Factors Affecting Hedgehog Distribution and Habitat Selection in Rural Landscapes



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This thesis is dedicated to

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Abstract

The UK population of hedgehogs (*Erinaceus europaeus*) has halved in rural areas between 2005 and 2015, and hedgehogs select urban areas over arable land. Explanations for the unsuitability of arable land for hedgehogs include: high predation risk by badgers (*Meles meles*), low prey densities, cold microclimates and low availability of nest sites. I investigated the reasons for hedgehog avoidance of arable land by measuring hedgehog habitat use, ranging behaviour, daily energy expenditure (DEE) and diet along a gradient of habitats from rural villages to arable farmland, under varying predation threat and temperatures. I also examined which factors affected hedgehog presence and abundance nationally. Hedgehogs preferentially selected urban habitats for both foraging and nesting, including gardens and buildings. A hedgehog's mean distance to buildings over a season was positively correlated with home range size and DEE, conceivably due to higher prey availability in rural villages and the need for increased movement on arable land to achieve sufficient food intake. I found little evidence that the prey taxa hedgehogs consumed changed along the gradient from buildings to arable land, although all hedgehogs consumed pet food, suggesting that supplementary feeding is one reason hedgehogs are attracted to buildings. On sites where badgers were present hedgehogs stayed closer to edge habitats and buildings, had smaller home ranges, spent less time on arable land, and had a lower DEE. Badger presence is one likely cause of hedgehogs' avoidance of arable land and their selection of rural villages, where badgers are found at lower densities. Nationally, badger abundance and fox (*Vulpes vulpes*) abundance was negatively associated with hedgehog abundance. Landowners on farms under Higher Level Stewardship (HLS) were more likely to report having seen hedgehogs than landowners on farms not under HLS. I conclude that rural villages are a key habitat for sustaining hedgehog numbers in the countryside and the connectivity between these island populations should be enhanced through the implementation of agri-environment schemes. Higher-tier schemes may also increase habitat complexity, which could potentially reduce the predation pressure from badgers, as well as enhancing hedgehogs' invertebrate food supply.

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Contents

Abstract i

Acknowledgements ii

Chapter 1: Introduction **1**

Biodiversity loss on arable land 2

The European hedgehog 3

Thesis aims 6

Thesis overview 7

Thesis chapters 8

References 9

Chapter 2: A pilot study of hedgehog (Erinaceus europaeus) habitat use and distribution in rural areas **15**

Abstract 17

Introduction 18

Review of hedgehog habitat use 20

Hedgehog survey 25

Hedgehog release study 27

Conclusions 34

References 35

Chapter 3: Hedgehog (*Erinaceus europaeus*) movement and habitat use on arable land under threat from badger (*Meles meles*) predation **40**

Abstract 42

Introduction 43

Methods 45

Results 52

Discussion 67

References 71

Appendix 76

Chapter 4: Daily energetic expenditure in the face of predation: hedgehog energetics in rural landscapes **78**
Abstract 80
Introduction 81
Methods 84
Results 92
Discussion 99
References 105
Appendix 111
Chapter 5: Hedgehog diet in rural Britain as revealed by molecular analysis **118**
Abstract 120
Introduction 121
Methods 123
Results 130
Discussion 142
References 148
Appendix 154
Chapter 6: National predictors of hedgehog distribution and decline in Britain **162**
Abstract 164
Introduction 165
Methods 167
Results 171
Discussion 189
References 196
Appendix 200
Chapter 7: Discussion **202**
Overview 203
Evidence for higher forage availability in rural villages 204
Risk of badger predation on arable land 205
Availability of nesting habitat in rural villages 208
The effect of microclimate on hedgehog distribution 208
Conservation implications 209
Further research 212
References 214

Introduction

Biodiversity loss on arable land

An alarming number of the world's species are becoming extinct. It has been argued that biodiversity losses at the current rate constitute a sixth major extinction event (Pimm *et al.* 1995; Barnosky *et al.* 2011). There are currently over 23 thousand species listed as 'threatened' worldwide, a figure which may be a considerable underestimate as not all species have been described and evaluated (IUCN Red List 2015). The greatest current threat to species persistence is habitat loss and degradation followed by direct exploitation and the introduction of invasive species (Hilton-Taylor 2000).

Arable land covers 11% of land on earth and 25% of the land in the UK (FAO 2012). In the UK, intensification of arable farming in the 20th century, accompanied by increases in the use of pesticides and other inputs, has been associated with severe losses of biodiversity (Stoate *et al.* 2001; Foley *et al.* 2005; Macdonald & Feber 2015). Intensification has resulted in trends towards larger farms with larger fields, coupled with the removal of edge habitat such as hedgerows, field margins and ditches (Stoate *et al.* 2001; Robinson & Sutherland 2002). The loss of edge habitat not only directly impacts on species on farmland (e.g. birds; Arnold 1983; Lack 1988; Cornulier *et al*. 2011), but also reduces connectivity between habitat patches (Forman & Baudry 1984; Michel, Burel & Butet 2006). Invertebrate feeders have been further impacted by the loss of prey resulting from chemical application (Moreby & Southway 1999; Wilson *et al.* 1999; Robinson & Sutherland 2002).

Intensification on arable land has been implicated in the decline of a range of species on farmland in the UK including: flowering plants (Sotherton & Self 2000), invertebrates (Aebischer 1990, 1991; Wilson *et al.* 1999; Sotherton & Self 2000), birds (Fuller *et al.* 1995; Chamberlain *et al.* 2000; Donald, Green & Heath 2001) and small mammals (Tattersall & Tew 2015). Here I focus on small mammal species, which are understudied in comparison with farmland birds. Small mammal declines in the UK, at least partially resulting from this intensification, have been documented in brown hares *Lepus europaeus* (Smith, Jennings & Harris 2005), water voles *Arvicola terrestris* (Jefferies, Morris & Mulleneux 1989; Strachan, Strachan & Jefferies 2000), field voles *Microtus agrestis* (Harris *et al.*

1995) and hedgehogs *Erinaceus europaeus* (Aebischer, Davey & Kingdon 2011; Roos, Johnston & Noble 2012).

As the impact of intensive farming on biodiversity was recognised, agri-environment schemes were introduced into Britain in 1987, with the aim of encouraging farmers to conserve natural features of the land in return for payment (Natural England 2009). These schemes are thought to increase the value of arable land for some small mammal species through increased set-aside (Macdonald *et al.* 2007), grassy field margins (Shore *et al.* 2005), hedgerows (Gelling, Macdonald & Mathews 2007) and prey abundance (Thomas *et al.* 2001; Vickery, Feber & Fuller 2009), yet there is little effective ecological monitoring on the ability of agri-environment schemes to curtail species declines (Kleijn & Sutherland 2003). Therefore, further research into the benefit of agri-environment schemes for small mammals is needed.

Here the European hedgehog is used as a model species to study the value of arable land and agri-environment schemes for small mammals. The hedgehog primarily feeds on macroinvertebrates (Yalden 1976; Wroot 1984) and therefore its occurrence indicates an abundance of invertebrates, which are not only prey for other small mammals, bats and birds (Wilson *et al.* 1999; Wickramasinghe *et al.* 2004), but are indicators of soil quality, such as microfauna assemblages, pH, and fertility (Paoletti 1999; Irmler 2003). Hedgehogs select edge habitats including hedgerows and field margins (Doncaster, Rondinini & Johnson 2001; Riber 2006; Hof & Bright 2010a, 2012) and therefore can be used to study connectivity of habitat patches on farmland.

The European hedgehog

The Western European hedgehog, *Erinaceus europaeus* (Linnaeus 1758), is a small nocturnal mammal in the sub-family Erinaceinae, or spiny hedgehogs, of the order Eulipotyphla. The current distribution of the species includes Western Europe- up to a longitude of 15^{o} East- the UK, the Republic of Ireland and Southern Scandinavia (Reeve 1994). In Britain the hedgehog is widespread but patchily distributed (Hof 2009; Aebischer *et al.* 2011; Roos *et al.* 2012). Hedgehogs are

traditionally associated with hedgerows on farmland (Hof & Bright 2010a), yet they are abundant in urban and suburban habitats and are common visitors to gardens (Hof & Bright 2009; Dowding *et al.* 2010a).

Hedgehogs are generalist predators, primarily feeding on macroinvertebrates such as earthworms, Carabid beetles and caterpillars, yet their diet also includes a wide range of other prey including amphibians, small mammals, birds eggs and scavenged human food waste (Yalden 1976; Wroot 1984). Hedgehogs spend up to 70% of their time foraging (Riber 2006) and are relatively mobile with males, which have larger home ranges than females (Reeve 1981, 1982; Kristiansson 1984; Hof & Bright 2010a; Haigh, O'Riordan & Butler 2013; Rautio, Valtonen & Kunnasranta 2013), frequently travelling over 1km in one evening (Reeve 1981, 1982). In Britain and Ireland hedgehogs hibernate from October/November until March/April, with common spontaneous arousals (Morris 1973; Haigh, O'Riordan & Butler 2012). Soon after emergence from hibernation, hedgehogs begin to mate and continue to do so throughout the active season, with a peak in May-August (Reeve 1981).

The main predator of the hedgehog on farmland is the European badger (*Meles meles)* (Doncaster 1992; Hof & Bright 2010a). Hedgehogs are also attacked by foxes and domestic dogs (Doncaster 1994; Reeve 1994), but badgers are the only predator thought to be able to uncurl a hedgehog from its defensive position (Neal 1986). The presence of badgers is thought to be particularly detrimental to hedgehogs because they are intraguild predators and compete with hedgehogs for earthworms (Neal 1986; Polis, Myers & Holt 1989; Doncaster 1992). Badgers may therefore exclude hedgehogs from productive habitats and alter their foraging behaviour (Doncaster 1992; Ward, Macdonald & Doncaster 1997; Ward, Austin & MacDonald 2000; Hof, Snellenberg & Bright 2012).

The hedgehog was voted Britain's National Species in a recent online poll (BBC Wildlife Magazine 2013). However, the hedgehog was not always well-loved in Britain; hedgehogs were disliked for stealing hen's eggs and in European folklore hedgehogs suckled milk from cows after dark (Reeve 1994; Morris 2006; Lovegrove 2007). Hedgehogs were therefore considered vermin and potentially

over half a million were killed from the sixteenth to the nineteenth century (Lovegrove 2007). Nowadays, not only have hedgehogs risen to meteoric popularity with the general public, they are recognised as an important indicator of the health of agricultural land.

The hedgehog decline

The British population of European hedgehogs is thought to have fallen from 1.5 million in 1995 (Harris 1995) to less than one million in 2015 (PTES & BHPS 2015), and the rural population of hedgehogs is thought to have halved in the last ten years (PTES & BHPS 2015). Additionally, radio-tracking studies of hedgehogs have shown that they typically avoid arable land (Doncaster 1992, 1994; Doncaster *et al.* 2001).

There are several potential causes of the hedgehog decline in rural areas. Hedgehog habitat use is linked to prey availability, particularly of earthworms (Micol, Doncaster & Mackinlay 1994; Young *et al.* 2006), which occur at relatively low abundances on intensively managed arable land (Curry, Byrne & Schmidt 2002; Smith *et al.* 2008). Agricultural chemicals cause a decrease in prey abundance (Moreby & Southway 1999; Wilson *et al.* 1999), but also may be toxic to hedgehogs through direct consumption (Brakes & Smith 2005) and bioaccumulation, particularly rodenticides and molluscicides (Dowding *et al.* 2010b).

Since 1945, 50% of the hedgerows in Britain have been removed (Robinson & Sutherland 2002) and less than 10% of remaining hedgerows on arable land are in good structural condition (Carey *et al.* 2008). Loss of edge habitat removes important foraging and nesting habitat for hedgehogs (Hof & Bright 2010a; Haigh *et al.* 2012). Hedgerows also offer vital shelter from predation (Hof & Bright 2012); hedgehogs radio-tracked on sites where badgers were present were found on average 38m closer to edge cover than hedgehogs on sites without badgers (Hof *et al.* 2012). A decrease in habitat structure, for example through the removal of hedgerows, therefore exacerbates the effects of intraguild predation on hedgehogs (Janssen *et al.* 2007). Changes in the productivity of a shared habitat can also alter the relationship between intraguild predators and their prey (Polis *et al.* 1989;

Holt & Polis 1997; Morin 1999), and thus a reduction in the availability of invertebrates on arable land may also increase predation pressure on hedgehogs.

The implementation of agri-environment schemes has not prevented the decline of hedgehogs on arable land in the UK. However, it is unknown whether hedgehog declines would have been more severe without agri-environment scheme enhancement. Despite arable land not being favoured by hedgehogs, when hedgehogs do use arable land, agri-environment hedgerows and field margins are highly selected (Hof & Bright 2010a). Grassy field margins sustain high numbers of macroinvertebrates (Thomas *et al.* 2001; Meek *et al.* 2002; Woodcock *et al.* 2007; Hof & Bright 2010b) and thus they are beneficial for hedgehogs (Hof & Bright 2010a). Agri-environment scheme hedgerows are valuable for nesting (Hof & Bright 2010a; Haigh *et al.* 2012), as refuge from badgers (Hof *et al.* 2012), and as dispersal corridors (Doncaster, Micol & Jensen 1996; Moorhouse *et al.* 2014).

Thesis aims

The aim of this thesis, at its inception in 2012, was to explore how agri-environment scheme options on arable land might be improved to increase their value for hedgehogs and other small mammals. It was hoped that assessment of habitat use, movement and nesting patterns would point to specific management options for this purpose. However, initial fieldwork undertaken in Oxfordshire (see Chapter 2) suggested that hedgehogs avoided arable land, regardless of the presence or type of agri-environment schemes in favour of rural villages. In the light of these preliminary observations, the thesis then took a new direction; investigating the specific factors that cause hedgehogs to favour village habitats over arable land. Unpicking the contribution of these factors will allow us to establish how arable land might be improved to sustain higher numbers of hedgehogs and slow the hedgehog decline in rural areas.

Thesis overview

A pilot study in Oxfordshire (Chapter 2) indicated five key factors that may cause hedgehogs to avoid arable land and select villages:

1) Badger presence; badgers are at higher numbers on farmland and thus villages act as a refuge from predation (Hof *et al.* 2012)
2) Lack of natural prey items, particularly earthworms, on arable land, which are abundant on mowed grass habitats in villages such as garden lawns and amenity grassland (Micol *et al.* 1994; Young *et al.* 2006; Dowding *et al.* 2010a)
3) An attraction to supplementary feeding in villages (Hubert *et al.* 2011)
4) A lack of nesting sites on arable land compared with in villages, such as under garden sheds and under shrubs (suggested by Reeve 1998)
5) Microclimate; cold temperatures on open farmland due to hedgerow removal and warmer microclimate in villages due to shelter from the wind and urban warming (Forman & Baudry 1984; Hubert *et al.* 2011)

This thesis will investigate each of the above factors in an attempt to provide evidence of the causes of the apparent unsuitability of arable land for hedgehogs. The research will result in outlining possible conservation measures to mitigate the effect of the unsuitable aspects of arable farmland for hedgehogs, thus permitting hedgehogs to use the land surrounding rural villages and halting the decline of hedgehogs in rural areas.

Thesis chapters

Chapter 2: A pilot study investigating hedgehog habitat used and distribution in rural areas. The work undertaken included a hedgehog survey on six predominately arable farms in Oxfordshire and the release and radio-tracking of 12 hedgehogs on three predominately arable farms in Oxfordshire.

Chapter 3: This chapter examines the contribution of expected drivers of hedgehog attraction to rural villages by quantifying hedgehog habitat use, home range size, and distance to key habitat features on four predominately arable sites, under varying predation threat and climatic conditions.

Chapter 4: This chapter investigates variation in hedgehog daily energetic expenditure- measured by the doubly labelled water method- body condition and ranging behaviour along a gradient of habitats from rural villages to arable land at sites, with and without badgers, to isolate the causes of the hedgehog's apparent preference for village habitats.

Chapter 5: Here I use molecular methods to amplify prey DNA from hedgehog faecal samples and assess differences in hedgehog diet on a gradient from rural villages to open arable farmland, under varying predation threat from badgers.

Chapter 6: This study uses a volunteer survey of mammal roadkill, Mammals on Roads (MoR), and a questionnaire sent to 4000 farmers, to examine which factors affect hedgehog presence, abundance and changes in hedgehog abundance nationally.

Chapter 7: Discussion: a synthesis of the overall findings in an attempt to draw conclusions on factors affecting hedgehog distribution in rural landscapes. I also discuss the conservation implications of this thesis.

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Chapter 2

A pilot study of hedgehog (*Erinaceus europaeus*) habitat use and distribution in rural areas

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Abstract

Hedgehogs are declining in the UK and the decline is thought to be the most severe in rural areas, with arable land being particularly unfavourable for hedgehogs. Possible reasons for this decline stem from the intensification of farming in the UK in the 1950s and include a reduction in invertebrate prey due to the increased use of pesticides and a lack of cover and nesting sites due to the removal of hedgerows. Agri-environment schemes were introduced in the UK in the 1908s with the aim of managing the land in an environmentally sensitive manner and therefore halting declines in farmland species. This study aimed to investigate hedgehog distribution and habitat use in relation to agri-environment features such as managed hedgerows and grassy field margins. The study included a review of hedgehog habitat use in rural areas of the UK, a footprint tunnel survey of six arable dominated farms in Oxfordshire and the release and radio-tracking of 12 hedgehogs onto three arable farms in Oxfordshire, to assess how dispersing hedgehogs behave in relation to agri-environment scheme enhancements. The studies reviewed here indicated that arable land and woodland are under-selected by hedgehogs at national, landscape and field scales in the UK and hedgehogs are associated with residential areas such as rural villages. Throughout the hedgehog survey only one set of hedgehog footprints was found, indicating a low abundance of hedgehogs on arable land in Oxfordshire. Eighty percent of the released hedgehogs, that were still being tracked after 30 days, left open farmland in favour of habitats associated with humans including villages, allotments and gardens. We conclude that hedgehogs show a clear preference for villages and gardens over open farmland, particularly arable land, and this is not affected by current agri-environment scheme measures. Possible reasons for the avoidance of arable land include a lack of invertebrate prey, the presence of the hedgehog's main predator the badger (*Meles meles*) on arable land, a lack of nest sites on arable land and a cold microclimate. These factors require further investigation in order to find conservation measures to prevent further declines of the hedgehog in rural areas.

Introduction

In the UK, intensification of arable farming in the 20th century, accompanied by increases in the use of pesticides and other inputs, has been associated with severe losses of biodiversity (Stoate *et al.* 2001; Foley *et al.* 2005; Macdonald & Feber 2015). Intensification on arable land has been implicated in the decline of a range of species on farmland in the UK including: flowering plants (Sotherton & Self 2000), invertebrates (Aebischer 1990, 1991; Wilson *et al.* 1999; Sotherton & Self 2000), birds (Fuller *et al.* 1995; Chamberlain *et al.* 2000; Donald, Green & Heath 2001) and small mammals (Tattersall & Tew 2015). One such small mammal in decline in the UK is the European hedgehog, the population of which is thought to have fallen from 1.5 million in 1995 (Harris 1995) to less than one million in 2015 (PTES & BHPS 2015), and the rural population of hedgehogs is thought to have halved in the last ten years (PTES & BHPS 2015).

There are several potential causes of the hedgehog decline in rural areas, many of which stem from agricultural intensification. Hedgehog habitat use is linked to prey availability, particularly of earthworms (Micol, Doncaster & Mackinlay 1994; Young *et al.* 2006), which occur at relatively low abundances on intensively managed arable land (Curry, Byrne & Schmidt 2002; Smith *et al.* 2008). Agricultural chemicals cause a decrease in prey abundance (Moreby & Southway 1999; Wilson *et al.* 1999), but also may be toxic to hedgehogs through direct consumption (Brakes & Smith 2005) and bioaccumulation, particularly rodenticides and molluscicides (Dowding *et al.* 2010b).

Since 1945, 50% of the hedgerows in Britain have been removed (Robinson & Sutherland 2002) and less than 10% of remaining hedgerows on arable land are in good structural condition (Carey *et al.* 2008). Loss of edge habitat removes important foraging and nesting habitat for hedgehogs (Hof & Bright 2010a; Haigh, O'Riordan & Butler 2012b). Hedgerows also offer vital shelter from predation (Hof & Bright 2012); hedgehogs radio-tracked on sites where badgers were present were found on average 38m closer to edge cover than hedgehogs on sites without badgers (Hof, Snellenberg & Bright 2012). A decrease in habitat structure, for example through the removal of hedgerows,

therefore exacerbates the effects of intraguild predation on hedgehogs (Janssen *et al.* 2007). Changes in the productivity of a shared habitat can also alter the relationship between intraguild predators and their prey (Polis, Myers & Holt 1989; Holt & Polis 1997; Morin 1999), and thus a reduction in the availability of invertebrates on arable land may also increase predation pressure on hedgehogs.

Agri-environment schemes were introduced into Britain in 1987, with the aim of encouraging farmers to conserve natural features of the land in return for payment (Natural England 2009). These schemes are thought to increase the value of arable land for some small mammal species through increased set-aside (Macdonald *et al.* 2007), grassy field margins (Shore *et al.* 2005), hedgerows (Gelling, Macdonald & Mathews 2007) and prey abundance (Thomas *et al.* 2001; Vickery, Feber & Fuller 2009). Agri-environment scheme hedgerows and field margins are highly selected by hedgehogs on arable land (Hof & Bright 2010a). Grassy field margins sustain high numbers of the hedgehog's macroinvertebrate prey (Thomas *et al.* 2001; Meek *et al.* 2002; Woodcock *et al.* 2007; Hof & Bright 2010b) and agri-environment scheme hedgerows are valuable for nesting (Hof & Bright 2010a; Haigh *et al.* 2012b), as refuge from badgers (Hof *et al.* 2012), and as dispersal corridors (Doncaster, Micol & Jensen 1996; Moorhouse *et al.* 2014).

This chapter details a pilot study undertaken in Oxfordshire to establish a preliminary picture of hedgehog habitat use and distribution in rural areas in relation to agri-environment scheme features. The aim was to ascertain which features should be promoted to improve arable land for hedgehogs and prevent further declines in rural areas. This introductory research comprised:

1) A literature review of existing studies into hedgehog habitat use in rural areas;
2) A survey of arable dominated farmland in Oxfordshire to assess the abundance and distribution of hedgehogs in relation to agri-environment scheme enhancements;

3) A hedgehog release onto arable land with fine scale radio-tracking of hedgehog habitat use to assess how dispersing hedgehogs behave in relation to agri-environment scheme enhancements.

Below I detail the above three pieces of preparatory work and discuss the implications of each.

Review of hedgehog habitat use

For the purposes of this review, I will mainly focus on studies in the UK in relation to hedgehog habitat selection. However, I do include studies from Europe where relevant. I will look at four main types of study; national surveys, local hedgehog surveys including spotlight surveys and footprint tunnel surveys, hedgehog release studies- where hedgehogs are translocated from existing populations or rehabilitated hedgehogs are released and tracked- and radio-tracking studies of wild hedgehogs. I will review the potential causes of hedgehog habitat selection and the possible reasons for the unsuitability of habitats that are avoided. A summary of key studies into hedgehog habitat selection is presented in Table 1.

National surveys in the UK have been carried out by recording volunteer sightings (Hof 2009; Hof & Bright 2009; Roos, Johnston & Noble 2012), game bag counts (Aebischer, Davey & Kingdon 2011), questionnaires (Hof & Bright 2012) and roadkill (Hof 2009). The evidence from all national surveys shows varying degrees of decline in hedgehogs in the UK in the last ten years, and there is regional variety in the strength of the decline (Aebischer *et al.* 2011; Roos *et al.* 2012), with hedgehogs being in highest abundance in the arable-dominated landscapes of the North East and East of England (Hof 2009; Hof & Bright 2012). An analysis of hedgehog sightings from the national survey HogWatch found that hedgehogs avoided arable land and selected coniferous woodland (Hof 2009). A questionnaire sent to 4000 farmers across Britain in 2006 found that hedgehogs were seen most frequently in gardens followed by grassland and deciduous woodland and were seen the least on heathland and, in disagreement to the national survey sightings, in coniferous woodland (Hof & Bright 2012).

Table 1 A review of habitat selection by hedgehogs in the UK from four types of hedgehog studies: national surveys, spotlight surveys, release studies and radio-tracking studies.

Study	Method	Location	Study area habitat	No. sites	Habitat preferences	Habitat avoidance	Suggested causes of habitat preference
Hof 2009	Volunteer sightings	National, UK	Gardens, roads, road verges	NA	Coniferous woodland	Arable	Badger numbers, roads
Hof & Bright 2012	Questionnaire to farmers	National, UK	Farmland	NA	Garden, grassland, deciduous woodland	Coniferous woodland, heathland	Badger numbers
Micol *et al.* 1994	Spotlight surveys	Oxfordshire, UK	Pasture, amenity grassland	6	Amenity grassland, suburban	Pasture	Badger activity, earthworm abundance, proximity to town
Young *et al.* 2006	Spotlight surveys	Midlands and South-West England, UK	Pasture, amenity grassland	10	Amenity grassland, suburban	Pasture	Badger sett density. earthworm abundance
Hubert *et al.* 2011	Spotlight surveys	Ardennes, France	Mixed farmland, urban	1	Garden lawns	Arable Woodland	Availability of pet food and earthworms, nest sites and microclimate
Doncaster 1992	Release study	Oxfordshire, UK	Woodland and pasture	2	Urban, grass fields	Arable Woodland	Badgers excluded hedgehogs from habitats with suitable prey
Doncaster 1994	Release study	Oxfordshire, UK	Mixed farmland, urban	3	Pasture, mowed grass fields, urban	Arable	Badger presence, earthworm abundance
Reeve 1998	Release study	Surrey, UK	Woodland, mixed farmland, urban	2	Urban	Woodland	Mate availability, prey availability, nest sites, villages, fewer badgers in urban areas
Doncaster *et al.* 2001	Release study	Oxfordshire, UK	Mixed farmland	4	Edge habitat, roads and urban	Arable	Badger numbers
Doncaster 1993	Radio-tracking	Oxfordshire, UK	Mixed farmland	1	Pasture	Arable	Prey availability
Riber 2006	Radio-tracking	Aarhus, Denmark	Arable land	1	Forest edge, woodland	Arable	Invertebrate density, microclimate
Huijser 2000	Radio-tracking	Elburg, Netherlands	Mixed farmland	1	Hedgerows, grassland, edge habitat	Forest, arable	Hedgerow used for resting and travelling, grassland for foraging

Table 1 *Continued*

Study	Method	Location	Study area habitat	No. sites	Habitat preferences	Habitat avoidance	Possible causes of habitat preference
Dowding *et al.* 2010	Radio-tracking	Bristol, UK	Urban	1	Rear gardens of terraced and semi-detached houses.	Roads, gardens of detached houses	Prey availability, risk from badger predation, road traffic
Hof & Bright 2010	Radio-tracking	Norfolk, UK	Arable land	1	Hedgerows and field margins. Females: village habitats	Centre of arable fields	Food availability, cover from predation, nest sites
Hof *et al.* 2012	Radio-tracking	Lincolnshire, Berkshire, Leicestershire, Norfolk, UK	Arable land	4	Edge habitats, village when badgers present	Centre of arable fields, open ground	Perceived risk of predation by badgers
Haigh *et al.* 2013	Radio-tracking	County Cork, Ireland	Mixed farmland	1	Gardens, arable	Woodland, marsh	Increase in invertebrate numbers on arable land after harvesting

Surveys on a local scale have assessed hedgehog occupancy by spotlight surveys, footprint tunnels and live captures, and spotlight surveys are thought to be particularly successful in detecting hedgehogs in rural areas (Haigh, Butler & Riordan 2012a). Micol *et al.* (1994) and Young (2006) carried out spotlight surveys in grass fields and found that hedgehogs show a preference for mowed amenity grassland fields in suburban areas over pasture fields on open farmland. Hubert *et al.* (2011) carried out spotlight surveys on transects in a range of habitats in rural France and found that over 70% of captures were on garden lawns compared with 14% in pasture fields, 4-6% on arable land and meadows and 0% in woodland. Yarnell *et al.* (2014) carried out footprint tunnel surveys at 111 sites across the UK and although there was no evidence for an effect of habitat on occupancy, the study found that hedgehogs were twice as likely to be present on sites without badgers than they were on sites occupied by badgers.

Doncaster carried out several perturbation studies involving the translocation of hedgehogs from high quality habitats to low quality habitats (Doncaster 1992, 1994; Doncaster *et al.* 2001). Dispersing hedgehogs showed a preference for suburban areas such as villages and gardens, edge habitats and grass fields and avoided arable land and woodland. Other studies have radio-tracked hedgehogs after rehabilitation. Reeve (1998) released ten hedgehogs into woodland and two hedgehogs into an urban area and found that hedgehogs released in woodland dispersed away from woodland in favour of residential areas and the two hedgehogs released in urban areas did not disperse.

Radio-tracking studies of wild hedgehogs on farmland have shown hedgehogs to have a preference for field edges such as field margins and hedgerows and pasture is preferred over arable land (Huijser 2000; Hof & Bright 2010a; Hof *et al.* 2012). Rural villages are also heavily used by hedgehogs, particularly by females (Hof & Bright 2010a). Habitat selection on arable land varies by month due to the changing nature of farmland throughout the season, for example during ploughing and after harvesting the centre of arable fields are utilised by hedgehogs (Haigh *et al.* 2013).

Although there was a range of methods used in these studies, there are similarities in the potential causes of hedgehog habitat selection raised by researchers. Badger predation is thought to regulate hedgehog populations in rural areas (Hof & Bright 2010a) and nationally hedgehog numbers are negatively correlated with badger numbers (Hof 2009; Hof & Bright 2012). At the field scale, spotlight surveys of grass fields found that hedgehog abundance was negatively correlated with the regional density of badger setts (Young *et al.* 2006) and with badger activity (Micol *et al.* 1994). Hedgehogs also prefer not to forage in the presence of badger odour (Ward, Macdonald & Doncaster 1997) and dispersal away from areas with high badger numbers is a common observation in release studies (Doncaster 1992, 1994; Doncaster *et al.* 2001). Badgers tend to be in lower numbers in urban areas, and thus village habitats may be preferred when badgers are present as they offer cover and lower risk from badger predation (Hof *et al.* 2012). Dowding *et al.* (2010a)

found that hedgehogs in urban areas selected the back gardens of terraced and semi-detached houses and females avoided the large back gardens of detached houses and they speculated this avoidance was due to larger gardens being favoured by badgers (Dowding *et al.* 2010a). Badger setts are often in woodland (Neal & Cheeseman 1996) and woodland was avoided by hedgehogs in several of the studies (Doncaster 1992; Reeve 1998; Hubert *et al.* 2011; Haigh *et al.* 2013). Studies of wild hedgehogs in countries with lower badger numbers than the UK have found hedgehogs to utilise woodland and open arable land (Riber 2006; Haigh *et al.* 2013).

Hedgehogs are generalist predators and a high proportion of their diet comprises macroinvertebrates (Yalden 1976; Wroot 1984). Mowed grass habitats in urban areas, such as amenity grassland and garden lawns, sustain high numbers of macroinvertebrate prey compared with intensively managed farmland (Micol *et al.* 1994; Curry *et al.* 2002; Young *et al.* 2006; Dowding *et al.* 2010b). Hedgehog presence on amenity grassland and pasture fields is positively correlated with earthworm abundance (Doncaster 1994; Micol *et al.* 1994; Young *et al.* 2006) and the selection of edge habitats in arable fields is associated with high invertebrate abundance on grassy field margins (Hof & Bright 2010a; b). Pasture has higher numbers of earthworms per unit area than arable land but is a preferred habitat of badgers (Kruuk *et al.* 1979). Badgers may exclude hedgehogs from habitats with suitable prey (Doncaster 1992), and badger numbers in the surrounding area may affect the numbers of hedgehogs in suburban habitats (Young *et al.* 2006).

Hedgehogs are known to eat supplementary food and scavenge for domestic waste in residential areas (Yalden 1976; Morris 1985). In rural France, hedgehog occupancy was positively correlated with counts of domestic cats in the area, a proxy for pet food availability (Hubert *et al.* 2011). Hubert *et al.* also raise the question of microclimate and hypothesised that urban warming in residential areas may be of possible benefit to hedgehogs during hibernation. Reeve (1998) suggested that another possible explanation for hedgehogs dispersal towards urban areas could be a lack of wild hedgehogs to mate with in the release area. However, this raises the question of why hedgehogs

were not in the release area to begin with. Reeve also suggested that there may be more secure nesting sites in urban areas, for example in out-houses and garden sheds.

In summary, the evidence from the studies reviewed here indicates that arable land and woodland are unfavourable for hedgehogs at national, landscape and field scales in the UK and hedgehogs are associated with residential areas and rural villages. Throughout the range of studies discussed, two factors are repeatedly raised as indicators of hedgehog selection of villages and gardens. Firstly the abundance of macroinvertebrate prey, in particular earthworms is typically higher in habitats associated with humans. Secondly, badger presence, which may manifest itself in two ways: by direct predation, which appears to be more likely on open farmland than in rural villages, and by hedgehogs avoiding badgers by selecting village habitats, which badgers are typically absent from. Other potential causes discussed here include, attraction to the warmer microclimate and higher abundance of supplementary food available in villages (typically pet food), a greater availability of secure nest sites in villages and an attraction to areas with a high number of conspecifics in villages.

Hedgehog survey

Methods

We used footprint tunnels, previously found to be a successful method for detecting hedgehog presence (Huijser & Bergers 2000; Yarnell *et al.* 2014), to survey six predominately arable farms in Oxfordshire in 2012 (Fig.1). The farms varied in agri-environment scheme options; two farms had 4-6m grassy margins, two were organic with 4-6m grassy and two were control farms with no field margins and non-organic farming (Table 2). The farms had predominately cereal crops, with some fields of oilseed rape and pasture, and one organic farm had several fields of set-aside. Ten baited tunnels were placed on each of the six farms in late March and April 2012. Tunnels were placed along hedgerows in arable fields, at least 100m apart and were checked once a day for six days. Sites were divided into two blocks, A and B, each containing a farm in each treatment type. Block A was

surveyed first and block B immediately after in order to minimise differences in environmental variables and the amount of time hedgehogs had been active since spring emergence.

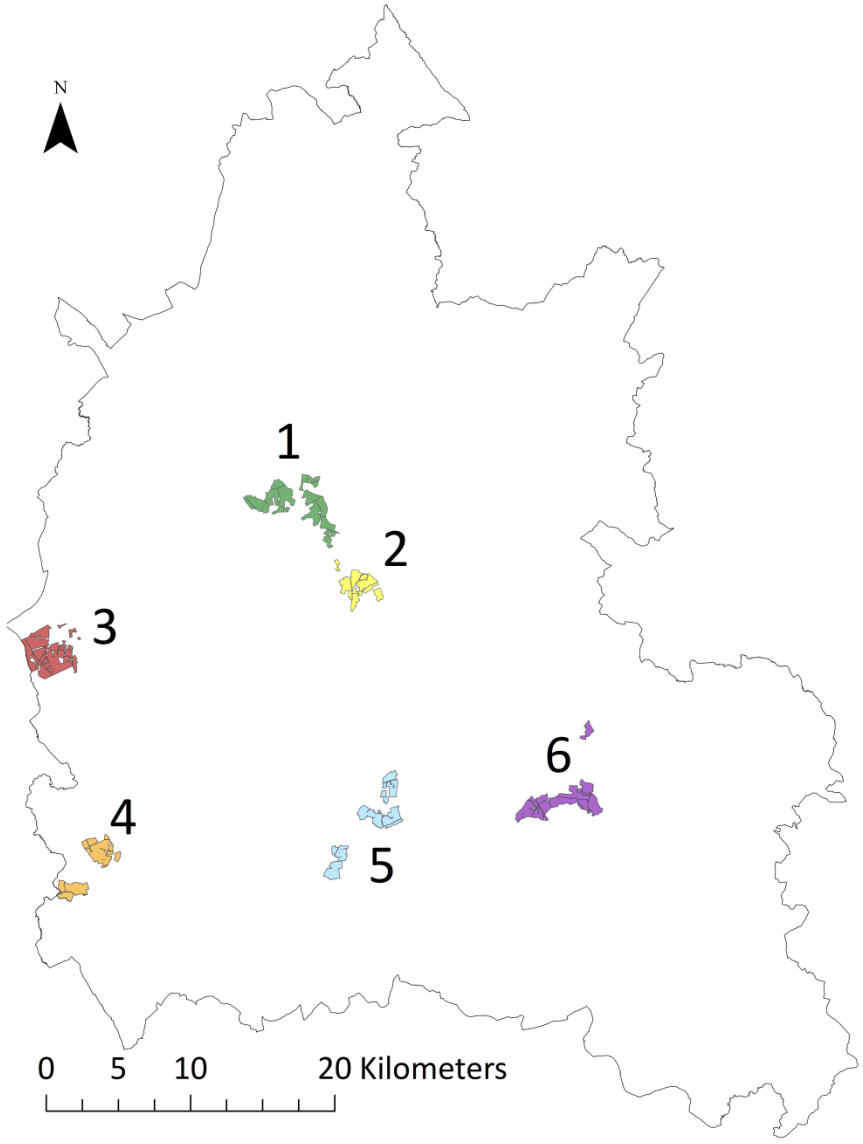


Fig.1 The location of six farms in Oxfordshire surveyed in 2012 for hedgehogs, using footprint tunnels

Table 2 Details of six farms in Oxfordshire surveyed in 2012 for hedgehogs, using footprint tunnels

Site	UK grid refs	Farm size (ha)	Agri-environment scheme	Type	Block	Survey date
1	SP 41162 17252	801	ELS	No margins	A	22/03/2012
2	SP 44982 12964	379	ELS	No margins	B	04/04/2012
3	SP 23667 07978	743	Organic ELS	Grassy margins	A	22/03/2012
4	SU 25248 94021	489	Organic ELS + HLS	Grassy margins	B	04/04/2012
5	SU 45495 96506	606	ELS	Grassy margins	A	22/03/2012
6	SU 59960 96328	708	ELS	Grassy margins	B	04/04/2012

ELS= Entry Level Stewardship, HLS= Higher Level Stewardship

Results

Throughout the survey only one set of hedgehog footprints was found. These footprints were found on one of the organic farms (Farm 4), in a barley field with 4m grassy margins. A further survey of this barley field, and the fields around it, in the week following the finding, detected no further footprints. The surveys were repeated in the pasture fields on the farms and one wholly pasture farm in order to ascertain whether hedgehogs were on the farms but simply avoiding the arable fields. No further hedgehog footprints were found.

Discussion

Previous validation studies of footprint tunnels across the UK have found that if hedgehogs are absent after 3.6 ± SE 2.9-4.6 days, it can be said with 95% confidence that hedgehogs are truly absent (Yarnell *et al.* 2014). Thus, the results of the study indicated a low abundance of hedgehogs on arable farmland in Oxfordshire. It appears that hedgehogs were not utilising either arable or pastoral farmland, despite agri-environment scheme enhancements on the farms studied. Previous studies have successfully used the release and radio-tracking of rehabilitated hedgehogs to lead researchers to wild hedgehogs on arable land (Hof & Bright 2010a), and therefore a hedgehog release onto the farms assessed here would be useful in ground-truthing the survey results.

Hedgehog release study

Methods

Twelve hedgehogs were released from wildlife rescue centres in Oxfordshire and Gloucestershire on three of the farms surveyed during the footprint tunnel survey. Hedgehogs had been admitted for a variety of reasons (Table 3) but were deemed to be in good health before release with a weight range of 739-1160g. A small patch of spines on the rump were clipped and a 10g radio-tag (TW-3 single celled tag; Biotrack, Wareham, UK) was glued to spines using epoxy resin. Hedgehogs were marked using six 1cm long pieces of heat-shrink tubing glued in a patch at the rear. Hedgehogs were released singly on three of the initial survey farms described above (Farms 2, 4 and 5; fig.2), one of

each treatment type: one with 4-6m grassy margins; one organic farm with 4-6m grassy margins and one with no field margins and non-organic farming. Hedgehogs were from locations far from the release sites and were not familiar with the landscape. Release sites were selected based on absence of badger setts, adequate cover and central location on the farm.

Hedgehogs were radio-tracked for their first two evenings and then at least twice a week for 30 days using a hand-held three element yagi directional antenna (Wildlife Materials International, Murphysboro, USA) and a TRX-1000S receiver (Wildlife Materials International, Murphysboro, USA). Hedgehogs were located every five minutes from 9pm until 3am and their GPS coordinates were recorded (as carried out in Dowding *et al.* 2010). Along with the GPS coordinates, the habitat the hedgehog was in recorded as: pasture, arable, set-aside, woodland, hedgerow, or agri-environment field margin. Behaviour was classified as in Riber (2006) into foraging (nose close to the ground/rooting/sniffing/eating), running (fast movement with nose off the ground), walking and resting (no movement, lack of modulation in radio-signal). When hedgehogs could not be seen their position was triangulated (Kenward 2000) and behaviour was established from modulation in the radio-tracking signal and speed of movement. Sightings of wild hedgehogs during the release study were recorded. The farms were visited before sunset and the GPS location of the released hedgehogs day nest was located.

Statistical analysis

The habitat available to a hedgehog was compared with the habitat used by a hedgehog by compositional analysis (Aebischer, Robertson & Kenward 1993). The habitat available to the hedgehog was calculated as that within a 1km diameter of the release site. For two of the hedgehogs that moved well outside this 1km diameter, a 1km diameter of habitat available was calculated for each position fix. To analyse the association of hedgehog behaviour with different habitats, t-tests between the percentages of position fixes in the hedgerow versus those in the

margin were performed for each activity (foraging, resting, walking or running and nesting) after arcsine square root transformation (Ahrens, Cox & Budhwar 1990).

