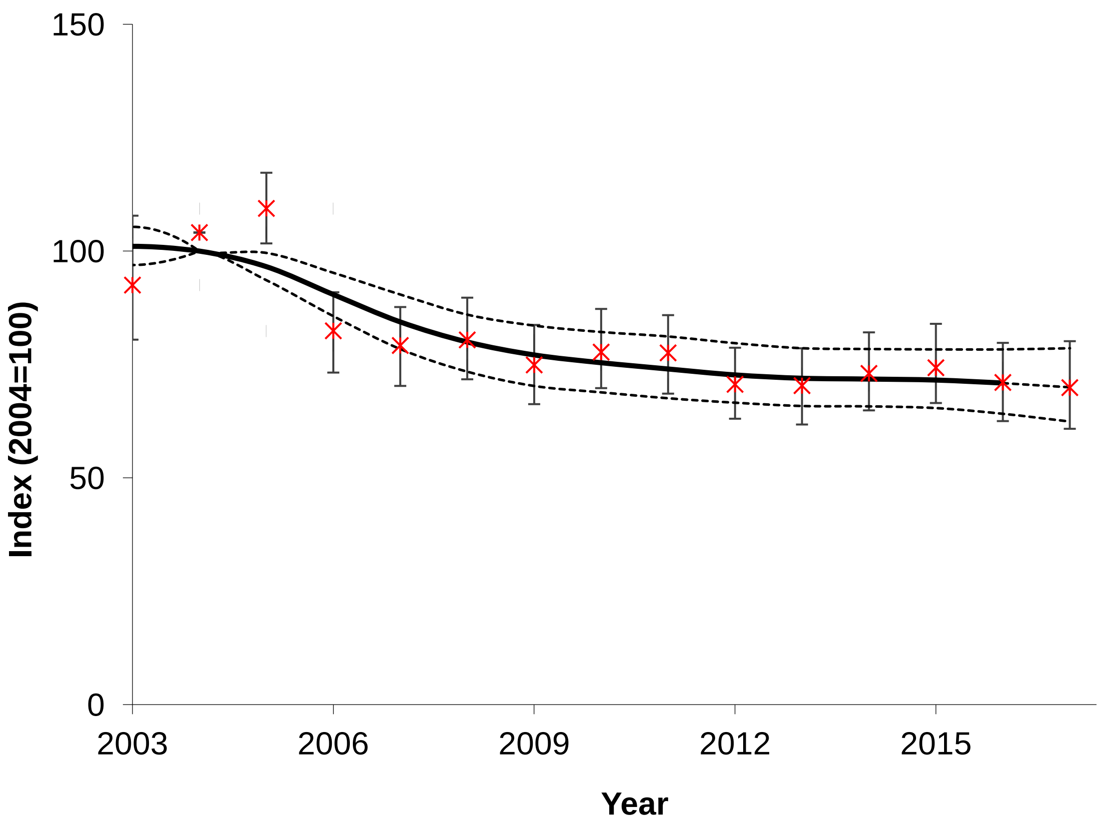


Table 7.4. Results of the exploratory modelling undertaken to identify demographic parameter estimates which would generate a growth rate matching that of the *Living with Mammals* monitoring programme (λ = 0.973). Values in bold represent values used in the initial base model for this exercise (based on Kristiansson 1990).

	DM1	**DM2**	**DM3**	**DM4**	**DM5**	**DM6**	**DM7**
JS	**0.53**	**0.53**	0.17	0.30	0.20	0.20	0.50
AS	**0.66**	0.01	**0.66**	0.40	0.40	0.60	0.55
F	0.78	**2.80**	**2.80**	2.00	3.00	2.40	1.00
λ	0.974	1.356	0.965	0.973	0.973	0.977	0.971

Discussion

The key results arising from this modelling exercise are: (1) there are relatively few published data on all aspects of hedgehog demographics currently available; and (2) that those data which are available do not appear to correlate with the population trends identified in ongoing hedgehog monitoring programmes in the UK. This discrepancy was substantial: even modelling the data stochastically, where standard deviations were set at 20% of mean values, only 2.7% of runs for the worst case scenario (LM12) resulted in negative growth. Estimates of age-specific fecundity rates and survival rates from both urban and rural hedgehog populations are, therefore, needed urgently.

Sensitivity analysis of those data that are available did, however, indicate that juvenile survival was the parameter that most influenced population growth rate. This was further reinforced in the exploratory analysis where parameter values were adjusted to force population growth rate to match that observed in the PTES's *Living with Mammals* programme: in this juvenile survival would have to decline by approximately 40-60%, and adult survival by approximately 40%. The latter would also affect the maximum age adults are likely to attain and their overall reproductive lifespan.

During the first year of life, juvenile hedgehogs are likely to be especially vulnerable as they are less able to protect themselves against badgers, but also other predators such as foxes (*Vulpes vulpes*) and, in urban areas, domestic dogs (*Canis domesticus*) and perhaps even domestic cats (*Felis catus*). In addition, juvenile hedgehogs have the additional pressure of having to attain a sufficient body mass (approximately 500g) to enable them to survive hibernation. At present, there are very few data on the survival rate of juveniles in their first year (see Table 7.3) but most especially in the period immediately after birth.