Table 3 The fate of 12 rehabilitated hedgehogs released on three predominately arable farms in Oxfordshire

ID	Sex	Release weight (g)	Reason for admission	Release date	Farm no.	No. of nights tracked	Days on farmland	Location after 30 days	Dist travelled (m)
1	F	1074	Dehydration	29/05/2012	5	2	?	Lost tag	NA
2	F	1093	Orphaned	31/05/2012	4	29	14	Farm gardens	1199
3	M	936	Orphaned	12/06/2012	5	30	12	Allotments	1270
4	M	1040	Tangled in football net	17/06/2012	4	49	12	Village	2354
5	M	830	Trapped in plant pot	19/06/2012	5	65	1	Farm gardens	429
6	F	1160	Strimming injury	25/06/2012	2	110	15	Village	1379
7	F	1012	Tangled in cricket nets	26/06/2012	2	15	0	Returned to rescue	902
8	M	1018	Foot injury	02/07/2012	4	84	6	Village	795
9	F	866	Disturbed nest	12/09/2012	5	39	1	Farm gardens	820
10	M	884	Broken Jaw	12/09/2012	5	39	?	Tag failed	NA
11	F	739	?	24/09/2012	4	34	30	Release farm	162
12	M	836	Orphaned	24/09/2012	4	34	30	Release farm	459

Dist travelled is the direct distance (m) from the release site to the final location the hedgehog was observed

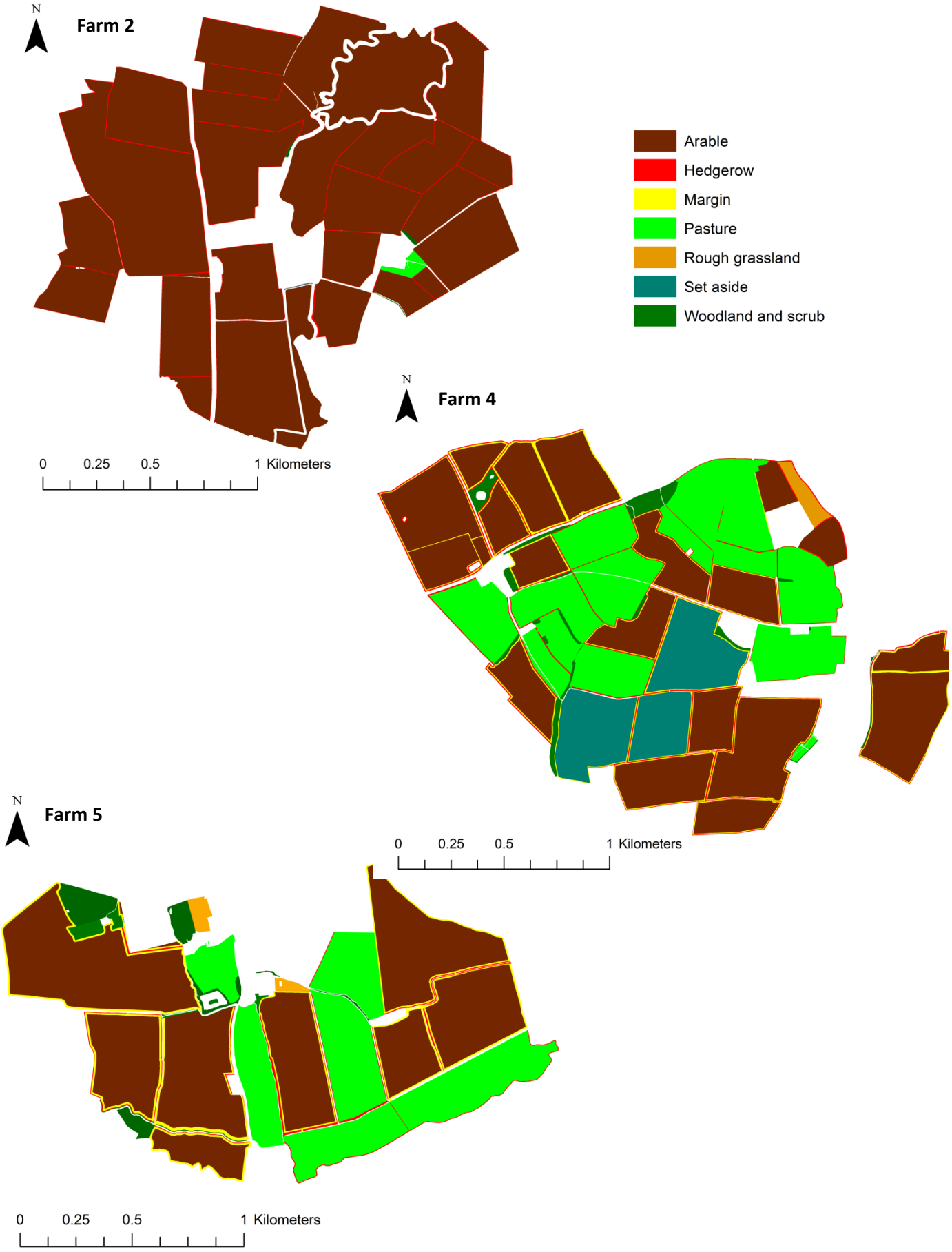


Fig.2 Three study farms in Oxfordshire used for hedgehog release and radio-tracking studies in 2012

Results

A summary of the fates of the 12 released hedgehogs is given in Table 3. Of the nine hedgehogs that were still being tracked after 30 days, only two were still on the release farm. The others left open farmland in favour of habitats associated with humans including villages, allotments and the gardens of isolated houses on the farms. Although hedgehog number seven was not in the study after 30 days, it left farmland on the release evening before being poisoned, possibly by slug pellets in a local village. Hence 80% of the released hedgehogs dispersed away from farmland to urban habitats.

A total of 1198 position fixes were obtained for the 12 hedgehogs while they were on farmland. Habitat use differed significantly from random (Table 4, λ=0.045, p= 0.002). The ranking of the habitats selected was; hedgerows >>> field margins > set-aside > pasture > arable, where >>> indicates a statistically significant difference in hedgehog preference between habitat groups. There were clear behavioural uses for each habitat type, particularly those ranking as the most selected in the compositional analysis (Fig.3). However, there was no significant difference between the proportions of time spent doing each activity in the hedge verses margin (t-tests: Foraging t= 0.588, p= 0.573, 8d.f; walking or running, t= 1.52, p=0.163, 9d.f; resting, t= 0.098, p=0.924, 9d.f, nesting t=1.783, p= 0.125, 6d.f).

Table 4 The ranking matrix produced by compositional analysis (Aebischer *et al.* 1993) with the four main habitat types used by 12 hedgehogs during a release study on predominately arable farmland in Oxfordshire

	Arable	Hedgerow	Margin	Pasture	Set aside	Rank
Arable	0	---	---	-	---	0
Hedgerow	+++	0	+++	+++	+++	4
Margin	+++	---	0	+++	+	3
Pasture	+	---	---	0	-	1
Set aside	+++	---	-	+	0	2

Habitat available to each hedgehog was deemed as that within a 1km diameter circle of the release site. For two highly mobile hedgehogs, a circle with 1km diameter was calculated for each position fix.

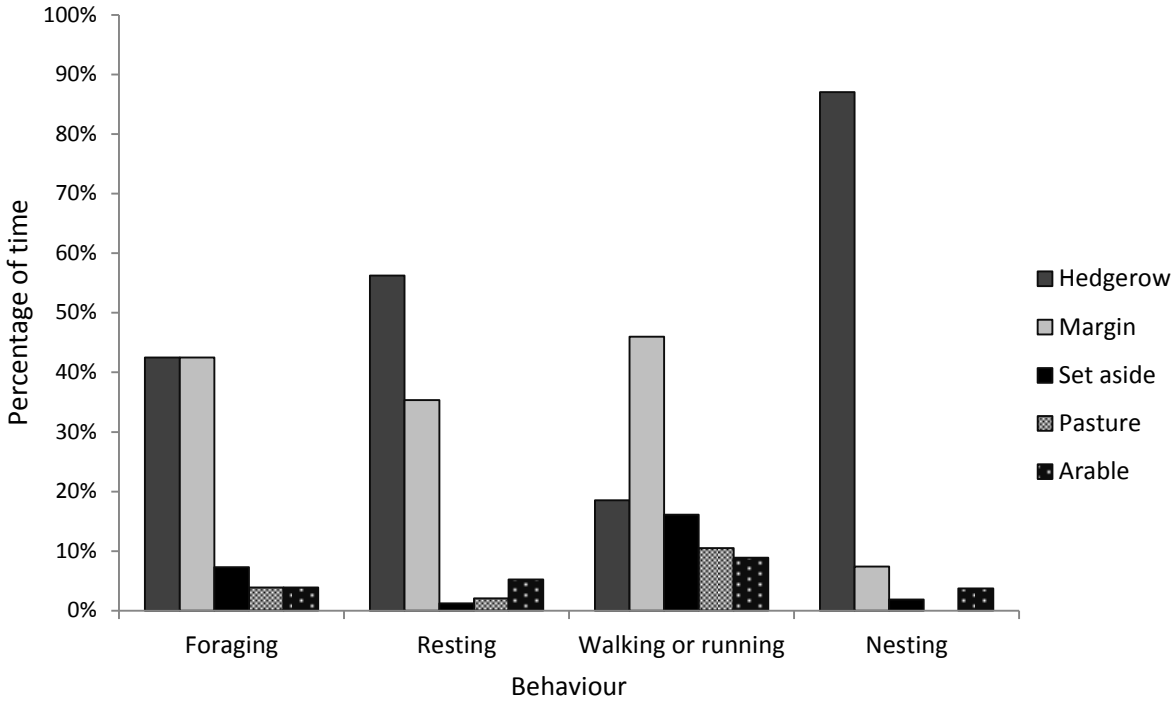


Fig.3 The percentage of time spent by 12 released hedgehogs in each of five habitats on farmland whilst foraging, resting, walking or running

The only wild hedgehog spotted on farmland during the radio-tracking of released individuals was a juvenile sighted in the same field that hedgehog footprints were detected in during the footprint tunnel survey on Farm 4. The field backed onto gardens from the local village and the hedgehog was recorded on a grassy field margin on the side of the field closest to gardens, 10m away from the gardens. Wild hedgehogs were observed in two rural villages that hedgehogs in the study settled in.

Discussion

We only observed one wild hedgehog throughout the radio-tracking of release hedgehogs and this supports the results of the footprint tunnel survey. Previous studies have successfully used released hedgehogs to find wild hedgehogs (Hof & Bright 2010a) and thus our results indicate an absence, or at least very low density of hedgehogs on arable farmland in Oxfordshire. Despite the overall dispersal away from agricultural land the hedgehogs were shown to select agri-environment scheme features while on the farms. The same habitat rankings were found in a study of wild hedgehogs on

arable land (Hof & Bright 2010a). There was no statistically significant difference in the behaviour observed in the hedgerow and margin but the hedgerow was particularly used for resting and nesting. Walking or running was most often observed in the margin, suggesting margins could be useful as dispersal corridors.

Although agri-environment scheme features were selected by hedgehogs at the field scale, neither arable land nor pasture was selected at the landscape scale. In fact, four of the hedgehogs dispersed through pasture fields. A study by Reeve (1998) found similar dispersal patterns in rehabilitated hedgehogs, where the release of 10 hedgehogs in rural woodland resulted in dispersal towards urban habitats. Doncaster (2001) also found that dispersing hedgehogs selected urban habitats. Hedgehogs are, however, present on arable and pasture fields elsewhere in Britain (Hof & Bright 2010a; Hof *et al.* 2012). Possible explanations for the dispersal away from farmland and towards residential areas in this study, also apparent in the studies of Reeve and Doncaster, include: low prey density, badger presence, lack of nest sites, microclimate and an absence of mates.

There was no evidence of a lack of nest sites on farmland in this study as all hedgehogs constructed nests from the first night onwards, most frequently in agri-environment scheme hedgerows, and were never observed exposed during the day. However, after dispersal to habitats associated with humans, hedgehogs often used man-made structures to nest under including wooden pallets, garden sheds and in hay barns. Observations in the field highlighted the warmer microclimate around villages and farm buildings. Hubert *et al.* (2011) suggested that urban warming may be a contributing factor to hedgehogs' attraction to urban areas. For a small endotherm, such as the hedgehog, energy expenditure is higher at lower ambient temperatures (Speakman 1997) and it would be energetically costly to forage in colder habitats.

As the footprint tunnel surveys proved, there were no, or very few, conspecifics on the release sites and hedgehogs may have left farmland in this study to seek out mates. Only one wild hedgehog was spotted on farmland during radio-tracking and wild hedgehogs were observed in the villages where

hedgehogs settled. Hedgehog numbers 11 and 12, the only hedgehogs that remained on farmland, were the last to be released, in late September. In October these hedgehogs exhibited behaviour which suggested they were preparing for hibernation rather than mating, for example, emerging to forage earlier in the evening than those released in the summer and spending more time building day nests (Rautio *et al.* 2014).

The hedgehogs released in this study may have had some 'memory' of urban areas given that they were all rescued from urban areas and therefore sought out villages and gardens. However, seven of the hedgehogs in the study were either autumn juveniles that overwintered in rescue centres or were juveniles from 2012 litters. As a result, over half of the released hedgehogs had not been in the wild as an adult and their experience with urban habitats was minimal. It could be argued that hedgehogs were undergoing juvenile dispersal rather than habitat selection (Berthoud 1978; Dobson 1982; Morris & Warwick 1994; Wolff 1994), and therefore future studies should also release hedgehogs into villages to confirm the preference for habitats close to buildings. Control releases were carried out by Reeve (1998) and the two hedgehogs released in to urban habitats did not disperse.

Conclusions

The literature reviewed here, a hedgehog survey across farms in Oxfordshire and a release study on arable land in Oxfordshire, all showed that hedgehogs in our study area evidenced a clear preference for villages, gardens and allotments over open farmland, particularly arable land, and this is not affected by current agri-environment scheme measures. From the work discussed here there are five key factors that may cause hedgehogs to avoid arable land and select villages:

1) Badger presence; badgers are at higher numbers on farmland and thus villages act as a refuge from predation (Hof *et al.* 2012)

2) Lack of natural prey items, particularly earthworms, on arable land, which are abundant on mowed grass habitats in villages such as garden lawns and amenity grassland (Micol *et al.* 1994; Young *et al.* 2006; Dowding *et al.* 2010a)
3) An attraction to supplementary feeding in villages (Hubert *et al.* 2011)
4) A lack of nesting sites on arable land compared with in villages, such as under garden sheds and under shrubs (suggested by Reeve 1998)
5) Microclimate; cold temperatures on open farmland due to hedgerow removal and warmer microclimate in villages due to shelter from the wind and urban warming (Forman & Baudry 1984; Hubert *et al.* 2011)

Further work should study the contribution of each of these factors to the hedgehog's avoidance of arable land in order to establish possible causes of the hedgehog decline in arable landscapes. This research would then result in possible conservation measures to improve arable land for hedgehogs and stem the decline of hedgehogs in rural areas.

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Chapter 3

Hedgehog (*Erinaceus europaeus*) movement and habitat use on arable land under threat from badger (*Meles meles*) predation

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Abstract

Built-up areas cover over 16,750 square kilometres of the UK. Although habitats associated with humans are often unfavourable for wildlife, some species can take advantage of the altered physical environment and human food waste. The European hedgehog *(Erinaceus europaeus)* is increasingly becoming associated with gardens and rural villages and less so with arable farmland. Suggested explanations for this include: predation by badgers *(Meles meles)* on arable land, attraction to higher prey densities, the availability of supplementary food and warmer microclimates in rural villages, and a greater range of day nest sites. Here we investigate the contribution of these drivers of habitat selection by radio-tracking hedgehogs on four arable sites in Norfolk and two in North Yorkshire, with one farm in each county with badgers present. Seventy-eight hedgehogs were tracked, with 52 yielding enough data to calculate home range sizes. Where badgers were present hedgehogs were found closer to cover, hedgerows and buildings and hedgehogs were found further from badger activity than a randomly generated set of points. Hedgehogs' home ranges were 11ha smaller on badger-occupied sites, when ranges were calculated by 100% minimum convex polygons. When hedgehogs were found closer to buildings, their ranges were smaller; whether or not badgers were present. Arable land and woodland were avoided by hedgehogs and on badger-occupied sites hedgehogs spent 50% less time on arable land compared with hedgehogs on sites without badgers. Over 60% of day nests were constructed in village habitats compared with 15% in woodland and 12% in pasture and arable. We found no evidence for an attraction to villages due to a warmer microclimate. We demonstrated that badger presence affects hedgehog habitat use and ranging behaviour and that this is one possible cause of hedgehogs' selection of rural villages. However, on sites with no badgers, hedgehogs also selected buildings and gardens over other habitats. We suggest that food availability also attracts hedgehogs to villages; this is supported by the smaller home range sizes of hedgehogs in villages. We recommend focusing conservation efforts on maintaining hedgehog populations in rural villages, and increasing connectivity between villages by increasing hedgerow cover on arable land, which will also act as protection from badger predation.

Introduction

Built-up areas cover over 16,750 square kilometres of the UK and over 50% of the land in the UK is developed or used for agriculture (The UK National Ecosystem Assessment 2011). An increase in the size of urban areas and intensively manged farmland has resulted in biodiversity losses in both urban and rural areas in the UK (Stoate *et al.* 2001; Foley *et al.* 2005; Macdonald & Feber 2015). Urbanisation may be particularly detrimental to wildlife, for example through habitat loss and fragmentation (Dickman 1987; Friesen, Eagles & Mackay 1995; Lehtinen, Galatowitsch & Tester 1999), road mortalities and the effect of roads as barriers to movement (Forman & Alexander 1998; Huijser & Bergers 2000; Rondinini & Doncaster 2002; Baker *et al.* 2004), human-wildlife conflict (Mosillo, Heske & Thompson 1999; Peine 2001; Gompper 2002; Hill, Carbery & Deane 2007; Delahay *et al.* 2009), and predation of native species by domestic pets (Baker *et al.* 2003; Woods, McDonald & Harris 2003).

There are also aspects of residential areas that are beneficial for wildlife, for example, low numbers of natural predators (Eden 1985; Gering & Blair 1999; Møller 2012), the availability of supplementary food (Doncaster *et al.* 1990; Fedriani, Fuller & Sauvajot 2001; Prange, Gehrt & Wiggers 2003; Fuller *et al.* 2008) and altered physical conditions, such as higher temperatures due to urban warming (Eden 1985; Pickett *et al.* 2008). These advantageous qualities have allowed some species to thrive in built-up areas, particularly omnivorous species, which can take advantage of anthropogenic waste (Fedriani *et al.* 2001; McKinney 2002; Chace & Walsh 2006).

Here we focus on the Western European hedgehog *(Erinaceus europaeus),* a generalist predator of macroinvertebrates, which is increasingly becoming associated with the human environment, such as rural villages, and less so with agricultural land (Hubert *et al.* 2011; Van De Poel, Dekker & Van Langevelde 2015). In the UK hedgehog numbers are declining, but with more severe declines in rural than urban areas (JNCC 2010; Aebischer, Davey & Kingdon 2011; Roos, Johnston & Noble 2012). Even within rural areas hedgehogs favour rural villages rather than open farmland and arable land is

particularly under selected (Hof & Bright 2010a; Hof, Snellenberg & Bright 2012). We examine the drivers of hedgehogs' increasing association with villages in rural areas, which will help in establishing the causes of their population declines in agricultural areas - and in doing so will highlight conservation measures.

Several factors might influence hedgehogs' attraction to rural villages over arable farmland. The hedgehog's diet is mainly composed of macroinvertebrates, with earthworms thought to be especially high-energy prey (Yalden 1976; Wroot 1984). Hedgehog abundance is positively correlated with the earthworm abundance of grass fields, and urban habitats such as amenity grassland and garden lawns sustain high numbers of earthworms compared with intensively managed arable fields (Doncaster 1994; Micol, Doncaster & Mackinlay 1994; Curry, Byrne & Schmidt 2002; Young *et al.* 2006). Hedgehogs also take advantage of waste and pet food left out by humans (Yalden 1976; Morris 1985). Rural villages may also act as refuges from predation (Hof *et al.* 2012). The European badger (*Meles meles*) is the main predator of hedgehogs and also competes with them for earthworms (Doncaster 1992). Badgers are thought to regulate hedgehog populations in rural areas (Hof & Bright 2010a) and hedgehog abundance on grass fields is negatively correlated with badger activity and sett density in the local area (Micol *et al.* 1994; Young *et al.* 2006). Badgers avoid excavating setts in urban areas (Neal & Cheeseman 1996) and although hedgehogs may face attack from domestic dogs and foxes (Doncaster 1994; Reeve 1994), badgers are the only predator thought to be proficient in uncurling a hedgehog from its defensive position (Neal 1986). Warmer temperatures may also attract hedgehogs to villages as, for a small endotherm, energy expenditure is high at low ambient temperatures (Schmidt-Nielsen 1976; Wroot 1984; Speakman 1997). Warmer temperatures may also result in higher availability of invertebrate prey for hedgehogs (Crawford-Sidebotham 1972; Edwards & Bohlen 1996; Honek 1997) and increase the chance of survival during winter hibernation (Hubert *et al.* 2011). Village habitats may also have a greater range of secure nest sites than on farmland, such as in garden sheds and compost heaps (Reeve 1998; Rautio *et al.* 2014).

Here we investigate the contribution of four expected drivers of hedgehog attraction to rural villages by measuring hedgehog habitat use, home range size, and distance to key habitat features on four predominately arable sites, under varying predation threat and climatic conditions. We hypothesise that village habitats will be selected over arable farmland and that:

1) Higher natural and supplementary food availability in villages than on the surrounding farmland (Doncaster 1994; Micol *et al.* 1994; Curry *et al.* 2002; Young *et al.* 2006; Hubert *et al.* 2011) will result in hedgehogs residing in villages having smaller home ranges than those that utilise arable land (Fortier & Tamarin 1998).
2) When badgers are present hedgehogs will avoid arable land and be found closer to buildings and cover (Doncaster 1994; Hof *et al.* 2012).
3) Due to the higher energetic costs associated with foraging at cold temperatures (Wroot 1984), when ambient temperatures are colder hedgehogs will be found closer to buildings and cover.
4) Hedgehogs will show a preference for nesting in villages, which will have a greater variety of secure nesting habitats than on arable land (Rautio *et al.* 2014).

Methods

Study sites

To select sites for radio-tracking studies a questionnaire was sent to 4000 farmers in Britain 2013 (for analysis of questionnaire data see chapter 6). The questionnaire asked if farmers had seen hedgehogs in the past year. Thirteen farms across England where farmers had observed hedgehogs were surveyed using red-filtered spotlights and four similarly-matched sites with hedgehogs present were selected for further study, two in North Norfolk (UK grid refs: TF 96061 25469 and TG 16716 36586; Fig.1) and two in North Yorkshire (SE 90511 81822 and SE 68646 24715; Fig.1). Badgers were present on one site in each county; presence was determined by surveys for tracks, setts and signs in October 2013 and April 2014. Each site comprised predominately arable farmland with a local rural

village (Table 1, Figs.2-5). Sites were all at least 65% arable land, predominately cereal crops, with some pasture and rough grassland fields (Table 1). Rural villages were within 2.5km of the farmland and all contained amenity grassland including parks, playing fields and church yards. Villages were surrounded by small pasture fields and arable land.

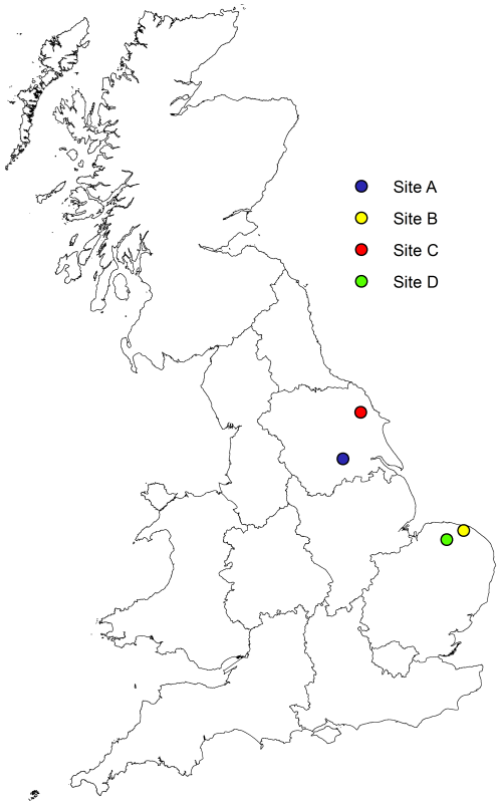


Fig.1 The location of four sites in a study of hedgehog movement and habitat use

Table 1 Details of four sites in England on which hedgehog radio-tracking studies took place in 2013 and 2014

Site	County	Size (ha)	Badger presence	% of buildings	% of hedgerow	% of arable	Agri-environment scheme
A	North Yorkshire	632	Absent	0.7	1.5	74.7	ELS
B	Norfolk	457	Absent	0.5	1.6	72	ELS
C	North Yorkshire	379	Two setts	0.9	1.7	72	ELS
D	Norfolk	280	Two setts	2.9	4	69.2	HLS

% is the percentage of the total site area made up of the given habitat
ELS= Entry Level Stewardship, HLS= Higher Level Stewardship

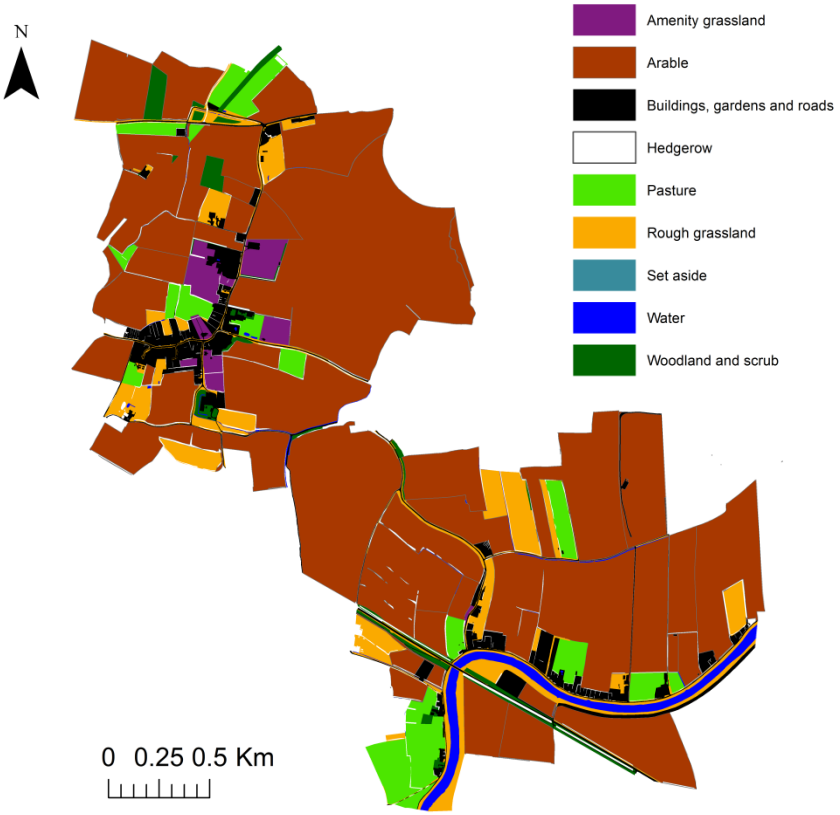


Fig.2 Site A situated in North Yorkshire

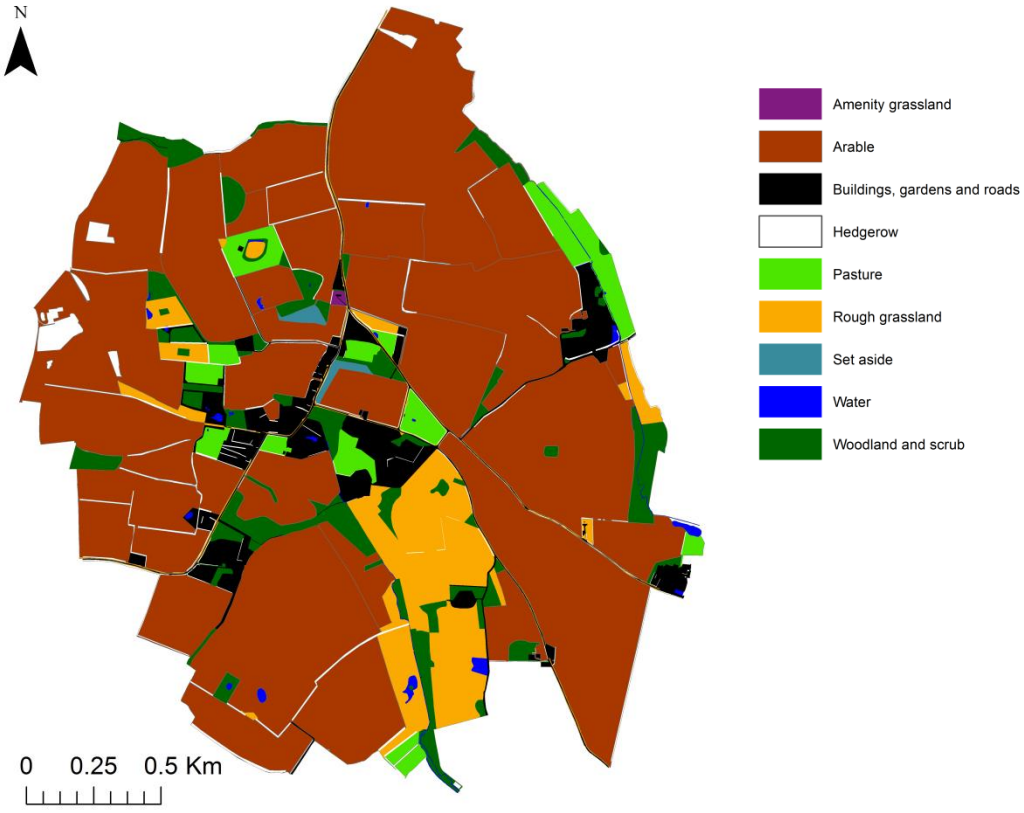


Fig.3 Site B situated in Norfolk

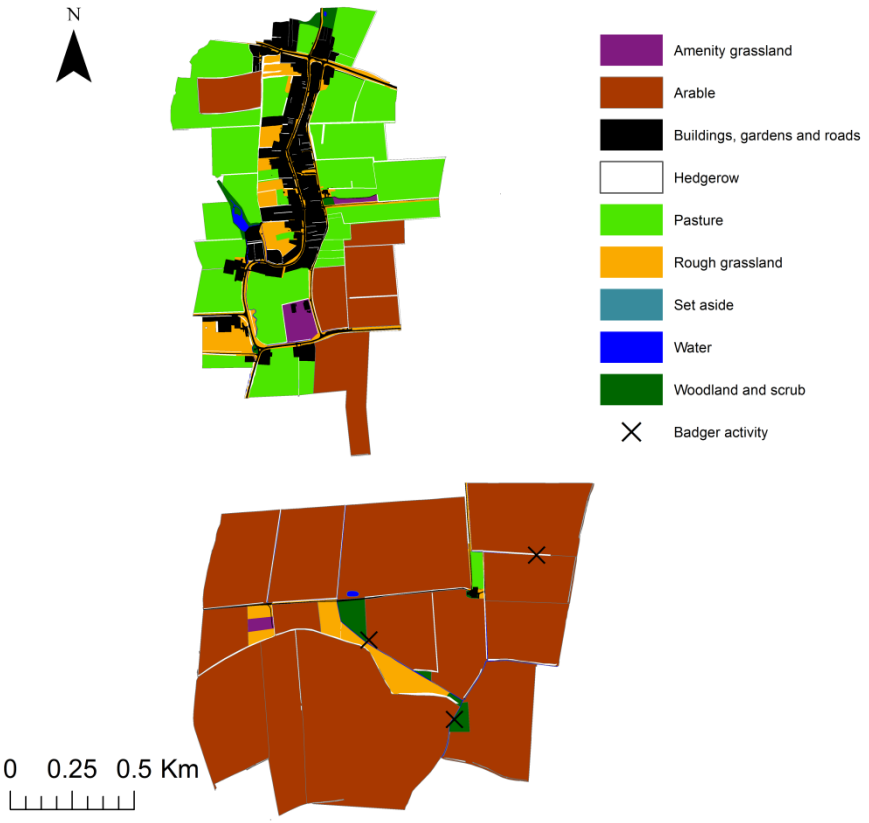


Fig.4 Site C situated in North Yorkshire. Badger activity includes latrines, setts and sightings

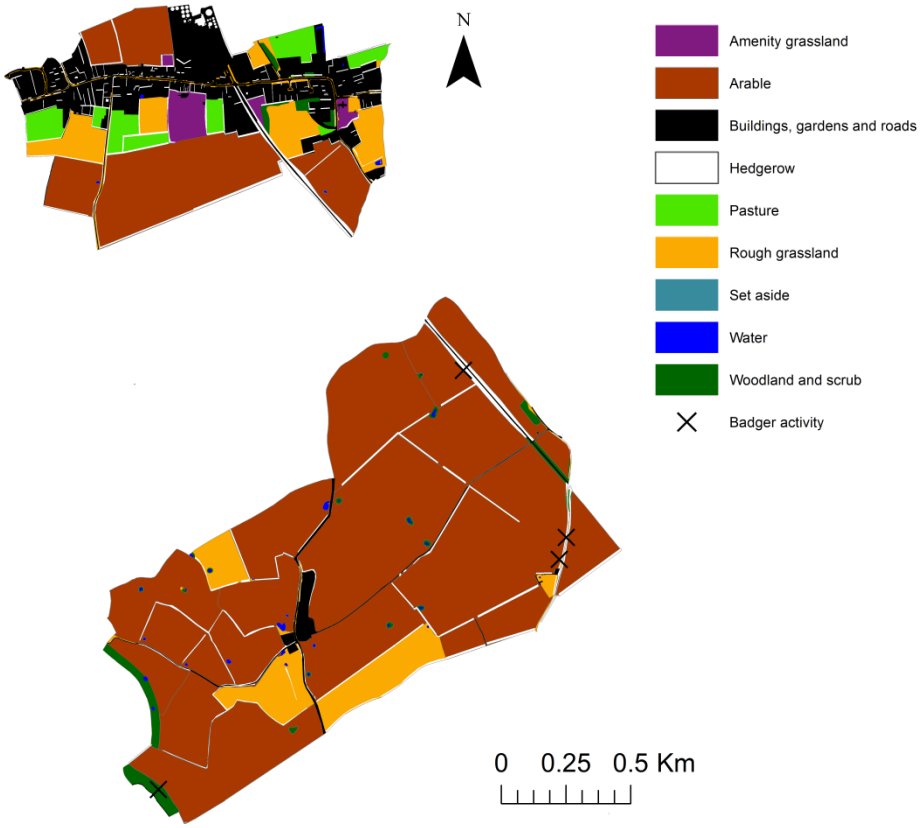


Fig.5 Site D situated in Norfolk. Badger activity includes latrines, setts and sightings

Hedgehog tracking

Hedgehogs were captured using red spotlights and anaesthetised using isoflurane (Natural England License 2014/SCI/0298, HO PIL 30/10293). A small patch of spines on the rump was clipped and a 10g radio-tag was glued to the clipped spines using epoxy resin. Hedgehogs were marked using six 1cm long pieces of coloured heat-shrink tubing glued in a patch at the rear. Hedgehogs were then tracked on the sites from July-October 2013 and April-September 2014. Each site was visited for between four and eight nights at a time in turn over the season. Whilst on site hedgehogs were tracked between sunset and 4am using a hand-held three element yagi directional antenna (Wildlife Materials International, Murphysboro, USA) and a TRX-1000S receiver (Wildlife Materials International, Murphysboro, USA). Every evening each hedgehog on the site was recorded at least three times. For each hedgehog we recorded its GPS location to the nearest five meters, the habitat it was found in, and its distance from cover, i.e. scrub, hedgerow or shrubs. The distance of the hedgehog at each tracking fix from hedgerows, buildings and badger activity (on sites with badgers) was estimated using proximity analysis in ArcGIS (Esri, Redlands, CA, USA). Often hedgehogs were in enclosed gardens we did not have access to; in these cases triangulation was performed (Kenward 2000). To test whether hedgehogs avoided arable land in the study, the percentage of radio-tracking fixes on arable land was calculated for each hedgehog.

Temperature

Ambient temperature was recorded using ten data loggers per site placed 30cm off the ground, two in the centre of arable fields, two in the hedgerow of arable fields, two outside farm buildings, two in gardens and two on amenity grassland. Logger placement was selected randomly in fields and gardens where access was granted and where they would offer minimal interference e.g. flower beds in gardens and under isolated trees in the centre of fields.

Nesting

The GPS location of the hedgehog's day nest was recorded along with the general and specific habitat the nest was found in. General habitat was categorised as: 'arable', 'pasture' and 'village' (including amenity grassland, gardens and buildings) and 'woodland'. The specific habitat within each of these general habitats was recorded as 'buildings', 'hedgerows', 'scrub' (including brambles and under bushes) and 'other'. Six hedgerows were randomly selected on each of the sites including hedgerows where hedgehogs had nested at some point during the 2013 and 2014 field seasons and surveys of these hedgerows were carried out in June 2015 following the DEFRA hedgerow survey handbook (DEFRA 2007).

Statistical analysis

Linear mixed effects models were constructed using the R software (R Core Team 2014) to test whether distance to buildings, distance to cover and distance to hedgerow varied between sites-characterised as with or without badgers present, between males and females and depending on the ambient temperature. Hedgehog ID was included as a random factor in each model. To analyse hedgehog distance from badger activity, including badger sightings latrines and setts, we generated a random number of spatial points on each badger-occupied site, equal to the number of actual radio-tracking fixes. We then constructed a linear model to test for differences in the distance of the random points to badger activity with the distance of the actual tracking fixes to badger activity.

To test for differences in home range size between hedgehogs that selected village habitats and those that selected arable habitats, on sites with and without badgers, a series of home range estimates was calculated for each hedgehog over the two seasons in the program Ranges (Anatrack Ltd, Dorset, UK). Estimates included: 100%, 95% and 90% minimum convex polygons (MCP) and 95%, 90% and 50% kernel density estimates. The predictor variables used were site, sex and mean distance to buildings during the two seasons (a measure of how much time a hedgehog spent in the village or close to human dwellings). The number of fixes obtained for each hedgehog varied

between 1 and 53 fixes. All tracking fixes were included in the analysis of distance to hedgerows, cover and buildings. For the analysis of home ranges using MCPs, only hedgehogs with at least 10 fixes over at least seven days were included, resulting in 52 hedgehogs in the analyses, with a mean of 24 fixes per hedgehog and a range of 10-53 fixes. For more in depth analysis of hedgehog core home range, analysed by kernel estimates, only 21 hedgehogs with at least 25 positional fixes were included.

Compositional analysis was performed to examine habitat use at the landscape scale using the above home ranges (selection of 100% MCP home range and 50% kernel home range within the landscape), and habitat use at the local scale (habitat selection within the hedgehog's 100% MCP home range and 50% kernel home range), following Aebischer (1993). For habitat selection at the landscape scale, an area of $5km^2$ around each site was digitised and categorised as: 'amenity grassland', 'arable land', 'buildings', 'gardens', 'hedgerow', 'pasture' and 'rough grassland', and 'woodland and scrub'. For the calculation of habitats available at the home range scale, 'buildings' and 'gardens' were merged into one category as it was often difficult to distinguish the precise habitat of a hedgehog in an enclosed garden. Only one of the four study sites had any set-aside (1.4ha) and therefore set-aside was not included in the analysis. Only two of the four sites had grassy field margins. Where this habitat was used, it was recorded in the pasture and rough grassland category.

To examine differences in the amount of time hedgehogs spent on arable land on sites with and without badgers, a generalised linear model was constructed with the proportion of fixes that each hedgehog was found on arable land as the response variable and site and sex as the explanatory variables, with a binomial link and weighted by the number of tracking fixes for each hedgehog. Only hedgehogs with over 10 tracking fixes were included in the analysis.

Compositional analysis was used to examine nest selection within the hedgehog's home range, measured by 100% MCP. Also, binomial logistic regression was used in order to assess whether the

attributes of a hedgerow could predict whether or not it was used for hedgehog nesting during 2013 and 2014. Due to only six hedgerows being selected by hedgehogs for nesting, only a small number of attributes could be included in the analysis, these included: hedgerow height, hedgerow width and the height from the ground to the base canopy. The identity of the site on which the hedgerow was located was included as a fixed blocking factor.

Results

Summary

A total of 46 hedgehogs was tracked in 2013 and 42 in 2014. Ten of the hedgehogs tracked in 2014 had also been captured in 2013, giving a total of 78 individuals, comprising 28 females and 50 males (See appendix Table A). We wished to capture an equal number of hedgehogs at each site, but twice as many hedgehogs were found on sites without badgers, 52, than with badgers, 26. For the 78 hedgehogs a total of 1324 GPS fixes was obtained (Figs.6-9). Sixty six day nest locations were recorded from 42 individuals.

Distance to habitat features

On the two sites where badgers were present hedgehogs were found a mean distance of 4.7 ± SE 1.1m closer to cover, 13 ± SE 1. m closer to hedgerows and 7.2 ± SE 3.5m closer to buildings (Fig.10a, Table 2), than on the sites without badgers. The distance a hedgehog was found from buildings was positively correlated with the distance that the hedgehog was from cover and hedgerows (cover: R^2=0.19, p<0.0001, 1201 tracking fixes from 78 hedgehogs; hedgerows: R^2=0.13, p<0.0001, 1250 fixes from 78 hedgehogs). When ambient temperature was lower hedgehogs were found further from cover (Table 2, Fig.11). There was no evidence for a difference in the distance found to each of these features between males and females (Table 2).