In addition to changes in mortality rates per se, declining population densities may further influence the long-term sustainability of hedgehog populations. Although potentially amenable to minimum population viability analysis (Moorhouse 2013), the paucity and relevance of those demographic data currently available make such exercises redundant. However, the concept of a minimum viable population is relevant, as it can be further extended to that of the corresponding minimum area required to support that population: all other things being equal, this minimum area would by necessity increase as the quality of the habitat declines, thereby reducing animal density. Those data from *Chapters Three* and *Six* of this theses indicate that hedgehog populations appear to becoming more patchy in nature, with animals increasingly associated with human habitations such that overall density has declined. As such, the carrying capacity of the landscape has declined, while certain mortality risks have likely increased (e.g. predation, road traffic). In combination, these factors would make hedgehogs more vulnerable. Reversing such declines will be dependent on a much more detailed understanding of hedgehog behaviour, density and demographics.

In summary, current data on hedgehog demographics is lacking. Consequently, some useful conservation tools (e.g. population modelling and population viability analysis) are unable to be utilised. The collection of such data, therefore, should be a priority and subsequently comparisons can be made with existing data to see what has changed in the 20 plus years since it was collected.

Acknowledgements

I would like to thank the Peoples Trust for Endangered Species for providing the data outputs from the *Living with Mammals* general additive models.

General Discussion

With much of the world under some form of farm management and increasing urbanisation the state of biodiversity is inherently dependent on humans and the decisions we take (Ellis & Ramankutty 2008; Baudron & Giller 2014). The intensification and changes in agricultural management in recent decades have led to well documented species declines (e.g. Green 1990; Robinson and Sutherland 2002; Burns *et al.* 2016; Hayhow *et al.* 2016). Indeed, agriculture is considered to have had the largest negative effect on nature out of all human activities (Balmford *et al.* 2012). Furthermore, urbanisation is reducing rural habitat availability and increasing pressures on an already strained countryside (Antrop 2004; UK National Ecosystem Assesment 2011; Hayhow *et al.* 2016). Conservation and food production cannot both be maximised simultaneously, therefore, management goals need to be clearly defined (Simons and Weisser 2017).

Central to wildlife conservation are two fundamental questions: (a) where does a species occur; and (b) where could that species occur (Peterson and Dunham 2003). The answers to these simple questions enable researchers to put in context the conservation status of focal species and monitor any conservation initiative implemented. Additionally, policy makers and practitioners are enabled to enact changes to help conserve the species in question. To be able to answer these questions robust survey methods are needed that are reliable, repeatable and economically viable (Pollock *et al.* 2002; Garden *et al.* 2007).

While the questions may be simple, it is not always easy to generate the answers, which are often complex. Ideally, species would be recorded directly as this minimises chances of error e.g. misidentification. Additionally, such techniques often enable abundance to be calculated. Examples include live trapping using a capture-mark-recapture framework and spotlight transects (Tuyttens *et al.* 1999; Heydon *et al.* 2000; Sharp *et al.* 2001). However, there are instances where direct observations are unfeasible; in these situations the use of field signs may be more practical. Well used examples of field sign surveys include sett surveys for badgers (*Meles meles*; Judge *et al.* 2014); spraint surveys for otters (*Lutra lutra*; Lanskzi *et al.* 2008); and latrine and burrow surveys for water voles (*Arvicola amphibius*; Woodroffe *et al.* 1990; Morris *et al.* 1998). However, some species are hard to detect directly and leave little to no readily found and identifiable field signs; in these situations it is necessary to develop alternative methods. For example, the use of raft to detect or catch mink (*Mustela vison*; Reynolds *et al.* 2004) or barn owl (*Tyto alba*) pellets to survey small mammals (Bonvicino and Bezerra 2003).

While surveys for some species are established by deploying well developed and accepted methodologies, other species and taxa lack suitable survey protocols (Harris and Yalden 2004). Often, this is because species are cryptic, requiring either intensive survey effort or advanced survey techniques. As such, novel survey methods need to be developed to enable cryptic species to be monitored (e.g. acoustic sampling; Lambert and Mcdonald 2014). While some techniques may be suitable for use on multiple taxa (e.g. Marques *et al.* 2013), others are species specific, developed or tailored purposely (Mills *et al.* 2016).

The development of new survey methods can be problematic, not least because it can be hard to verify their effectiveness. Traditionally, new methods would be compared and verified against existing methods that have been validated (Langbein *et al.* 1999; Newey *et al.* 2018). Where no accepted method exists, or the costs are too high to utilise existing methods, an alternative approach to verifying the new technique is required. In such circumstances new methods may be verified using statistical techniques (Barata *et al.* 2017).

Here, a novel method for surveying hedgehogs was developed and validated for use in urban (*Chapter Four*) and rural habitats (*Chapters Two* and *Three*). The method was validated using occupancy analysis; a maximum likelihood method that incorporates detection probability based on repeated site surveys so that an overall occupancy estimate can be obtained.

The development of novel survey methods is needed now to provide data that has historically been lacking. Such data are becoming increasingly required as many species are becoming threatened with extinction and are increasingly vulnerable to e.g. climate change (Moritz and Agudo 2013), urbanisation (Sol *et al.* 2014), and intensive agriculture (Donald *et al.* 2001; Shackelford *et al.* 2015).

Throughout the world agriculture is becoming more intensive, as the demand for food to feed an ever growing human population increases (Tilman *et al.* 2011). The tendency for more intensive farming has been seen throughout Europe and linked to declines in a range of species (Kleijn *et al.* 2009). There is increasing awareness among the general public and policy makers of the anthropogenic impact on, and need to protect, the natural environment for the future (e.g. Rodman 1999).