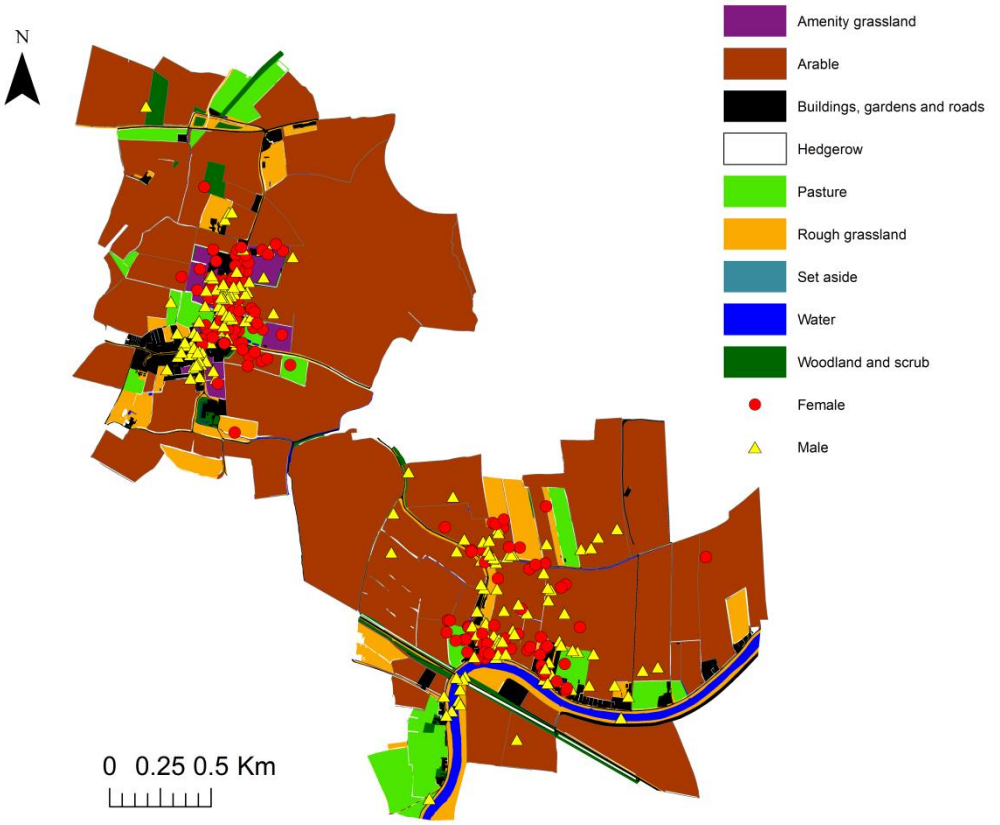


Fig.6 Site A situated in North Yorkshire showing radio-tracking fixes from male and female hedgehogs

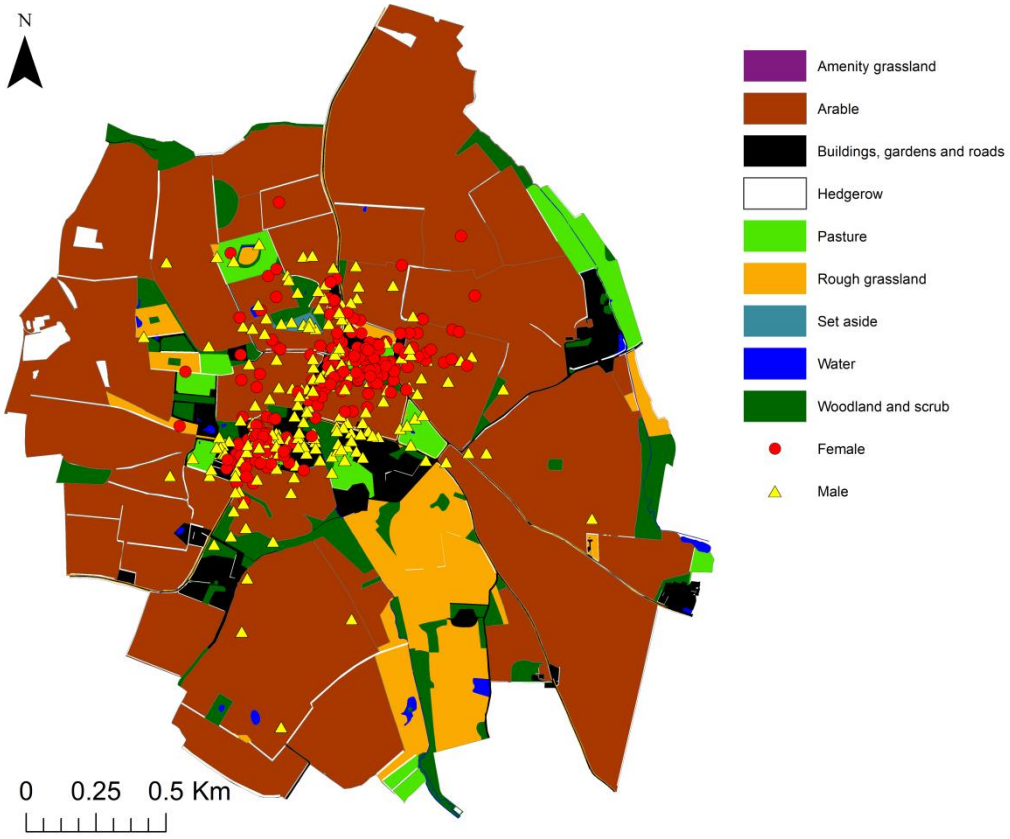


Fig.7 Site B situated in Norfolk showing radio-tracking fixes from male and female hedgehogs

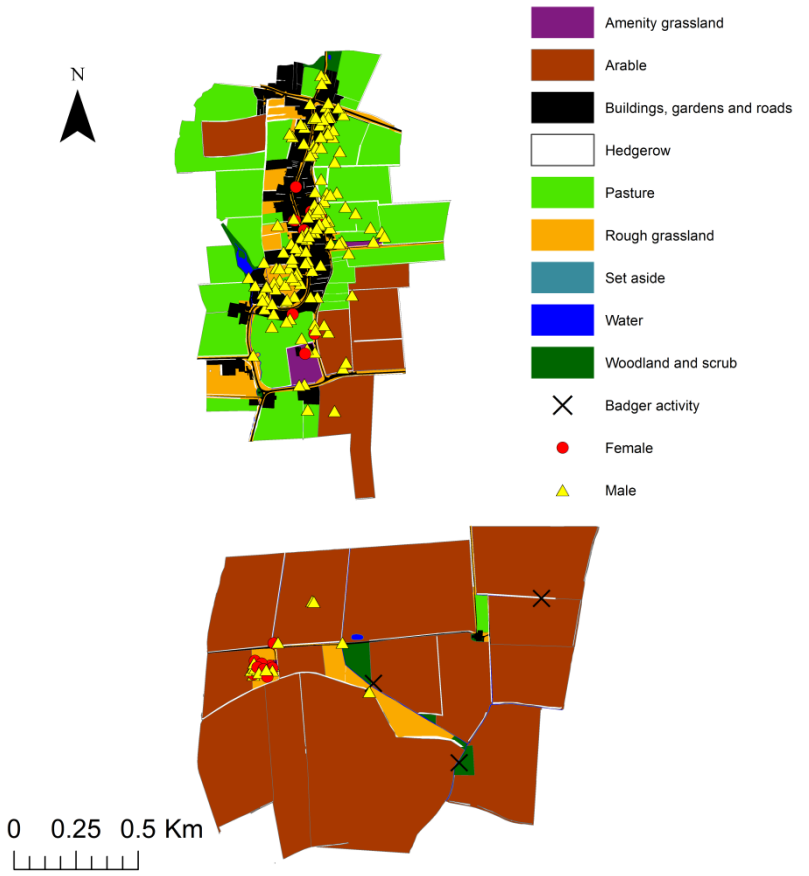


Fig.8 Site C situated in North Yorkshire showing radio-tracking fixes from male and female hedgehogs

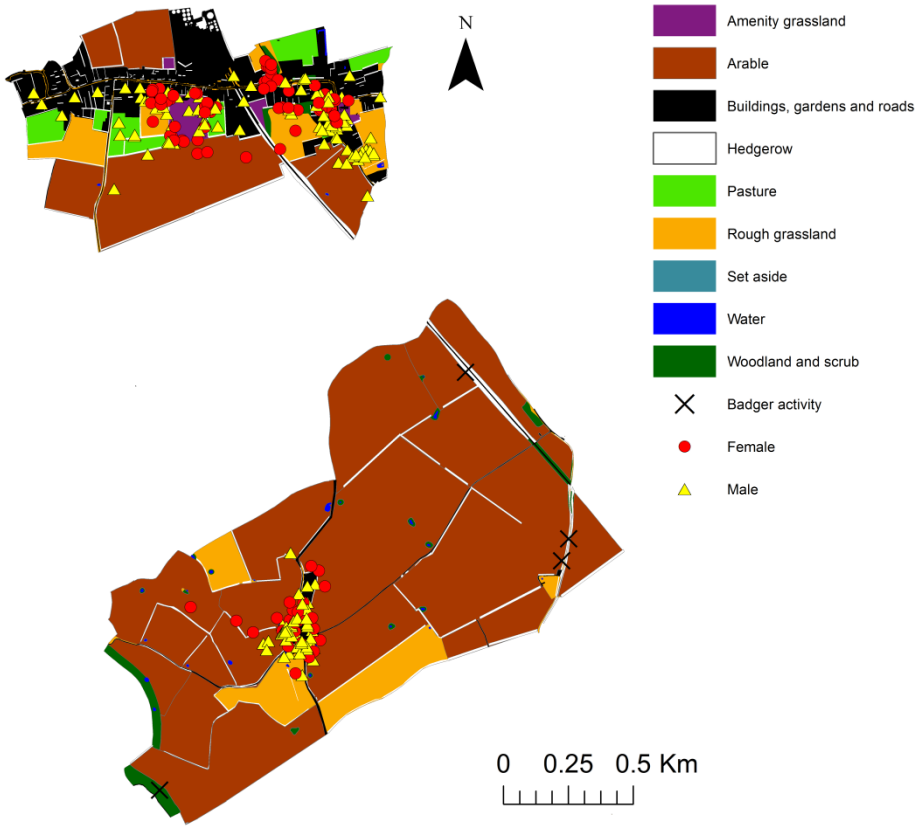


Fig.9 Site D situated in Norfolk showing radio-tracking fixes from male and female hedgehogs

Table 2 The results of three linear models to test the differences in the distance a hedgehog was found to hedgerow, cover and buildings on sites with and without badgers, between males and females and with ambient temperature

Response	Variable	Df	F statistic	P value	Effect size	95% CI
Distance to hedgerow	Site B *NO BADGERS*	3, 55	3.088	0.034*	0.443	-0.290, 1.195
	C BADGERS				-0.025	-1.006, 0.975
	D BADGERS				-0.860	-1.725, 0.007
	Ambient temperature	1, 914	0.180	0.672	-0.011	-0.061, 0.039
	Sex *MALE*	1, 50	0.196	0.660	0.137	-0.475, 0.760
Distance to cover	Site B *NO BADGERS*	3, 53	3.428	0.023*	-0.216	-0.562, 0.127
	C BADGERS				-0.652	-1.122, -0.191†
	D BADGERS				-0.462	-0.864, -0.064†
	Ambient temperature	1, 886	7.908	0.005**	-0.039	-0.066, -0.012†
	Sex *MALE*	1, 48	0.804	0.374	0.128	-0.155, 0.414
Distance to building	Site B *NO BADGERS*	3, 59	2.536	0.065.	0.246	-0.207, 0.702
	C BADGERS				-0.508	-1.104, 0.098
	D BADGERS				-0.199	-0.738, 0.332
	Ambient temperature	1, 904	0.757	0.384	-0.012	-0.039, 0.015
	Sex *MALE*	1, 55	1.498	0.226	0.233	-0.144, 0.616

Site A (no badgers) and females are the reference categories
***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 .near significance
† 95% confidence interval of the effect size does not contain zero

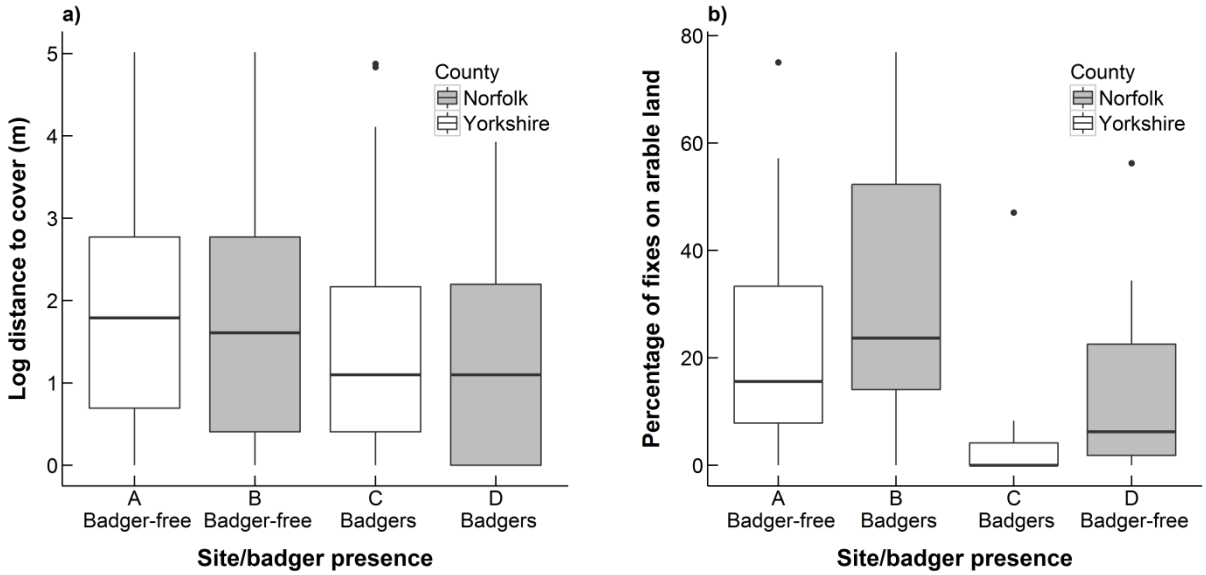


Fig.10 a) The distance hedgehogs were found to cover, including hedgerows, scrub and shrubs and b) The percentage of radio-tracking fixes that a hedgehog was found on arable land, in radio-tracking studies carried out on four sites in Norfolk and Yorkshire in July-October 2013 and April-September 2014

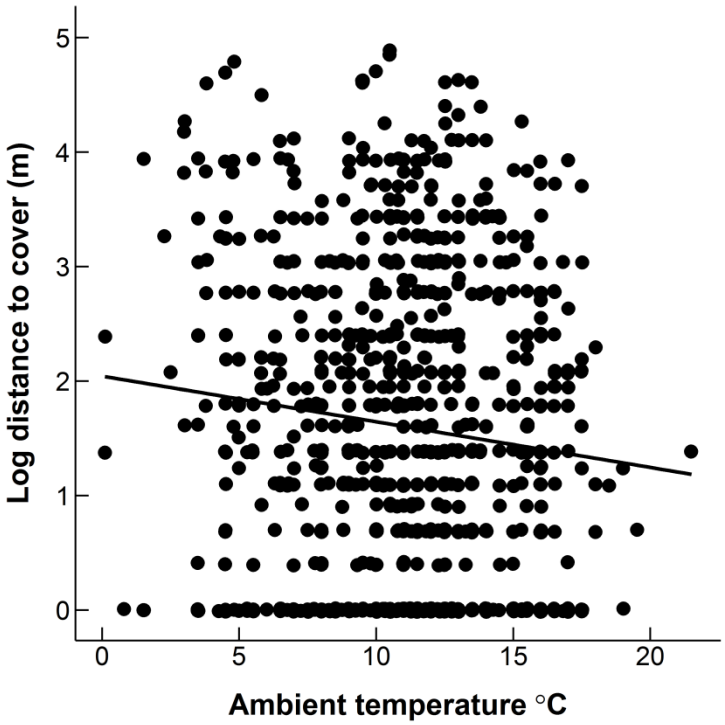


Fig.11 The relationship between ambient temperature, measured by data loggers on site, and the distance a hedgehog was found from cover- including hedgerows, scrub and shrubs- in radio-tracking studies carried out on four sites in Norfolk and Yorkshire in July-October 2013 and April-September 2014.

We found a significant difference between the distance randomly generated tracking fixes were from badger activity and the distance that actual tracking fixes were found from badger activity (ANOVA, $F_{1,246}$=82.3, p<0.0001). The actual fixes were found a mean of 728 ± 16m to badger activity compared with 473 ± 23m for the randomly generated points.

Home range size

Home ranges calculated using 100% MCPs are displayed in Figs.12-15. All home range size estimates increased with distance from buildings (Table 3, Fig.16c). Where badgers were present, hedgehogs had smaller home ranges, but this was statistically significant only when 100% of tracking fixes were included and home range was calculated using the MCP method (Table 3, Fig.16a). Using this method, on sites with badgers present, hedgehogs had a mean home range of 9.7 ± SE 2.4ha compared with a home range of 20.7 ± SE 3.9ha. Hedgehogs generally did not move between villages but there was often movement between rural villages and nearby hamlets or isolated houses

on farmland. Males had consistently larger home ranges than females, for example when using 100% MCP males had a mean range of 21.9 ± SE 4.4ha compared with a female range of 10 ± SE 2ha (Table 3, Fig 16b).

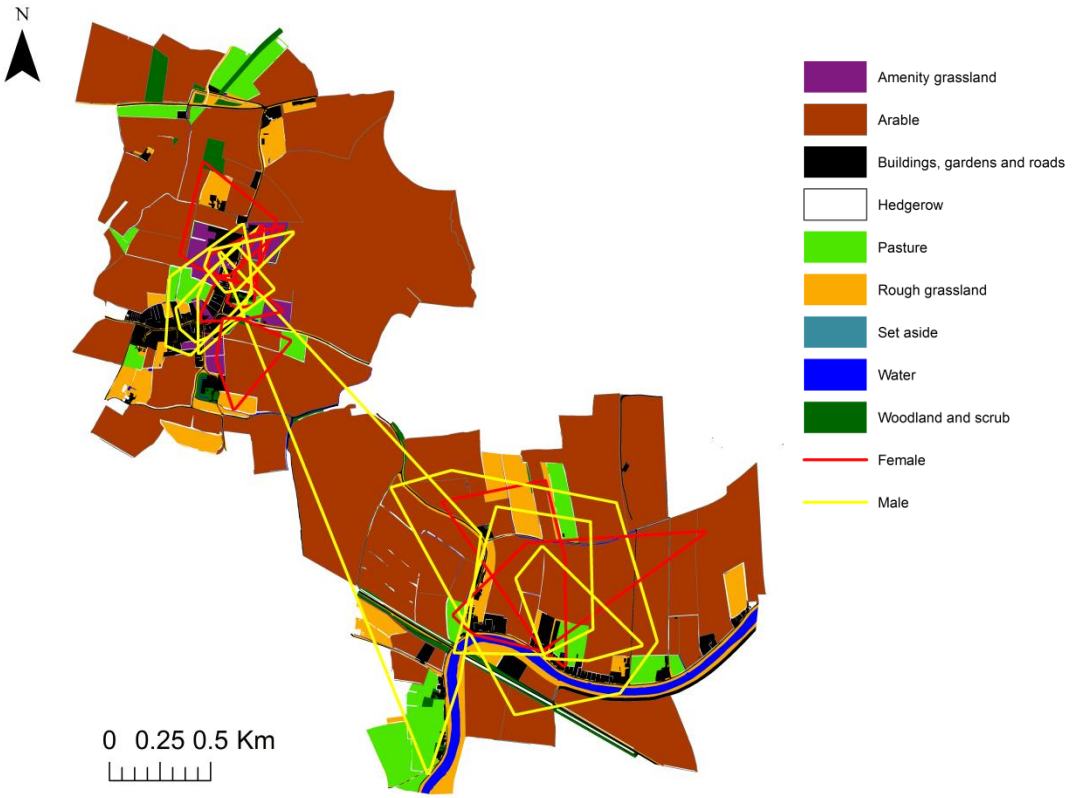


Fig.12 Site A situated in North Yorkshire showing male and female home ranges calculated by 100% minimum convex polygons

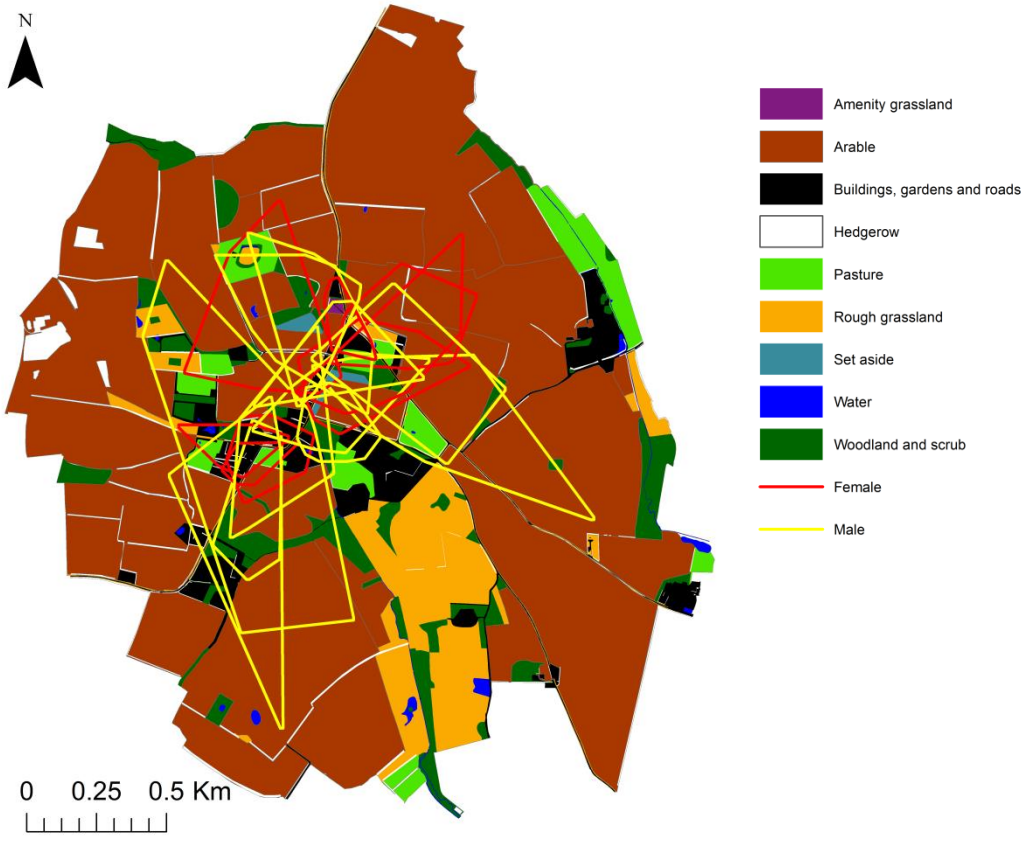


Fig.13 Site B situated in Norfolk showing male and female home ranges calculated by 100% minimum convex polygons (MCPs)

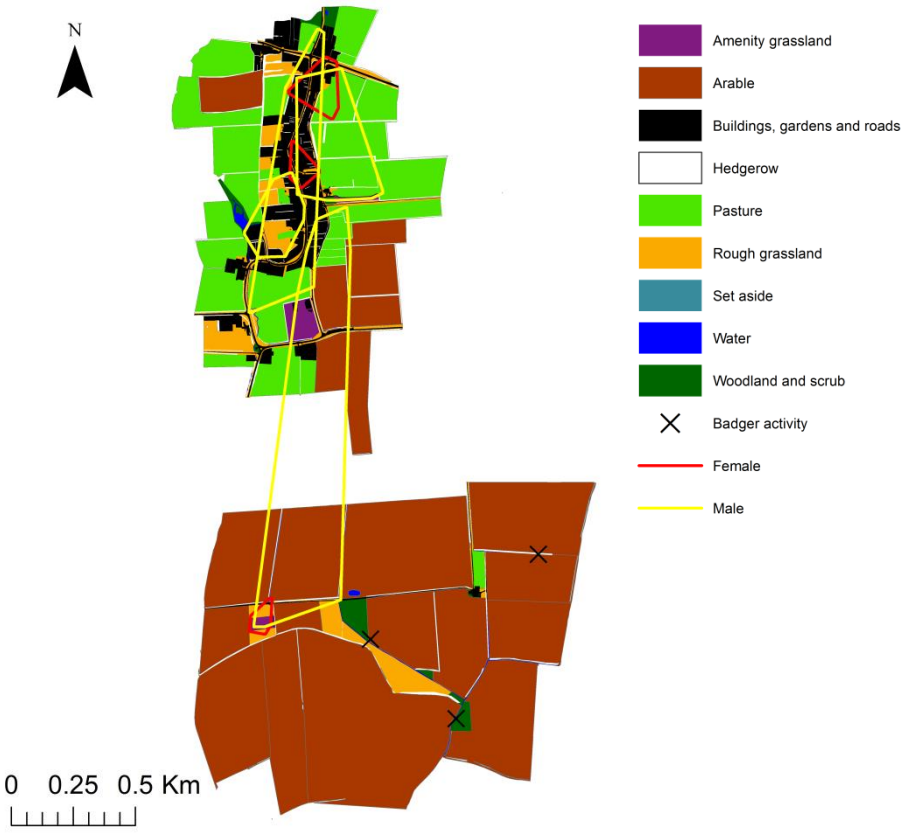


Fig.14 Site C situated in North Yorkshire showing male and female home ranges calculated by 100% minimum convex polygons

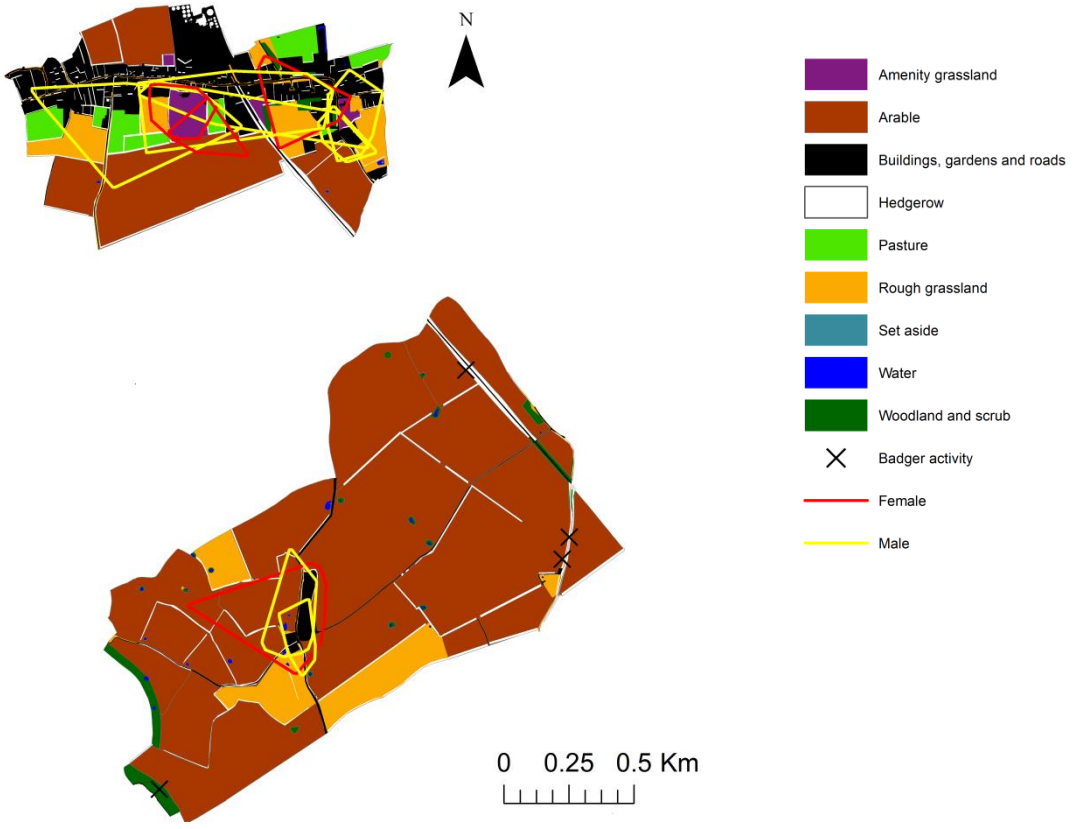


Fig.15 Site D situated in Norfolk showing male and female home ranges calculated by 100% minimum convex polygons (MCPs)

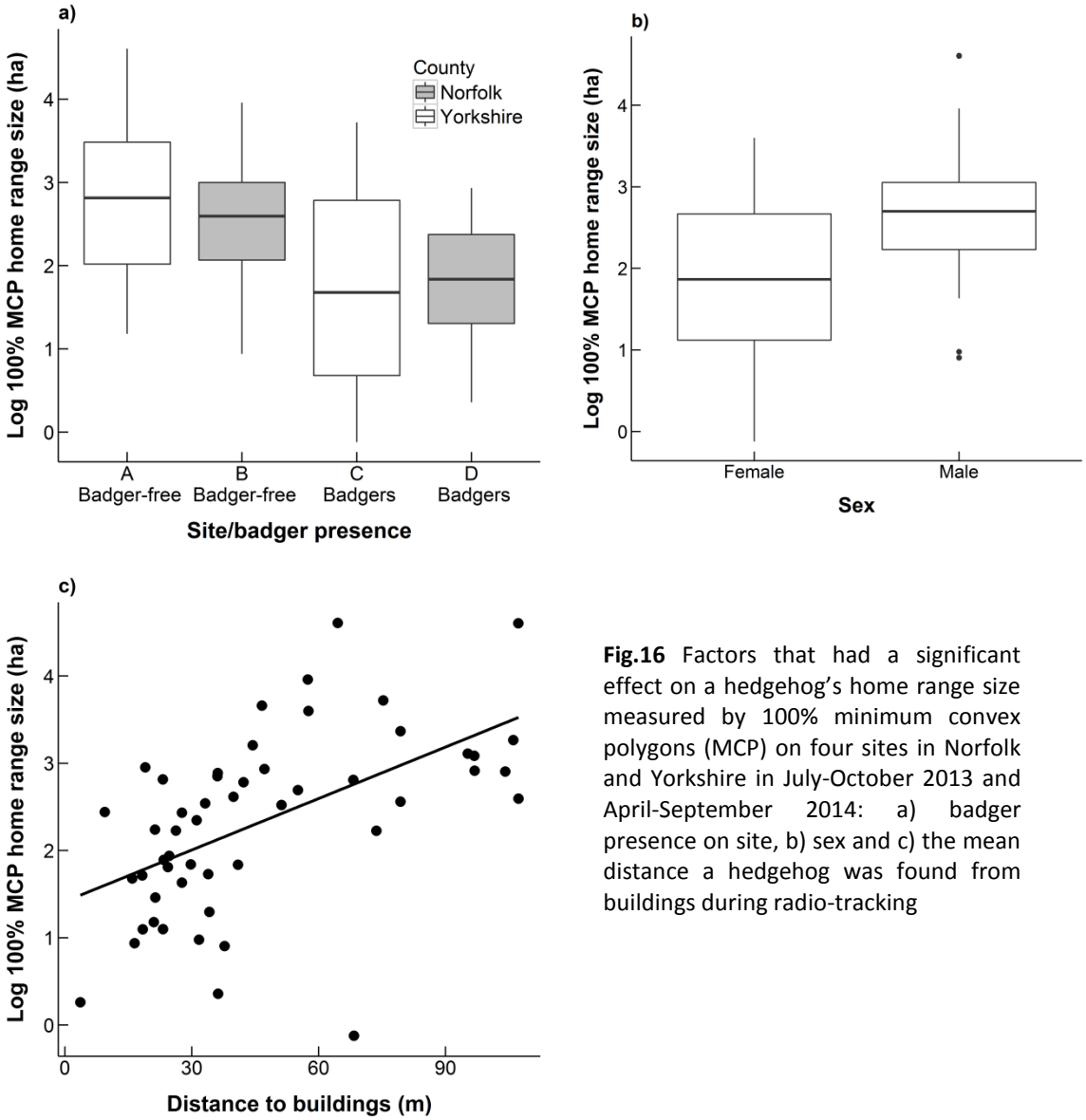


Fig.16 Factors that had a significant effect on a hedgehog's home range size measured by 100% minimum convex polygons (MCP) on four sites in Norfolk and Yorkshire in July-October 2013 and April-September 2014: a) badger presence on site, b) sex and c) the mean distance a hedgehog was found from buildings during radio-tracking

Table 3 The results of six linear models to test the differences in hedgehog home range size on sites with and without badgers, between males and females and with the mean distance a hedgehog was found from buildings. Home range was calculated by minimum convex polygons (MCP) with 100% of radio-tracking fixes and with the outermost 5% and 10% of fixes removed, and by 95%, 90% and 50% kernel estimates

Response	Variable	Df	F statistic	P value	Effect size	95% CI
100% MCP	Site *B NO BADGERS*	3, 46	5.169	0.004**	-0.406	-0.928, 0.116
	C BADGERS				-0.812	-1.510, -0.115†
	D BADGERS				-0.818	-1.426, -0.211†
	Distance to buildings	1, 46	21.099	<0.0001***	0.002	0.009, 0.024†
	Sex *MALE*	1, 46	9.655	0.0003***	0.003	0.382, 1.231†
95% MCP	Site *B NO BADGERS*	3, 46	1.628	0.196	-0.178	-0.723, 0.365
	C BADGERS				-0.311	-1.039, 0.416
	D BADGERS				-0.407	-1.040, 0.226
	Distance to buildings	1, 46	11.447	<0.0001***	0.012	0.008, 0.024†
	Sex *MALE*	1, 46	9.025	0.0004***	0.775	0.406, 1.290†
90% MCP	Site *B NO BADGERS*	3, 46	1.513	0.224	-0.284	-0.817, 0.249
	C BADGERS				-0.308	-1.021, 0.404
	D BADGERS				-0.372	-0.992, 0.248
	Distance to buildings	1, 46	14.634	<0.0001***	0.014	0.011, 0.026†
	Sex *MALE*	1, 46	8.190	0.0005***	0.703	0.374, 1.241†
95% Kernel	Site *B NO BADGERS*	3, 15	2.775	0.078**.**	-0.562	-1.232, 0.133
	C BADGERS				-0.102	-1.131, 0.976
	D BADGERS				-0.169	-0.873, 0.565
	Distance to buildings	1,15	21.084	0.0004***	0.029	0.016, 0.043†
	Sex *MALE*	1,15	1.876	0.191	0.374	-0.198, 0.912
90% kernel	Site *B NO BADGERS*	3, 15	2.883	0.071**.**	-0.562	-1.238, 0.114
	C BADGERS				-0.102	-1.146, 0.941
	D BADGERS				-0.169	-0.881, 0.543
	Distance to buildings	1,15	20.900	0.0004***	0.029	0.016, 0.042†
	Sex *MALE*	1,15	2.103	0.168	0.374	-0.176, 0.924
50% kernel	Site *B NO BADGERS*	3, 15	3.206	0.054**.**	-0.523	-1.138, 0.091
	C BADGERS				-0.089	-1.038, 0.860
	D BADGERS				-0.148	-0.796, 0.499
	Distance to buildings	1,15	25.366	0.0001***	0.029	0.017, 0.041†
	Sex *MALE*	1,15	2.767	0.117	0.390	-0.110, 0.890

Distance to building is the mean distance each hedgehog was found to the nearest building during two seasons of radio-tracking in 2013 and 2014. Site A (no badgers) and females are the reference categories.

***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 **.**near significance

† 95% confidence interval of the effect size does not contain zero

Ranges were log transformed before analysis

Habitat use

Habitat use rankings at the landscape and local scales using both 100% MCP and Kernel estimates are summarised in Tables 4 and 5. Habitat use was statistically significantly non-random apart from at the local scale using kernel estimates, when it was near significance, and at the local scale on sites where badgers were present using 100% MCP. At all scales gardens and buildings were the highest ranked habitats compared with their availability, on sites with and without badgers, and with both methods of home range calculation. Woodland was the least selected habitat in all analyses, apart from at the local scale with 50% kernel estimates. Arable land was the next least selected habitat after woodland. Other habitats were interchangeable depending on the scale and the home range method applied. Hedgerow was ranked highly at the landscape scale but became less selected within home ranges. Pasture was selected above amenity grassland when analysis was performed using kernel estimates and vice versa when using 100% MCP.

There was a difference in habitat selection at the landscape scale on sites with and without badgers when analysis was performed with 100% MCP (Table 4). On sites with badgers, buildings were ranked first, and on sites with no badgers gardens and hedgerow were ranked above buildings. There was no difference between hedgehog habitat selection at the home range scale between sites with and without badgers. There were too few hedgehogs with over 25 fixes (21) to analyse differences between the habitat selection of hedgehogs on sites with and without badgers when using 50% kernel estimates.

Table 4 The ranking of habitats selected by radio-tracked hedgehogs at the landscape scale in a) 100% minimum convex polygon (MCP) estimate of home range, c) 50% kernel estimate of home range, and b) and d), the hedgehog habitat selection within these home ranges

a) 100% MCP home range selection in the landscape									
Rank	6	5	4	3	2	1	0	p	λ
All	GA >>>	BD >>>	HR >>>	PA >	AM >	AB >	WD	0.002**	0.40
Males	GA >>>	BD >>>	HR >>>	PA >	AM >	WD >	AB	0.002**	0.17
Females	GA >	BD >	HR >	PA >	AM >	AB >>>	WD	0.002**	0.31
Badgers	BD >	GA >	PA >	HR >	AM >>>	AB >	WD	0.002**	0.10
No badgers	GA >>>	BD >	HR >>>	PA >	AB >	WD >	AM	0.002**	0.18

b) Habitat selection within 100% MCP home range								
Rank	5	4	3	2	1	0	p	λ
All	BD & GA >	PA >	AM >	AB >>>	WD >	HR	0.006**	0.51
Males	BD & GA >	PA >	AB >	AM >	WD >	HR	0.022*	0.44
Females	BD & GA >	AM >	PA >	HR >	AB >	WD	0.018*	0.31
Badgers	BD & GA >	PA >	AM =	AB =	WD =	HR	0.158	0.28
No badgers	BD & GA >	PA >	AM>	AB >	HR >	WD	0.030*	0.50

c) 50% Kernel Home-range selection in the landscape									
Rank	6	5	4	3	2	1	0	p	λ
All	GA >>	BD >>	HR >	PA >	AM >>	AB >	WD	0.002**	0.034
Males	GA >	BD >>	HR >	PA >	AM >>	WD >	AB	0.002**	0.029
Females	GA >>	BD >>	HR >	AM >	PA >	AB >	WD	0.03*	0.030
Badgers	BD >	GA >>	HR >	PA >	AM >>	AB >	WD	0.028*	0.003
No badger	GA >>	BD >>	HR >	PA >	AM >	AB >	WD	0.002**	0.021

d) Habitat selection within 50% Kernel home range								
Rank	5	4	3	2	1	0	p	λ
All	BD & GA >>	PA >	AM =	AB =	WD >	HR	0.056.	0.233

Coding: AB=arable, AM=amenity grass, BD=buildings, GA=gardens, HR=hedgerow, PA=pasture, WD=woodland
Habitats are ranked from most selected to least from left to right
>>> indicates a statistically significant difference in hedgehog preference between habitat groups
> indicates a non-significant difference and = indicates no difference
Habitat selection with 100% MCPs includes 52 hedgehogs
Habitat selection with 50% kernel includes 21 hedgehogs
Ranking was carried out following (Aebischer *et al.* 1993)

Table 5 A ranking matrix (Aebischer *et al.* 1993) of habitats selected by radio-tracked hedgehogs at the landscape scale in a) 100% minimum convex polygon (MCP) estimate of home range, c) 50% kernel estimate of home range, and b) and d), hedgehog habitat selection within these home ranges

a) 100% MCP home range selection in the landscape

	Amenity	Arable	Buildings	Gardens	Pasture	Hedgerow	Woodland	Rank
Amenity	0	+	---	---	-	---	+++	2
Arable	-	0	---	---	---	---	+	1
Buildings	+++	+++	0	---	+++	+++	+++	5
Gardens	+++	+++	+++	0	+++	+++	+++	6
Pasture	+	+++	---	---	0	---	+++	3
Hedgerow	+++	+++	---	---	+++	0	+++	4
Woodland	---	-	---	---	---	---	0	0

b) Habitat selection within 100% MCP home range

	Amenity	Arable	Village	Grassland	Hedgerow	Woodland	Rank
Amenity	0	+	-	-	+++	+	3
Arable	-	0	---	-	+	+++	2
Village	+	+++	0	+	+++	+++	5
Grassland	+	+	-	0	+++	+++	4
Hedgerow	---	-	---	---	0	+	1
Woodland	-	---	---	---	-	0	0

c) 50% Kernel Home-range selection in the landscape

	Amenity	Arable	Buildings	Gardens	Pasture	Hedgerow	Woodland	Rank
Amenity	0	+++	---	---	-	-	+++	2
Arable	---	0	---	---	---	---	+	1
Buildings	+++	+++	0	---	+++	+++	+++	5
Gardens	+++	+++	+++	0	+++	+++	+++	6
Pasture	+	+++	---	---	0	-	+++	3
Hedgerow	+	+++	---	---	+	0	+++	4
Woodland	---	-	---	---	---	---	0	0

d) Habitat selection within 50% Kernel home range

	Amenity	Arable	Village	Grassland	Hedgerow	Woodland	Rank
Amenity	0	+	-	-	+	-	2
Arable	-	0	---	-	+	+	2
Village	+	+++	0	+++	+++	+	5
Grassland	+	+	---	0	+++	+	4
Hedgerow	-	-	---	---	0	-	0
Woodland	+	-	-	-	+	0	2

+ indicates habitat was positively selected over comparison habitat and – vice versa. A triple sign indicates the preference was statistically significant

Habitat selection with 100% MCPs includes 52 hedgehogs

Habitat selection with 50% kernel includes 21 hedgehogs

The percentage of hedgehog tracking fixes recorded on arable land varied with site (ANOVA, X^2=38.8, p<0.0001, 3 df, Fig.10b). On sites where badgers were present a lower percentage of tracking fixes was recorded on arable land: 13.7 ± 5.1% compared with 27.3 ± 3.8%, on sites without badgers. There was no difference in the percentage of fixes recorded on arable land between males and females (ANOVA, X^2=0.26, p=0.61, 1 df).