The need to help safeguard the natural world has been recognised, primarily for the ecosystem services that many habitats, species and taxa provide (Chan *et al.* 2016). For example, it has been estimated that pollinators provide €153 billion worth of economic value worldwide each year (Gallai *et al.* 2009) and hedgerows can be a valuable tool in carbon sequestration (Axe *et al.* 2017). Additionally, the natural world is valued for its intrinsic value and the benefit it can bring to human wellbeing (e.g. Sandifer *et al.* 2015). However, assigning a monetary value to such attributes is problematic and there are no agreed upon values (Natural Capital Committee 2018). Consequently, it is often the ecosystem service value that is considered when assigning monetary values to aspects of the natural environment. To help conserve the natural world governmental bodies may implement national initiatives to incentivise and reward farmers and landowners for undertaking activities that are beneficial to wildlife (Batáry *et al.* 2015); in Europe the Argri-Environment Scheme (AES) is the chief mechanism employed to achieve this.

The AES was first introduced in England in 1987, through the implementation of Environmentally Sensitive Areas (ESA), as a response to the rapid agricultural intensification and loss of wildlife being witnessed (Natural England 2009). In 1991 The Countryside Stewardship Scheme (CSS) was launched to help conserve the most important areas not in the ESA scheme (Natural England 2009). Following a review in 2005 a major overhaul was seen with the introduction of Environmental Stewardship (ES) and the closure of ESA and CSS to new applicants (Natural England 2009). The new ES scheme built on the knowledge and experience gained under its predecessor schemes and was also multi-objective in nature (Natural England 2009). There are two levels in the scheme: Entry Level Stewardship (ELS) which rewards simple environmental management and is open to all; and Higher Level Stewardship (HLS) which sees higher levels of environmental management rewarded and is targeted towards land and features with the greatest environmental value (Natural England 2009). ELS and HLS agreements last for five and ten years respectively (Natural England 2009). These schemes are currently funded through the European Union (EU) Common Agricultural Policy (CAP) and are administered through Defra as the managing authority for the UK (Natural England 2009). In the period 2014-2020 the total CAP budget is €408.31 billion, with the UK estimated to receive €28 billion (European Commission 2017). One common criticism of the current EU method of farm subsidies is that the CAP Basic Payment Scheme pays land owners for the amount of productive land rather than for the environmental benefit that they provide; this is aimed to subsidise framers main income enabling economic food production (Swinbank 2017).

Currently, the UK participates in the EU farm subsidy systems; however, with the UK due to leave the EU in early 2019 it is likely that a new system will be implemented (Swinbank 2017); the creation of which presents an opportunity for a major overhaul. While the detail of any such system is not yet known, it is likely that farms will receive a lower subsidy and a greater focus will be put on environmental enrichment (e.g. the creation, restoration and management of hedgerows, wildflower field margins, dew ponds, copses; Swinbank 2017). Indeed, the government wants this generation to be the first to leave the natural environment in a better condition than it was inherited (HM Government 2011, 2018).

Habitat enhancements will often be beneficial to a range of species, not just the target species, providing a wide range of benefits; indeed, some are likely to be directly, or indirectly, beneficial to hedgehogs (Hedgehog Street 2018). It is worth acknowledging that, while habitat improvements are welcomed by conservationists, their full benefit will often not be realised for many years (Reid & Grice 2001); consequently, a long term view should be taken and the protection of existing beneficial habitats should be prioritised over the creation of new habitats.

In contrast, when the UK leaves the EU there are likely to be other trade opportunities that open up; some of which may look to lower environmental or animal welfare standards. For example, a trade deal with the United States of America (USA) may mean the lowering of animal welfare standards and consequently have negative environmental impacts (Swinbank 2017). While there is ample opportunity to put the natural environment at the centre of the new system, the lack of an overarching governing body may mean that subsequent governments could weaken environmental regulation more easily (Dhingra *et al.* 2016). As such, strong safeguards should be implemented that provide reassurance to the public and farmers that any system implemented will have sufficient longevity to adequately (i) protect the environment, and (ii) plan financially for the future. For instance, if subsidies for field margins are removed at short notice, farmers may decide to turn that area of land over to a more productive and profitable use.

Defra's 25 year plan provides some reassurance to the public, farmers, and wildlife conservation organisations and professionals that the natural world will be afforded some protection, helping it to regain and retain "good health" (HM Government 2018). The plan is fairly comprehensive and broad in scope, including aspects on connecting people with the environment as well as habitat improvements and waste management. The government plans to use a natural capital approach (which would be a world first) where everything in nature is assigned a value (HM Government

2018). The basic principle is that without a value assigned nature has no value and is, therefore, easier to dismiss when decisions are being taken. However, if values on nature are too low then it will be easy for these values to be superseded by e.g. development and the associated economic benefits. It is likely that broad values will be assigned; for example an average monetary value for every unit area of woodland, however, this may fail to distinguish between areas and recognise the local importance of certain features or habitat. Consequently, such an approach needs to be well designed with safeguards in place to ensure that the natural environment is adequately protected. These values are being developed by the Natural Capital Committee (NCC) in collaboration with the Office for National Statistics (ONS) and Defra with the goal of creating a set of 'accounts' by 2020; however, there are some substantial hurdles that will need to be overcome to enable this deadline to be met (Natural Capital Committee 2018).

While looking forwards involves much speculation about what will be implemented and how, it does appear that the protection and enhancement of the natural world will be taken seriously and play a key role in how the UK develops moving forwards. Indeed, one of the four Grand Challenges of the Industrial Strategy is Clean Growth (HM Government 2017), indicating its importance in the government's development plans.