Nesting

The general habitat used for nesting was non-random (λ= 0.37, p=0.002). Habitats used were ranked as follows village >>> woodland > pasture > arable, where >>> indicates a significant difference between habitats. Forty of the 66 nests studied were within villages and 48% of these were constructed in scrub, 25% in buildings and 23% in hedgerows (Fig.17). Nests in hedgerows in villages were in the hedgerows of amenity grassland or garden hedgerows. Across the four villages 28% of hedgerows were conifer, 19% privet and 19% hawthorn. Only eight nests were constructed in arable fields and 8 in pasture fields. When farmland was used hedgerows were by far the most chosen habitat (Fig. 17). Hedgerows on farmland tended to be predominately hawthorn and blackthorn with brambles. Ten nests were constructed in scrub in woodland.

The mean total width of the hedgerow was wider in farmland hedgerows where hedgehogs nested than hedgerows never used for nests, but this was only near significance in a logistic regression (Fig.18, z= 7.13, p=0.08). For nests made with natural materials, 67% contained leaf litter, 56% dry grass and 50% were in brambles. Three hedgehogs used holes in both living and dead trees. A variety of man-made structures were used for nesting in villages including garden sheds, hay barns, compost heaps and under tarpaulin.

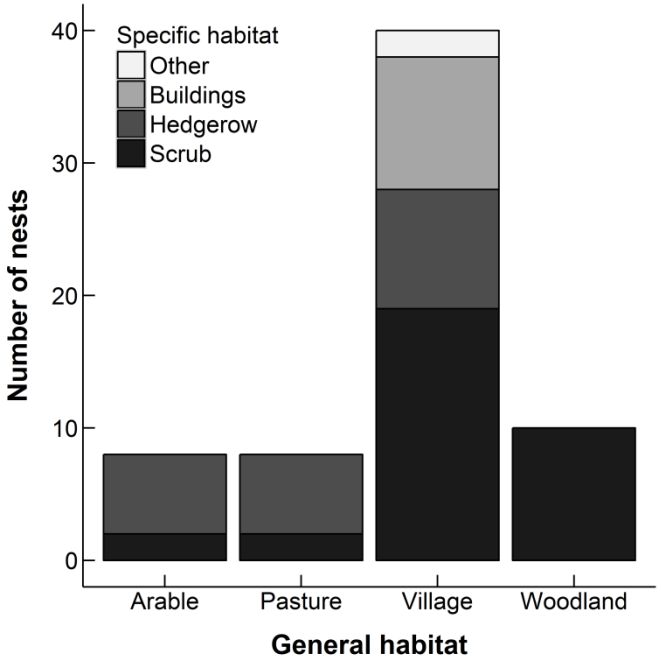


Fig.17 The general habitat (x axis) and the specific habitat (see legend) in which 66 hedgehog day nests were constructed. Selection of the general habitat used for nesting was non-random (λ= 0.37, p=0.002). Nest habitats were recorded during a radio-tracking study of hedgehogs on four sites in Norfolk and Yorkshire in July-October 2013 and April-September 2014

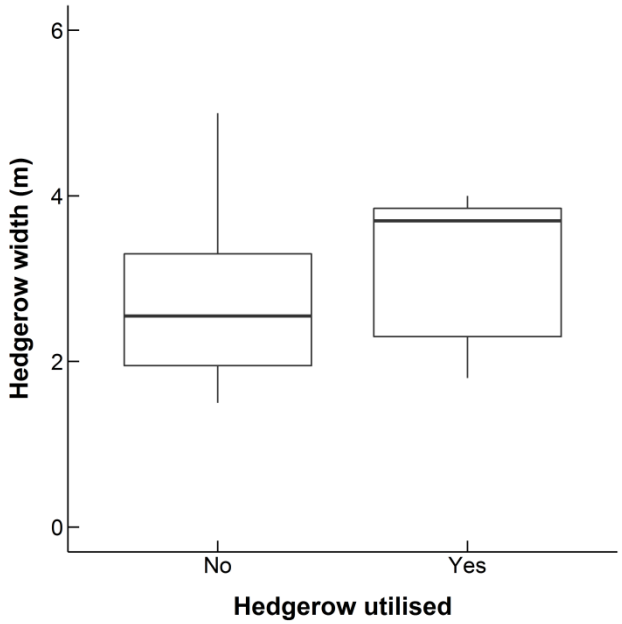


Fig.18 The width of hedgerows surveyed on four sites in Norfolk and Yorkshire. Hedgerow utilised indicates whether or not the hedgerow was utilised as a nest site during radio-tracking studies in July-October 2013 and April-September 2014. Hedgerow width was near statistical significance in determining whether hedgehogs nested in a hedgerow or not (Logistic regression, z= 7.13, p=0.08)

Discussion

The evidence presented in this study demonstrates that hedgehogs favour habitats in and around rural villages rather than those on the surrounding arable farmland. Gardens and buildings were strongly favoured over all farmland habitats, at both the landscape and home range scale, and woodland was avoided (Tables 4 and 5). This habitat selection is in line with previous studies of wild hedgehogs in rural areas and the results of release studies (Doncaster 1994; Reeve 1998; Doncaster *et al.* 2001).

Badger presence is thought to cause hedgehogs to select rural villages, where badger numbers are lower than on the surrounding farmland (Young *et al.* 2006; Hof *et al.* 2012). The results from this study support this: on the two badger-occupied sites buildings were ranked before gardens and hedgerows at the landscape scale and vice versa when badgers were absent. Also, the hedgehogs tracked in this study were found further from badger activity than a randomly generated set of tracking fixes. Furthermore, on badger-occupied sites hedgehogs spent less time on arable land, supporting the notion that arable land is a 'landscape of fear' for hedgehogs (Micol *et al.* 1994; Laundre, Hernandez & Ripple 2010; Hof *et al.* 2012). Woodland was particularly avoided at both the landscape and home range scale, on sites with and without badgers, although hedgehogs did nest in small coppices of woodland on both of the badger-free sites. All the active badger setts observed in this study were in woodland, which could be one reason for hedgehog's avoidance of woodland.

Hedgehogs were found closer to cover and hedgerows when badgers were present, a finding that accords with the results of a study of hedgehogs on four further sites in England by Hof *et al.* (2012). Studies of other small mammals also show a trade-off between prey availability and distance to cover in the presence of predators (Lima & Dill 1990; Kotler *et al.* 1991; Hughes & Ward 1993; Orrock 2004). We can speculate that hedgehogs may perceive a greater threat from badger presence further from cover, on sites where badgers are present. The distance a hedgehog was found from buildings was positively correlated with the distance that the hedgehog was from cover

and hedgerows, suggesting that villages provide a range of habitats in which hedgehogs are able to take refuge from badgers.

Home range size was larger on sites where badgers were not present but this was significant only when all tracking fixes were included in the calculation of the home range size. There was no evidence of an effect on the size of the core range. One possible reason for these findings is that hedgehogs range less overall as a result of staying closer to cover and hedgerows when badgers are present (Hof & Bright 2012; this study). It is plausible that this restricted movement and affinity for cover in the presence of badgers may hamper a hedgehog's ability to forage and this warrants further investigation.

Although badger presence was a key driver of hedgehog habitat use in this study, hedgehogs on badger-free sites still selected village habitats over arable land, suggesting villages may be favoured by hedgehogs for other reasons in combination with refuge from immediate predation. We found a positive correlation between the mean distance a hedgehog was found from buildings and home range size, regardless of the method used to calculate the home range size. This finding may be due to a lower availability of resources, i.e. lower earthworm abundance, on arable land than on mown grass habitats in rural villages (Doncaster 1992, 1994; Doncaster *et al.* 2001), and hedgehogs must put in more effort per prey item captured on arable land. Increased locomotion may be energetically costly (Kenagy & Hoyt 1989; Covell, Miller & Karasov 1996) and this could at least partly explain why hedgehogs select villages.

This study also provides evidence that villages offer a wide range of day nesting habitats for hedgehogs, in corroboration with previous study in Finland, where over half of day nests in urban areas were constructed in built-up areas (Rautio *et al.* 2014). Village habitats were ranked as the most selected habitat for nesting and within village habitats scrub was the most used habitat. In this study scrub included bushes and areas of brambles and weeds, which were plentiful in gardens. Nest sites in villages were often inaccessible such as under garden sheds, which supports the hypothesis

that nest sites may be more secure in villages, although human disturbance of nests in urban areas is potentially problematic, for example from domestic dogs (Reeve 1994). Hedgerows were still selected in villages and were the most common habitat used for nesting on farmland, as in a study by Haigh *et al.* (2012b) in Ireland, where 82% of 16 nests on farmland were found in hedgerows.

Hedgerow width was an indicator of whether it was likely to be used for nesting or not. However, this was not statistically significant, possibly as the number of hedgerows utilised on arable farmland was low compared with those not utilised (20 not used, 8 used). Hedgerows that hedgehogs nested in were also shorter than those never utilised. Short, wide, compact hedgerows are arguably more dense than tall, slim hedgerows and it has previously been suggested that hedgehogs will not nest in hedgerows that are particularly bare at the base (Hof & Bright 2010b). The hedgerow BAP target states that the minimum width for a favourable hedgerow for biodiversity should be 1.5 m (DEFRA 2007). The mean width of hedgerows used for day nests in this study was 3.18 ± SE 0.33m compared with 2.78 ± SE 0.25m for those unused, giving some indication that hedgehogs may require a width greater than that currently deemed as favourable, although a larger study is needed to substantiate this.

Another explanation of hedgehogs' selection of villages in this study could be an attraction to higher numbers of mates in villages. In this study we encountered far fewer hedgehogs on arable land than in rural villages so it may be that hedgehogs have to travel further to look for mates on arable land. Male hedgehogs tend to search actively for females, whereas females are more sedentary (Reeve 1994), yet in this study both male and female home ranges were positively correlated with mean distance from buildings indicating that it is not purely seeking out mates causing hedgehogs to range further on arable land.

We found no evidence of hedgehogs' attraction to the warmer microclimate in rural villages in this study. Hedgehogs were in fact found further from cover when it was colder (Fig.2). The reason for this finding is unclear. We found no evidence that the relationship was due to hedgehogs utilising

the centre of arable fields after harvesting when temperatures are colder. We also tested for an effect of time in the evening, as temperatures are warmer earlier on in the evening when hedgehogs may be closer to edge habitats because they have just emerged from the nest, but found no effect.

Unlike in previous studies (Hof & Bright 2010b), hedgerow was selected less than arable land at the home range scale. It may be that hedgerows are only heavily used when hedgehogs are on arable land, as cover from predation (Hof *et al.* 2012), but in this study, as hedgehogs spent much of their time in the village, there was other cover available e.g. shrubs, scrub and out-houses. Alternatively, in this study hedgerows may have been selected for nesting rather than foraging and thus hedgehogs selected home ranges with high availability of hedgerow but did not utilise hedgerows during nightly tracking (mean percentage of area that was hedgerow at the landscape scale on the four sites: 1.83 ± SE 0.05%, mean percentage of hedgerow at the home range scale: 3.36 ± SE 0.22%). It is also worth noting that the type of hedgerow available in rural villages differs from that on open arable land; there was a range of hedgerow types such as conifer and privet whereas on arable land hedgerows were predominately hawthorn and blackthorn.

Summary

This study demonstrates that hedgehogs are currently associated with rural villages rather than farmland, particularly arable land. There is evidence that badger presence alters hedgehog habitat use, especially in respect to avoidance of arable land and badger activity and the use of cover, and that this is one potential cause of hedgehogs' preference for rural villages. However, on sites with no badgers, hedgehogs also selected buildings and gardens over any other habitat; we suggest that food availability also attracts hedgehogs to villages. This is supported by the finding that hedgehogs that spent more time closer to buildings had smaller home range sizes. Further research into hedgehog diet in rural landscapes is needed to establish the contribution of food availability to hedgehog distribution. Our study of nest sites confirms that hedgehogs prefer to build day nests in villages than on arable land and that a range of habitats are available to build secure nests.

The research presented here indicates the importance of rural villages in sustaining hedgehog numbers in the UK countryside. Our findings suggest a two-pronged approach for hedgehog conservation: firstly, maintaining hedgehog subpopulations in rural villages by improving garden management and preserving green spaces and secondly, improving the surrounding arable land, chiefly in respect to connectivity between rural villages and cover from predation. Although this research shows that residential areas are selected by hedgehogs, hedgehogs are also in decline in urban areas and they face a suite of problems which were beyond the scope of this study including: poisoning from molluscicides and rodenticides (Keymer, Gibson & Reynolds 1991; Dowding *et al.* 2010), a lack of habitat connectivity due to enclosed gardens (Hof & Bright 2009) and deaths on roads (Huijser & Bergers 2000; Rondinini & Doncaster 2002). Wildlife friendly gardening and the consideration of habitat connectivity in urban planning may reduce some of these threats to hedgehogs (Hof & Bright 2009). On arable land, increasing hedgerows and cover will offer protection from badger predation, and provide nest sites and dispersal corridors between rural villages (Moorhouse *et al.* 2014). These recommendations are relevant to many species struggling to survive in landscapes dominated by human habitation and intensively managed farmland.

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Appendix

Table A Details of the 78 hedgehogs captured and radio-tracked during the course of the study

ID	Date captured	County	Site	Sex	Weight (g)	Years tracked	No. of fixes
1	03/07/2013	Yorkshire	A	F	836.6	2013 & 2014	27*†
2	03/07/2013	Yorkshire	A	F	1184.7	2013	5
3	05/07/2013	Yorkshire	C	M	862.7	2013	8
4	16/07/2013	Norfolk	D	F	869	2013 & 2014	37*†
5	17/07/2013	Norfolk	D	M	820.6	2013	19*
6	17/07/2013	Norfolk	D	M	790.9	2013	4
7	17/07/2013	Norfolk	D	M	1119	2013	20*
8	18/07/2013	Norfolk	D	F	688.6	2013	22*
9	19/07/2013	Norfolk	D	M	761.2	2013	16*
10	20/07/2013	Norfolk	D	M	640.8	2013	16*
11	24/07/2013	Norfolk	B	F	711.8	2013 & 2014	53*†
12	24/07/2013	Norfolk	B	M	707.2	2013 & 2014	29*†
13	25/07/2013	Norfolk	B	M	708.9	2013	1
14	25/07/2013	Norfolk	B	F	606.2	2013	22*
15	25/07/2013	Norfolk	B	M	728.2	2013 & 2014	38*†
16	25/07/2013	Norfolk	B	M	688.3	2013	2
17	25/07/2013	Norfolk	B	M	783.8	2013	2
18	25/07/2013	Norfolk	B	M	841.4	2013	2
19	26/07/2013	Norfolk	B	M	809.8	2013	2
20	26/07/2013	Norfolk	B	F	728.1	2013	2
21	26/07/2013	Norfolk	B	M	754.9	2013	2
22	26/07/2013	Norfolk	B	F	797.6	2013 & 2014	52*†
23	26/07/2013	Norfolk	B	M	744.2	2013	2
24	29/07/2013	Yorkshire	A	F	1101.4	2013	9
25	30/07/2013	Yorkshire	A	M	956	2013	15*
26	30/07/2013	Yorkshire	A	F	954.2	2013	13*
27	30/07/2013	Yorkshire	A	M	1179.1	2013 & 2014	9
28	30/07/2013	Yorkshire	A	F	737.1	2013 & 2014	32*†
29	31/07/2013	Yorkshire	A	M	1032.5	2013	2
30	31/07/2013	Yorkshire	A	M	791.6	2013	7
31	31/07/2013	Yorkshire	A	M	985.5	2013	11*
32	31/07/2013	Yorkshire	A	F	995.4	2013	17*
33	31/07/2013	Yorkshire	A	M	999.8	2013	2
34	01/08/2013	Yorkshire	C	F	781.2	2013 & 2014	24*
35	02/08/2013	Yorkshire	C	F	828.3	2013	3
36	02/08/2013	Yorkshire	C	F	845.4	2013	12*
37	02/08/2013	Yorkshire	C	M	911.7	2013	3
38	02/08/2013	Yorkshire	C	F	827.6	2013	2
39	02/08/2013	Yorkshire	C	M	892.6	2013	3
40	03/08/2013	Yorkshire	C	M	1022.1	2013 & 2014	18*

Table A *Continued*

ID	Date captured	County	Site	Sex	Weight (g)	Years tracked	No. of fixes
41	04/08/2013	Yorkshire	C	M	1120.6	2013	2
42	04/08/2013	Yorkshire	C	F	901	2013	10*
43	28/08/2013	Yorkshire	A	M	1113.5	2013	9
44	04/09/2013	Norfolk	B	F	741.3	2013	13*
45	04/09/2013	Norfolk	B	M	810.7	2013	16*
46	04/09/2013	Norfolk	B	M	665.4	2013	16*
47	22/04/2014	Norfolk	B	M	813.4	2014	4
48	22/04/2014	Norfolk	B	M	869.2	2014	20*
49	25/04/2014	Norfolk	B	F	726.4	2014	21*
50	07/05/2014	Norfolk	B	M	801.2	2014	25*†
51	08/05/2014	Norfolk	B	F	678.9	2014	32*†
52	08/05/2014	Norfolk	B	F	673.7	2014	17*
53	16/05/2014	Yorkshire	C	M	707.1	2014	5
54	20/05/2014	Yorkshire	C	M	516.4	2014	43*†
55	27/05/2014	Norfolk	D	M	1019	2014	34*†
56	31/05/2014	Norfolk	D	F	1015.8	2014	34*†
57	06/05/2014	Norfolk	B	M	791.8	2014	32*†
58	10/06/2014	Norfolk	B	M	742.8	2014	18*
59	16/06/2014	Norfolk	D	M	802.2	2014	27*†
60	19/06/2014	Norfolk	D	M	662.8	2014	26*†
61	20/06/2014	Norfolk	D	F	825.7	2014	28*†
62	26/06/2014	Yorkshire	C	M	612.1	2014	25*†
63	04/07/2014	Yorkshire	A	M	989.1	2014	29*†
64	06/07/2014	Yorkshire	A	F	889.3	2014	24*
65	06/07/2014	Yorkshire	A	M	980.3	2014	25*†
66	06/07/2014	Yorkshire	A	M	706.1	2014	25*†
67	06/07/2014	Yorkshire	A	F	802.4	2014	33*†
68	08/07/2014	Yorkshire	A	M	852	2014	8
69	10/07/2014	Yorkshire	A	M	765.1	2014	23*
70	21/07/2014	Yorkshire	A	M	NA	2014	19*
71	30/07/2014	Norfolk	B	M	867.6	2014	17*
72	30/07/2014	Norfolk	B	F	736.2	2014	21*
73	30/07/2014	Norfolk	B	M	747.8	2014	20*
74	13/08/2014	Yorkshire	C	M	970.5	2014	22*
75	15/08/2014	Yorkshire	A	F	1275.5	2014	11*
76	15/08/2014	Yorkshire	A	F	811.6	2014	3
77	18/08/2014	Norfolk	B	M	820.9	2014	16*
78	27/08/2014	Yorkshire	A	M	944.3	2014	12*

*****Indicates that the hedgehog was included in MCP home range analysis

†Indicates that the hedgehog was included in kernel home range analysis

Chapter 4

Daily energetic expenditure in the face of predation: hedgehog energetics in rural landscapes

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Abstract

Daily energy expenditure (DEE) gives a measure of energy balance in the face of environmental conditions. Failure to maintain energy balance can have an impact on survival and reproduction, and therefore impact on the persistence of populations. Here we study patterns in the DEE of the European hedgehog (*Erinaceus europaeus*). This species is declining in the UK, and studies dating back twenty years have shown that hedgehogs favour gardens and amenity grassland over arable land. One of the main threats the hedgehog faces on arable land is thought to be predation by badgers *(Meles meles).* We hypothesise that there is a gradient of suitable habitat for hedgehogs which decreases the further they are from buildings. This gradient is a result of fewer food resources, a higher risk from predation and colder ambient temperatures, as distance to the nearest building increases. Here the doubly labelled water (DLW) method was used to obtain 44 measures of DEE from hedgehogs in predominately arable areas, to determine the energetic costs associated with proximity to buildings, on sites with and without badgers. We also recorded hedgehog condition, by regressing the natural logarithm of body mass on the natural logarithm of rear thigh length, and ranging behaviour. The mean DEE was 508.9 ± SE 34.8 KJ/day and there was large variation in DEE between individuals, ranging from 226.7 KJ/day to 1271.7 KJ/day. DEE increased the further a hedgehog was from buildings, possibly because they ranged larger distances to find sufficient prey on arable land. Hedgehogs had a 30% lower DEE on sites where badgers were present. We speculate that on badger-occupied sites hedgehogs may restrict foraging in response to a perceived threat from predation and thus have reduced DEE. Hedgehogs on the site with the highest DEE were in the greatest condition and those on the site with the lowest DEE were in the poorest condition. Hedgehog condition was poorer on badger occupied sites, but this variation was attributed to the poor condition of hedgehogs on one site with badgers. These findings support the hypothesis that hedgehogs expend more energy the further they are from buildings, which potentially explains their attraction to residential areas. Furthermore, on badger-occupied sites hedgehogs may seek refuge in villages where the perceived threat of predation is lower.

Introduction

Energy balance is essential in all animal species for survival and reproduction. The cost of homeostasis, in particular body temperature regulation, in mammals can be high (Nagy 1987), and small mammals must maintain a high metabolic rate relative to their body size to maintain endothermy (McNab 1983). In addition to maintaining the body at rest, energy must be allocated for activity, growth, reproduction and survival (Brown *et al.* 2004). An animal's field metabolic rate, or daily energy expenditure (DEE), gives a measure of the total energy an individual spends on these processes, in the face of environmental conditions. DEE varies between species (Bryce *et al.* 2001; Speakman & Król 2010), between individuals of the same species (Zub *et al.* 2011; Fletcher *et al.* 2012) and within individuals at different points in time (Speakman *et al.* 1994; Fletcher *et al.* 2012).

Failure to maintain balance between energy input and output can affect the survival of individuals (Zub *et al.* 2011) and the amount of energy that is apportioned for reproduction (Speakman 2008; Rutkowska *et al.* 2011). Examining differences in DEE between populations of a declining species, in varying habitats, may therefore be useful in examining factors contributing to species' declines. It is hypothesised that habitat productivity may influence DEE in two different ways: in low-productivity habitats an individual's resting metabolic rate (RMR), and therefore DEE, may be forced up, conversely, in higher productivity habitats, higher RMRs and thus higher rates of DEE may be enabled (Speakman *et al.* 2003; Bozinovic, Muñoz & Cruz-Neto 2007; Burton *et al.* 2011). Additionally, energy expenditure increases with locomotion (Kenagy & Hoyt 1989; Covell, Miller & Karasov 1996) and ranging behaviour varies in response to resource availability (Ford 1983).

Predation risk is an understudied factor which is also likely to affect an individual's behaviour and therefore energetic expenditure (McNab 1986; Lima 1998). When there is a perceived threat of predation, individuals may expend energy by fleeing or burrowing (Vleck 1979; Kenagy, Sharbaugh & Nagy 1989), or due to increased physiological stress (Boonstra *et al.* 1998; Tidhar, Bonier & Speakman 2007). Alternatively, individuals may be forced to alter habitat use (Kotler *et al.* 1991), or

restrict foraging to avoid predation (Banks, Hume & Crowe 1999; Ergon *et al.* 2004). Thus, predator presence can have a detrimental effect on body mass, survival and reproduction (Hik 1995; Ergon *et al.* 2004; Monarca, Mathias & Speakman 2015a; Monarca *et al.* 2015b).

The European hedgehog (*Erinaceus europaeus*) is a model species for studying the effects of habitat productivity and predator presence on DEE. The hedgehog is declining and patchily distributed in the UK (Hof 2009; Aebischer, Davey & Kingdon 2011; Roos, Johnston & Noble 2012) and declines are thought to be more severe in rural areas (JNCC 2010). Nationally, declines in rural areas have been attributed to changes in farmland management practices (Harris *et al.* 1995), and predation by European badgers (*Meles meles*) (Hof & Bright 2012). Locally, hedgehog release studies have shown arable land to be particularly under-selected by dispersing hedgehogs, which show an attraction to rural villages and gardens (Doncaster 1992, 1994; Doncaster, Rondinini & Johnson 2001). Hedgehog avoidance of arable land in favour of rural villages may be due to poor habitat quality or predator presence on arable land and evidence shows it is most likely a combination of the two (Micol, Doncaster & Mackinlay 1994; Hof, Snellenberg & Bright 2012).

Hedgehogs prey on macroinvertebrates (Yalden 1976; Wroot 1984) and arable land may be unfavourable for hedgehogs due to a lack of natural prey, resulting from agricultural intensification (Moreby & Southway 1999; Wilson *et al.* 1999; Robinson & Sutherland 2002; Macdonald & Feber 2015a; b). Conversely, rural villages are abundant in mown grass habitats, such as amenity grassland and garden lawns (Doncaster 1992, 1994), which have higher earthworm abundance per unit area than arable fields (Kruuk *et al.* 1979). Hedgehogs may also benefit from supplementary feeding in villages (Morris 1985; Hubert *et al.* 2011) and warmer ambient temperatures than on arable land (see Hubert *et al.* 2011). Badgers are more abundant on open farmland than in rural villages (Neal & Cheeseman 1996) and hedgehog presence is negatively correlated with the abundance of badger setts (Micol *et al.* 1994; Young *et al.* 2006). The presence of badgers is thought to be particularly detrimental because they are intraguild predators and compete with hedgehogs for earthworms

(Neal 1986; Polis, Myers & Holt 1989; Doncaster 1992). Badgers may therefore exclude hedgehogs from productive habitats and alter their foraging behaviour (Doncaster 1992; Ward, Macdonald & Doncaster 1997; Ward, Austin & MacDonald 2000; Hof *et al.* 2012). Hedgehogs may also be predated by foxes on arable land (Reeve 1994).

For hedgehogs in rural landscapes, food availability, temperature and risk from badger predation all vary with distance to rural villages (Fig.1). Therefore studying what factors govern their preference for villages may shed light on why hedgehogs appear to be declining nationwide, and lead to solutions to conserve them. Our study investigated variation in hedgehog DEE, body condition and ranging behaviour along a gradient of habitats from rural villages to arable at sites, with and without resident badger populations, to dissect the causes of hedgehogs' apparent preference for villages. We predicted that hedgehogs would face an increasing gradient of pressures further away from buildings and those which spend more of their time further from buildings will have higher energetic costs to those residing close to buildings. Hedgehogs may have higher costs further from buildings due to physiological stress from badger presence (Ward *et al.* 1996), having to increase foraging range to meet energy requirements, or experiencing increased costs of thermoregulation. Alternatively, hedgehogs may have lower energy expenditure further from buildings as activity is restricted to avoid predation (Hof *et al.* 2012), because hedgehogs may be smaller due to restricted foraging (Monarca *et al.* 2015a; b), or as energy expenditure is constrained due to insufficient food resources.

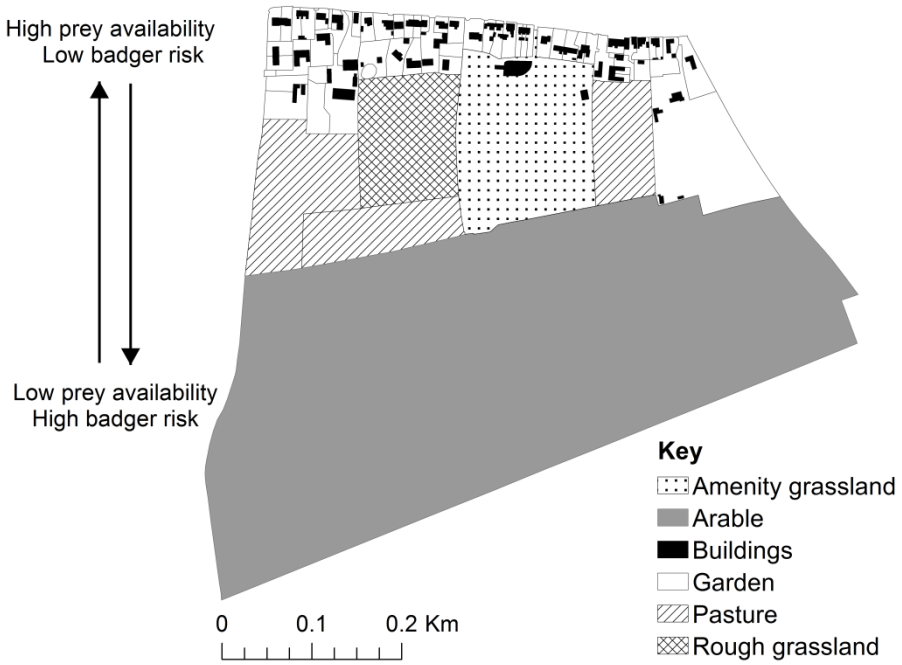


Fig.1 A portion of Site D, where hedgehog energetic experiments took place, showing the gradient of habitat suitability for hedgehogs in predominately arable rural areas

Methods

Study design

We wished to test whether hedgehog DEE, condition and ranging behaviour varied the further from buildings that a hedgehog resided, and whether these varied with and without badger presence. To select sites for the study a questionnaire was sent to 4000 farmers in Britain in 2013 (for analysis of questionnaire data see chapter 6). The questionnaire asked if farmers had seen hedgehogs in the past year. Thirteen farms across England where farmers had observed hedgehogs were surveyed using red-filtered spotlights and four similarly-matched sites with hedgehogs present were selected for further study, two in North Norfolk (UK grid refs: TF 96061 25469 and TG 16716 36586; Table 1) and two in North Yorkshire (SE 90511 81822 and SE 68646 24715; Table 1). Each site consisted of arable farmland with a rural village within 2.5km. Each village consisted of houses and rural gardens with village edge habitats, including small pasture fields and amenity grassland. To test the effect of badger presence on DEE, we selected one site in each county where badgers were present and one

site where they were absent. Badger presence was determined by surveys in October 2013 and April 2014 by inspecting woodland, coppices and hedgerows, for setts, latrines and tracks. Badger sightings during hedgehog radio-tracking were also recorded. To ascertain if hedgehogs were patchily distributed on the study sites, we recorded the number of encounters of untagged individuals on each site in the village, village edge habitats and surrounding arable land.

Table 1 Details of four sites in England on which hedgehog energetics studies took place in 2013 and 2014

Site	County	Size (ha)	Badger presence	% of buildings	% of hedgerow	% of arable	Agri-environment scheme
A	North Yorkshire	632	Absent	0.7	1.5	74.7	ELS
B	Norfolk	457	Absent	0.5	1.6	72	ELS
C	North Yorkshire	379	Two setts	0.9	1.7	72	ELS
D	Norfolk	280	Two setts	2.9	4	69.2	HLS

% is the percentage of the total site area made up of the given habitat
ELS= Entry Level Stewardship, HLS= Higher Level Stewardship

Hedgehog capture

Adult hedgehogs were captured, by hand, across the four sites in July-September 2013 and April-September 2014 (Natural England License 2014/SCI/0298, HO PIL 30/10293). Hedgehogs were anaesthetised using inhalation anaesthesia (IsoFlo, Zoetis, London, UK) weighed, sexed and fitted with a 10g radio-tag (Biotrack, Dorset, UK), which was glued to a patch of clipped spines on the rump using epoxy resin. Hedgehogs were marked with six 1cm pieces of coloured heat-shrink tubing, which were glued over spines in a patch on the rear (Molony *et al.* 2006). As DEE may vary with reproductive state in small mammals (Kenagy *et al.* 1989; Poppitt, Speakman & Racey 1993, 1994; Key & Ross 1999; Fletcher *et al.* 2012), we measured testes length and female hedgehogs were checked for signs of lactation and pregnancy. Hedgehogs were given three weeks to become accustomed to the radio-tag and then re-captured for energetics experiments.

Doubly labelled water experiments

Daily energy expenditure was measured by the doubly labelled water (DLW) technique (Lifson, Gordon & McClintock 1955; Nagy 1980, 1983; Butler *et al.* 2004). In addition to the hedgehogs tagged three weeks prior, 12 hedgehogs were captured during the experiments and were fitted with a tag and injected with DLW at the same time. There was no difference in the mean DEE between those given time to acclimatise and those injected and tagged at the same time (Anova, $F_{1,42}$ =0.25, p=0.62); hedgehogs that had time to acclimatise to the tag: 501.6 ± 40.2 KJ/day and those tagged during the DLW experiments: 528.2 ± 71.8 KJ/day, which suggests that hedgehogs do not need time to become acclimatised to tags, and tagging has no immediate effect on energy expenditure. Radio-tags were 0.87-1.84% of the hedgehog's body mass in the study and small tags relative to body mass have previously been shown to have no effect on DEE in small mammals (Berteaux *et al.* 1996a).

Hedgehogs were all given the same dose of DLW (0.6 ml; 61,3671 PPM ^{18}O and 33,4163 PPM ^{2}H), injected ventrally and subcutaneously under anaesthesia. To calculate the exact dose, administered trials were conducted in the laboratory to assess the mean volume of DLW left in the syringe after injection (4d.p.). After injection hedgehogs were placed in a recovery box whilst the isotopes reached equilibrium in the body. Hedgehogs were re-anesthetised and an initial 100µl blood sample was taken from the left hind leg. In 2013, hedgehogs were held for one hour before the initial blood sample (time based on species of a similar body mass with the same method of injection see Speakman 1997), but this proved to be insufficient time for the isotopes to reach equilibrium in some individuals. Therefore, at the beginning of the 2014 field season a trial was performed to optimise the procedure. Three hedgehogs were captured and a 100µl blood sample was taken from each hedgehog at one, two and three hours after the DLW injection. Analysis indicated the optimal time for equilibrium was two hours and consequently this was used for the remainder of the 2014 season.

After the initial blood sample, hedgehogs were allowed to recover from anaesthesia before being released at the point of capture. Hedgehogs were re-captured for a second 100µl blood sample, from the right hind leg, as close to 96h after release as possible. Collecting samples across 96h minimises the large daily variability in DEE (Speakman *et al.* 1994; Berteaux *et al.* 1996b). Background blood samples were taken from two hedgehogs on each site before injection, in order to obtain a measure of the background levels of the isotopes in the local environment. All blood samples were flame-sealed in heparin-free glass capillaries (Vitrex Medical, Herlev, Denmark) and capillary ends were dipped in sealing wax to prevent air leaks. Samples were stored at 4^{o}C until analysis.

Blood sample analysis

The blood-filled capillary tubes were vacuum distilled (Nagy 1983) and the resulting water samples were analysed for their enrichment of ^{2}H and ^{18}O on a liquid water isotope analyser (Los Gatos Research, California, US). Fifteen replicates were measured for each sample, which were run alongside three global water standards; Standard Mean Ocean Water (SMOW), Standard Light Antarctic Precipitation (SLAP) and Greenland Ice Sheet Precipitation (GISP) and three in house laboratory standards, encompassing the range of enrichments expected. Measures of the degree of enrichment of ^{2}H and ^{18}O in the water samples were converted into DEE measures using a single pool model (equation 7.17: Speakman 1997), the optimal method for small mammals (Speakman 1997; Speakman & Król 2005). In 2013, six of the 14 individuals had low isotope enrichments in the initial blood sample, indicating that the isotopes had not reached equilibrium in the body during the one hour holding period. For these animals, their initial enrichment values were estimated based on initial enrichment readings of other hedgehogs that had reached equilibrium in the 2013 dataset, the known volume injected and the individual's body mass. There was no difference in DEE between these six individuals and the other individuals in the 2013 dataset (Anova, $F_{1,12}$ =0.43, p=0.52).

Hedgehog condition

Measures of hedgehog condition were taken from those in the energetics study and also from hedgehogs that were part of an ongoing radio-tracking study on the same field sites. Rear thigh length was measured and the natural logarithm of the hedgehog's body mass was regressed against the natural logarithm of thigh length (Fig.2). The residuals of the regression were used as a condition index (Schulte-Hostedde *et al.* 2005b). For the analysis of hedgehog condition the mean distance to buildings was calculated for each hedgehog over the season.

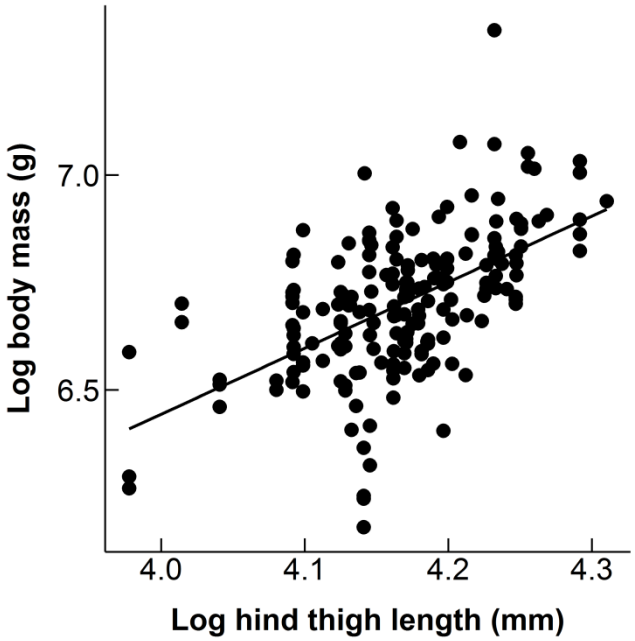


Fig.2 The relationship between hind thigh length and body mass (192 measurements from 69 hedgehogs)

Ranging behaviour

During the 96 hours that hedgehogs were released, hedgehogs were radio-tracked from 9pm-4am, obtaining at least three tracking fixes per hedgehog per evening using a hand-held three element yagi directional antenna (Wildlife Materials International, Murphysboro, USA) and a TRX-1000S

receiver (Wildlife Materials International, Murphysboro, USA). GPS location and habitat found at the site of each fix were recorded. The distance travelled by each hedgehog during the release period was calculated using Ranges7 (Anatrack Ltd, Dorset, UK). Proximity analysis was performed in ArcGIS to measure the distance of each location fix to the nearest building. The mean distance to buildings during the 96 hour release period was calculated for each hedgehog.

Ambient Temperature

To test for the predicted differences in temperature between rural habitats, we placed data loggers (Thermochron ibutton, Maxim Intergrated, CA, USA) 30cm off the ground in a range of habitats including: arable fields, hedgerows of arable fields, farm buildings, amenity grassland and village gardens. Loggers recorded hourly from 19:00-07:00hrs. Ambient temperature was correlated with day in the season and the quadratic term of day in the season in this study (R^2=0.21), as temperature increased from April until July and began to fall again in August. Therefore only day in the season, with 1st of April set as day one for each year, was included in the analysis of hedgehog DEE, condition and ranging behaviour to avoid collinearity (Graham 2003).

Statistical analysis

We wished to test the effect of proximity to buildings and site, categorised by having badgers or not, on DEE in hedgehogs. A series of linear models were constructed in R (R Foundation for Statistical Computing, Vienna, Austria) corresponding to different plausible hypotheses, as recommended by Anderson (2008), listed in Table 2a. Explanatory variables included mean distance to buildings, site, the day in the study period, the quadratic of day, year, individual body mass and sex. Due to the varying badger abundance with distance to buildings, the interaction between site and distance to building was included. Hedgehog ID was not added as a random effect as repeated measures were carried out on only three hedgehogs, and therefore the effects of pseudoreplication from this source were deemed to be negligible. The continuous explanatory variables were scaled to two standard deviations following Gelman (2008).

For assessing the effects of proximity to buildings and badger presence on condition, a series of mixed effects models were constructed with hedgehog ID as a random factor (Table 2b). The explanatory variables included mean distance to buildings, site- categorised as having badgers present or not- day in the season, the quadratic of day, sex, year and the interaction between site and distance to building. For assessing the effects of proximity to buildings and badger presence on ranging behaviour during the energetics studies, linear models were constructed with the distance travelled by each hedgehog in the 96 hour release period as the response variable (Table 2c). The explanatory variables included were mean distance to buildings, site, categorised as having badgers present or not, day in the season, sex and year.

To test for statistically significant differences in the nightly ambient temperature of rural habitats, a linear mixed model was constructed with habitat and site as fixed explanatory variables and date and time as random factors. Pairwise t-tests to test for differences in ambient temperatures between habitats were performed using the Bonferroni correction (Dunn 1961). All results are stated as mean ± standard error.