To date much focus on hedgehog conservation has been placed on trying to understand the rate of decline rather than the mechanisms behind it. Moreover, there has been no attention paid to how management actions could help to reverse declines. This is, in part, associated with a lack of understanding about the driving forces behind the decline. A key problem to date has been the limitations associated with the various survey methods (see *Chapter One* for a brief discussion on this). The primary aim of this work, therefore, was to validate and use a novel method for surveying hedgehogs to assess their current occupancy in Britain and investigate the factors influencing hedgehog occupancy in rural and suburban / urban habitats. Additional work was undertaken to investigate causes of hedgehog-vehicle-collisions; better understand the genetic structure of hedgehog populations; and investigate hedgehog demographics and population trends. Overall, the work presented in this thesis aims to help fill some of the key knowledge gaps hindering hedgehog conservation. Furthermore, it can be fed directly into national management plans and be used to help gain a better understanding of the conservation status of *E. europaeus* in the UK and throughout Europe. Much of the data used for hedgehogs in the recent review of British mammal populations (Mathews *et al.* 2018) was obtained over twenty years ago, and is likely to be out of date (e.g. *Chapter Seven*). The findings presented here may be included in future models helping to enhance estimates of hedgehog occupancy and abundance nationally.

Chapter One provided an overview of why this work is important and set the context. *Chapter Two* focused on demonstrating the validity of a novel method for surveying hedgehogs, footprint tunnels, and how this could be integrated with recently developed occupancy analysis. *Chapters Three* and *Four* focused on assessing hedgehog occupancy in rural and suburban / urban habitats respectively using footprint tunnels and occupancy analysis. A shift in focus was seen in *Chapter Five* which investigated the causes of hedgehog-vehicle-collisions in rural and suburban / urban habitats. *Chapter Six* used a panel of microsatellite markers to help understand hedgehog population structure and investigate gene flow in Southern England. Finally, *Chapter Seven* identified current gaps in knowledge of hedgehog demographics and highlighted areas for further research.

Overall, the results indicate that whilst hedgehogs are widely distributed they are not ubiquitous in rural or suburban / urban habitats. Hedgehog presence is negatively influenced by badger presence and / or abundance in all habitats and they appear to have a positive association with the built environment. However, the results also show that badger presence / abundance is not the sole reason for lack of occupancy, and hence decline. Indeed, work presented here (*Chapter Three*) suggests badger numbers would have to increase considerably throughout all of Britain to extirpate hedgehogs completely. Therefore, my work suggests that there is an underlying issue of habitat suitability in both rural and suburban / urban environments that warrants further investigation.

Below, I summarise the work undertaken throughout this thesis to investigate the influence of habitat, predator and anthropogenic variables on hedgehog occupancy and survival throughout Britain in rural and suburban / urban habitats. The work is summarised by chapter detailing the key findings and associated implications for hedgehog conservation before drawing it all together to consider the implications of the findings on hedgehog conservation and identifying areas that require further research.

Chapter Two

In *Chapter Two* I tested and validated a novel method for monitoring hedgehogs in rural habitat. The method was designed to be used with recently developed occupancy analysis (MacKenzie *et al.* 2006) to account for imperfect detection. Results were positive, indicating good hedgehog detection rates (59.3%) with a low false absence rate (0.5%) if tunnels were used for five nights. Power analysis indicated that the method would be suitable to use at a national scale and that if 621 sites could be surveyed a change in occupancy of 25% could be detected.

Benefits to the use of footprint tunnels over traditional methods (e.g. spotlighting, road-kill counts, live trapping) were many but primarily included their suitability for volunteer / citizen-scientist use and ability to be used on a small scale e.g. individual farm so that environmental and management covariates could be included in analysis and were cheap enough to be rolled out nationally.

The successful trial and validation of the method using occupancy analysis allowed for the method to be used for the first ever national survey of hedgehogs (*Chapter Three*) using indirect and non biased methods.

Chapter Three

In *Chapter Three* I investigated hedgehog occupancy throughout rural England and Wales, producing the first unbiased estimate at a landscape scale. All seven land classes were surveyed in proportion to their coverage and sites were selected randomly. Data on the number of badger setts was obtained from the recent (2011-2013) national badger sett survey (Judge *et al.* 2014), and were included in the models along with data on habitat and land management practices.

No significant influence of habitat availability or complexity was detected. Hedgehog occupancy, however, was positively affected by an increase in the built environment and road density. This association has been noted in other studies and is thought to be related to reduced badger abundance, increased food availability and / or novel refugia in suburban / urban areas (Doncaster 1992; Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012; van de Poel *et al.* 2015; Pettett *et al.* 2017b).

The most influential variable in the models, however, was badger sett density. Indeed, results from both single-species and two-species occupancy models indicated a negative relationship between hedgehog occupancy and badger sett density. However, this relationship appears complex with hedgehogs and badgers found to coexist at the 1km^2 scale. Furthermore, hedgehogs were not detected at some sites with no badger setts and predicted hedgehog occupancy in the absence of badgers was still low at only 31%. Indeed, my work indicates that badger main sett density would have to increase more than six fold from that reported by Judge *et al.* (2014) for badgers to completely extirpate hedgehogs from England and Wales. Taken together, these results indicate that much of the rural countryside in Britain is unsuitable for hedgehogs.

The findings here indicate that the wider landscape in England and Wales is not well suited to hedgehog occupancy at the $1km^2$ scale; therefore, further work is needed to help understand what practical changes could be made in the rural environment to make it more suitable.

Chapter Four

In *Chapter Four* I investigated hedgehog garden occupancy in a large town, Reading, Berkshire, UK. Occupancy (*c*. 37%) was in line with that of previous studies e.g. Living with Mammals (Roos *et al.* 2012). Given that suburban areas such as residential gardens appear to be the hedgehogs preferred habitat (e.g. Hubert *et al.* 2011) it is noteworthy that almost two thirds of those studied did not have hedgehogs visit them; this could be due to (i) lack of access; (ii) lack of hedgehogs in the area; or (iii) poor quality gardens.

In line with the rural findings the presence of badgers negatively affected hedgehog occupancy. Furthermore, the two-species occupancy modelling indicated that hedgehogs show avoidance of gardens used by badgers; this avoidance was not detected with respect to foxes indicating that fear of predation is the driver rather than competition for food. However, neither the two-species occupancy modelling, Fisher's exact test nor the single-species occupancy modelling showed badger presence to have a significant effect on hedgehog garden occupancy. This may be explained by (i) too few sites to detect a significant difference in a complex habitat; (ii) the relatively short amount of time since badgers have also made extensive use of the urban area i.e. it is too soon to detect the effect (Davison *et al.* 2009; Huck *et al.* 2008); or (iii) the increased food availability and refuge options in a suburban setting are able to mitigate the pressures badgers impose on hedgehogs. Further work in this area would be beneficial and findings may be able to be extrapolated to the rural environment; for example, if food availability is found to help mitigate in the suburban environment then work could be undertaken to increase food availability in the rural environment and the response monitored.

This work partially disagrees with the findings of Williams *et al.* (2014) who reported residents were unable to accurately predict the presence / absence of hedgehogs in their gardens; this is likely due to the number of gardens tested, 47 compared to 151 in this study. However, there was some difference between residents predictions and detections, with 34.7% of households unable to correctly predict hedgehog presence / absence. These findings do call into question the use of questionnaire surveys, particularly for cryptic or elusive species. Therefore, while it may be an acceptable trade off to use questionnaires to gather such data providing responses are high, the use of footprint tunnels would be recommended, particularly if few gardens are to be studied or accurate information is needed for a particular garden or area.

Further work should be undertaken to investigate the use of gardens by hedgehogs and competitors / predators with the aim of ensuring that suburban / urban areas remain a stronghold for hedgehogs. Understanding why hedgehogs are absent from more than half of gardens also warrants further investigation.

Chapter Five

In *Chapter Five* I investigated hedgehog-vehicle-collisions in rural and suburban / urban habitats. Numbers of casualties differed by month, as would be expected, and matched the findings of Haigh *et al.* (2014). Significant clustering of carcasses was also found at all spatial scales indicating non random occurrence; visual analysis pointed towards suburban / urban areas as hot-spots.

In both rural and urban habitat fatalities occurred more on roads with a speed limit of 30mph or less. As one would expect greater vigilance and a shorter stopping distance at these speeds the higher incidence of collisions in these areas is likely due to increased hedgehog abundance in these areas, which are often residential. Alternatively, hedgehogs may show less avoidance of crossing these roads than of roads with higher speed limits as has been shown for other species (e.g. Husby and Husby 2014). In rural areas the presence of a junction nearby was also associated with hedgehog carcasses; it is unclear if this is due to reduced driver awareness or increased hedgehog crossings in these areas and investigations into this are warranted.

Whilst some similarities were detected in carcass positions between rural and urban habitats differences were also noted, highlighting the importance of habitat when investigating such phenomenon. All detected influential factors were based on fine scale data and not e.g. surrounding habitat; as this is the scale much work is conducted (e.g. Clevenger *et al.* 2003; Seiler 2005; for a review see: Gunson *et al.* 2011) I recommend that future research considers the scale investigated carefully to ensure that the results are meaningful and able to answer the research question. Furthermore, researchers and practitioners should be wary about extrapolating from studies based in only one habitat or spatial scale.

I contend that as road speed was a key factor in influencing hedgehog road kill in both rural and urban habitats and given that many road kill surveys and monitoring schemes (e.g. PTES's Mammal on Roads) predominantly focus on main roads with higher speed limits and avoid urban areas the numbers of road kill nationally may be underestimated. Further work to determine by how much would be useful and allow the effect at a population level to be better understood. In addition, incorporating the factors highlighted in this study into analysis of long-term monitoring data such as the Mammals on Roads survey is important and would allow for more robust conclusions to be drawn.

The reasons behind the clustering are unknown and warrant further investigation; however, the work in this chapter may go some way in helping to explain this. For example, at larger spatial scales hedgehog carcasses appear to cluster around urban areas and at smaller spatial scales they appear to cluster around junctions and residential areas.

Chapter Six

In *Chapter Six* I investigated the population structure and gene flow of hedgehogs in rural Southern England. This work is the basis for determining factors that restrict gene flow among rural hedgehog populations that may lead to fragmented populations. Additional work will be undertaken to build on that presented here to gain a more comprehensive understanding of the landscape genetics of hedgehogs.

Originally it was planned to obtain a Home Office licence to allow the collection of blood samples for DNA analysis. However, this was not granted which delayed sample collection and necessitated alternative methods to be used. Ultimately, DNA samples were obtained from tissue from deceased hedgehogs (e.g. road kill or wildlife rescues) and buccal swabs from live hedgehogs (live cage trapped under licence from Natural England and wildlife rescues).

In total 289 samples were collected; with all ten polymorphic primers with location data available amplifying in 199 samples. Genetic diversity was comparable to other studies in the UK and Europe on *Erinaceus europaeus*. No population structure was detected in the data, indicating, at least some, gene flow between individuals in different towns / villages. Preliminary landscape genetic analysis is inconclusive and further work is needed to more fully explore the data using additional analytical techniques and comparing further covariates e.g. badger density.