Table 2 A range of models constructed to assess the predictors of a) Hedgehog daily energy expenditure (DEE;KJ/day), measured by the doubly labelled water method (DLW), b) Hedgehog condition; the residuals of hind thigh length regressed against body mass, and c) The distance a hedgehog travelled in a four day release period

	Model	logLik	R^2	AIC_c	ΔAIC_c	W
a)	Dist to building+Year+Sex+Site	-1.44	0.53	22.99	0.00	0.38
	Dist to building+Year+Sex+Site+Mass	-0.41	0.55	24.11	1.12	0.22
	DayL+Dist to building+Year+DayQ+Sex+Site	1.10	0.58	24.47	1.48	0.18
	DayL+Dist to building+Year+DayQ+Sex+Mass	-3.18	0.49	26.48	3.49	0.07
	DayL+Dist to building+Year+DayQ+Sex+Site+Mass	1.73	0.60	26.78	3.79	0.06
	DayL+Dist to building+Year+Sex+Site+Mass	-0.27	0.56	27.20	4.21	0.05
	DayL+Dist to building+DayQ+Sex+Site+Mass	-1.16	0.54	28.98	5.99	0.02
	DayL+Year+DayQ+Sex	-7.84	0.37	29.95	6.96	0.01
	DayL+Dist to building+Year+DayQ+Site+Mass	-1.93	0.52	30.53	7.54	0.01
	Year+Sex+Mass	-9.68	0.32	30.95	7.96	0.01
	DayL+Year+DayQ+Sex+Mass	-7.28	0.39	31.67	8.68	0.00
	DayL+Year+DayQ+Mass	-9.84	0.31	33.95	11.0	0.00
	DayL+DayQ+Mass	-11.84	0.25	35.25	12.3	0.00
	DayL+Dist to buildings+Year+DayQ+Sex+Site+Mass+ Dist to buildings*Site	3.27	0.27	35.94	13.0	0.00
	Dist to building+Site	-13.71	0.18	41.70	18.7	0.00
	Dist to building+Site+Dist to building*Site	-12.50	0.23	48.29	25.3	0.00
b)	Year+DayL+DayQ+Sex+Site	153.98	0.59	-286.7	0.00	0.27
	DayL+DayQ+Dist to building+Sex+Site	153.97	0.59	-286.7	0.01	0.26
	Year+DayL+DayQ+Dist to building+Site	153.67	0.59	-286.1	0.61	0.19
	Year+DayL+DayQ+Dist to building+Sex+Site+ Dist to building* Site	158.20	0.60	-286.0	0.71	0.19
	Year+DayL+DayQ+Dist to building+Sex+Site	154.02	0.58	-284.6	2.16	0.09
	Year+DayL+DayQ+Sex	144.04	0.60	-273.5	13.3	0.00
	Year+DayL+DayQ+Dist to building+Sex	144.24	0.60	-271.7	15.0	0.00
	Dist to building+Site	138.53	0.50	-262.4	24.3	0.00
	Dist to building+Site+Dist to building* Site	141.51	0.51	-261.8	24.9	0.00
	Year+Dist to building+Sex+Site	138.82	0.50	-258.7	28.1	0.00
c)	Dist to building+Sex	-19.38	0.42	47.78	0.00	0.60
	Day+Dist to building+Sex	-18.96	0.43	49.50	1.72	0.26
	Dist to building+Sex+Site	-17.38	0.47	51.86	4.08	0.08
	Day+Dist to building	-22.59	0.33	54.21	6.42	0.02
	Day+Dist to building+Sex+Site	-17.09	0.48	54.29	6.50	0.02
	Dist to building+Site	-20.70	0.39	55.66	7.88	0.01
	Day+Dist to building+Site	-20.59	0.39	58.29	10.5	0.00
	Day+Sex	-27.00	0.18	63.03	15.2	0.00
	Day+Sex+Site	-26.53	0.20	70.18	22.4	0.00

logLik is the log likelihood for each model. Dist to building is the mean distance each hedgehog was found to the nearest building during the energetics experiments. DayL is the linear term of day in the season, with April 1st being assigned day one, and DayQ is the quadratic term of day

Results

Forty four measures of DEE in free-living hedgehogs were obtained (see appendix Table A for details of study subjects). The mean DEE was 508.9 ± 34.8 KJ/day with a mean body mass of 808.1 ± 18.9g. There was large variation in DEE between individuals in the study ranging from 227 KJ/day to a rate over five times greater at 1272 KJ/day. We obtained 382 GPS fixes for hedgehogs during the 96 hour release period. We took 192 measures of condition, from 69 hedgehogs (see appendix Table B), in July-October 2013 and April-September 2014 and condition ranged from -0.48 to 0.54. We obtained over 11,000 measurements of ambient temperature.

Hedgehog density

Despite aiming to capture equal numbers of hedgehogs in village habitats and on arable land, only two of the 44 hedgehogs in the energetics study were found on arable land (Fig.3). Seventeen hedgehogs were found in village edge habitats including amenity grassland, small pasture fields and set-aside. The majority of hedgehogs, 25, were found in village habitats such as gardens and road verges. Although 36 hedgehogs did use arable land at some point during the 96 hour release period, most of these used the arable land infrequently; only 13 hedgehogs spent 30% or more of their time on arable land. Hedgehog density varied with site; 35% more hedgehogs were encountered on sites where badgers were absent (Fig. 3).

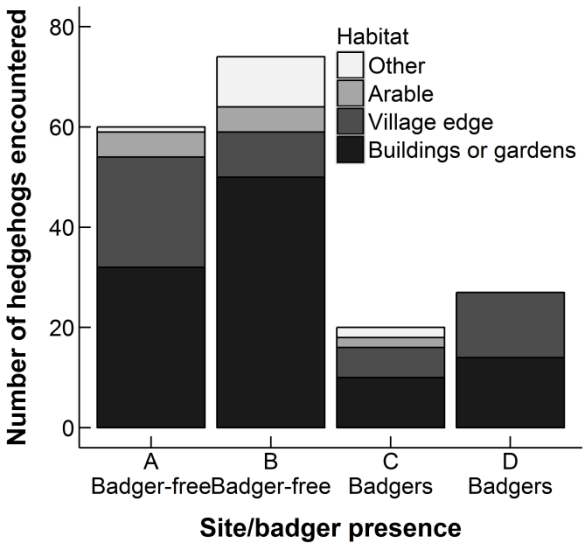


Fig.3 The effect of site and badger presence on the number of hedgehogs encountered in 2013 and 2014 in a variety of rural habitats. Sites A and C were in North Yorkshire and sites B and D were in Norfolk.

Daily energy expenditure

Daily energy expenditure varied significantly between sites and was 30% lower on sites where badgers were present (Fig.4, Table 3). Daily energy expenditure increased with the mean distance hedgehogs were found from buildings (Fig.5, Table 3). The interaction between site and distance to buildings did not feature in the top models by AIC and we can conclude it probably was not a significant predictor of DEE. Female hedgehogs had significantly higher energy expenditure than males in two of the three top models (560.7 ± 55.3 and 473 ± 44.2 KJ/day respectively, Fig.6a, Table 3). Six hedgehogs were noted to be in the late stages of pregnancy or lactating during the energetics experiments and these females had a higher DEE than females which were not pregnant (Fig.6b). Daily energy expenditure was significantly higher in 2013 than in 2014 (Fig.5c, Table 3). There was a weak relationship between body mass and DEE and this was near significance in the second of the top three models (Fig.5a, Table 3). There were positive relationships between day in the season and the quadratic of day with DEE in the third best model, yet the confidence intervals for the effect size included zero indicating the relationship was not statistically significant (Table 3).

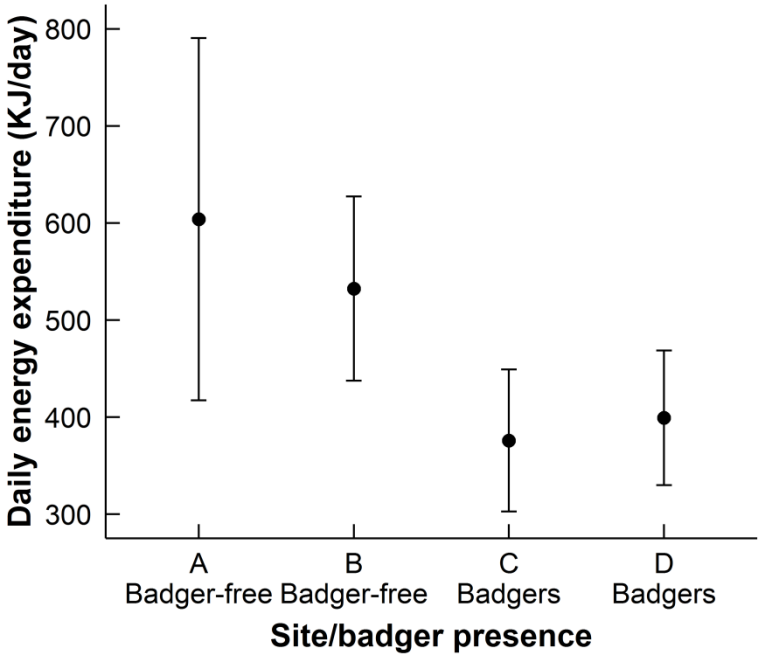


Fig.4 The effect of site and badger presence on hedgehog daily energy expenditure (DEE) in 44 hedgehogs

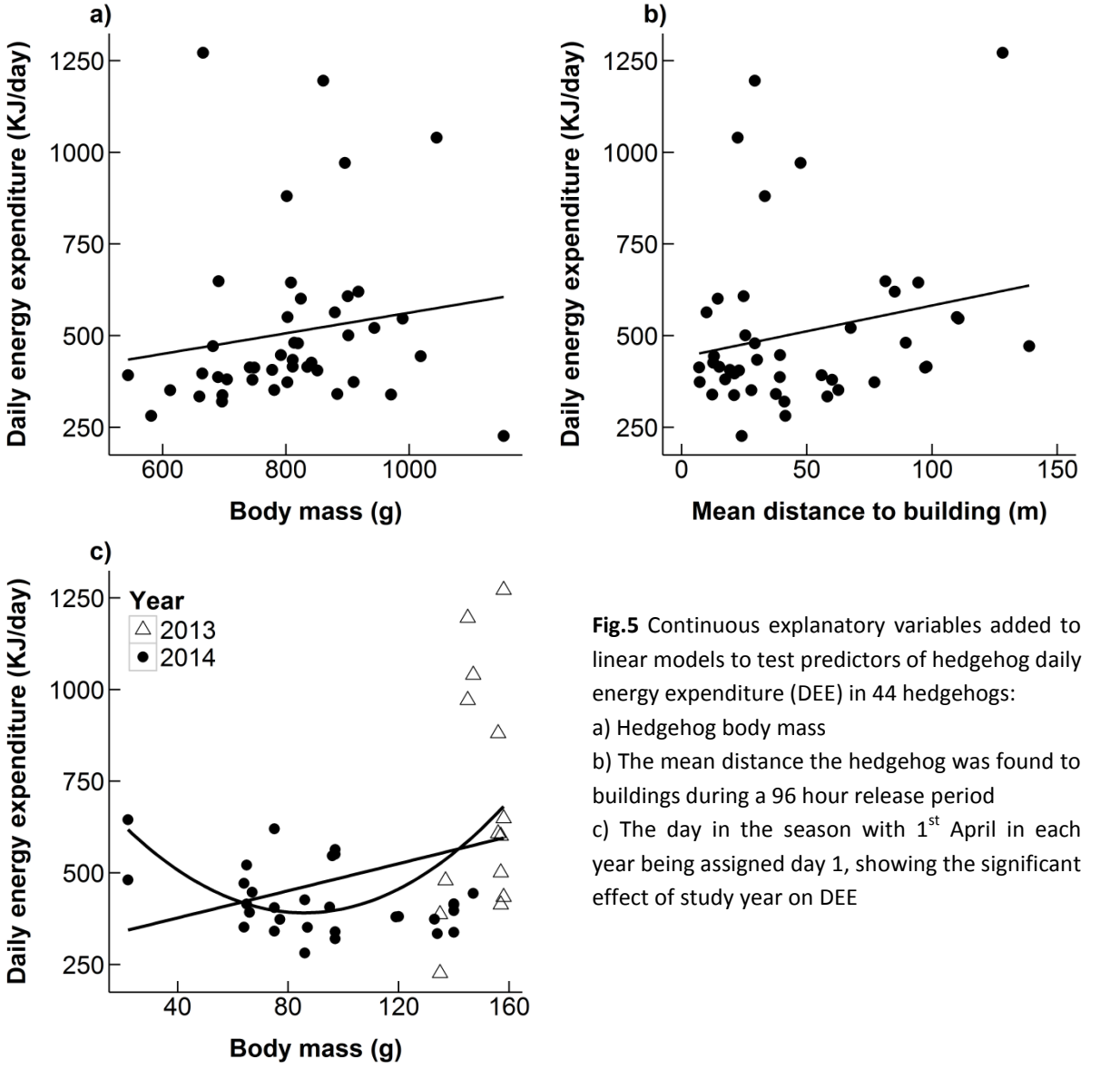


Fig.5 Continuous explanatory variables added to linear models to test predictors of hedgehog daily energy expenditure (DEE) in 44 hedgehogs:
a) Hedgehog body mass
b) The mean distance the hedgehog was found to buildings during a 96 hour release period
c) The day in the season with 1st April in each year being assigned day 1, showing the significant effect of study year on DEE

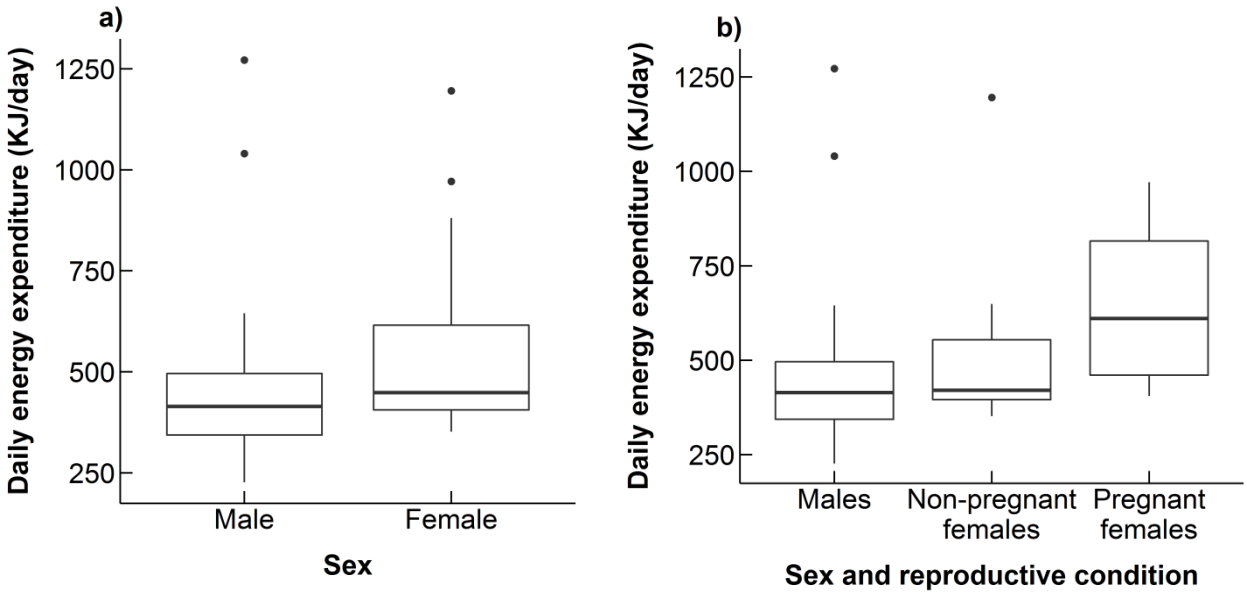


Fig.6 a) the effect of sex on hedgehog daily energy expenditure, measured by the doubly labelled water method (DLW) on 44 hedgehogs, and b) the effect of reproductive condition on female DEE, where pregnant females includes hedgehogs thought to be pregnant or lactating

Table 3 The significance of variables in the three best fitting models with the lowest AIC to explain variability in a-c) Hedgehog daily energy expenditure (DEE;KJ/day), measured by the doubly labelled water method (DLW), d-f) Hedgehog condition; the residuals of body mass regressed on rear thigh length, and g-i) The distance a hedgehog travelled in a four day release period

	Response	Variables in model	Df	F statistic	P value	Effect size	95% CI
a)	DEE	Dist to buildings	1,37	4.624	0.038*	0.004	0.001, 0.006†
		Year *2014*	1,37	24.25	0.00002***	0.094	-0.657, -0.274†
		Sex *Male*	1.37	3.397	0.073**.**	-0.164	-0.335, 0.008
		Site *B No Badgers*	3,37	3.294	0.031*	-0.187	-0.400, 0.027
		C Badgers				-0.144	-0.479, 0.191
		D Badgers				-0.345	-0.595, -0.096†
b)	DEE	Dist to buildings	1,36	4.715	0.037*	0.004	0.002, 0.007†
		Year *2014*	1,36	21.74	0.00004***	-0.443	-0.636, -0.250†
		Sex *Male*	1,36	4.976	0.032*	-0.184	-0.357, -0.011†
		Site *B No Badgers*	3,36	3.359	0.029*	-0.144	-0.366, 0.077
		C Badgers				-0.093	-0.434, 0.248
		D Badgers				-0.332	-0.580, -0.083†
		Body mass	1,36	3.198	0.082	0.121	-0.066, 0.307
c)	DEE	Dist to buildings	1,35	4.909	0.033*	0.004	0.001, 0.006†
		Year *2014*	1,35	5.415	0.026*	-0.355	-0.664, -0.045†
		Sex *Male*	1,35	8.329	0.007**	-0.202	-0.376, -0.027†
		Site: *B No badgers*	3,35	3.497	0.026*	-0.323	-0.571, -0.075†
		C Badgers				-0.165	-0.492, 0.161
		D Badgers				-0.333	-0.582, -0.084†
		Day linear	1,35	7.541	0.009**	0.149	-0.190, 0.488
		Day quadratic	1,35	12.343	0.001**	0.518	-0.022, 1.059
d)	Condition	Site: *B No badgers*	3,70	7.502	0.0002 ***	-0.112	-0.176, -0.050†
		C Badgers				-0.190	-0.277, -0.101†
		D Badgers				-0.057	-0.132, 0.016
		Day linear	1,160	11.700	0.0008 ***	0.058	0.024, 0.091†
		Day quadratic	1,177	30.505	1.17e-07 ***	0.148	0.095, 0.201†
		Sex *Male*	1,71	0.731	0.396	-0.022	-0.071, 0.029
		Year *2014*	1,162	0.114	0.736	-0.007	-0.051, 0.037
e)	Condition	Dist to buildings	1,106	0.100	0.753	-0.0001	-0.001, 0.001
		Site: *B No badgers*	3,72	7.279	0.0002 ***	-0.111	-0.175, -0.049†
		C Badgers				-0.189	-0.277, -0.100†
		D Badgers				-0.059	-0.134, 0.015
		Day linear	1,157	12.675	0.0005***	0.059	0.026, 0.091†
		Day quadratic	1,174	31.565	7.51e-08 ***	0.146	0.095 , 0.197†
		Sex *Male*	1,72	0.670	0.416	-0.021	-0.071, 0.030
f)	Condition	Dist to buildings	1,101	0.1084	0.743	-0.0001	-0.001, 0.001
		Site: *B No badgers*	3,70	7.529	0.0002 ***	-0.114	-0.178, -0.051†
		C Badgers				-0.191	-0.279, -0.103†
		D Badgers				-0.061	-0.137, 0.013
		Day linear	1,160	11.541	0.0009***	0.057	0.024, 0.091†
		Day quadratic	1,177	30.134	1.39e-07 ***	0.147	0.094 , 0.200†
		Year *2014*	1,159	0.062	0.804	-0.005	-0.049, 0.039
g)	Locomotion	Dist to buildings	1,41	22.953	0.00002***	0.555	0.315, 0.796†
		Sex *Male*	1,41	6.950	0.012*	0.315	0.074, 0.556†
h)	Locomotion	Day	1,40	0.765	0.387	-0.109	-0.361, 0.143
		Dist to buildings	1,40	22.821	0.00002***	0.524	0.272, 0.776†
		Sex *Male*	1,40	6.910	0.012*	0.322	0.079, 0.564†
i)	Locomotion	Dist to buildings	1,38	23.302	0.00002***	0.618	0.368, 0.868†
		Sex *Male*	1,38	7.056	0.012*	0.299	0.056, 0.542†
		Site: *B No badgers*	3,38	1.208	0.320	-0.236	-0.534, 0.062
		C Badgers				0.078	-0.386, 0.543
		D Badgers				-0.142	-0.495, 0.211

Site A (no badgers) and females were the reference categories ***Significant at p<0.001, **Significant at p<0.01 , *significant at p<0.0, **.** near significant, † 95% confidence interval of the effect size does not contain zero

Hedgehog Condition

Hedgehog condition was poorer on badger occupied sites, but this variation can be attributed to the poor condition of hedgehogs on site C (badgers present: -0.04 ± 0.02, badgers absent: 0.02 ± 0.01, Fig.7, Table 3). There was no relationship between a hedgehog's mean proximity to buildings and its condition, and no effect of sex on condition (Table 3). There was a positive relationship between hedgehog condition and testes length (Fig.8).

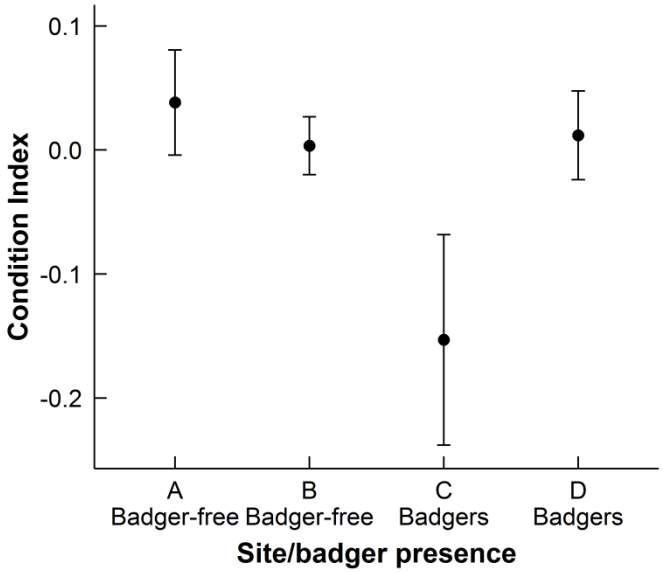


Fig.7 The effect of site and badger presence on hedgehog condition, the residuals of body mass regressed against hind thigh length, from 192 measurements on 62 hedgehogs

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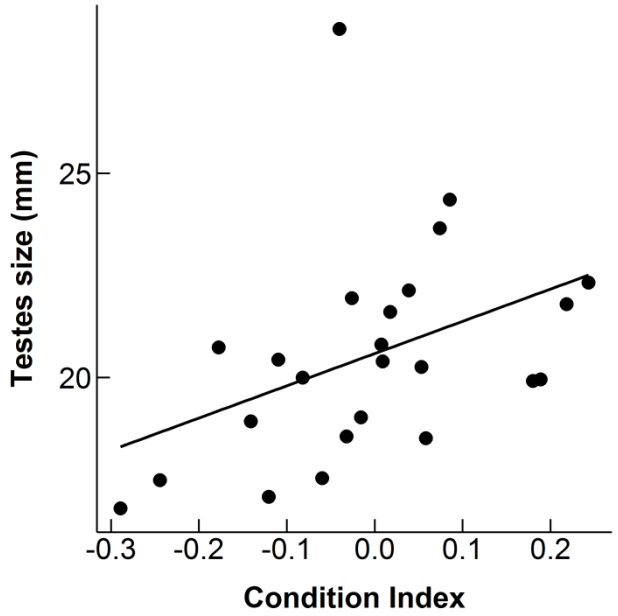


Fig.8 The relationship between condition, the residuals of body mass regressed against hind thigh length, and testes size, in 24 hedgehogs the doubly labelled water (DLW) method was carried out on

Ranging behaviour

Male hedgehogs travelled one and a half times further than female hedgehogs during the release period (1483 ± 158m, and 949 ± 155m respectively) and hedgehogs that spent more of their time away from buildings in the release period travelled further (Fig.9). There was no difference in the mean distance travelled by hedgehogs on each site, and on sites with and without badgers during the study (with badgers: 1259 ± 140m, without: 1267 ± 159m). However, the home range size over the season for hedgehogs in this study was larger for hedgehogs on sites where badgers were absent (Home range calculated by 100% minimum convex polygon; with badgers: 9.68 ± 1.67ha, without: 16.67 ± 3.44ha).

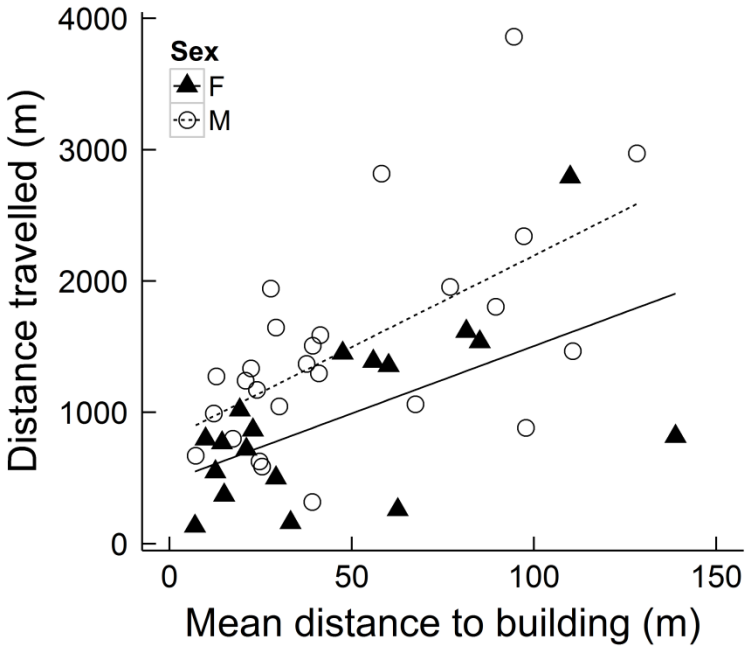


Fig.9 The relationship between the mean distance that male (M) and female (F) hedgehogs were found in relation to buildings, during a 96 hour release period, and the distance they travelled, calculated from the distance between hourly radio-tracking fixes

Ambient temperature

Mean hourly night temperature differed between rural habitat types (Table 4). The mean temperature was coldest in arable fields (10.7 ± 0.09^{o}C) and this habitat was significantly colder than all other habitat types (Table 4, Fig. 10). The next coldest habitat was the hedgerows of arable fields (11.4 ± 0.07^{o}C), which was significantly colder than all none-arable habitats. The warmest habitat was village gardens (11.9 ± 0.07^{o}C). There were no differences in the mean ambient temperature between farm buildings, village gardens and amenity grassland (Table 4). Day in the season, a proxy for temperature, was positively correlated with DEE. We verified this finding by running the models again and replacing day in the season with the mean logger temperature during the release period. Temperature was present in the model with the third lowest AIC and was significantly positively correlated with DEE ($F_{1,34}$=18.1, p=0.002, Effect size= 0.18).

Table 4 a) The significance of variables in a linear mixed effects model to test for differences in ambient temperature between five rural habitats at five sites in July-October 2013 and April-September 2014. b) Pairwise t-tests between the ambient temperatures in five rural habitats with a Bonferroni correction applied

a)	**Variable**		**DF**	**T statistic**	**P value**	**Effect size**	**95% CI**
	Habitat	*Farm buildings*	4, 10955	172.040	<0.0001***	0.201	0.082, 0.319†
		Arable hedge				-0.437	-0.551, -0.323†
		Arable field				-1.077	-1.193, -0.960†
		Village garden				0.039	-0.074, 0.153
	Site	B	3, 353	19.945	<0.0001***	-1.066	-2.153, 0.029
		C				-2.857	-3.825, -1.887†
		D				0.108	-0.987, 1.207

b)		**Amenity grassland**	**Farm buildings**	**Arable hedge**	**Arable field**	**Village garden**
	Farm buildings	1.00	-	-	-	-
	Arable hedge	<0.0001***	<0.0001***	-	-	-
	Arable field	<0.0001***	<0.0001***	<0.0001***	-	-
	Village garden	1.00	1.00	0.0004***	<0.0001***	<0.0001***

Temperature was measured hourly from 19:00-07:00hrs.
The reference habitat is Amenity grassland and the reference site is site A.
***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05, **.** near significance
† 95% confidence interval of the effect size does not contain zero

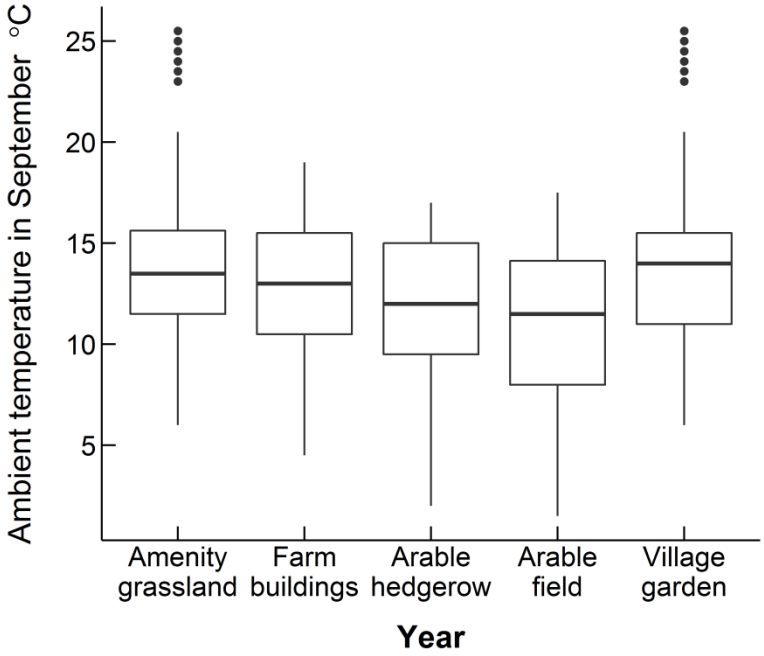


Fig.10 The ambient temperature in five rural habitats on four sites, two in North Norfolk and two in North Yorkshire, in September 2014

Discussion

Daily energy expenditure

In this study hedgehogs on badger-occupied sites had a lower DEE than those on badger-free sites. Previous intraspecific studies of DEE and resting metabolic rate (RMR) have shown that in higher productivity habitats, higher RMRs and thus higher rates of DEE may be enabled (Speakman *et al.* 2003; Bozinovic *et al.* 2007; Burton *et al.* 2011)– and conversely DEE may be lower in lower productivity habitats. Although in this study we did not measure the productivity of arable land, the finding that hedgehogs have a lower DEE where badgers are present may reflect the inability of hedgehogs to take advantage of available resources when under risk from predation. For example, Hof *et al*., (2012) found that when badgers were present hedgehogs stayed closer to hedgerows and Ward *et al*. (1997) found that hedgehogs preferred not to forage in the presence of badger odour. This finding supports the suggestion by Hof *et al.* (2012) and Micol *et al.* (1994) that arable land is a 'landscape of fear' for hedgehogs as they are excluded from potentially suitable habitat due to a

perceived risk of predation (Laundre, Hernandez & Ripple 2010). And when on badger-occupied arable land hedgehogs may spend more foraging time taking cover or being vigilant.

Individual voles (*Microtus agrestis*) with a higher DEE have been found to have a higher chance of survival and a greater capability to reproduce under some conditions (Speakman *et al.* 2003). These results indicate that badgers may not only control hedgehog populations by direct predation (Neal 1986; Doncaster 1992, 1994; Morris & Warwick 1994; Hof & Bright 2010), but also by negative impacts on a hedgehog's ability to survive and reproduce, resulting from the landscape of fear effect; i.e. non-lethal predation (Lima 1998; Valeix *et al.* 2009). This conclusion is supported by encounter rates on each site over two seasons: on sites where hedgehogs had a low DEE we encountered fewer hedgehogs (Figs. 3 and 4). However, it is not clear if hedgehogs are absent from these sites because they were predated upon, whether the population was diminished by the effects of indirect predation, or if hedgehogs simply dispersed to sites with lower badger abundance. Also, we did not find an effect of badger presence on hedgehog condition.

We found a positive relationship between daily energy expenditure and the mean distance a hedgehog was from buildings in the four day release period, which supports our hypothesis that hedgehogs face higher energetic costs the further they are from buildings. We speculate that this finding arose from lower prey densities and food availability in arable habitats, compared with villages (in which supplementary feeding may take place), requiring hedgehogs to spend more time looking for food in arable habitats. Locomotion accounts for a large proportion of a small mammal's energy budget (Kenagy & Hoyt 1989; Covell *et al.* 1996) and increased movement is energetically costly. Additionally, we found significant differences in temperature between arable land and village habitats. Although the difference was only around 1^{o}C, it may contribute to higher energetic costs the further hedgehogs are from buildings due to a higher cost of maintaining endothermy. To maintain energy balance it would pay to stay in close proximity to buildings, which explains why

previous studies, and the encounter rates in this study, have found hedgehogs to be attracted to habitats close to buildings (Doncaster 1994; Micol *et al.* 1994; Doncaster *et al.* 2001).

We found no interaction between site and distance from buildings on DEE. The lack of an interaction suggests that badgers have an impact on hedgehog DEE regardless of a hedgehog's proximity to buildings. Although hedgehogs may use villages as a refuge from badgers, this habitat selection does not completely mitigate the risk of predation by badgers. For example, Young *et al.* (2006) found that hedgehog numbers on amenity grassland were lower when badger sett density was higher in surrounding areas, suggesting that where badgers are present, there is a knock on effect on hedgehog survival on the outskirts of residential areas. Also, when badgers are in high abundance they may utilise villages, particularly in rural settlements with large gardens (Davison *et al.* 2009), meaning in some areas badger risk may be more constant across rural habitats. Finally, when badgers are present hedgehogs may stay closer to buildings (Doncaster 1994), indicating that mean distance to building was confounded with badger presence to some extent and therefore the analysis of an interaction could be inappropriate.

Female hedgehogs had a higher DEE than males, despite male hedgehogs travelling further than females during the four day release period. The energetic costs of reproduction are high for female small mammals, particularly during lactation (Poppitt *et al.* 1993; Speakman 2008; Fletcher *et al.* 2012), which may explain why females in this study had higher rates of energy expenditure than males. We found that the high daily energy expenditure of pregnant or lactating females strongly influenced the mean DEE for female hedgehogs which corroborates this hypothesis (Fig.6b).

Hedgehog DEE was higher in 2013 than in 2014. A potential explanation is that it was slightly colder in 2013 than 2014 (mean nightly ambient temperature in September 2013: 10.65 ± 0.16^{o}C, and in 2014: 12.45 ± 0.11^{o}C) and energetics experiments went on later into September in 2013 (Fig.5c). The colder temperatures in 2013 may have resulted in higher measures of DEE due to the increased energetic costs of endothermy. A more likely explanation may be that during the autumn hedgehogs

forage intensively to increase fat stores for hibernation (Dowding *et al.* 2010; Haigh, O'Riordan & Butler 2012) and rates of foraging result in high energy expenditure (Bryce *et al.* 2001; Humphries *et al.* 2002). Consequently, we surmise that we only captured the effects of intensive autumn foraging in 2013.

Hedgehog condition

Hedgehog condition varied by site and showed a similar pattern to differences in DEE across sites (Figs. 3 and 7). Hedgehogs on Site A, a badger-free site in Yorkshire, had the highest DEE and the highest condition and on Site C, a badger-occupied site in Yorkshire, had the lowest DEE and poorest condition. Changes in foraging habits due to the avoidance of predators and/or competitors can have a negative impact on an individual's condition (Harrington *et al.* 2009). Condition was poorer on badger occupied sites, but this variation was down to the mean poor condition on Site C. It is not clear if the poor condition on Site C can be attributed to badger presence. Site C was the most northerly site and we recorded the coldest night temperatures here which may have been a contributing factor. The variation in condition between sites may give a measure of the ability of hedgehogs on that site to survive and reproduce. In this study there was a positive relationship between hedgehog condition and testes size, which is linked to ejaculate production in small mammals (Schulte-Hostedde, Millar & Hickling 2005a). Condition is also linked to winter survival in the hedgehog (Jensen 2004; Haigh *et al.* 2012).

We found a positive relationship between condition with day in the season and the quadratic term of day. This relationship may be because hedgehog body mass increases throughout the season, beginning with low body mass on emergence after hibernation and ending with a high body mass prior to hibernation (Morris 1984; Reeve 1994; Dowding *et al.* 2010; Haigh *et al.* 2012). As day in the season and ambient temperature were correlated in the study, the results may reflect a relationship between hedgehog condition and temperature. The activity of macroinvertebrate prey increases

with temperature (Crawford-Sidebotham 1972; Edwards & Bohlen 1996; Honek 1997) which may result in increases in hedgehog activity and condition.

We found no relationship between hedgehog condition and their mean distance to buildings. This finding is contrary to what we would expect; hedgehogs that spend more time in villages, rather than on the surrounding arable farmland, should possibly be in better condition, due to increased prey availability.

Ranging behaviour

Hedgehogs that stayed closer to buildings did not travel as far in the four day release period as those which resided further away from buildings. An individual will use the minimum area possible to obtain enough food to meet energy needs (Tufto, Andersen & Linnell 1996), and this result may suggest that hedgehogs maintain their condition on arable land by foraging over greater distances. However a diet study is needed to ascertain if hedgehogs are eating different prey types on arable land and in villages, or if they are travelling further to find the same prey. Male hedgehogs travelled further than female hedgehogs in the four day release period, which is unsurprising given that male hedgehogs are known to have larger home ranges than females (Reeve 1994; Haigh, O'Riordan & Butler 2013; Rautio, Valtonen & Kunnasranta 2013). Male hedgehogs on arable land may also have to travel further to find mates, or cross open arable land to visit females, which were at higher densities in villages in this study.

Hedgehogs on badger-occupied sites travelled the same distance in the release period as hedgehogs on sites without badgers, yet over the season hedgehogs on badger-occupied sites had smaller home range sizes than on sites without badgers. This behaviour may be a result of hedgehogs using rural villages as refuge when badgers are present (Hof *et al.* 2012) and, as discussed above, hedgehogs that stay closer to buildings do not travel as far.

Ambient temperature

We found that in arable habitats, including in the cover of hedgerows, the mean night temperature was colder than village habitats. In this study when hedgehogs used open arable land they often selected habitat close to buildings on the farm, particularly isolated houses and this could be one possible cause: it may pay to forage close to buildings where the energetic cost of thermoregulation is lower. We found that day in the season, a proxy for temperature, was positively correlated with DEE, the opposite to the theory that DEE would increase in colder temperatures. This relationship has been found in previous studies of intraspecific DEE (Bryce *et al.* 2001; Fletcher *et al.* 2012) and Dowding *et al*. (2010) found that hedgehog activity, and therefore energy expenditure, increased with temperature, due to increased prey activity, which is corroborated by our finding that condition increased with day in the season.

Conclusions and implications for hedgehog conservation

Although these constitute preliminary findings on a complex issue, the observed gradient in hedgehog abundance with increased distance from buildings is at least partially explicable by increasing energetic costs, related to food abundance and temperature - although the disentangling of these effects requires further investigation. The results also show a lower hedgehog DEE on sites with badgers, indicating that predator presence may alter hedgehog energy budgets, potentially by reducing their ability to forage. A perceived predation risk on badger-occupied sites may also cause hedgehogs to move closer to the cover of buildings. These findings suggest a partial explanation for hedgehogs' preference for residing in close proximity to buildings in arable areas and show that DEE is a useful tool in assessing habitat quality for small mammals.

These results are of conservation concern for hedgehogs; 25% of the land in the UK is arable land (FAO 2012), resulting in large areas of unsuitable habitat for hedgehogs and low connectivity between rural villages. Increasing macroinvertebrate prey on arable land by increasing grassy field margins (Hof & Bright 2010) and reducing pesticide use, may decrease foraging costs for hedgehogs

and also provide alternative prey for badgers. Badger numbers have increased on arable land in the past thirty years (Judge *et al.* 2014) but there is evidence that species in an intraguild relationship can co-exist (Polis & Holt 1992; Holt & Polis 1997; Kamler *et al.* 2012). There has been mass removal of hedgerows since the 1950's (Stoate *et al.* 2001; Robinson & Sutherland 2002) and less than 10% of remaining hedgerows on arable land are in good structural condition (Carey 2008). A lack of habitat structure can impact negatively on intraguild prey, in this case the hedgehog, due to a lack of cover from predation (Janssen *et al.* 2007). We therefore suggest an increase in hedgerow cover and habitat complexity on arable land to mitigate the effect of badgers, which, as this study has shown, will have the added benefit of increasing local temperatures on arable land. Further investigation is warranted to assess the feasibility of these conservation proposals, particularly in respect to the level of hedgerow cover required to mitigate the negative effects of badgers on arable land.

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Appendix

Table A The subjects of doubly labelled water (DLW) experiments on hedgehogs in 2013 and 2014

ID	Sex	Site	Date	Pregnant	Body mass (g)	Thigh length (mm)	Testes size (mm)	Condition Index	Mean temp (^{o}C)
4	F	D	14/06/2014	Yes	917.5	69.04	NA	0.02	12.82
5	M	D	15/08/2013	NA	819.4	66.81	28.54	-0.04	15.14
7	M	D	13/08/2013	NA	1153	70.49	21.8	0.22	14.1
10	M	D	13/08/2013	NA	689.8	62.53	20.44	-0.11	13.97
11	F	B	03/09/2013	Yes	801.3	61.1	NA	0.08	13.88
11	F	B	04/06/2014	No	834.6	59.82	NA	0.15	10.85
12	M	B	04/09/2013	NA	901.2	65.99	23.66	0.07	12.53
14	F	B	04/09/2013	Yes	824.1	62.33	NA	0.07	12.11
15	M	B	03/09/2013	NA	900	65.45	24.36	0.09	13.72
15	M	B	22/04/2014	NA	808.1	64.21	20.81	0.01	8.82
22	F	B	05/09/2013	No	690.7	62.68	NA	-0.11	10.78
25	M	A	25/08/2013	NA	1044.2	67.78	19.92	0.18	13.04
28	F	A	23/08/2013	Yes	895.6	61.76	NA	0.17	15.23
28	F	A	04/07/2014	No	777.5	63.3	NA	-0.01	12.83
32	F	A	23/08/2013	No	860.5	66.24	NA	0.02	15.11
34	F	C	25/06/2014	No	841.4	68.47	NA	-0.05	9.69
44	F	B	04/09/2013	Yes	741.3	60.65	NA	0.01	12.07
45	M	B	05/09/2013	NA	810.7	62.27	18.52	0.06	10.89
46	M	B	05/09/2013	NA	665.4	59.16	17.54	-0.06	11.1
47	M	B	22/04/2014	NA	813.4	55.38	22.33	0.24	9.17
49	F	B	05/06/2014	No	543.7	53.39	NA	-0.10	11.4
50	M	B	04/06/2014	NA	943.2	63.11	19.96	0.19	10.87
51	F	B	03/06/2014	No	780.8	61.87	NA	0.03	10.73
52	F	B	03/06/2014	No	681.3	56.86	NA	0.03	10.73
54	M	C	25/06/2014	NA	581.3	62.87	16.8	-0.29	9.68
55	M	D	14/06/2014	NA	883.1	66.63	22.14	0.04	13.11
56	F	D	14/06/2014	Yes	850.8	64.15	NA	0.06	12.83
57	M	B	06/06/2014	NA	791.8	64.32	19.03	-0.02	11.94
58	M	B	18/08/2014	NA	748.6	64.75	20	-0.08	9.12
59	M	D	16/06/2014	NA	802.2	65.3	21.95	-0.03	11.37
60	M	D	29/07/2014	NA	704.2	60.27	18.56	-0.03	15.27
61	F	D	28/07/2014	No	745.6	64.67	NA	-0.08	15.27
62	M	C	26/06/2014	NA	612.1	63.14	17.49	-0.24	9.94
63	M	A	05/07/2014	NA	989.1	73.08	20.4	0.01	12.83
64	F	A	06/07/2014	No	879.3	64.83	NA	0.08	12.52
65	M	A	06/07/2014	NA	970.3	70.15	20.26	0.05	12.52
66	M	A	06/07/2014	NA	696.1	64.18	18.93	-0.14	11.96
67	F	A	06/07/2014	No	802.4	66.45	NA	-0.05	12.52
69	M	A	12/08/2014	NA	659.5	NA	NA	NA	12.68

Table A *Continued*

ID	Sex	Site	Date	Pregnant	Body mass (g)	Thigh length (mm)	Testes size (mm)	Condition Index	Mean temp (^{o}C)
70	M	A	11/08/2014	NA	909.7	68.86	21.61	0.02	12.69
72	F	B	18/08/2014	No	664.3	62.07	NA	-0.14	9.16
73	M	B	18/08/2014	NA	696.7	65.75	20.74	-0.18	9.15
74	M	C	25/08/2014	NA	1018.3	NA	NA	NA	13.18
77	M	B	18/08/2014	NA	810.9	69.89	17.08	-0.12	9.11

If a hedgehog ID is given twice, this hedgehog was sampled in 2013 and 2014
Date is the date of the DLW injection
Mean temp is the mean temperature on arable land during the four days of DLW experiments

Table B 192 measures of hedgehog condition taken from 69 hedgehogs in 2013 and 2014

ID	Sex	Site	Date	Weight (g)	Thigh length (mm)	Testes size (mm)	Condition Index
1	F	A	03/07/2013	836.6	63.2	NA	0.06
1	F	A	22/08/2013	932.2	63.2	NA	0.17
2	F	A	03/07/2013	1184.7	67.22	NA	0.31
3	M	C	05/07/2013	862.7	66.03	NA	0.02
4	F	D	16/07/2013	869	69.92	NA	-0.06
4	F	D	13/08/2013	893.3	69.92	NA	-0.03
4	F	D	26/09/2013	991	69.92	NA	0.07
5	M	D	17/07/2013	820.6	66.81	28.54	-0.04
5	M	D	15/08/2013	821.4	66.81	NA	-0.04
6	M	D	17/07/2013	790.9	65.34	21.94	-0.05
6	M	D	13/08/2013	842.5	65.34	NA	0.02
7	M	D	17/07/2013	1119	70.49	21.8	0.18
7	M	D	12/08/2013	1155	70.49	NA	0.22
8	F	D	18/07/2013	688.6	67.5	NA	-0.24
8	F	D	14/08/2013	914	67.5	NA	0.05
9	M	D	19/07/2013	761.2	64.81	18.4	-0.07
9	M	D	13/08/2013	854.4	64.81	NA	0.04
10	M	D	20/07/2013	640.8	62.53	20.44	-0.19
10	M	D	12/08/2013	691.8	62.53	NA	-0.11
11	F	B	24/07/2013	711.8	61.1	NA	-0.05
11	F	B	03/09/2013	803.3	61.1	NA	0.07
12	M	B	24/07/2013	707.2	65.99	23.66	-0.17
12	M	B	04/09/2013	903.2	65.99	NA	0.07
13	M	B	25/07/2013	708.9	63.65	22.56	-0.12
14	F	B	25/07/2013	606.2	62.33	NA	-0.24
14	F	B	04/09/2013	826.1	62.33	NA	0.07
15	M	B	25/07/2013	728.2	65.45	24.36	-0.13
15	M	B	02/09/2013	900	65.45	NA	0.08
15	M	B	08/10/2013	723	65.45	NA	-0.14
16	M	B	25/07/2013	688.3	65.35	22.17	-0.19
17	M	B	25/07/2013	783.8	66.87	23.52	-0.09
18	M	B	25/07/2013	841.4	69.46	20.86	-0.08
19	M	B	26/07/2013	809.8	62.22	23.93	0.05
19	M	B	07/10/2013	936	62.22	NA	0.20
20	F	B	26/07/2013	728.1	64.2	NA	-0.10
21	M	B	26/07/2013	754.9	64.67	23.77	-0.08
22	F	B	26/07/2013	797.6	62.68	NA	0.03
22	F	B	04/09/2013	692.7	62.68	NA	-0.12
23	M	B	26/07/2013	744.2	65.72	20.52	-0.12
24	F	A	29/07/2013	1101.4	62.91	NA	0.34
25	M	A	30/07/2013	956	67.78	19.92	0.09
25	M	A	25/08/2013	1046.2	67.78	NA	0.18
26	F	A	30/07/2013	954.2	67.79	NA	0.08

Table B *Continued*

ID	Sex	Site	Date	Weight (g)	Thigh length (mm)	Testes size (mm)	Condition Index
27	M	A	30/07/2013	1179.1	68.86	24.16	0.27
28	F	A	30/07/2013	737.1	61.76	NA	-0.03
28	F	A	23/08/2013	895.6	61.76	NA	0.16
29	M	A	31/07/2013	1032.5	74.46	21.23	0.02
30	M	A	31/07/2013	791.6	67.55	18.16	-0.10
31	M	A	31/07/2013	985.5	71.02	20.48	0.05
32	F	A	31/07/2013	995.4	66.24	NA	0.16
32	F	A	23/08/2013	862.5	66.24	NA	0.02
33	M	A	31/07/2013	999.8	71.42	19.64	0.05
34	F	C	01/08/2013	781.2	68.25	NA	-0.13
35	F	C	02/08/2013	828.3	68.37	NA	-0.07
36	F	C	02/08/2013	845.4	65.59	NA	0.01
39	M	C	02/08/2013	892.6	69.22	20.15	-0.01
43	M	A	28/08/2013	1113.5	70.8	19.53	0.17
44	F	B	04/09/2013	741.3	60.65	NA	0.00
45	M	B	04/09/2013	810.7	62.27	18.52	0.05
46	M	B	04/09/2013	665.4	59.16	17.54	-0.07
46	M	B	08/10/2013	680	59.16	NA	-0.04
1	F	A	11/08/2014	967.6	65.05	NA	0.16
1	F	A	08/09/2014	776.1	65.05	NA	-0.06
4	F	D	28/05/2014	1038.1	69.04	NA	0.14
4	F	D	14/06/2014	917.5	69.04	NA	0.02
4	F	D	18/06/2014	901.1	69.04	NA	0.00
11	F	B	07/05/2014	814.7	59.82	NA	0.12
11	F	B	04/06/2014	834.6	59.82	NA	0.14
11	F	B	08/06/2014	826.9	59.82	NA	0.13
11	F	B	30/07/2014	773.5	59.82	NA	0.07
11	F	B	21/08/2014	677.7	59.82	NA	-0.07
11	F	B	16/09/2014	897.9	59.82	NA	0.22
12	M	B	24/04/2014	890	66.13	19.78	0.05
15	M	B	22/04/2014	808.1	64.21	20.81	0.00
15	M	B	26/04/2014	790	64.21	NA	-0.02
22	F	B	06/05/2014	839.6	59.87	NA	0.15
22	F	B	04/06/2014	693.6	59.87	NA	-0.04
22	F	B	08/06/2014	723.6	59.87	NA	0.00
22	F	B	30/07/2014	755.5	59.87	NA	0.04
22	F	B	19/08/2014	735.2	59.87	NA	0.01
22	F	B	02/09/2014	768.1	59.87	NA	0.06
22	F	B	16/09/2014	911.2	59.87	NA	0.23
28	F	A	04/07/2014	777.5	63.3	NA	-0.01
28	F	A	08/07/2014	732.1	63.3	NA	-0.08
34	F	C	15/05/2014	853.7	68.47	NA	-0.04
34	F	C	25/06/2014	841.4	68.47	NA	-0.06

Table B *Continued*

ID	Sex	Site	Date	Weight (g)	Thigh length (mm)	Testes size (mm)	Condition Index
34	F	C	29/06/2014	889.7	68.47	NA	0.00
40	M	C	18/04/2014	985	68.95	21.26	0.09
47	M	B	22/04/2014	813.4	55.38	22.33	0.24
47	M	B	25/04/2014	778.8	55.38	NA	0.19
48	M	B	22/04/2014	869.2	63.87	18.72	0.08
49	F	B	25/04/2014	726.4	53.39	NA	0.18
49	F	B	05/06/2014	543.7	53.39	NA	-0.11
49	F	B	09/06/2014	529.2	53.39	NA	-0.14
50	M	B	07/05/2014	801.2	63.11	19.96	0.02
50	M	B	04/06/2014	943.2	63.11	NA	0.18
50	M	B	08/06/2014	910.6	63.11	NA	0.15
50	M	B	21/08/2014	875.6	63.11	NA	0.11
50	M	B	05/09/2014	941.2	63.11	NA	0.18
50	M	B	16/09/2014	959.4	63.11	NA	0.20
51	F	B	08/05/2014	678.9	61.87	NA	-0.12
51	F	B	03/06/2014	780.8	61.87	NA	0.02
51	F	B	07/06/2014	731.2	61.87	NA	-0.04
51	F	B	20/08/2014	741.5	61.87	NA	-0.03
51	F	B	03/09/2014	777.4	61.87	NA	0.02
51	F	B	16/09/2014	835.5	61.87	NA	0.09
52	F	B	08/05/2014	673.7	56.86	NA	0.01
52	F	B	03/06/2014	681.3	56.86	NA	0.02
52	F	B	07/06/2014	639.4	56.86	NA	-0.05
53	M	C	16/05/2014	707.1	66.86	19.89	-0.19
54	M	C	20/05/2014	516.4	62.87	16.8	-0.41
54	M	C	25/06/2014	581.3	62.87	NA	-0.30
54	M	C	29/06/2014	519.7	62.87	NA	-0.41
54	M	C	25/08/2014	483.3	62.87	NA	-0.48
55	M	D	27/05/2014	1019	66.63	22.14	0.18
55	M	D	14/06/2014	883.1	66.63	NA	0.03
55	M	D	17/06/2014	855.3	66.63	NA	0.00
55	M	D	16/07/2014	902.9	66.63	NA	0.06
55	M	D	20/08/2014	901.4	66.63	NA	0.05
56	F	D	31/05/2014	1015.8	64.15	NA	0.23
56	F	D	14/06/2014	850.8	64.15	NA	0.05
56	F	D	18/06/2014	927.7	64.15	NA	0.14
56	F	D	22/08/2014	872.3	64.15	NA	0.08
57	M	B	06/05/2014	791.8	64.32	19.03	-0.02
57	M	B	09/06/2014	759.3	64.32	NA	-0.06
57	M	B	19/08/2014	901.8	64.32	NA	0.11
57	M	B	01/09/2014	950.3	64.32	NA	0.16
57	M	B	16/09/2014	987.2	64.32	NA	0.20
58	M	B	10/06/2014	742.8	64.75	20	-0.10

Table B *Continued*

ID	Sex	Site	Date	Weight (g)	Thigh length (mm)	Testes size (mm)	Condition Index
58	M	B	18/08/2014	748.6	64.75	NA	-0.09
58	M	B	22/08/2014	749.1	64.75	NA	-0.09
58	M	B	03/09/2014	854.4	64.75	NA	0.04
58	M	B	17/09/2014	840	64.75	NA	0.03
59	M	D	16/06/2014	802.2	65.3	21.95	-0.03
59	M	D	20/06/2014	776.7	65.3	NA	-0.06
60	M	D	19/06/2014	662.8	60.27	18.56	-0.10
60	M	D	17/07/2014	709.3	60.27	NA	-0.03
60	M	D	29/07/2014	704.2	60.27	NA	-0.04
60	M	D	01/08/2014	796.9	60.27	NA	0.09
60	M	D	16/09/2014	965.2	60.27	NA	0.28
61	F	D	20/06/2014	825.7	64.67	NA	0.01
61	F	D	16/07/2014	724.4	64.67	NA	-0.12
61	F	D	28/07/2014	745.6	64.67	NA	-0.09
61	F	D	01/08/2014	700.2	64.67	NA	-0.15
61	F	D	20/08/2014	793.4	64.67	NA	-0.03
62	M	C	26/06/2014	612.1	63.14	17.49	-0.25
62	M	C	30/06/2014	558.2	63.14	NA	-0.34
62	M	C	14/08/2014	756.1	63.14	NA	-0.04
63	M	A	04/07/2014	989.1	73.08	20.4	0.00
63	M	A	08/07/2014	919.8	73.08	NA	-0.07
63	M	A	27/08/2014	956.5	73.08	NA	-0.03
63	M	A	08/09/2014	1103.4	73.08	NA	0.11
63	M	A	25/09/2014	1133.2	73.08	NA	0.14
64	F	A	06/07/2014	889.3	64.83	NA	0.08
64	F	A	06/07/2014	879.3	64.83	NA	0.07
64	F	A	10/07/2014	840	64.83	NA	0.03
64	F	A	21/07/2014	828.1	64.83	NA	0.01
65	M	A	06/07/2014	980.3	70.15	20.26	0.06
65	M	A	06/07/2014	970.3	70.15	NA	0.05
65	M	A	10/07/2014	929.3	70.15	NA	0.01
65	M	A	21/07/2014	968.1	70.15	NA	0.05
66	M	A	06/07/2014	706.1	64.18	18.93	-0.13
66	M	A	06/07/2014	696.1	64.18	NA	-0.15
66	M	A	10/07/2014	683.5	64.18	NA	-0.16
66	M	A	22/07/2014	653.5	64.18	NA	-0.21
66	M	A	13/08/2014	702.5	64.18	NA	-0.14
67	F	A	06/07/2014	802.4	66.45	NA	-0.06
67	F	A	10/07/2014	751.3	66.45	NA	-0.12
67	F	A	27/08/2014	802.3	66.45	NA	-0.06
67	F	A	08/09/2014	851	66.45	NA	0.00
67	F	A	25/09/2014	605	66.45	NA	-0.34
70	M	A	11/08/2014	909.7	68.86	NA	0.01

Table B *Continued*

ID	Sex	Site	Date	Weight (g)	Thigh length (mm)	Testes size (mm)	Condition Index
70	M	A	15/08/2014	947.2	68.86	NA	0.05
70	M	A	25/09/2014	1537	68.86	NA	0.54
71	M	B	30/07/2014	867.6	68.92	21.6	-0.04
71	M	B	19/08/2014	843.2	68.92	NA	-0.06
71	M	B	03/09/2014	906.2	68.92	NA	0.01
71	M	B	16/09/2014	928.5	68.92	NA	0.03
72	M	B	30/07/2014	736.2	62.07	NA	-0.04
72	F	B	18/08/2014	664.3	62.07	NA	-0.14
72	F	B	22/08/2014	672.2	62.07	NA	-0.13
72	F	B	04/09/2014	826.7	62.07	NA	0.08
72	F	B	16/09/2014	758.6	62.07	NA	-0.01
73	M	B	30/07/2014	747.8	65.75	20.74	-0.11
73	M	B	18/08/2014	696.7	65.75	NA	-0.18
73	M	B	22/08/2014	740.9	65.75	NA	-0.12
73	M	B	02/09/2014	818.5	65.75	NA	-0.02
76	F	A	15/08/2014	811.6	61.76	NA	0.07
77	M	B	18/08/2014	820.9	69.89	17.08	-0.11
77	M	B	22/08/2014	813.1	69.89	NA	-0.12
77	M	B	02/09/2014	826.2	69.89	NA	-0.11
77	M	B	17/09/2014	910.5	69.89	NA	-0.01

Condition index is the residuals of body mass regressed on rear thigh length

Chapter 5

Hedgehog diet in rural Britain as revealed by molecular analysis

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Abstract

The European hedgehog (*Erinaceus europaeus*) is a generalist predator of macroinvertebrates in decline in the UK. Between 2000 and 2015 the rural population is estimated to have fallen by approximately 50%. Hedgehogs are known to favour gardens and amenity grassland over arable farmland. There are two principal, and non-mutually exclusive, explanations. Firstly, that the availability of the hedgehog's main prey, macroinvertebrates, is responsible. Secondly, hedgehog foraging behaviour may be limited by the distribution of the badger (*Meles meles*), which is both the principal predator of hedgehogs and a competitor for invertebrate food. We used five universal primer sets to amplify and sequence DNA from hedgehog faecal samples to identify dietary components and assess the evidence that diet and predator presence are responsible for the preference of hedgehogs for rural villages over arable farmland. We radio-tracked hedgehogs to ascertain if their mean distance to buildings in a given season was related to the presence or abundance of prey families. We also explored how diet varied with badger presence, month and between males and females. We found 35 prey families in 57 faecal samples. The most commonly detected prey items were: Carabid beetles, present in 100% of samples, Lumbricidae in 95%, Lepidoptera in 89%, Bovidae in 93% and Suidae in 89% of samples. Laboratory trials indicated that Bovidae and Suidae DNA was likely to be from pet food consumed by hedgehogs. We found no effect of hedgehogs' mean distance to buildings, between the sexes or between hedgehogs foraging on sites with and without badgers on the prey families present in hedgehog faecal samples. We found seasonal, site and annual differences in the abundance of prey families consumed. These findings indicate that a lack of suitable prey may not be a major contributing factor of hedgehog preference of rural villages over the surrounding arable farmland. However, the presence of DNA surmised to be from pet food in all faecal samples suggests this is at least partly responsible for hedgehogs' preference for gardens.

Introduction

Optimal foraging theory predicts that, where possible, animals will opt to spend more time foraging in productive habitats, where search time for prey is low (Krebs & Davies 2009). In habitats where prey items are patchily distributed predators must rely on a higher number of prey types in order to sustain adequate energy intake (Macarthur & Pianka 1966). Therefore, prey density influences an animal's diet composition, home range size, habitat use and time-budget (Krebs, Ryan & Charnov 1974; Charnov 1976; Ford 1983; Litvaitis, Sherburne & Bissonette 1986; Tufto, Andersen & Linnell 1996). Predator presence can modify optimal foraging behaviour as individuals may alter habitat use or restrict foraging time to reduce predation risk (Lima, Valone & Caraco 1985; Kotler *et al.* 1991; Banks, Hume & Crowe 1999; Ergon *et al.* 2004).

Prey density, particularly of invertebrate prey, has decreased on arable farmland in Britain due to agricultural intensification carried out since the 1950s, leading to changes in distribution and population declines in insectivorous species (Harris *et al.* 1995; Wilson *et al.* 1999; Robinson & Sutherland 2002; Macdonald & Feber 2015). The European hedgehog (*Erinaceus europaeus)* is a generalist predator of macroinvertebrates in decline in the UK. The British population of European hedgehogs is thought to have fallen from 1.5 million in 1995 (Harris 1995) to less than a million in 2015 (PTES & BHPS 2015), leading to a patchy distribution particularly in rural areas (JNCC 2010; Noble *et al.* 2012; Roos, Johnston & Noble 2012). Between 2000 and 2015 the rural population of hedgehogs fell by approximately half, whereas the urban population fell by approximately a third (PTES & BHPS 2015). In rural areas arable land is particularly avoided by hedgehogs in comparison to village habitats such as gardens and allotments (Doncaster 1994; Hof & Bright 2010).

There are several possible reasons for the hedgehog's distribution in the UK countryside: rural villages may be preferred over the surrounding arable farmland because of greater food availability, a warmer microclimate, lower numbers of predators and a greater availability of nest sites (Reeve 1998; Doncaster, Rondinini & Johnson 2001; Hubert *et al.* 2011; Hof, Snellenberg & Bright 2012).

Here we focus on the contribution of prey distribution. Prey density has been shown to affect hedgehog distribution at the field scale (Haigh, Butler & O'Riordan 2012a). Hedgehogs consume mainly macroinvertebrates, particularly earthworms, gastropods, beetles and caterpillars. About 15% of the diet is vertebrate prey such as bird's eggs, game bird chicks, small mammals and amphibians (Yalden 1976; Wroot 1984; Dickman 1988). Plant material is also frequently ingested, yet possibly accidentally or in the guts of prey (Yalden 1976; Wroot 1984). Hedgehogs may be in relatively higher abundance in gardens and amenity grassland as a result of the reduction in macroinvertebrate availability on arable land. Earthworm abundance is low in arable fields (Curry, Byrne & Schmidt 2002; Smith *et al.* 2008), whereas short grass habitats such as amenity grassland and garden lawns may sustain high numbers of earthworms and therefore hedgehogs (Micol, Doncaster & Mackinlay 1994; Young *et al.* 2006). Hedgehogs may also be attracted to artificial food sources near buildings, such as food provided for pets by homeowners and specifically for hedgehogs (Morris 1985; Hubert *et al.* 2011).

The second principal hypothesis explaining hedgehog foraging behaviour is that the distribution of the hedgehog's main predator on arable land, the European badger (*Meles meles*), is responsible. Hedgehog density on grass fields is inversely correlated with the density of local badger populations, or with distance from badger setts, (Micol *et al.* 1994; Young *et al.* 2006) and hedgehogs may favour rural villages to avoid badgers on the surrounding arable land (Hof *et al.* 2012). The hedgehog-badger relationship is an example of asymmetrical intraguild predation (Polis, Myers & Holt 1989), as badgers not only prey on hedgehogs but also compete for macroinvertebrates (Neal 1986) and may force hedgehogs out of suitable foraging habitat (Doncaster 1992).

Establishing how diet shapes hedgehog distribution in rural landscapes has the potential to provide an evidence base for conservation action to prevent further population declines in rural areas. For example, if we find key prey items are lacking in the diet of hedgehogs on arable land we can focus on restoring or improving invertebrate-friendly habitats on farmland (Hof & Bright 2010). Previous

studies of hedgehog diet involved analysis of gut or faeces contents to identify prey items from their morphology, which is time consuming as prey items such as gastropods and earthworms are difficult to identify (Yalden 1976; Wroot 1984). Additionally, artificial food, i.e. pet food, which may constitute a large part of a hedgehogs' diet, may be difficult to detect using such methods. More recently, studies employing molecular methods have used universal DNA barcoding primer sets to amplify and then sequence the DNA of a specific group of species present in predator faecal or stomach contents (Deagle, Kirkwood & Jarman 2009; Soininen *et al.* 2009; Bohmann *et al.* 2011; Razgour *et al.* 2011; Zeale *et al.* 2011). These studies were initially limited to one prey type, but now studies can examine complex, omnivorous diets using several universal primer sets (De Barba *et al.* 2014). The amplification of prey DNA has been tested successfully in identifying amphibian DNA in hedgehog faecal and stomach contents (Egeter, Bishop & Robertson 2014) and can also be used to detect the species present in pet food (Okuma & Hellberg 2015).

Here we use molecular methods, capable of detecting previously problematical items such as pet food and macroinvertebrates, to assess if there are variations in hedgehog diet on a gradient from rural villages to open arable farmland, and under varying predation threat from badgers. We can then make inferences as to whether dietary differences contribute to hedgehog distribution in the countryside. We tested if the presence or abundance, determined from the abundance of prey DNA sequences present, of prey items was correlated with a hedgehog's mean distance from buildings over a season and examined whether diet differed on sites with and without badgers.

Methods

Sample collection

Hedgehogs were captured at four sites in July–September 2013 and April–September 2014, two in North Norfolk (UK grid refs: TF 96061 25469 and TG 16716 36586) and two in North Yorkshire (SE 90511 81822 and SE 68646 24715). Each site consisted of predominately arable farmland and a neighbouring village. Hedgehogs were caught by hand and fitted with 10g VHF radio-tags (Biotrack,

Dorset, UK) under inhalation anaesthesia (HO license no: PIL 30/10293, Natural England license no: 2014/SCI/0298). Hedgehogs were individually marked with coloured heat-shrink tubing, which was super-glued to six spines. They were sexed and weighed. During tagging an enema was performed by slowly syringing 5ml warm water in to the anus, to obtain a faecal sample for diet analysis. Each of the four sites was visited in turn throughout the season for 4–8 days at a time and tagged hedgehogs were captured and re-anaesthetised as part of ongoing energetics studies. At each opportunity an enema was performed. However, enemas proved unsuccessful and therefore samples were also collected in the anaesthesia recovery box and opportunistically from unknown hedgehogs in areas where hedgehogs were frequently found foraging, such as amenity grassland and gardens. Faecal samples were stored in absolute ethanol until analysis.

Radio-tracking

Radio-tracking was used to assess hedgehogs' association with residential areas with a hand-held three element yagi directional antenna (Wildlife Materials International, Murphysboro, USA) and a TRX-1000S receiver (Wildlife Materials International, Murphysboro, USA). Hedgehogs were radio-tracked throughout each season from 9pm–4am, with at least three tracking fixes for each hedgehog obtained each evening during each 4–8 day site visit. For each fix, GPS coordinates, accurate to 5m were recorded. If hedgehogs were in gardens which were not accessible, their position was triangulated. The distance of each position fix to the closest building(s) was computed in ArcGIS desktop (ESRI, Redlands, CA, US). Here buildings were defined as any man-made structure with a roof and walls including: houses, out-houses, sheds and farm buildings. The mean distance of each tagged hedgehog to buildings was calculated for each hedgehog for the 2013 and 2014 seasons. In early October 2013 and April 2014 badger surveys were carried out to ascertain presence or absence on each site. Hedgerows and coppices were walked and checked for tracks, signs and setts and badger sightings during radio-tracking were recorded.

Primer selection

Four universal primer sets were selected for regions of mitochondrial DNA and one for chloroplast DNA (Table 1), with amplicon sizes <300bp to increase the chance of successful amplification with potentially degraded prey DNA (Deagle, Eveson & Jarman 2006) and also allow sequencing on the MiSeq platform (Illumina, CA, USA). The primer sets were tested on a range of potential prey items (Yalden 1976; Wroot 1984), both from DNA that was donated to the project, from DNA extracted from prey collected in local parks and from wet and dry cat and dog food in several flavours (see Appendix: Table A). DNA was extracted from tissues and pet food by following the ammonium acetate precipitation method (see Appendix). PCR reactions were performed in 10µl, with 1µl of extracted DNA, 4µl Taq PCR Master Mix Kit (Qiagen, Venlo, Netherlands), 1µl of 5µM forward and reverse primer and 3µl distilled H_2O. Touch-down PCR was run from 60–48^{o}C, decreasing by one degree per cycle. The PCR conditions were as follows: 15 mins at 95^{o}C followed by 14 cycles of 30s at 95^{o}C then 30s at 60^{o}C (decreased by 1^{o}C per cycle) and 90s at 72^{o}C, followed by 25 cycles of 30s at 95^{o}C, 30s at 48^{o}C and 30s at 72^{o}C, followed by a final incubation of 10 mins at 72^{o}C. PCR products were sequenced on a ABI 3730 capillary sequencer, sequences were aligned (CodonCode Ltd, MA, US), and compared against the NCBI nucleotide database using BLAST with the default settings (Altschul *et al.* 1990) to confirm sequence identity.

Universal primers used to amplify potential hedgehog vertebrate prey will also amplify predator DNA, in this case hedgehog DNA (Deagle *et al.* 2006; Vestheim & Jarman 2008). Previous studies have resolved co-amplification of predator DNA by using blocking primers (Vestheim & Jarman 2008; Leray *et al.* 2013). However, this process risks blocking potential prey items similar to predator DNA at barcoding regions. Modern sequencing platforms can produce millions of reads, of which thousands will be of target DNA (Piñol *et al.* 2014), thus negating the need for blocking primers. Therefore, blocking primers were not used in this study.

Table 1 Universal primer sets selected to amplify target plant and animal prey in hedgehog faecal samples

Set no.	Target prey	Name	Region	Product size (bp)	Primer sequence	PCR temp	Source
1	Earthworm	185F	12s	225-236	TGTGTACTGCCGTCGTAAGCA	60 °C	Harper *et*
		14233R			AAGAGCGACGGGCGATGTGT		*al.*, 2005
2	Vertebrate	L1085	12s	215	CCCAAACTGGGATTAGATACCC	58 °C	Kitano *et*
		H1259			GTTTGCTGAAGATGGCGGTA		*al.*, 2007
3	Vertebrate	L2513	16s	244	GCCTGTTTACCAAAAACATCAC	56 °C	Kitano *et*
		H2714			CTCCATAGGGTCTTCTCGTCTT		*al.*, 2007
4	Invertebrate	ZBJ-ArtF1c	COI	157	AGATATTGGAACWTTATATTTTATTTTTGG	55 °C	Zeale *et*
		ZBJ-ArtR2c			WACTAATCAATTWCCAAATCCTCC		*al.*, 2011
5	Plant	A49325	trnL	254-767	CGAAATCGGTAGACGCTACG	56 °C	Taberlet *et*
		B49863			GGGGATAGAGGGACTTGAAC		*al.*, 2007

On each row the forward primer is on line 1 and the reverse primer is on line 2
Animal primers targeted regions of mitochondrial DNA, plant primers targeted chloroplast DNA

DNA extraction and amplification

Faecal samples were dried on tissue paper and DNA was extracted from 20mg (dry weight) using the QIAamp DNA stool minikit (Qiagen, Venlo, Netherlands), following the manufacturer's guidelines and alongside negative controls. Extractions were quantified on agarose gel and with fluorometry. Both forward and reverse primers were 5'-tagged with a 6bp identifier sequence to allow pooled Illumina MiSeq sequencing of individual uniquely-tagged samples and allowing the assignment of sequences to individual faecal samples after sequencing (see Appendix: Table B). All PCR reactions were prepared in a separate lab from where the testing of primers on potential prey items was performed, using filter tips. PCR reactions were carried out in 30µl with 12µl of Taq PCR Master Mix Kit (Qiagen, Venlo, Netherlands), 6µl distilled H_2O, 3µl of tagged forward, 3µl of tagged reverse primer (primers at a concentration of 5µM) and 6µl of extracted DNA. The PCR conditions were as follows: 15 mins at 95°C followed by 35 cycles of 30s at 95°C then 30s at primer temperature (see Table 1) and 30s at 72°C, followed by a final incubation of 10 mins at 72°C. Each PCR reaction was performed in duplicate alongside negative controls. PCR products were run on a 0.01% agarose gel and quantified using a fluorometer. PCR products from each primer set were pooled for each faecal sample in equal concentrations based on the strength of products from gel electrophoresis. PCR

products for each sample were cleaned using a QIAquick PCR purification kit (Qiagen Venlo, Netherlands), following manufacturer's guidelines, and quantified with fluorometry. PCR products from all samples were then pooled in equimolar ratios.

Analysis of sequence data

Raw reads were trimmed to remove Illumina sequencing adapters and low quality sequences using Trimmomatic (Bolger, Lohse & Usadel 2014), with reads trimmed using a 4bp sliding window and a quality threshold of 20, and any reads shorter than 135bp after trimming removed. The remaining paired reads were aligned using FLASH (Magoč & Salzberg 2011), allowing a maximum overlap of 250bp. Aligned pairs were combined with any trimmed but unaligned or unpaired reads, and sequence files were subsequently split into those from different regions using the primer sequence, and then assigned to samples using the dual 6bp identifiers before primer sequences were trimmed off using Mothur (Schloss *et al.* 2009). Reads for each gene were clustered in Usearch (Edgar 2010) and identical reads and chimeric sequences were removed. Remaining reads were clustered using an identity threshold of 97% with 90% sequence coverage. Clusters consisting of just one read (singletons) were discarded. A representative sequence from each cluster was compared against the NCBI nucleotide database using BLAST (Altschul *et al.* 1990), considering only matches with 98% sequence identity and 100% sequence coverage.

Primer performance

Results of primer optimisation indicated that the five selected primer sets would be efficient in amplifying the key prey items in the hedgehog's diet and products would be suitable for comparing to reference databases at the family level (Appendix: Table A). Results of trials on pet food found that the extracted DNA, particularly of wet food, was commonly assigned to pig (*Sus scrofa*) or cow (*Bos taurus*), regardless of the advertised flavour (Appendix: Table A). This is likely to be due to the gelatine present in the jelly of wet pet food. The presence of these species would offer a good

indication of pet food presence as other species such as chicken or rabbit could be consumed naturally, for example as chicken eggs or carrion.

Negative controls

Negative controls both of DNA extraction for faecal matter and of PCR reactions produced no PCR products when gel electrophoresis on agarose gel was performed. However, we found a large number of DNA sequences in the samples after sorting with Mothur (Schloss *et al.* 2009). Looking at the origins of the samples in more detail we found this contamination to be the repeat sequencing of a small number of molecules of DNA present in the controls. For true samples there was a larger range of sequences which would by far drown out this effect. Therefore, we conclude this hasn't affected our ability to analyse differences in diet between hedgehogs.

Morphological analysis

For samples where sufficient faecal matter remained after molecular analysis a coarse morphological analysis was performed to ground-truth the findings of the molecular study. The contents of four 5g sub-samples of each faecal sample were identified under a x10-50 microscope and presence/absence of prey items recorded.

Statistical analysis

We were unable to confidently BLAST to species level and therefore analysis was performed at the family level. We grouped Lepidoptera at the order level and Gastropods at the class level, as some families were very scarce, and removed other prey families that were present in fewer than 5% of samples from analyses. Prey family accumulation curves were constructed using the program EstimateS 9.1 (Colwell 2005). For analyses where it was not possible to add hedgehog ID as a random factor, i.e. diversity and similarity indices, we removed repeats by keeping the first sample collected for a given hedgehog and discarding remaining samples, to give a data set free of pseudoreplication.

To test for differences in diversity and evenness in the prey families present in faecal samples between males and females, sites, counties and samples from sites with and without badgers, we calculated Shannon indices, to give a measure of richness and evenness (Shannon & Weaver 1949), and Simpson's Indices, to give a measure of prey family evenness and dominance (Simpson 1949), in the R software package Vegan (R Core Team 2014; Oksanen *et al.* 2015). Similarity indices between groups were calculated in PAST 3.0 (Hammer, Harper & Ryan 2001).

To test for an effect of distance to buildings on the prey families present in a hedgehog faecal sample, whilst controlling for other factors which may affect hedgehog diet composition including seasonal availability of prey items(Yalden 1976; Wroot 1984; Haigh, O'Riordan & Butler 2013) and sex (Yalden 1976), we used Canonical Correspondence Analysis (CCA). CCA is an ordination method which reduces the variation in a data matrix, in this case a list of prey families present in each sample, at the same time constraining the ordination using predictor variables (Ter Braak 1986; Legendre & Legendre 2012). We performed CCA in the R software package Vegan (Oksanen *et al.* 2015) with "mean distance to buildings over the season", site and sex as constraining variables. The year the faecal sample was collected was added as a conditioning or 'nuisance' variable (covariable). The statistical significance of the predictor variables in constraining the ordination is tested by randomisation.

To test for differences in the abundance of prey items present, the number of sequences clustered for BLASTing was used as a measure of the number of DNA sequences of each prey family present in each sample. It is worth noting that this measure can be used to look at the number of sequences assigned to each prey family between individuals but care must be taken when determining the proportion of prey items within an individual faecal sample (Deagle *et al.* 2010; Srivathsan *et al.* 2014). DNA from various prey items may be amplified differentially during the PCR reactions (Polz & Cavanaugh 1998) and prey items may be digested at different rates and to varying degrees (Deagle *et al.* 2010). For this reason, in this study we analysed only differences in prey family DNA sequence

abundance between individuals. Linear mixed effects models were constructed to test for differences in the number of sequences obtained for commonly occurring prey families. The explanatory variables were distance to buildings, site, sex, month and calendar year. Hedgehog ID was again added as a random factor.

Results

Summary

Fifty seven faecal samples were obtained, 50 from tagged individuals and seven from key foraging habitats. Of the 50 samples from tagged individuals, 32 were from unique individuals. We successfully extracted DNA from all 57 faecal samples. A total of 9,189,958 sequences were obtained from MiSeq. After trimming and clustering reads 1,330,033 sequences remained. After clustering sequences for comparison to the NCBI Nucleotide database, BLAST produced matches for 46,926 sequences; of these 27,500 were assigned to hedgehog and 168 to human, both of which were discarded. We also discarded non-target sequences including those assigned to bacteria, nematodes and ticks. We performed morphological analysis on 41 faecal samples.

We detected 35 prey families in the 57 samples, listed in Table 2. After grouping Lepidoptera and Gastropoda, removing families appearing in less than 5% of samples and removing repeat samples from individuals replicated at a different sampling time, 23 prey groups remained. Of these the most common invertebrate family in the diet was Carabid beetles, which were found in every sample, followed by Lumbricidae and Lepidoptera (from five families), found in 97% of samples (Fig.1a). The most common families of vertebrate prey were not usual hedgehog prey items: Suidae and Bovidae in 91% of samples (Fig.1b). The most common 'natural' vertebrate prey family in the samples was Bufonidae, which was present in 72% of samples. No plant DNA was detected in the molecular analysis. Prey accumulation curves (Fig.2) provide evidence that we were able to describe a high proportion of prey families in the hedgehog's diet with the sample size in this study.