Chapter Seven

In *Chapter Seven* I constructed basic deterministic Leslies matrix population models based on data in the literature and compared the outputs to 15 years of data obtained from the Living with Mammals (LwM) survey 2003 - 2017.

An extensive desk based literature search was undertaken to determine the likely demographic data on hedgehog populations. Data were inconsistent between studies leading to uncertainty; therefore, multiple models were constructed and outputs compared to data collected nationally to determine the most likely combination.

Age structure analysis indicated juveniles make up *c*.75% of the hedgehog population. As the current UK hedgehog population level is unknown (Croft *et al.* 2017; Mathews *et al. 2018*) it was impossible to accurately assess when the population may become extinct if the current growth trend continues. The influence of all demographic variables was assessed, showing juvenile survival and fecundity to be most influential in the model, respectively. In conjunction with this uncertainty analysis was used to determine where future research efforts should be focused; variables assessed to be highly influential and uncertain should take priority. Consequently juvenile survival should be the focus of future research and conservation efforts. Indeed, small changes in either adult or juvenile survival has the ability to change the population growth rate substantially; analysis showed that a positive change as small as 5% in either could change the population growth rate from negative to positive. The best fitting model with LwM data was Fecundity: 3.0, Adult Survival: 40%, and Juvenile Survival: 30%.

The chief aim of this work was to identify priorities for further research by determining for which demographic variables data are deficient and which have the greatest influence on hedgehog population growth rate. This has been successful and it is now hoped that further research will be prioritised accordingly allowing for the dynamic use of population modelling in the conservation of hedgehogs.

While this work was able to identify the key areas where conservation effort should be focused further research is needed to identify the current causes of mortality and ways to reduce it, allowing hedgehog populations to recover. Further work is also needed to reduce uncertainty around some of the basic demographic factors, this data would greatly increase the ability of the models to predict population changes and be used in real time. Given that the data in the literature do not appear to match the current decline it calls into question their use and the validity of the results from research using them e.g. Moorhouse (2013)

Implications for hedgehog conservation

It is widely accepted that the hedgehog population in Britain is in decline; however, the extent and causes are still not fully understood. Nevertheless, key patterns are starting to emerge from research presented here and by others. For example, badgers are consistently cited as a key cause of decline (Young *et al.* 2006; Parrott *et al.* 2014; Trewby *et al.* 2014) while suburban / urban areas appear to be favoured by hedgehogs (Doncaster 1992; Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012; van de Poel *et al.* 2015; Pettett *et al.* 2017b). While these broad areas are known to play a role the exact mechanisms behind them are not fully known. Likewise, other factors, as discussed in *Chapter One*, may also be playing a role but to a lesser extent, and as such less work has been undertaken to understand their effects. Here, I consider the work in this thesis and its implications for hedgehog conservation and make recommendations for future research.

Roads

As outlined in *Chapter's One* and *Five* roads cause loss and fragmentation of habitat. Furthermore, they are a direct cause of mortality; a recent study by Wembridge *et al.* (2016) estimated that 167,000 - 335,000 hedgehogs could be killed annually in Britain. This may constitute a large enough proportion of the population to be having a considerable negative effect. Indeed, Huijser and Bergers (2000) estimate that hedgehog populations may be reduced by up to 30% due to roads and traffic.

Factors influencing hedgehog road-kill were investigated in *Chapter Five* in two contrasting habitats (rural and suburban / urban). Results showed hedgehogs to be killed more readily near urban areas and on roads with speed limits ≤ 30mph. The later is thought to be liked to residential areas which typically have such speed restrictions in place for human safety. Results also indicated that fine scale road characteristics play a role; therefore, getting a better understanding of these may allow mitigation measures to be implemented. Results from *Chapter Three* indicated hedgehogs preferred habitat with a high density of roads; however, this is also likely linked to their presence in urban areas. Therefore, I contend this relationship is due to increased hedgehog density in residential areas rather than a preference for roads themselves.

Previously, hedgehogs have been shown to avoid crossing major roads (Rondinini and Doncaster 2002) leading to speculation that they may lead to increased habitat fragmentation. Indeed, Becher and Griffiths (1998) noted genetic differences between local villages in rural Oxfordshire, UK. However, work presented here shows no genetic structure in hedgehogs sampled across Wiltshire, Berkshire and beyond.

Badgers

Given that badgers are the principal predator of the hedgehog in the UK (Doncaster 1992, 1994; Micol *et al.* 1994), compete for the same food (Morris 2006) and their numbers have increased considerably over recent decades (Harris *et al.* 1995; Wilson *et al.* 1997; Macdonald and Burnham 2011; Judge *et al.* 2014, 2017) it is of little surprise that a negative association between them and hedgehogs is often reported (e.g. Young *et al.* 2006; Parrott *et al.* 2014; Trewby *et al.* 2014; Pettett *et al.* 2017a). While the reasoning behind this association is clear, the mechanisms driving it are not. For instance, logic would suggest that both predation and competition could play a role but we do not know if hedgehogs are absent from badger dominated areas, or at least present with reduced abundance, due to being out competed, predated upon or avoidance e.g. to minimise predation risk.