Table 2. List of prey families identified in 57 hedgehog faecal samples from four sites in Norfolk and North Yorkshire in 2013 and 2014. % is the percentage of samples found to have the prey item present

Class	Order	Family	No. samples	% samples
Actinopterygii	Clupeiformes	Clupeidae	5	9
Amphibia	Anura	Bufonidae	38	67
		Ranidae	9	16
	Caudata	Salamandridae	6	11
Arachnida	Araneae	Lycosidae	1	2
Aves	Columbiformes	Columbidae	17	30
	Galliformes	Phasianidae	4	7
Clitellata	Haplotaxida	Lumbricidae	54	95
Diplopoda	Julida	Julidae	3	5
Entognatha	Entomobryomorpha	Paronellidae	27	47
Gastropoda	Limacoidea	Agriolimacidae	2	4
	Sigmurethra	Arionidae	2	4
		Limacidae	1	2
Insecta	Coleoptera	Carabidae	57	100
		Cerambycidae	8	14
		Staphylinidae	1	2
		Tenebrionidae	4	7
	Diptera	Anthomyiidae	2	4
		Phoridae	12	21
		Tipulidae	13	23
	Lepidoptera	Crambidae	2	4
		Geometridae	1	2
		Hepialidae	1	2
		Noctuidae	49	86
		Nymphalidae	1	2
	Orthoptera	Acrididae	5	9
Mammalia	Artiodactyla	Bovidae	53	93
		Suidae	51	89
	Carnivora	Canidae	22	39
		Felidae	21	37
		Mustelidae	2	4
	Lagomorpha	Leporidae	3	5
	Perissodactyla	Equidae	3	5
	Rodentia	Muridae	21	37
	Soricomorpha	Soricidae	4	7

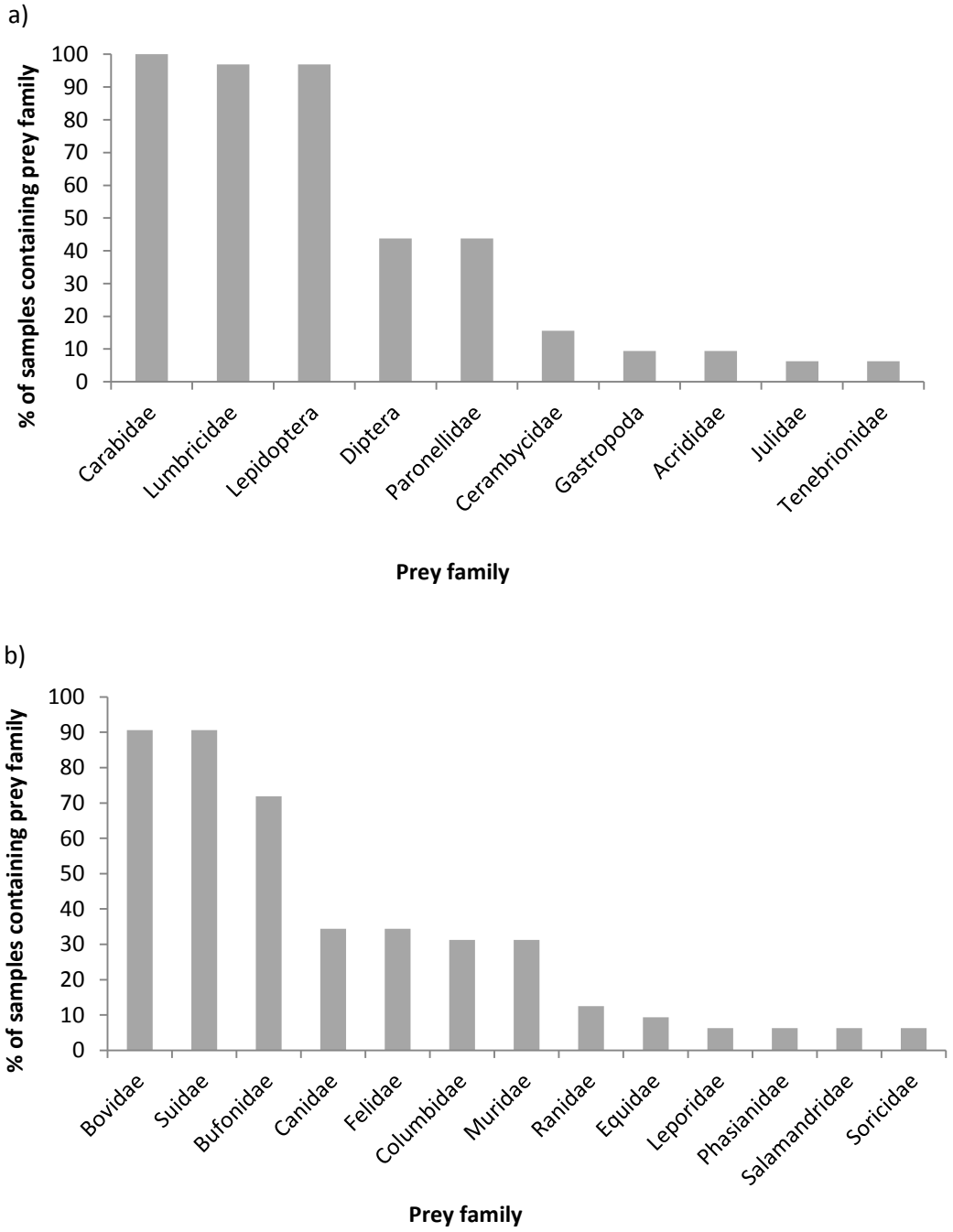


Fig.1 a) The percentage occurrence of invertebrate prey families in 32 unique hedgehog faecal samples and b) the percentage occurrence of vertebrate prey families in 32 hedgehog faecal samples. Samples were collected from radio-tagged individuals on four sites in Norfolk and Yorkshire. Prey families were grouped for Lepidoptera, Diptera and Gastropoda

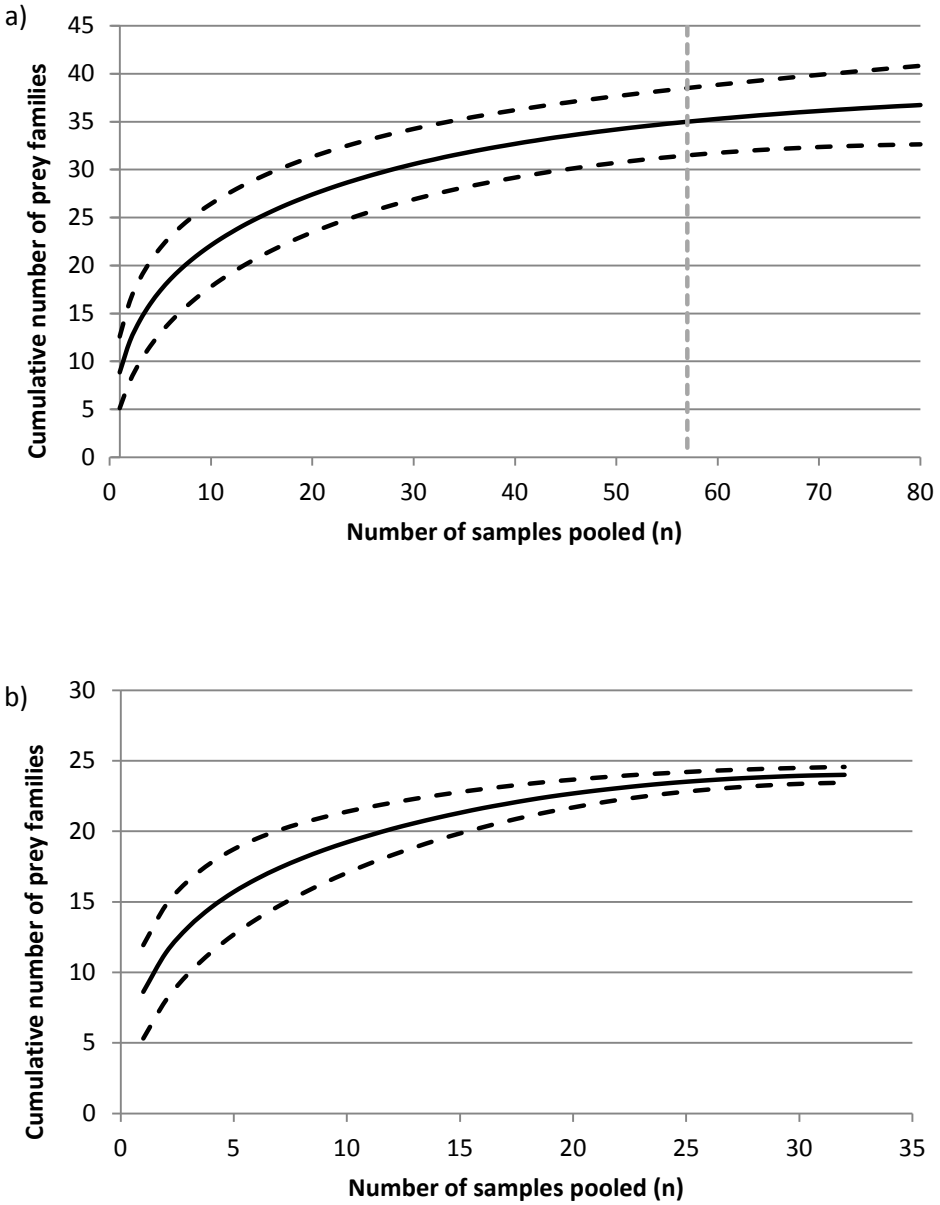


Fig.2 a) An accumulation curve of prey families in 57 hedgehog faecal samples. b) An accumulation curve for the same dataset with repeats from individual hedgehogs removed, samples from unknown hedgehogs removed, families present in less than 5% of samples removed and Lepidoptera, Diptera Gastropoda families grouped together. Data was resampled 100 times for each curve. Dashed lines indicate 95% confidence intervals. The curve past the dashed vertical line in plot a) indicates a simulation of the number of prey families expected if the sample size was increased to n=80, following Colwell et al. (2012).

Richness and diversity

Shannon and Simpson indices are present in Table 3. When faecal samples were divided into groups according to the sex of the hedgehog, badger presence, county and site, the Simpson index was nearly constant between groups (0.91-0.93, Table 3) whereas there were small differences in the Shannon index between groups (2.48-2.77, Table 3). The similarity of prey families eaten between hedgehog groups was confirmed by the results of similarity indices (Table 4). For example, the mean Bray-Curtis index between groups was 0.68, indicating high similarity between sample groups (Bray & Curtis 1957). The greatest dissimilarities were between samples from different sites, particularly in respect to Site B. The difference between Site B and C was 0.52 and between Site B and Site D was 0.54 (Table 4).

Table 3 The richness and diversity of prey families found in faecal samples from 32 unique hedgehogs collected from hedgehogs radio-tracked in Norfolk and Yorkshire in July-October 2013 and April-September 2014

Sample group	No. of samples	Family Richness	Shannon Index	Simpsons Index
All	32	23	2.72	0.92
Males	16	21	2.69	0.92
Females	16	22	2.71	0.92
Badgers present	11	19	2.63	0.91
Badgers absent	21	22	2.73	0.92
Norfolk	18	23	2.77	0.93
Yorkshire	14	18	2.56	0.91
Site A	9	18	2.52	0.91
Site B	12	18	2.76	0.93
Site C	5	13	2.48	0.91
Site D	6	21	2.59	0.91

Shannon and Simpson indices were calculated in the R package Vegan (R Core Team 2014; Oksanen *et al.* 2015)

Table 4 Comparisons of the number of prey families and the similarity of the families present found in hedgehog faecal samples, in different groups, from 32 hedgehog faecal samples collected from hedgehogs radio-tracked in Norfolk and Yorkshire in July-October 2013 and April-September 2014

Comparison	Shared Families	Unique Families	Jaccard	Sorensen	Bray-Curtis	Spearman's Rho
Badger Vs No badger	18	5	0.78	0.88	0.62	0.84
Male Vs Female	20	3	0.86	0.93	0.89	0.85
Norfolk Vs Yorkshire	18	5	0.78	0.88	0.79	0.81
Site A Vs Site B	16	6	0.73	0.84	0.74	0.77
Site A Vs Site C	12	6	0.67	0.80	0.64	0.84
Site A Vs Site D	13	9	0.59	0.74	0.68	0.66
Site B Vs Site C	13	8	0.62	0.76	0.52	0.89
Site B Vs Site D	16	7	0.70	0.82	0.54	0.66
Site C Vs Site D	12	7	0.63	0.77	0.74	0.73

Similarity indices were calculated using PAST 3.0 (Bray & Curtis 1957; Hammer *et al.* 2001)

Canonical Correspondence Analysis

The CCA explained just 19% of variation in the presence or absence of prey families between samples. The conditioning variable year explained 4% whereas the constraining variables distance to buildings, sex and site explained 12% of inertia. The results of the CCA indicated no effect of distance to buildings on the prey families present in a hedgehog faecal sample (X^2=0.04, p=0.29). However, the site from which the faecal sample was collected explained a significant amount of variation between samples (X^2=0.13, p=0.04). There was variation between all four sites rather than between sites with and without badgers or sites in Norfolk or Yorkshire (Fig.3), providing no evidence for an effect of badger presence on the prey families present in a hedgehog faecal sample (Fig.3). We found no effect of sex on the diet families present in a faecal sample (X^2=0.03, p=0.54).

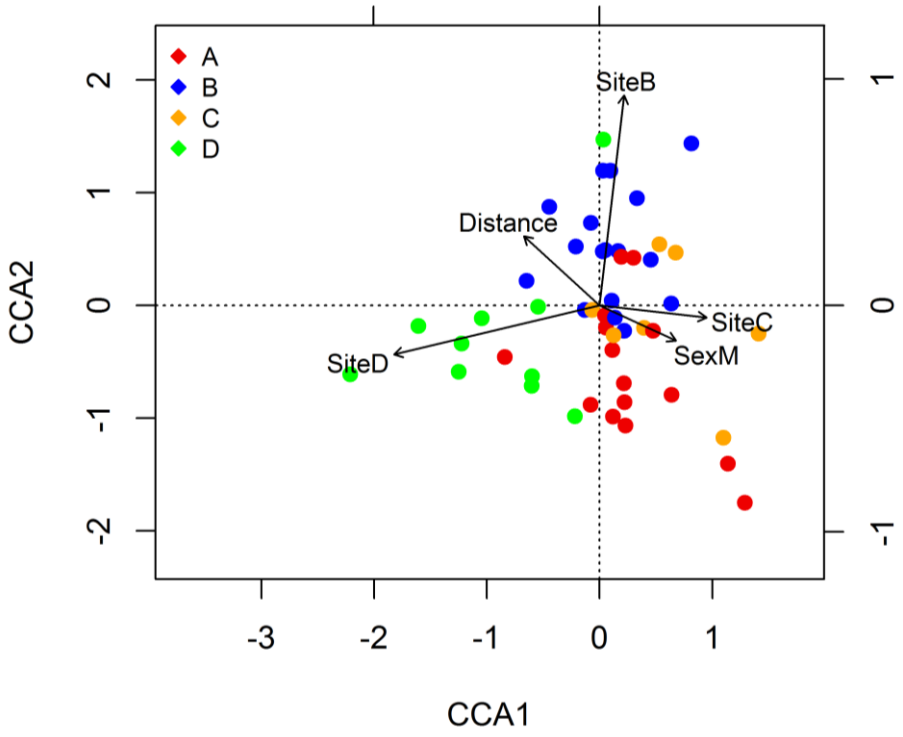


Fig.3 The results of a Canonical Correspondence Analysis (CCA) to test for variance in the prey families present in hedgehog faecal samples. The mean distance the hedgehog that provided the sample was found to buildings over the season, site and sex were added as constraining variables. The year the faecal sample was collected was added as a conditioning variable

Prey abundance

Using the number of prey family DNA sequences making up each unique cluster as a measure of abundance, we studied differences in the abundance of the following key prey families: Lumbricidae, Carabidae, Lepidoptera, Bovidae and Suidae (See appendix Table C for the total number of prey DNA sequences attributed to each of the 35 prey families in this study). We found no relationship between the abundance of DNA sequences detected from these prey families in a faecal sample and the mean distance a hedgehog was found to buildings (Table 5).

Table 5 Results of linear models to test the effect of a hedgehog's mean distance to buildings, site (with or without badgers), month, sex and year on the number of prey DNA sequences of Lumbricidae, Carabidae, Suidae and Bovidae detected in a faecal sample from the tracked hedgehog. Samples were collected from hedgehogs in Norfolk and Yorkshire in July-October 2013 and April-September 2014

Response	**Variable**	**Df**	**F**	**P value**	**Effect size**	**95% CI**
Lumbricidae	Year *2014*	1,50	21.30	<0.0001**	1.847	1.047, 2.647†
	Distance to buildings	1,50	1.551	0.219	0.010	-0.006, 0.025
	Site (*A BADGER-FREE)*	3,50	3.646	0.148		
	Site B badger-free				0.703	-0.184, 1.589
	Site C badgers				-0.597	-2.096, 0.902
	Site D badgers				0.592	-0.439, 1.623
	Month (*APRIL)*	4,50	3.65	0.011*		
	Month May				3.274	0.239, 6.310†
	Month June				2.750	0.274, 5.226†
	Month July				3.986	1.627, 6.345†
	Month August				3.973	1.589, 6.358†
	Sex *MALE*	1,50	0.347	0.558	-0.224	-0.982, 0.53
Carabidae	Year *2014*	1,50	0.773	0.384	0.244	-0.311, 0.799
	Distance to buildings	1,50	0.957	0.333	0.005	-0.006, 0.016
	Site (*A BADGER-FREE)*	3,50	2.146	0.106		
	Site B badger-free				0.521	-0.094, 1.136
	Site C badgers				-0.424	-1.464, 0.615
	Site D badgers				-0.107	-0.822, 0.608
	Month (*APRIL)*	4,50	4.084	0.006**		
	Month May				2.523	0.869, 4.177†
	Month June				2.991	1.356, 4.627†
	Month July				2.893	1.176, 4.610†
	Month August				3.545	1.440, 5.650†
	Sex *MALE*	1,50	0.008	0.927	0.024	-0.502, 0.550
Lepidoptera	Year *2014*	1,50	6.152	0.02*	-0.734	-1.325, -0.143†
	Distance to buildings	1,50	0.331	0.568	-0.003	-0.015, 0.008
	Site (*A BADGER-FREE)*	3,50	9.955	<0.0001***		
	Site B badger-free				1.541	0.885, 2.197†
	Site C badgers				0.066	-1.043, 1.174
	Site D badgers				0.167	-0.596, 0.929
	Month (*APRIL)*	4,50	3.228	0.020*		
	Month May				-0.158	-1.922, 1.606
	Month June				-0.956	-2.701, 0.788
	Month July				-0.817	-2.648, 1.014
	Month August				0.821	-1.424, 3.066
	Sex *MALE*	1,50	3.150	0.082.	-0.498	-1.059, 0.063

Table 5 *Continued*

Response	Variable	Df	F	P value	Effect size	95% CI
Suidae	Year *2014*	1,50	21.317	<0.0001***	-1.082	-1.550, -0.614†
	Distance to buildings	1,50	0.188	0.667	-0.002	-0.011, 0.007
	Site (*A BADGER-FREE)*	3,50	1.542	0.215		
	Site B badger-free				-0.058	-0.577, 0.461
	Site C badgers				-0.376	-1.253, 0.502
	Site D badgers				-0.575	-1.178, 0.029
	Month (*APRIL)*	4,50	7.540	<0.0001***		
	Month May				-0.809	-2.205, 0.587
	Month June				-1.799	-3.180, -0.418†
	Month July				-0.424	-1.873, 1.026
	Month August				-0.494	-2.272, 1.283
	Sex *MALE*	1,50	0.158	0.693	0.088	-0.356, 0.532
Bovidae	Year *2014*	1,50	0.003	0.952	0.021	-0.659, 0.700
	Distance to buildings	1,50	0.719	0.400	-0.006	-0.019, 0.008
	Site (*A BADGER-FREE)*	3,50	1.217	0.313		
	Site B badger-free				0.054	-0.842, 0.624
	Site C badgers				-1.052	-2.327, 0.219
	Site D badgers				-0.340	-1.216, 0.535
	Month (*APRIL)*	4,50	1.841	0.136		
	Month May				1.033	-0.222, 4.934
	Month June				0.546	-1.533, 2.673
	Month July				0.570	-1.457, 2.549
	Month August				2.356	-0.993, 3.058
	Sex *MALE*	1,50	0.854	0.360	-0.298	-0.942, 0.346

Dependent variables were all log transformed for analysis

Words in italics following categorical variables indicate the reference category.

***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 **.**near significance

† 95% confidence interval of the effect size does not contain zero

The abundance of key prey families varied between years. We found a higher number of Lumbricid worm DNA sequences in 2014 than in 2013 and a higher number of Lepidoptera and Suidae sequences in 2013 than in 2014 (Table 5, Fig.5). The abundance of Lumbricid worm DNA was higher in samples collected later in the season (Table 5, Fig. 6) and the abundance of Suidae DNA sequences found in samples was higher at the beginning and end of the season in April and August and lower in the middle of the season in July (Table 5, Fig. 6). The abundance of Carabid beetles also varied with month, with the lowest number of DNA sequences found in samples at the beginning and end of the

season (Table 5, Fig. 6). The abundance of Lepidoptera DNA varied between sites, with a particularly high number of Lepidoptera sequences obtained from samples collected on Site B (Table 5, Fig. 6).

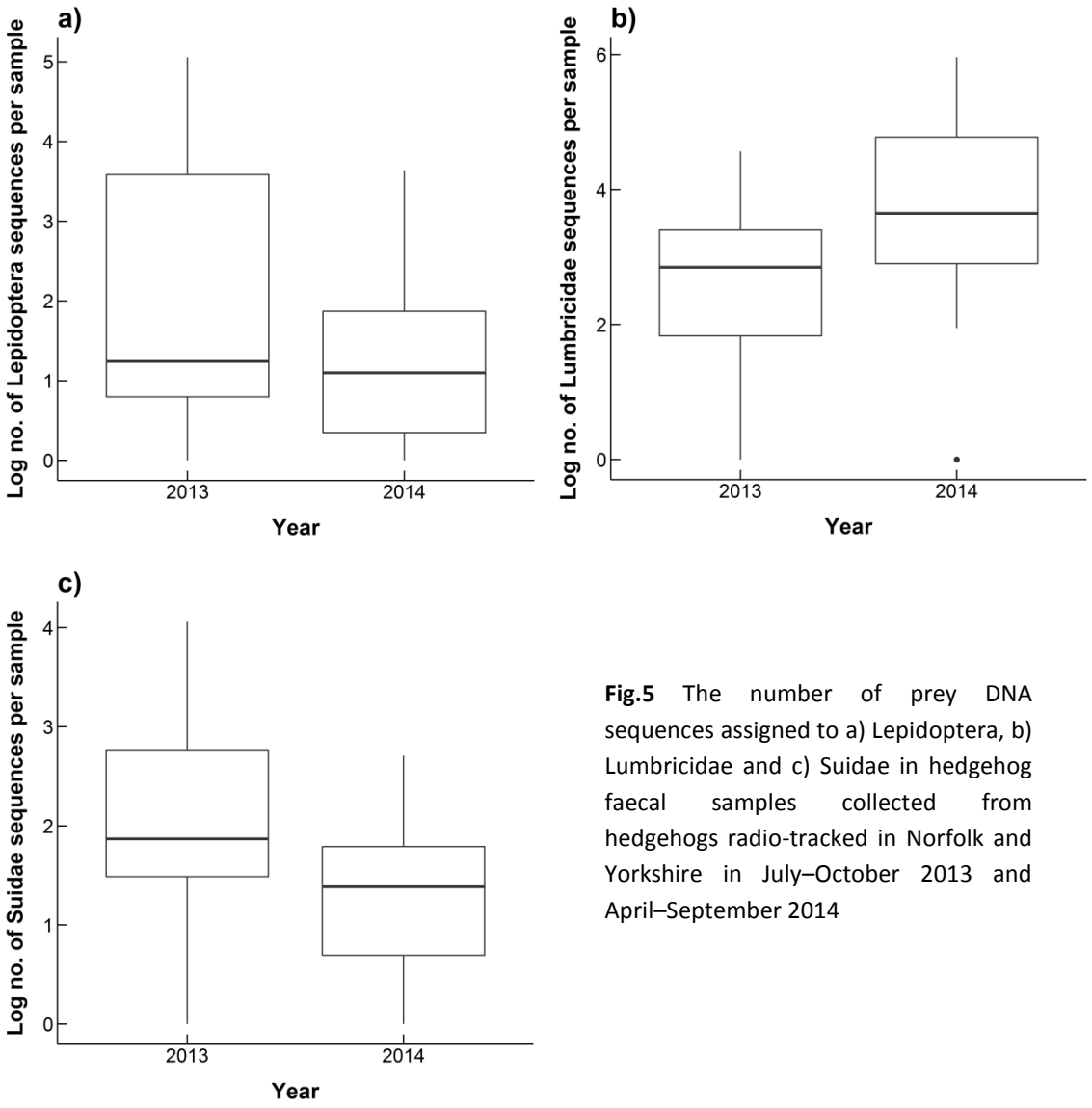


Fig.5 The number of prey DNA sequences assigned to a) Lepidoptera, b) Lumbricidae and c) Suidae in hedgehog faecal samples collected from hedgehogs radio-tracked in Norfolk and Yorkshire in July–October 2013 and April–September 2014

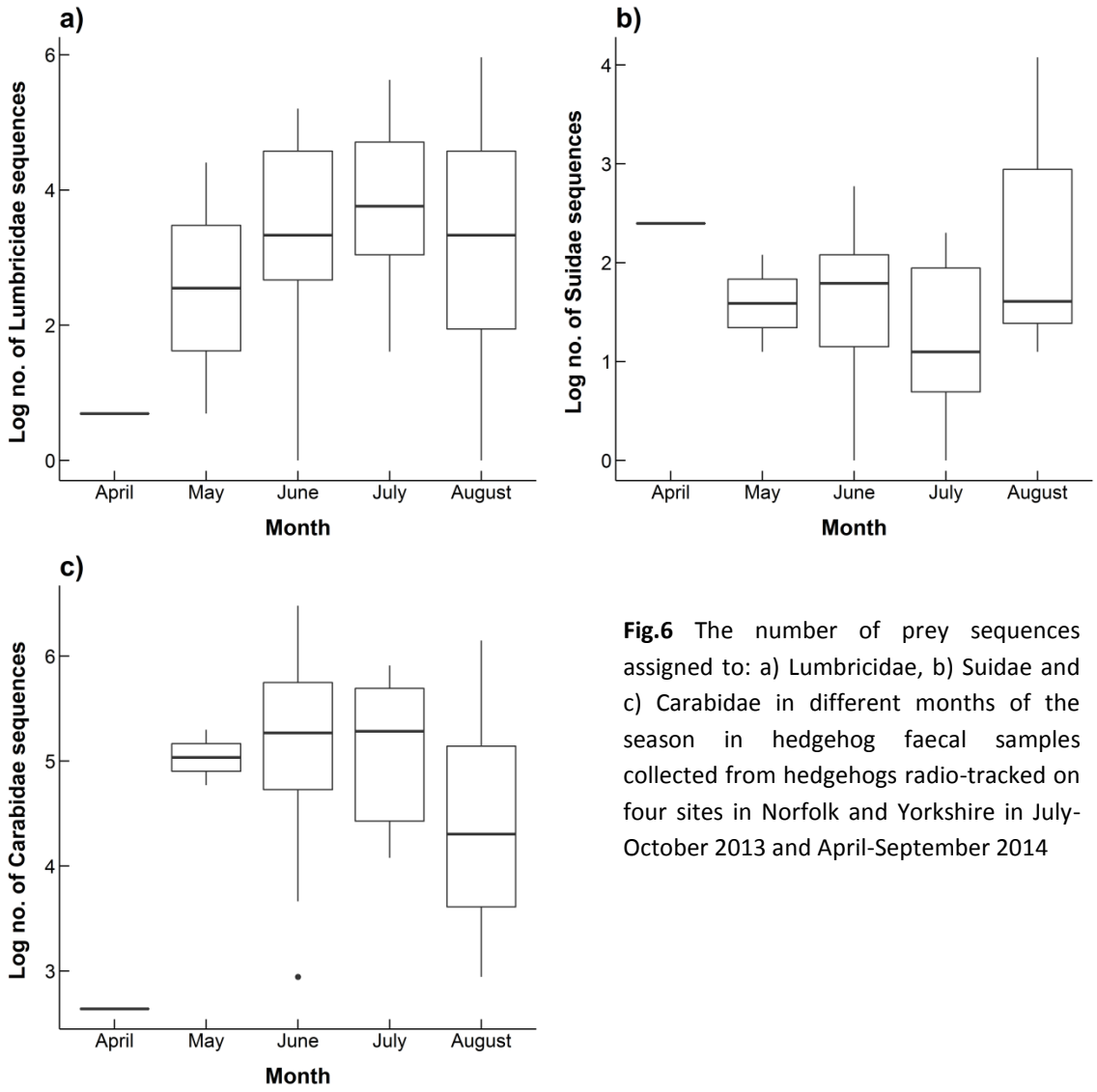


Fig.6 The number of prey sequences assigned to: a) Lumbricidae, b) Suidae and c) Carabidae in different months of the season in hedgehog faecal samples collected from hedgehogs radio-tracked on four sites in Norfolk and Yorkshire in July-October 2013 and April-September 2014

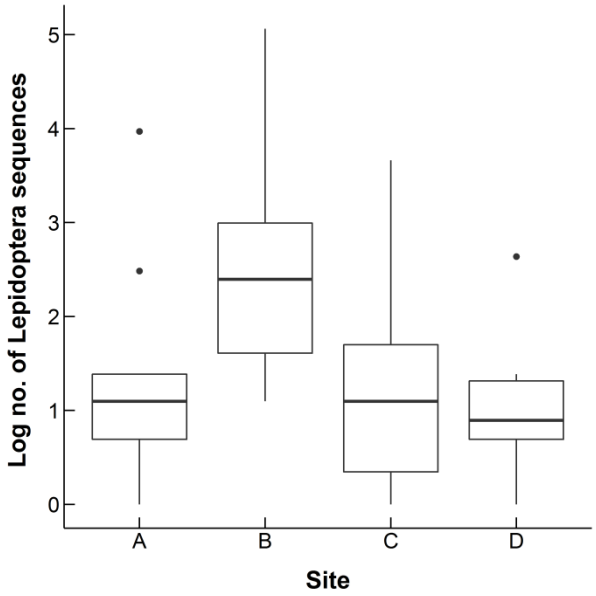


Fig.7 The number of prey sequences assigned to Lepidoptera in hedgehog faecal samples collected from hedgehogs radio-tracked on four sites in Norfolk and Yorkshire in July-October 2013 and April-September 2014

Morphological analysis

During the coarse morphological analysis the most common prey items were Carabid beetles in 95% of samples, grass in 61% of samples and Lepidopteran larvae in 24%. Other items of interest included seeds, bones, snail shell and chunks of meat (Table 6). The grass, plant matter and seeds observed during morphological analysis, suggest that there was failure in the ability of the trnL primer set in detecting plant DNA present in hedgehog faeces in this study.

Table 6 Prey items found in morphological analysis of 41 hedgehog faecal samples

Prey item	No. samples	% samples
Carabid beetle	39	95
Grass	25	61
Lepidoptera	10	24
Seed	9	22
Bone	6	15
Lumbricid earthworm	5	12
Woody plant	5	12
Hair	4	10
Meat	3	7
Crane fly	3	7
Aphid	3	7
Fibrous plant	2	5
Snail shell	2	5

Discussion

As in previous studies, hedgehogs were found to eat a wide range of invertebrates and vertebrates (Yalden 1976; Wroot 1984). We found that every sample contained either Suidae or Bovidae DNA, which laboratory trials indicated could be from pet food. The presence of Suidae and Bovidae therefore indicates that hedgehogs in the rural landscape frequently consume supplementary food, regardless of their mean distance to buildings. Evidence from sightings of hedgehogs radio-tracked to food bowls in gardens, and discussion with inhabitants of local villages supports the conclusion that hedgehogs frequently consumed pet food across all four sites. We may have found no relationship between the presence of Bovidae and Suidae with distance to buildings because previous studies have shown food addition may not alter home range size or nesting location of hedgehogs inhabiting urban or suburban areas (Morris 1985; Cassini, Krebs & Behavioural 1994). We also found Clupeidae in 9% of samples which may also be from pet food or possibly scavenged. Pet food has previously been linked to hedgehog attraction to urban areas in France (Hubert *et al.* 2011) and this study indicates a similar scenario in England.

Richness and diversity

The Shannon index, in this case calculated using presence or absence of prey families, is usually on a scale from 1.5–3.5 in ecological studies (Magurran 2013), and therefore a score of 2.72 indicates a relatively high prey family richness and evenness in the hedgehog's diet. For the Simpson index a result of 1 indicates complete evenness (Magurran 2013), and therefore the score of 0.92 suggests low diversity of prey families in the diet. When samples were grouped into males and females, samples from different counties and samples from different sites, we found minimal differences in diet between the sample groups. The lowest similarity indices were between Site B and Site C and D, which may be a result of the higher sample size at Site B, 12, than at Sites B and C, which had samples from 5 and 6 hedgehogs, respectively.

Canonical Correspondence Analysis

The CCA found no effect of a hedgehog's mean distance to buildings on the prey families present in its diet. This finding indicates that the preference of village habitats over arable farmland by hedgehogs is not due to the absence of natural prey families on predominately arable farmland. We must take into account that hedgehogs were never far from buildings in the study: the mean distance a hedgehog was from buildings in the study ranged from 9–112m with a mean of 42 ± SE 4m. To put this into perspective, male hedgehogs may travel up to 1158m a night and females 660m (Morris 1985). Therefore, all hedgehogs were always well within reach of buildings and tended to only use the centre of arable fields late in the season after harvesting. Had hedgehogs foraged more frequently further from buildings, variations in diet may have been more evident. Again, site was the only variable found to explain differences in the prey families present in a hedgehog faecal sample. This finding is expected due to local differences in climate and habitat availability at each of the sites, for example, the coldest temperatures were recorded at the most northerly site, Site C in Yorkshire, and Site B was the only site to have areas of set-aside.

Prey abundance

In addition to finding no effect of distance to buildings on prey families present in the diet, we found no evidence to suggest differences in the abundance of these prey items with a hedgehog's mean distance to buildings. We found a higher number of Lumbricid worm DNA sequences in 2014 than in 2013 and a higher number of Lepidoptera and Suidae sequences in 2013 than in 2014. The observed difference in the abundance of natural prey families in the diet between years is likely to be due to variability in environmental conditions between years, which is known to affect invertebrate abundance on farmland (Curry 1994; Roy *et al.* 2001; Bradbury *et al.* 2003). It was colder in summer 2013 than in 2014. Data loggers on the sites measured a mean temperature of 13 ± SE 0.1^{o}C in July, August and September 2014 and a temperature of 12.7 ± SE 0.2^{o}C in 2013. Earthworm activity is lower in colder temperatures (Edwards & Bohlen 1996) and we can speculate that the increases in

consumption of Lepidoptera and pet food in 2014 were to compensate for the lower earthworm availability than in 2013.

The most abundant and frequently occurring family of Lepidoptera in the study was Noctuidae. Many species of Noctuid larvae are active at night close to the ground and are therefore easily accessible to hedgehogs (Hofmann & Marktanner 1995). The abundance of Lepidoptera DNA varied between sites, with a particularly high number of sequences obtained from samples collected on Site B. A key difference between Site B and the other sites in the study was the presence of set-aside, predominately consisting of *Trifolium repens*. The abundance of invertebrates, including Lepidoptera, is often higher on set-aside than arable fields possibly due to the availability of larval food plants and the spraying of pesticides on arable land (Van Buskirk & Willi 2004; Macdonald *et al.* 2007; Alanen *et al.* 2011; Macdonald & Feber 2015).

The abundance of Lumbricid worm DNA was higher in samples collected later in the season. This finding is in line with previous studies of hedgehogs that have observed them using the centre of arable fields after harvesting when earthworm availability is high (Haigh *et al.* 2012a, 2013). Faecal samples obtained in May, June and July contained the highest abundance of Carabid beetle DNA, and this is to be expected as Carabid beetle activity is seasonal and peaks in mid-summer for some species (Thomas *et al.* 2001). A higher abundance of Suidae was consumed early on in the season in April and later on in the season in August. This pattern corresponds to periods when hedgehogs are building up fat stores, firstly after emergence from hibernation, and secondly before hibernation (Morris 1984; Jensen 2004; Haigh, O'Riordan & Butler 2012b), and thus we can speculate that hedgehogs consumed more pet food during these periods of intensive foraging. This behaviour was corroborated by observations during radio-tracking, for example, with one male hedgehog limiting its nightly activity to one garden where wet pet food was provided during late August and September 2014.

Morphological analysis

The coarse morphological analysis, as in the molecular analysis, showed Carabid beetles to be present in a high proportion of samples, 95%, and Lepidoptera to be an important prey item, present in 24% of samples. Prey families difficult to detect under the microscope were likely to have been under-represented, such as Lumbricid worms, only found in 12% of samples compared with 95% of samples in the molecular analysis, and gastropods, present in 7% of samples for the molecular analysis but in no samples during the morphological analysis. The morphological study confirmed that the Lepidoptera DNA detected is likely to be from caterpillars rather than moths or butterflies on the wing. The presence of chunks of meat in two faecal samples validated that Suidae and Bovidae DNA in the samples is likely to be the result of consuming pet food.

Predator presence

We found no evidence to suggest that badger presence affected the presence of prey items or the abundance of key prey families in the diet. Badgers are also omnivores and prey on earthworms, insects and fruit (Roper 1994; Neal & Cheeseman 1996) and we can infer that their presence indicates a reasonable availability of invertebrates. On sites with badgers the abundance of invertebrates may have been high enough to sustain both badgers and hedgehogs. Hedgehogs have been observed foraging close to badgers on arable land in the Republic of Ireland, where badger numbers are low (Haigh *et al.* 2012a). Additionally, amateur footage in gardens has recorded hedgehogs and badgers feeding side by side at food bowls, which we know were available on the sites in this study. Where food availability and habitat heterogeneity is high intraguild species can co-exist (Polis & Holt 1992; Morin 1999; Finke & Denno 2002; Janssen *et al.* 2007).

Study limitations

Prey DNA may still be detected in hedgehog faeces over 30 hours after the prey was consumed (Egeter *et al.* 2014). However, as hedgehogs eat a wide range of prey types and this varies with availability, the study of individual faecal samples gives us only a snapshot of the prey families each

hedgehog may eat over the season. Thus, the absence of a prey family in one sample does not mean that hedgehog did not consume the prey item at another point in time.

We detected no plant DNA in the faecal samples, but morphological observations indicated that plant matter was present. Other studies have found plant matter in hedgehog faecal and stomach samples but concluded it was often accidental ingestion whilst consuming invertebrates or chewed grass from the stomachs of caterpillars (Yalden 1976; Wroot 1984). The trials of the trnL primers were effective on a range of vegetables and fruits and have been successful in a study of faecal samples from the brown bear (*Ursus arctos*) (De Barba *et al.* 2014). One possible cause is the variability in the PCR product size for the plant primers (Table 1), which may have resulted in products that were too long for sequencing on the MiSeq platform. After further investigation, we found 64 sequences of plant DNA were filtered from the analyses as they were too long for alignment. These sequences could not be assigned to samples, but included sequences assigned to the families: Asteraceae, Poaceae, Urticaceae, Rosaceae, Fabaceae, Plantaginaceae, Brassicaceae and Ranunculaceae. Further study should optimise a plant primer set with a shorter product size.

We found gastropod DNA in 7% of samples, and in all cases sequences were assigned to slugs not snails. During morphological analysis we observed snail shell in two faecal samples. Primer testing indicated a 50% success rate in amplifying slug and snail DNA and therefore it is possible that any snail DNA present in the samples was not amplified and the occurrence of this prey in hedgehog diet may be higher. Future studies should include a specific gastropod primer set.

Thirty seven percent of the 57 samples contained Felidae DNA and 39% Canidae. It is not unusual for some species to consume the faeces of cats or dogs to capitalise on any remaining undigested food (McKeown, Luescher & Machum 1988; Birkhead 2010), and this may have been the cause of cat and dog DNA present in hedgehog faeces. Hedgehogs 'self-anoint', a process where the hedgehog responds to substances with a strong odour, first chewing the substance then spitting the saliva onto its spines (Burton 1957). Hedgehogs have been observed self-anointing in response to dog faeces

(Lindemann 1951; Herter, Krumbach & Kükenthal 1957; Reeve 1994) and possibly horse faeces (Brockie 1976). Hedgehogs on the study sites would certainly have encountered dog and cat faeces around buildings. Horses were present on all four sites, pigs were present on one site and cows in another and hedgehogs were observed foraging in these fields. However, self-anointing is relatively rare (Brockie 1976; Reeve 1994) and was only observed twice during the radio-tracking of the hedgehogs in this study. Hedgehogs may also accidentally consume faeces whilst foraging, for example, for worms in slurry, which could also contribute to the common occurrence of Bovidae and Suidae. Research into the mislabelling of pet food found that no samples tested positive for horse meat suggesting it is unlikely the horse DNA present in the samples came from pet food (Okuma & Hellberg 2015). There is a chance that hedgehogs ingested hair or saliva from cats or dogs whilst feeding from bowls left out for pets. Bohmann *et al.* (2011) found dog DNA in a study of bat diet and discarded it as contamination.

Summary

The prey accumulation curves presented here indicate that we were able to gain a comprehensive list of prey families present in the hedgehog's diet in rural areas. Despite being unable to quantify the relative proportions of each prey family eaten by each individual, overall we found no relationship between a hedgehog's association with buildings and the presence or abundance of prey items in its diet. These findings do not provide evidence that lack of suitable prey is a major factor contributing to the preference of hedgehog preference for rural villages over the surrounding arable farmland. However, all hedgehogs in the study used habitats associated with humans to some degree. We detected DNA surmised to be from pet food in all faecal samples and this may be one reason hedgehogs are active close to buildings. We also found evidence that hedgehogs may frequently consume cat and dog faeces. We found no evidence that the occurrence of badgers had an impact on the presence and abundance of prey families found in hedgehog faeces.

Further work should perfect molecular analysis by better quantifying the amount of each prey type consumed. Quantification can be achieved through real-time PCR and can be verified with feeding trials (Deagle & Tollit 2007; Bowles *et al.* 2011; Srivathsan *et al.* 2014). Additionally, the performance of plant and gastropod primers should be optimised.