The fact that hedgehogs appear to move from badger dominated areas (Doncaster 1994) suggests avoidance is a key driver. However, avoidance may only be short term (e.g. Ward *et al.* 1997). Furthermore, some studies have reported high predation rates indicating that both are still found in the same areas (Doncaster 1992; Hof and Bright 2010a). The results from *Chapter Three* also support the fact that both species can co-exist, at least at the 1km^2 scale. Additional work from *Chapter Three*, not presented here, also indicates that hedgehogs do not avoid badger setts, with no difference detected in the median distance to setts between tunnels that did and did not detect hedgehogs. In urban gardens hedgehogs showed no change in garden occupancy with the presence / absence of foxes; therefore, as foxes will also readily compete for food with hedgehogs, particularly in an urban environment, competition does not appear to be a driving force in determining occupancy, at least not in urban areas where food is abundant.

Hedgehog density is known to increase with a reduction in badger density (Trewby *et al* 2014*)*; similarly, areas with higher badger abundance have been shown to support fewer hedgehogs (e.g. Young *et al.* 2006). Furthermore, hedgehogs have been found to move from badger dominated areas upon release (Doncaster 1992). The negative association between badgers and hedgehogs has been found in rural and urban habitats (e.g. Doncaster 1992; Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012; Pettett *et al.* 2017b). Indeed, the work presented here also found badgers to negatively affect hedgehog abundance in both rural (*Chapters Two* and *Three*) and urban (*Chapter Four*) habitats; although, this was not significant in urban areas.

Predator control, i.e. culling badgers, is likely to have a positive effect on hedgehog populations (Trewby *et al* 2014). However, this may not be popular with many people and culling one species to conserve another may be morally questionable. Furthermore, while predation may cause local extinctions it rarely causes population extinctions on a large scale (Holyoak and Lawler 2007). Additionally, results from *Chapter Three* suggest that hedgehogs are also absent from areas with no badgers and that even with no badgers in Britain occupancy levels would be only *c.* 31% nationally. This suggests that whilst badgers are impacting on hedgehog populations other factors are at play as well e.g. loss of hedgerows, larger field sizes, reduced prey availability.

Research to better understand the interactions between badgers and hedgehogs and the pressures badgers exert on hedgehogs is needed, particularly in rural areas where hedgehogs are declining fastest (Wilson and Wembridge 2018) and appear to be significantly negatively affected by badgers (*Chapters Two* and *Three*; Doncaster 1992; Young *et al.* 2006; Hubert *et al.* 2011; Hof *et al.* 2012; Pettett *et al.* 2017b). Investigations looking at how badgers and hedgehogs co-occur in the landscape would be particularly beneficial. Understanding the issues will allow for effective mitigation to be implemented to help alleviate the negative effects. How much of the negative effect badgers have on hedgehogs is down to purely the increase in badger numbers is unknown and other factors such as a changing landscape, climate change and a reduction in food availability are likely to be compounding the issue. I suggest work is undertaken to look at how both badgers and hedgehogs use the landscape temporally and spatially when both species are present with particular focus on interactions, food availability and spatial refugia. Further work is also required to look at how hedgehogs use the landscape in the absence of badgers to see if there are any differences and determine what practical changes could be made in the rural environment to make it more suitable for hedgehogs, particularly in the presence of badgers.

Urban areas

While hedgehogs are generalists and able to live in a variety of habitats (e.g. Reeve 1994) they prefer a heterogeneous habitat and require suitable nesting sites and adequate food availability (Morris 2012). Recent agricultural intensification in Britain resulting in the loss of hedgerows and increased field sizes coupled with increased badger numbers may have made large areas unfavourable to hedgehogs (e.g. Pettett *et al.* 2017b). Furthermore, the increased use of pesticides and more homogeneous landscape is likely to have reduced the invertebrate prey availability (Hayhow *et al*. 2016).

Conversely, urban areas are largely heterogeneous providing a plethora of feeding and refuge opportunities. Furthermore, badger numbers are typically lower in urban areas reducing chances of predation and levels of competition. However, urban areas can also prove hazardous environments with a high road density providing a constant mortality risk (see *Roads* above; *Chapter Five*). While hedgehogs are subject to an increased range of potentially lethal hazards and anthropogenic harm in urban areas they are also widely appreciated and cared for by the public. For example, many residents provide additional food and nesting opportunities in their gardens and take sick or injured hedgehogs to receive care at wildlife rescue centres (e.g. Molony *et al.* 2007; Grogan and Kelly 2013; Barnes and Farnworth 2017).

Despite the potential dangers hedgehogs often show a preference for urban areas over the rural countryside (e.g. Pettett *et al.* 2017a); indeed, they often appear to thieve in these habitats (e.g. Hubert *et al.* 2011). The primary reasons for this appear to be reduced badger abundance and increased food availability (e.g. Hubert *et al.* 2011; Pettett *et al.* 2017a). Even with badgers becoming more prevalent in urban areas (Huck *et al.* 2008; Davison *et al.* 2009) there may be enough food to negate the effects of competition and enough refuge areas and habitat complexity to minimise the chances of contact between the two species and, consequently, predation.

Further detailed research in urban areas understanding hedgehog movements and contact rates with badgers would be beneficial. Such data on hedgehog movement would also help with mitigation of road-kill and enable better understanding of habitat fragmentation and gene flow. Until fairly recently the use of Very High Frequency (VHF) transmitters was the only practical way to monitor movements; however, this method can be problematic, particularly in urban areas; VHF signal can easily be bounced off buildings making it hard to pin point the source location. Furthermore, access restrictions can make it hard to determine the location of the source; for example, which garden it is originating from. Additionally, time between fixes is likely to create gaps in data so a complete picture of the subjects travels or time spent in particular habitat / location is unknown. The advancement of Global Positioning System (GPS) transmitters could prove valuable and allow much finer resolution of data collection (Glasby and Yarnell 2013, Braaker *et al.* 2014).

However, GPS devices are costly and their use on hedgehogs in the UK would require a licence; therefore, the use of footprint tunnels and / or questionnaires may be more feasible in many cases. While these methods will not provide movement data which is needed to answer some questions they may be able to gather data that could be implemented into e.g. a Joint Species Distribution Model (JSDM) to help untangle some of the issues that hedgehogs, and other species, face in the urban environment.

In such a complex habitat extensive data is required to determine which factors are most important. Research is particularly needed to understand the roles of badgers, foxes, access, and food availability on hedgehogs.

While hedgehogs appear to prefer urban areas (e.g. Pettett *et al.* 2017a), they still appear to be in decline in this habitat (e.g. Wilson and Wembridge 2018). Therefore, work is needed to help understand the mechanisms behind this to help safeguard their preferred habitat. Additionally, understanding the benefits of an urban over a rural environment for hedgehogs may allow improvements to be made to the countryside to benefit hedgehogs. If hedgehogs become confined to urban areas then fragmented populations will become a reality and many smaller villages may not be able to sustain healthy populations (Becher and Griffiths 1998; Moorhouse 2013).

Recommendations for future work

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

1. The development and validation of a method to accurately assess hedgehog abundance in (i) rural and (ii) suburban / urban habitats. This would allow for a proper assessment of the population level of hedgehogs. Furthermore, it would be particularly useful to determine density trends. One key limitation of the work here is the inability to estimate abundance levels at individual sites; therefore, all sites with hedgehog presence are considered equal.

There is the possibility that modelling could estimate abundance from footprint tunnels; however, preliminary tests were not promising and, therefore, not pursued.

2. Unravelling the relationship between badgers and hedgehogs will aid conservation efforts. This could be done by either (i) detailed monitoring of hedgehogs and badgers where they co-exist and compare to sites with hedgehogs only; or (ii) field manipulations. While removal of badgers to conserve hedgehogs may be morally questionable the current badger cull provides an opportunity to assess how hedgehogs respond in such situations (Trewby *et al.* 2014). It would be beneficial to not only monitor abundance as has been done previously (e.g. Trewby *et al.* 2014) but also how hedgehogs use of the landscape and habitat features change. This would require a period of monitoring before any cull took place. Additionally, there may be sites where badger numbers are increasing steadily, or expected to do so (e.g. after a period of culling), where monitoring hedgehog abundance and movement would prove useful.
3. Given the low estimated national rural occupancy of hedgehogs with complete badger removal it is imperative that a better understanding of how hedgehogs use the landscape and different habitat is obtained with a view to make habitat improvements. Enhancing the rural environment for hedgehogs is key to their sustainable conservation and is also likely to help other species.
4. Investigating how hedgehogs, foxes and badgers interact, in suburban / urban habitats and monitoring changes in this as badger density increases will help safeguard current hedgehog strongholds and may provide insight about what could be done in rural habitats to help conserve hedgehogs.
5. Assessing the impact of creating better access between gardens, as is recommended by Hedgehog Street (www.hedgehogstreet.org: a joint initiative between the British Hedgehog Preservation Society and Peoples Trust for Endangered Species) will aid conservation efforts and inform the practical levels residents are willing to go to.
6. A study looking at how long hedgehog carcasses persist for on roads within differing habitats, weather conditions and traffic volumes will help with analysis of road-kill data and allow for better estimates of the numbers killed per unit length annually.
7. Work building on *Chapter Five* to see if hedgehog road kill hot spots are consistent through time and space are warranted before costly mitigation measures are implemented. Ideally such work would also incorporate data on hedgehog density so that effects at a population level could also be investigated. Furthermore, such data would help determine if collisions are occurring due to increase abundance or road / roadside characteristics.

8. Reducing uncertainty around hedgehog demographics will allow conservation efforts to be properly targeted. Working with hedgehog carers / rescues may be of some use to collect this data. For instance, data on litter size and sex ratio could be recorded in these situations easily without the need to get a licence or disturb wild hedgehogs.
9. Investigating hedgehog decline in the absence of predators and competitors, e.g. on Jersey, could provide novel insight and prove valuable to hedgehog conservation. Such work could be compared to similar work in the presence of predators and competitors and help to separate the issues of habitat, food, predation and competition.
10. Little is known about when hedgehogs disperse and how far they move. Dispersal is fundamental to gene flow within and between populations; therefore, such studies would be beneficial particularly in agricultural landscapes and between towns / villages.
11. There is some evidence that hedgehogs are not always released back to the same areas they originated. While this may be helping to overcome obstacles to gene flow it could also be facilitating the spread of e.g. disease and parasites (Chipman *et al.* 2008). Current advice is to release individuals back to the site of origin, wherever possible. Work is warranted to get a better understanding of the current protocols wildlife rescues use and the extent to which hedgehogs are translocated.

Conclusion

To conclude, in this thesis I have validated a novel method for monitoring hedgehog occupancy in rural and suburban / urban habitats and identified the key factors influencing this. In addition, I investigated how roads affect hedgehog populations through potential fragmentation and causes of road-kill. Finally, I undertook a desktop exercise to gain a better understanding of hedgehog population demographics and identify areas requiring further research.

I contend that whilst hedgehogs are still declining in Britain the future does have hope and that given new monitoring methods and a better understanding of the drivers of decline small changes can have a big impact on their survival.

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