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Appendix

DNA Extraction from tissue: Ammonium acetate precipitation protocol

1) Place 250µl Digsol buffer and 10µl Proteinase K (10mg/ml) in a 1.5ml flip-top tube (Eppendorf, Hamburg, Germany). Keep on ice.
2) Add tissue sample and Vortex
3) Place in a rotating oven at 55^{o}C overnight
4) Once digested (straw colour) add 300µl 4M ammonium acetate to each sample
5) Vortex several times over a period of at least 15 minutes at room temperature
6) Centrifuge for 10 minutes at 13,000rpm
7) Aspirate supernatant into clean labelled 1.5ml flip-top tubes
8) Add 1ml 100% ethanol and invert tubes gently several times to precipitate DNA
9) Centrifuge for 10 minutes at 13,000rpm
10) Pour off ethanol taking care not to lose DNA pellet
11) Add 500µl 70% ethanol and invert several times to rinse pellet
12) Pour off ethanol in a smooth movement and stand tubes upside-down on clean tissue (approx. 30-60 minutes)
13) Once dry add 100µl Tris-EDTA (T10 E0.1).
14) Flick sample to dislodge pellet
15) Place in water bath for 30 minutes at 65^{o}C to dissolve pellet (flicking every 10 mins)
16) Store at -20^{o}C long term or 4^{o}C short term

Table A. List of the species and artificial foods used to test the capability of four primer sets in amplifying prey items from hedgehog faecal samples

Description	**Family**	**Species**	**Primer set**	**PCR success**	**BLAST match**
Lumbricid earthworm	Lumbricidae	Unidentified	1	Yes	*Allolobophora chlorotica*
Lumbricid earthworm	Lumbricidae	Unidentified	1	Yes	*Dendrodrilus rubidus*
Lumbricid earthworm	Lumbricidae	Unidentified	1	Yes	*Aporrectodea caliginosa*
Lumbricid earthworm	Lumbricidae	Unidentified	1	Yes	*Lumbricus terrestris*
Nursey web spider	Pisauridae	Unidentified	4	Yes	*Pisaura mirabilis*
Slug	Gastropoda	Unidentified	4	Yes	*Arion owenii*
Slug	Gastropoda	Unidentified	4	No	NA
Snail	Gastropoda	Unidentified	4	Yes	*Bekkochlamys sp.*
Snail	Gastropoda	Unidentified	4	No	NA
Spider	Unidentified	Unidentified	4	Yes	*Pardosa prativaga*
Millipede	Julidae	Unidentified	4	Yes	*Agabus audeni*
Mealworm	Tenebrionidae	*Tenebrio molitor*	4	Yes	Yes
Ground beetle	Unidentified	Unidentified	4	Yes	*Pterostichus niger*
Ground beetle	Unidentified	Unidentified	4	Yes	*Loricera pilicornis*
Fruit fly	Drosophilidae	Unidentified	4	Yes	*Anastrepha obliqua*
Pea aphid	Aphididae	*Acyrthosiphon pisum*	4	Yes	Yes
Noctuid moth	Noctuidae	Unidentified	4	Yes	*Scoliopteryx libatrix*
Butterfly	Unidentified	Unidentified	4	Yes	*Pararge aegeria aegeria*
Butterfly	Unidentified	Unidentified	4	Yes	*Pararge aegeria aegeria*
Cricket	Gryllidae	*Gryllus campestris*	4	Yes	Yes
Woodlouse	Oniscidea	Unidentified	4	No	NA
Common toad	Bufonidae	*Bufo bufo*	2	No	NA
Common toad	Bufonidae	*Bufo bufo*	2	No	NA
Common toad	Bufonidae	*Bufo bufo*	3	Yes	Yes
Common toad	Bufonidae	*Bufo bufo*	3	Yes	Yes
Common frog	Ranidae	*Rana temporaria*	2	No	NA
Common frog	Ranidae	*Rana temporaria*	3	Yes	Yes
Palmate newt	Salamandridae	*Lissotriton helveticus*	2	No	NA
Palmate newt	Salamandridae	*Lissotriton helveticus*	3	Yes	Yes
Smooth newt	Salamandridae	*Lissotriton vulgaris*	2	No	NA
Smooth newt	Salamandridae	*Lissotriton vulgaris*	3	No	NA
Newt	Salamandridae	Unidentified	2	No	NA
Newt	Salamandridae	Unidentified	3	Yes	*Triturus helveticus*
Mallard	Anatidae	*Anas platyrhynchos*	2	Yes	Yes
Mallard	Anatidae	*Anas platyrhynchos*	3	No	NA
Greylag goose	Anatidae	*Anser anser*	2	Yes	Yes
Greylag goose	Anatidae	*Anser anser*	3	Yes	Yes

Table A *Continued*

Description	Family	Species	Primer set	PCR success	Blast match
Blue Duck	Anatidae	*Hymenolaimus sp.*	2	No	NA
Blue Duck	Anatidae	*Hymenolaimus sp.*	3	No	NA
Duck	Anatidae	Unknown	2	Yes	*Anas platyrhynchos*
Duck	Anatidae	Unknown	3	Yes	*Anas platyrhynchos*
Lapwing	Charadriidae	*Vanellus vanellus*	2	Yes	Yes
Lapwing	Charadriidae	*Vanellus vanellus*	3	No	NA
Wood pigeon	Columbidae	*Columba palumbus*	2	Yes	Yes
Wood pigeon	Columbidae	*Columba palumbus*	3	No	NA
Domestic chicken	Gallus	*Gallus gallus*	2	Yes	Yes
Domestic chicken	Gallus	*Gallus gallus*	2	No	NA
Guinea fowl	Numididae	Unknown	2	Yes	*Numida meleagris*
Guinea fowl	Numididae	Unknown	3	Yes	*Numida meleagris*
Japanese quail	Phasianidae	*Coturnix japonica*	2	No	NA
Japanese quail	Phasianidae	*Coturnix japonica*	3	No	NA
Turkey	Phasianidae	*Meleagris gallopavo*	2	No	NA
Turkey	Phasianidae	*Meleagris gallopavo*	3	No	NA
Common pheasant	Phasianidae	*Phasianus colchicus*	2	Yes	Yes
Common pheasant	Phasianidae	*Phasianus colchicus*	2	No	NA
Common pheasant	Phasianidae	*Phasianus colchicus*	3	No	NA
Common pheasant	Phasianidae	*Phasianus colchicus*	3	No	NA
Red grouse	Phasianidae	*Phasianus colchicus*	2	No	NA
Red grouse	Phasianidae	*Phasianus colchicus*	3	No	NA
Great tit	Paridae	*Parus major*	2	Yes	Yes
Great tit	Paridae	*Parus major*	3	No	NA
House sparrow	Passeridae	*Passer domesticus*	2	Yes	Yes
House sparrow	Passeridae	*Passer domesticus*	3	No	NA
Eurasian blackbird	Turdidae	*Turdus merula*	2	Yes	Yes
Eurasian blackbird	Turdidae	*Turdus merula*	3	No	NA
Domestic cattle	Bovidae	*Bos taurus*	2	Yes	Yes
Domestic cattle	Bovidae	*Bos taurus*	3	Yes	Yes
Domestiic sheep	Bovidae	*Ovis aries*	2	Yes	Yes
Domestiic sheep	Bovidae	*Ovis aries*	3	Yes	Yes
Domestic pig	Suidae	*Sus scrofa domesticus*	2	Yes	Yes
Domestic pig	Suidae	*Sus scrofa domesticus*	3	Yes	Yes
European rabbit	Leporidae	*Oryctolagus cuniculus*	2	Yes	Yes
European rabbit	Leporidae	*Oryctolagus cuniculus*	3	Yes	Yes
Short tailed vole	Cricetidae	*Microtus agrestis*	2	Yes	*Microtus subterraneus*
Short tailed vole	Cricetidae	*Microtus agrestis*	3	Yes	*Eothenomys regulus*
Bank vole	Cricetidae	*Myodes glareolus*	2	Yes	*Microtus subterraneus*
Bank vole	Cricetidae	*Myodes glareolus*	2	Yes	*Microtus subterraneus*
Bank vole	Cricetidae	*Myodes glareolus*	3	No	NA

Table A *Continued*

Description	Family	Species	Primer set	PCR success	Blast match
Yellow-necked mouse	Muridae	*Apodemus flavicollis*	2	No	NA
Bank vole	Cricetidae	*Myodes glareolus*	3	Yes	Yes
Vole	Cricetidae	Unidentified	2	Yes	*Myodes glareolus*
Vole	Cricetidae	Unidentified	3	Yes	*Myodes glareolus*
Yellow-necked mouse	Muridae	*Apodemus flavicollis*	3	Yes	*Rattus rattus*
Wood mouse	Muridae	*Apodemus sylvaticus*	2	Yes	Yes
Wood mouse	Muridae	*Apodemus sylvaticus*	3	Yes	*Rattus rattus*
Brown rat	Muridae	*Rattus norvegicus*	2	Yes	Yes
Brown rat	Muridae	*Rattus norvegicus*	3	Yes	Yes
Mouse	Muridae	Unidentified	2	Yes	*Apodemus sylvaticus*
Mouse	Muridae	Unidentified	3	Yes	*Rattus rattus*
Red squirrel	Sciuridae	*Sciurus vulgaris*	2	Yes	Yes
Red squirrel	Sciuridae	*Sciurus vulgaris*	3	Yes	Yes
Water shrew	Soricidae	*Neomys fodiens*	2	Yes	Yes
Water shrew	Soricidae	*Neomys fodiens*	3	Yes	Yes
Common shrew	Soricidae	*Sorex araneus*	2	Yes	*Sorex cylindricauda*
Common shrew	Soricidae	*Sorex araneus*	3	Yes	*Sorex minutus*
Pygmy shrew	Soricidae	*Sorex minutus*	2	Yes	*Sorex cylindricauda*
Pygmy shrew	Soricidae	*Sorex minutus*	3	Yes	Yes
European mole	Talpidae	*Talpa europaea*	2	Yes	Yes
European mole	Talpidae	*Talpa europaea*	3	No	NA
Carrot	Apiaceae	*Daucus carota*	5	Yes	Yes
Sweetcorn	Poaceae	*Zea mays*	5	Yes	Yes
Banana	Musaceae	*Musa acuminata*	5	Yes	Yes
Spinach	Amaranthaceae	*Spinacia oleracea*	5	Yes	Yes
Peanut	Fabaceae	*Arachis hypogaea*	5	Yes	Yes
Pea	Fabaceae	*Pisum sativum*	5	Yes	Yes
Hazel	Betulaceae	*Corylus avellana*	5	Yes	*Corylus sp.*
Apple	Rosaceae	*Malus domestica*	5	Yes	Yes
Plum	Rosaceae	*Prunus domestica*	5	Yes	*Prunus sp.*
Pear	Rosaceae	*Pyrus communis*	5	Yes	*Pyrus sp.*
Raspberry	Rosaceae	*Rubus idaeus*	5	Yes	Yes
Blackberry	Rosaceae	*Rubus ulmifolius*	5	Yes	*Rubus sp.*
Orange	Rutaceae	*Citrus reticulata*	5	Yes	Yes
Grape	Vitaceae	*Vitis vinifera*	5	Yes	Yes
Salmon cat food (wet)	Salmonidae	*Salmo salar*	2	Yes	*Bos Taurus*
Salmon cat food (wet)	Salmonidae	*Salmo salar*	3	Yes	*Bos Taurus*
Duck cat treats	Anatidae	Unknown	2	Yes	*Anas platyrhynchos*
Duck cat treats	Anatidae	Unknown	3	Yes	*Anas platyrhynchos*
Chicken cat food (wet)	Gallus	*Gallus gallus*	3	Yes	*Sus Scrofa*
Chicken cat food (wet)	Gallus	*Gallus gallus*	2	Yes	*Sus Scrofa*

Table A *Continued*

Description	Family	Species	Primer set	PCR success	Blast match
Chicken cat food (dry)	Gallus	*Gallus gallus*	2	Yes	Yes
Chicken cat food (dry)	Gallus	*Gallus gallus*	2	Yes	Yes
Chicken cat food (dry)	Gallus	*Gallus gallus*	3	No	NA
Chicken cat food (dry)	Gallus	*Gallus gallus*	3	Yes	*Sus Scrofa*
Beef dog food (wet)	Bovidae	*Bos taurus*	2	No	NA
Beef dog food (wet)	Bovidae	*Bos taurus*	3	Yes	*Sus Scrofa*
Lamb dog food (wet)	Bovidae	*Ovis aries*	2	Yes	Yes
Lamb dog food (wet)	Bovidae	*Ovis aries*	3	Yes	*Sus Scrofa*

Universal primer sets targeted several mitochondrial regions and groups:
Set 1: 12s earthworms (Harper *et al.* 2005)
Set 2 and 3: 12s and 16s vertebrates (Kitano *et al.* 2007)
Set 4: COI invertebrates (Zeale *et al.* 2011)
Set 5: TrnL plants (Taberlet *et al.* 2007)
PCR success indicates where PCR products were observed after gel electrophoresis
Where BLAST species did not match the species or the species was unidentified before the experiment the BLAST result is given

Table B The unique primer tags used to sequence 57 faecal samples, along with negative controls, in parallel on the MiSeq platform (Illumina, CA, USA).

Sample No.	Forward name	Forward sequence	Reverse name	Reverse sequence
1	fw2	CCGGAA	rv2	CCGGAA
2	fw3	AGTGTT	rv2	CCGGAA
3	fw4	CCGCTG	rv2	CCGGAA
4	fw5	AACGCG	rv2	CCGGAA
5	fw6	GGCTAC	rv2	CCGGAA
6	fw7	TTCTCG	rv2	CCGGAA
7	fw8	TCACTC	rv2	CCGGAA
8	fw9	GAACTA	rv2	CCGGAA
9	fw2	CCGGAA	rv3	AGTGTT
10	fw3	AGTGTT	rv3	AGTGTT
11	fw4	CCGCTG	rv3	AGTGTT
12	fw5	AACGCG	rv3	AGTGTT
13	fw6	GGCTAC	rv3	AGTGTT
14	fw7	TTCTCG	rv3	AGTGTT
15	fw8	TCACTC	rv3	AGTGTT
16	fw9	GAACTA	rv3	AGTGTT
17	fw2	CCGGAA	rv4	CCGCTG
18	fw3	AGTGTT	rv4	CCGCTG
19	fw4	CCGCTG	rv4	CCGCTG
20	fw5	AACGCG	rv4	CCGCTG
21	fw6	GGCTAC	rv4	CCGCTG
22	fw7	TTCTCG	rv4	CCGCTG
23	fw8	TCACTC	rv4	CCGCTG
24	fw9	GAACTA	rv4	CCGCTG
25	fw2	CCGGAA	rv5	AACGCG
26	fw3	AGTGTT	rv5	AACGCG
27	fw4	CCGCTG	rv5	AACGCG
28	fw5	AACGCG	rv5	AACGCG
29	fw6	GGCTAC	rv5	AACGCG
30	fw7	TTCTCG	rv5	AACGCG
31	fw8	TCACTC	rv5	AACGCG
32	fw9	GAACTA	rv5	AACGCG
33	fw2	CCGGAA	rv6	GGCTAC
34	fw3	AGTGTT	rv6	GGCTAC
35	fw4	CCGCTG	rv6	GGCTAC
36	fw5	AACGCG	rv6	GGCTAC
37	fw6	GGCTAC	rv6	GGCTAC
38	fw7	TTCTCG	rv6	GGCTAC
39	fw8	TCACTC	rv6	GGCTAC
40	fw9	GAACTA	rv6	GGCTAC
41	fw2	CCGGAA	rv7	TTCTCG
42	fw3	AGTGTT	rv7	TTCTCG

Table B *Continued*

Sample No.	Forward name	Forward sequence	Reverse name	Reverse sequence
43	fw4	CCGCTG	rv7	TTCTCG
44	fw5	AACGCG	rv7	TTCTCG
45	fw6	GGCTAC	rv7	TTCTCG
46	fw7	TTCTCG	rv7	TTCTCG
47	fw8	TCACTC	rv7	TTCTCG
48	fw9	GAACTA	rv7	TTCTCG
49	fw2	CCGGAA	rv8	TCACTC
50	fw3	AGTGTT	rv8	TCACTC
51	fw4	CCGCTG	rv8	TCACTC
52	fw5	AACGCG	rv8	TCACTC
53	fw6	GGCTAC	rv8	TCACTC
54	fw7	TTCTCG	rv8	TCACTC
55	fw8	TCACTC	rv8	TCACTC
56	fw9	GAACTA	rv8	TCACTC
57	fw2	CCGGAA	rv9	GAACTA
58 (control)	fw3	AGTGTT	rv9	GAACTA
59 (control)	fw4	CCGCTG	rv9	GAACTA

Primers were made with the unique tag sequence at the beginning of the forward and reverse primer sequence for each of the five primer sets used in the study, to give 59 unique combinations for each primer set

Table C The number of DNA sequences of each prey family making up the cluster sequences that were compared to the NCBI nucleotide database using BLAST

Class	Order	Family	No.of seqs
Actinopterygii	Clupeiformes	Clupeidae	7
Amphibia	Anura	Bufonidae	95
Amphibia	Anura	Ranidae	16
Amphibia	Caudata	Salamandridae	32
Arachnida	Araneae	Lycosidae	1
Aves	Columbiformes	Columbidae	50
Aves	Galliformes	Phasianidae	19
Clitellata	Haplotaxida	Lumbricidae	3919
Diplopoda	Julida	Julidae	3
Entognatha	Entomobryomorpha	Paronellidae	48
Gastropoda	Limacoidea	Agriolimacidae	2
Gastropoda	Sigmurethra	Arionidae	4
Gastropoda	Sigmurethra	Limacidae	4
Insecta	Coleoptera	Carabidae	10112
Insecta	Coleoptera	Cerambycidae	25
Insecta	Coleoptera	Staphylinidae	1
Insecta	Coleoptera	Tenebrionidae	46
Insecta	Diptera	Anthomyiidae	4
Insecta	Diptera	Phoridae	215
Insecta	Diptera	Tipulidae	38
Insecta	Lepidoptera	Crambidae	4
Insecta	Lepidoptera	Geometridae	1
Insecta	Lepidoptera	Hepialidae	1
Insecta	Lepidoptera	Noctuidae	609
Insecta	Lepidoptera	Nymphalidae	1
Insecta	Orthoptera	Acrididae	8
Mammalia	Artiodactyla	Bovidae	586
Mammalia	Artiodactyla	Suidae	365
Mammalia	Carnivora	Canidae	39
Mammalia	Carnivora	Felidae	74
Mammalia	Carnivora	Mustelidae	3
Mammalia	Lagomorpha	Leporidae	6
Mammalia	Perissodactyla	Equidae	3
Mammalia	Rodentia	Muridae	37
Mammalia	Soricomorpha	Soricidae	5

Clustering was performed with 98% sequence identity and 100% sequence coverage.
BLAST was performed using default settings

Chapter 6

National predictors of hedgehog distribution and decline in Britain

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In preparation for: *Mammal Review*

Abstract

The British population of European hedgehogs is thought to have fallen from 1.5 million in the 1995 to under a million in 2015. Possible causes of the decline include urbanisation, mortalities on roads, agricultural intensification, and predation by badgers *(Meles meles)* and red foxes (*Vulpes vulpes*). This study uses a volunteer survey of mammal roadkill (Mammals on Roads (MoR)), including nearly 12,000 hedgehog records compiled between 2001 and 2011, to examine the evidence for which factors affected hedgehog abundance and changes in hedgehog abundance nationally. Hedgehogs were more abundant in the North and East of Britain and in Scotland than in the South and South West. Hedgehogs appeared to select arable land and urban areas relative to their availability. Badger abundance and fox abundance were negatively associated with hedgehog abundance at the $10km^2$ scale. Trend analyses, performed at the county level, between years 2001 and 2011 showed the negative effect of badger numbers on hedgehog numbers was stronger in 2011 than in 2001, suggesting the possibility that increases in badger numbers are having a negative effect on hedgehog numbers. At the county level, fox numbers were positively correlated with hedgehog numbers and this positive effect was stronger in 2011 than in 2001. Results of a farmer questionnaire corroborated the MoR findings: 47% of respondents had seen a hedgehog in the year before the survey and a higher number of respondents from arable and dairy farms had seen hedgehogs than had respondents from livestock or mixed farms. However, 73% of respondents answered that they usually saw hedgehogs in gardens rather than on arable or pastoral farmland. On farms under Higher Level Stewardship (HLS), 56% of respondents had seen hedgehogs, compared with 44% of respondents from farms not under HLS. We compared the results of the 2012 farmer questionnaire with the same questionnaire sent out in 2006 by Hof and Bright (2012) and found the positive relationship between hedgehogs and HLS farms was stronger in 2012 than in 2006. HLS may offer improved nesting and foraging habitat for hedgehogs and also increase habitat complexity, which may reduce the predation pressure from badgers and foxes.

Introduction

There are currently over 23 thousand species listed as 'threatened' worldwide, an underestimate as not all species have been described and evaluated (IUCN Red List 2015). With global biodiversity loss occurring at an alarming rate (Pimm *et al.* 1995; Barnosky *et al.* 2011), citizen science is being frequently drawn on in order to obtain wide scale information on species trends and distribution (Cooper *et al.* 2007; Bonney *et al.* 2009; Dickinson, Zuckerberg & Bonter 2010; Buesching *et al.* 2015). Citizen science involves the recruitment of the general public to collect and feed back data such as volunteer wildlife surveys. In Britain several such surveys currently exist, for example Garden BirdWatch (BTO) and the National Mammal Atlas Project (The Mammal Society), allowing for country-wide analysis of population trends that may otherwise be impossible.

The European hedgehog is a widespread charismatic species with which the public is engaged; the hedgehog was voted Britain's National Species in a recent online poll (BBC Wildlife Magazine 2013). The British population of European hedgehogs is thought to have fallen from 1.5 million in 1995 (Harris 1995) to fewer than one million individuals by 2015 (PTES & BHPS 2015). Several national volunteer surveys have contributed to the evidence for this decline including: HogWatch (PTES & BHPS; Hof, 2009), Living with Mammals (PTES; Hof & Bright, 2009), Mammals on Roads (PTES; Roos *et al.*, 2012; PTES & BHPS, 2015; Wembridge, 2011), the National Gamebag Census (GWCT; Aebischer, N.J. Davey, P.D. Kingdon, 2011), the Breeding Birds Survey BTO/JNCC/RSPB (BTO, JNCC & RSPB; Roos *et al.*, 2012), Garden BirdWatch (BTO; Roos *et al*., 2012) and the Waterways Breeding Bird Survey (BTO; Roos et al., 2012).

Possible causes of decreases in hedgehog numbers on a national scale include urbanisation, through removal of amenity grassland and tendency towards enclosed gardens (Hof & Bright 2009); roads, through mortalities and as barriers to dispersal (Huijser & Bergers 2000; Rondinini & Doncaster 2002); changes in the rural landscape such as the removal of hedgerows and use of pesticides (Hof & Bright 2010); direct predation and intra-guild competition from badgers *(Meles meles)* (Doncaster

1992; Hof & Bright 2012; Hof, Snellenberg & Bright 2012; Van De Poel, Dekker & Van Langevelde 2015), and predation by red foxes (*Vulpes vulpes*) (Doncaster 1994; Reeve 1994).

Here we validate the results of previous nation-wide hedgehog volunteer surveys by using the Mammals on Roads (MoR) dataset in order to assess which of the above identified factors affect hedgehog presence, abundance and changes in hedgehog abundance, including land use, badger numbers, hedgehog numbers and traffic flow. The MoR dataset contains hedgehog, badger and fox records allowing a comparison of distributions of the three species which is not confounded by differing survey methodologies. We also build on work by Hof and Bright (2012) by repeating a questionnaire that was sent to farmers in 2006 (six years before the current study) with the aim of assessing which farm attributes correlate with hedgehog distribution and the downward trend in hedgehog numbers. Spotlight surveying was also carried out on a selection of respondent's farms to ground-truth the questionnaire results. Our aim was to identify the principal correlates of the hedgehog's decline in the UK, and in so doing indicate potential conservation measures.

The datasets

Mammals on Roads

Mammals on Roads is a citizen science survey organised by People's Trust for Endangered Species (PTES), carried out yearly since 2001. The survey entails volunteers recording dead or alive animals sighted during journeys of over 20 miles, from July-September, during daylight hours while driving on the UK's roads. Participants record the species sighted, the number of each species at each sighting, the start and end points of their journey and the mileage reading at the start of the journey and when each sighting is made. This information permits sightings to be given a spatial reference to map yearly hedgehog presence, abundance and distribution.

MoR contains over 11,979 hedgehog sightings made between 2001 and 2011, 99% of which were of dead hedgehogs. Previous usages of these data have suggested they are sufficient to detect a hedgehog decline of 10% or more, with 80% power, in five to ten years (Roos *et al.* 2012) and data

from the surveys have already been used to show a national decline in hedgehog numbers (Wembridge 2011; Roos *et al.* 2012; PTES & BHPS 2015). Here we extend previous analyses to ask which predictor variables are most closely associated with variation in patterns of hedgehog decline. There are 2802 badger sightings and 2940 fox sightings in the database for the same period allowing for a comparison between the distribution of hedgehogs and their predators.

Farmer questionnaire

As part of previous hedgehog research in 2006 a questionnaire was sent to 4000 farmers and landowners across the UK (Hof & Bright 2012). In 2012, in collaboration with PTES, we repeated the questionnaire survey, which was sent to the same 4000 farmers (See Appendix). The questionnaire asked if hedgehogs had been observed in the past year on the respondent's farm and if so how often: fewer than three times, three-six times or more than six times. The respondent was asked which habitat hedgehogs tended to be observed in, including: gardens, rough grassland, lowland heath, arable, pasture, deciduous woodland or coniferous woodland. The questionnaire also collected information on the type and size of the farm, the length of hedgerows on the farm and if the farm was entered into an agri-environment scheme. Using the postcodes of respondents we were able to map the presence or absence of hedgehogs across the UK and ascertain whether any of the farm attributes can predict if hedgehogs were present or absent. We could also analyse changes in responses between 2006 and 2012 and model changes in hedgehog numbers against changes in farm attributes and predator numbers, taken from the Mammals on Roads database.

Methods

Mammals on Roads: hedgehog distribution

To examine predictors of hedgehog distribution we constructed a raster coverage with a cell size of 10km^2 for all years of the study combined using ArcGIS desktop (ESRI, Redlands, CA, US). For each cell the number of hedgehogs seen was summed giving a total number of hedgehogs seen per grid cell. To each grid cell we added information on the number of badgers and foxes seen in that grid cell

during the study and the total number of mammals spotted in the grid cell, which provides a measure of survey effort. We also added the most common land cover class in the grid cell using the CEH land cover map 2007 (Morton *et al.* 2014).

Although participants were encouraged to report journeys with no sightings, none were recorded, suggesting a reluctance to report these 'null' observations. This is likely to introduce a bias in the data set, such that relative abundance is over-estimated where hedgehogs (and other species) are uncommon. The database does, however, contain journeys on which several other common species were sighted, including rabbit, deer, foxes and hares. Where another species was observed and no hedgehogs were observed these journeys can be considered as journeys with genuine negative hedgehog sightings. We used journeys with rabbit sightings, but no hedgehog sightings, as negative sightings of hedgehogs and did likewise for negative sightings of badgers and foxes.

A generalised linear model was constructed using the software R (R Core Team 2014) testing the factors which may have affected the number of hedgehogs in a $10km^2$ grid cell. The model was constructed with a Poisson link and the explanatory variables: region, number of badgers sighted in the grid cell, number of foxes sighted in the grid cell and land cover category of the grid cell. The number of journeys per cell fell in each year of the survey, and so the models were offset by the total number of mammals sighted per grid cell to control for observer effort.

As a further measure of habitat selection, and to take into account the areas of each land cover class available to hedgehogs, we calculated resource selection ratios (wi) in the R package adehabitat (Calenge 2006; Manly *et al.* 2007; R Core Team 2014) at the $1km^2$ level. We calculated a ratio for each land cover class from the area of each class in the UK, taken from CEH land cover map 2007 (Morton *et al.* 2014), and the number of hedgehogs seen in the land class. A wi calculation greater than one indicates a preference for the habitat, whereas less than one indicates avoidance of the habitat. The package produces p values to test for statistically significant differences of wi from 1, with a Bonferroni correction for the number of land classes.

Mammals on Roads: trend analyses

We performed an overall trend analysis of hedgehog numbers in the Mammals on Roads dataset at the journey level including, for each journey, the number of hedgehogs observed during the journey, the number of badgers and foxes observed and the year. To incorporate changes in habitat and traffic flow, trend analyses were carried out at the county level and between the number of hedgehogs sighted in 2001 and sighted in 2011. We used the counties of England but, due to the availability of land use data, we had to group counties into larger areas for Wales and Scotland. Scotland was grouped by sub-regions (ScotStat 2015) and Wales was grouped into Dyfed, Gwynedd, Glamorgan and Gwent and Powys. We summed the number of hedgehogs, badgers and foxes sighted per county in 2001 and the number sighted in 2011. We compiled land use statistics at the county level including the proportion of the area that was arable land and farm woodland. These data were available in different years for the three countries in the study: for changes in land use in counties in England we used the years 2000 and 2010, for Wales we used the years 2002 and 2012, and for Scotland we used 2001 and 2011. We calculated the mean AADF in each county in 2001 and 2011. Data were compiled in the 'long' format with each county's information present twice, once for 2001 and once for 2011.

To perform the overall trend analysis we constructed a generalised linear model with a Poisson link and the number of hedgehogs seen on a journey as the dependent variable and the number of badgers observed, foxes observed and year as continuous explanatory variables. We also added the quadratic term of year as an explanatory variable, to test for oscillation in the hedgehog trend over the ten years. We constructed a linear model in the R software with the number of hedgehogs seen in each county as the dependent variable and the explanatory variables: year (2001 or 2011), region, number of badgers seen in the county, number of foxes seen, proportion of arable land in the county, proportion of woodland in the county and the mean AADF on roads in the county as explanatory variables. To test for an effect of year on the relationship between the explanatory variables and hedgehog numbers in the county we added interactions between year and each of the

explanatory variables in the model. We added the number of journeys carried out in each county in each year as an offset.

Farmer questionnaire: hedgehog distribution

Hof and Bright (2012) present an analysis of the 2006 farmer questionnaire data. Here we used the 2012 results to assess factors which affected hedgehog presence on farmland, for comparison with their 2006 data. Using the spatial reference of the post code of the surveyed farm we added predator numbers in the area from the Mammals on Roads dataset by constructing two raster layers, one of all badger sightings and one of all fox sightings in ArcGIS desktop (ESRI, Redlands, CA, US) with grid cells of 10km^2 and the number of each predator summed for each grid cell. We then overlaid the point locations of survey respondents and extracted the badger and fox information for each farm.

For statistical analysis of the 2012 data we constructed a generalised linear model in the R software with a binomial link and whether the respondent had seen hedgehogs or not on their farm in the last year as the dependent variable. The explanatory variables were: region, the number of badgers, the number of foxes, the farm type (arable and horticultural, dairy, livestock or mixed), the length of hedgerow on the farm in meters, the farm's organic status, if the farm was entered into an agri-environment scheme and if the farm was entered into a higher Level agri-environment scheme (HLS).

Farmer questionnaire: trend analyses

Trend analyses were performed on the farmer questionnaire data set using data from landowners who responded in both 2006 and 2012. A model was constructed with a binomial link and whether the respondent had seen hedgehogs or not on their farm in the last year as the dependent variable. The explanatory variables were year (2006 or 2012), region, number of badgers, number of foxes, farm type, length of hedgerow on the farm, organic status, agri-environment scheme status and HLS status. To test for an effect of year on the relationship between the explanatory variables and whether hedgehogs were observed on a farm we added interactions between year and each of the explanatory variables in the model.

Spotlight survey

As part of site selection for ongoing hedgehog radio-tracking studies on farmland, thirteen predominately arable farms, where hedgehogs had been observed in the past year by farmers during the 2012 farmer questionnaire, were chosen to be surveyed. These visits were used to partially ground-truth the results of the 2012 questionnaire. Spotlight surveys were conducted from 9pm-3am in April-June 2013, for two evenings per farm. All the hedgerows on each farm were walked in turn with a red spotlight and pasture fields scanned. When the hedgerows were all surveyed we began the route again taking care to alter the route the second evening so that hedgerows were surveyed at different times of night on each evening. If no hedgehogs were seen, a third night of spotlight surveying was carried out.

Results

Mammals on Roads: hedgehog distribution

There was a negative trend in hedgehog numbers from 2001-2011 (Fig. 1). We found an effect of region on the number of hedgehogs sighted in a 10km^2 grid cell (Table 1). There was a higher number of hedgehogs sighted per journey in the East of the country, including the North East, East Midlands, East of England and Yorkshire, than in the South East, South West and Wales (Fig. 2). The highest number of hedgehogs sighted per journey was in Scotland (Fig.2).

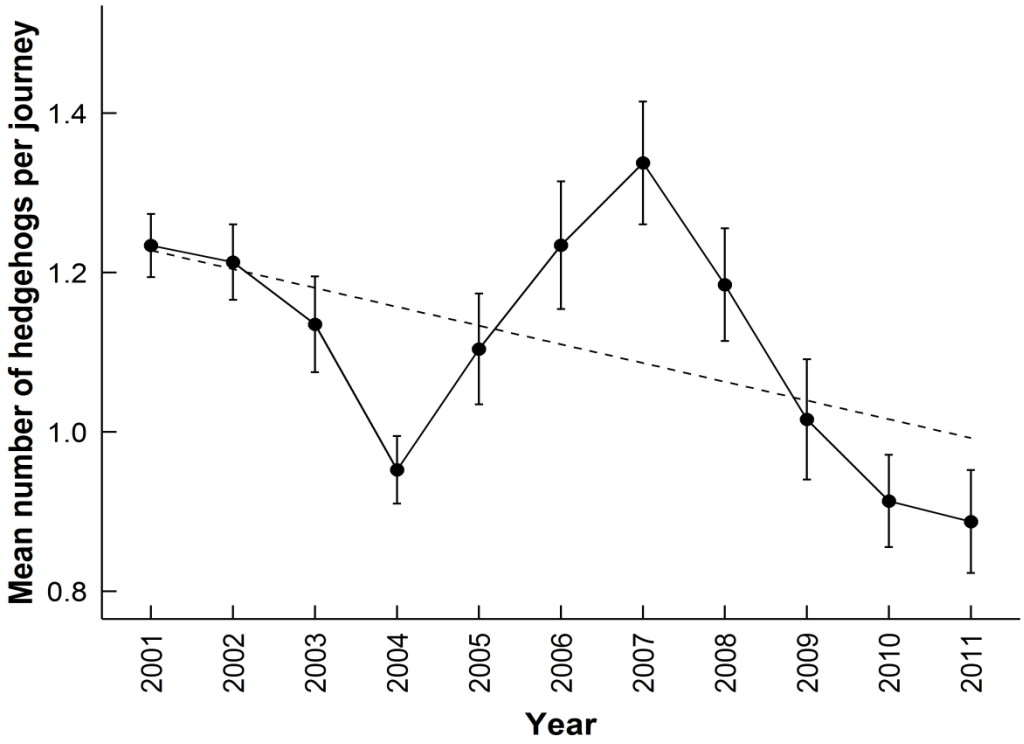


Fig.1 The mean number of hedgehogs seen per journey in each year of the Mammals on Roads survey 2001-2011. Error bars show the standard error of the mean and the dashed line shows the linear trend

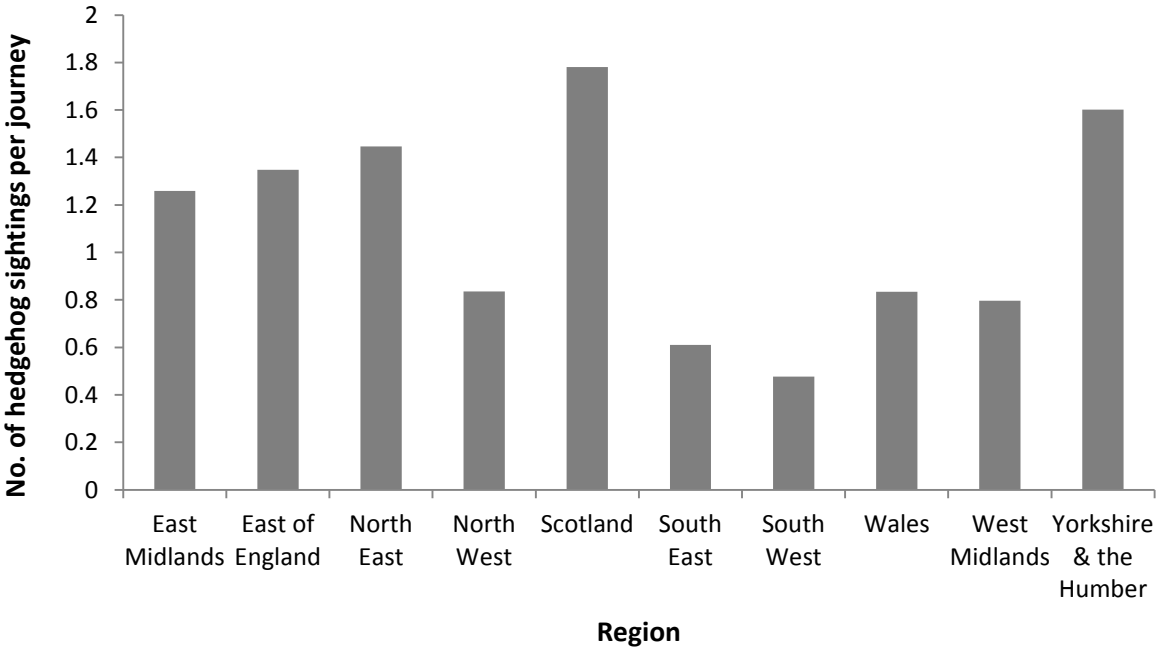


Fig.2 The number of hedgehogs, dead or alive, seen per journey in each region of the UK during the Mammals on Roads survey 2001-2011

Table 1 The results of a linear model to test the effect of badger numbers, fox numbers, traffic flow, land cover, year and region on the number of hedgehogs sighted in a 10km^2 grid cell of Great Britain, from the Mammals on roads survey 2001-2011

Variable	Factor Level	Df	Residual Deviance	P value	Effect size	95% CI
Region	*(EAST MIDLANDS)*	10, 1872	4815.5	<0.0001***		
	East of England				-0.006	-0.070, 0.058
	London				0.123	-0.381, 0.557
	North East				-0.174	-0.280, -0.070†
	North West				-0.059	-0.162, 0.042
	Scotland				0.416	0.338, 0.493†
	South East				-0.251	-0.327, -0.176†
	South West				-0.466	-0.553, -0.380†
	Wales				0.048	-0.046, 0.141
	West Midlands				-0.105	-0.186, -0.025†
	Yorkshire & the Humber				0.191	0.109, 0.272†
Land cover	*(ARABLE)*	6, 1866	4626.6	<0.0001***		
	Broadleaf woodland				-0.119	-0.227, -0.014†
	Coniferous woodland				0.080	-0.009, 0.167
	Improved grassland				-0.278	-0.402, -0.158†
	Mountain, heath & bog				-0.074	-0.122, -0.027†
	Semi-natural grassland				-0.617	-0.711, -0.525†
	Urban				-0.144	-0.239, -0.052†
No. of badgers		1, 1865	4567.1	<0.0001***	-0.016	-0.023, -0.009†
No. of foxes		1, 1864	4539.7	<0.0001***	-0.020	-0.028, -0.013†

The model was offset by the total number of mammal sightings in each 10km^2 grid cell
Words in italics following categorical variables indicate the reference category.
***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 **.**near significance
† 95% confidence interval of the effect size does not contain zero

Land cover had an effect on the number of hedgehogs seen (Table 1). The land class in which the greatest number of hedgehogs was seen was arable land followed by improved grassland (Fig.3a). The land class with the next greatest number of hedgehogs seen was in urban areas, despite participants being asked not to record in built-up areas for safety reasons. However, sampling effort in different habitats could not be taken into account as we only had information on the start and end

points of the journey and where sightings took place, rather than all of the habitats a journey passed through. Resource selection ratios at the 1km^2 level indicated non-random habitat selection (Log-likelihood =3217, p<0.0001, 6 d.f). The habitats with the highest selection ratio were arable land (wi=1.50, p<0.0001) and built-up areas and gardens (wi=1.45, p<0.0001). Broadleaf woodland and improved grassland were also selected and semi-natural grassland, coniferous woodland and mountain heath and bog were avoided (Fig.3b).

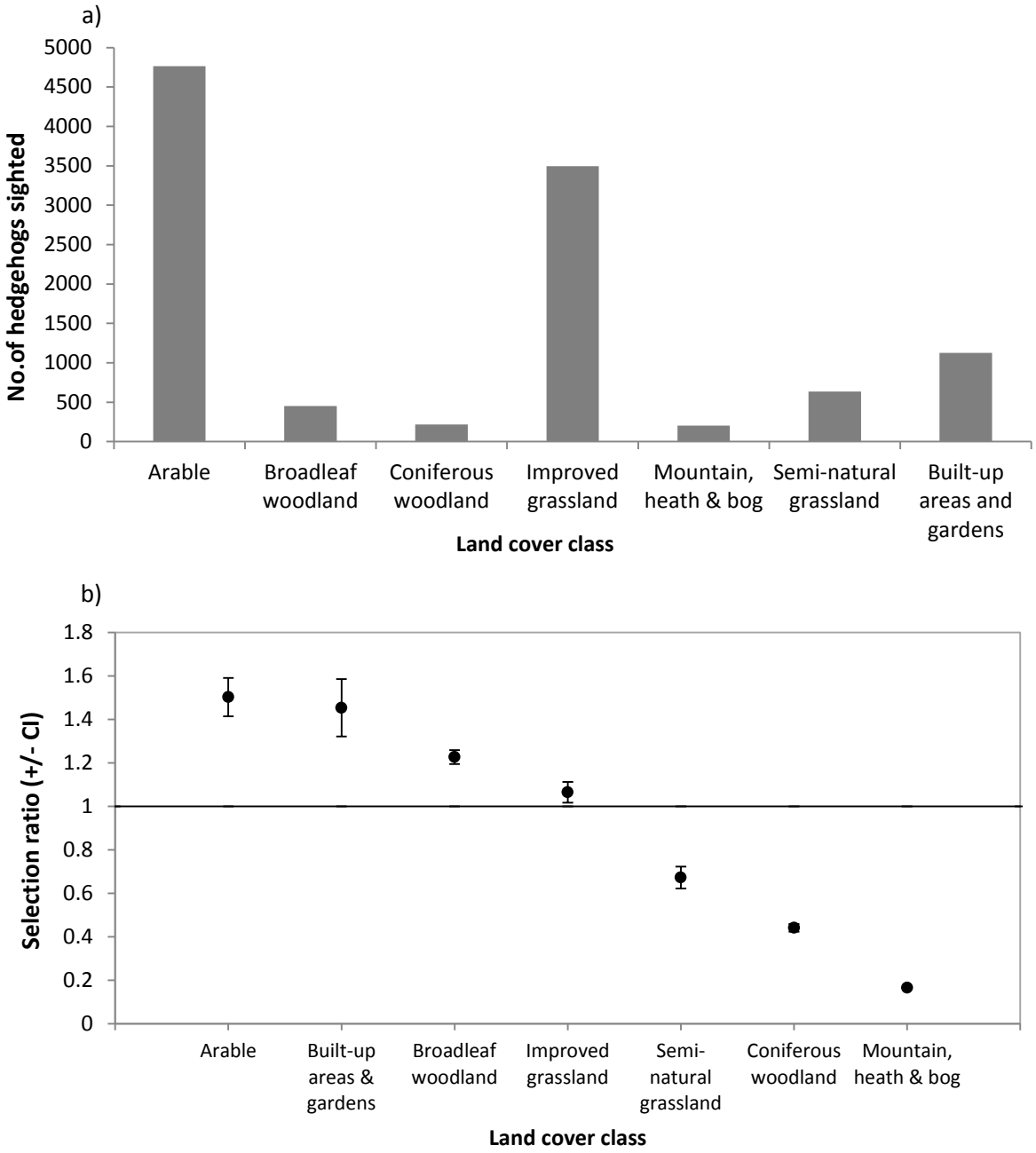


Fig.3 a) The number of hedgehogs seen in each land class of the UK during the Mammals on Roads survey 2001-2011 and b) the selection ratio (Manly *et al.* 2007) of land classes in the UK by hedgehogs seen during the Mammals on Roads survey 2001-2011 at the 1km^2 level

We found a negative effect of both badger numbers and fox numbers on hedgehog numbers (Table 1, Figs.4 and 5). The effect size was slightly stronger for fox numbers (Table 1), although Fig.4 indicates that when badger numbers were high observers were less likely to see hedgehogs than when fox numbers were high.

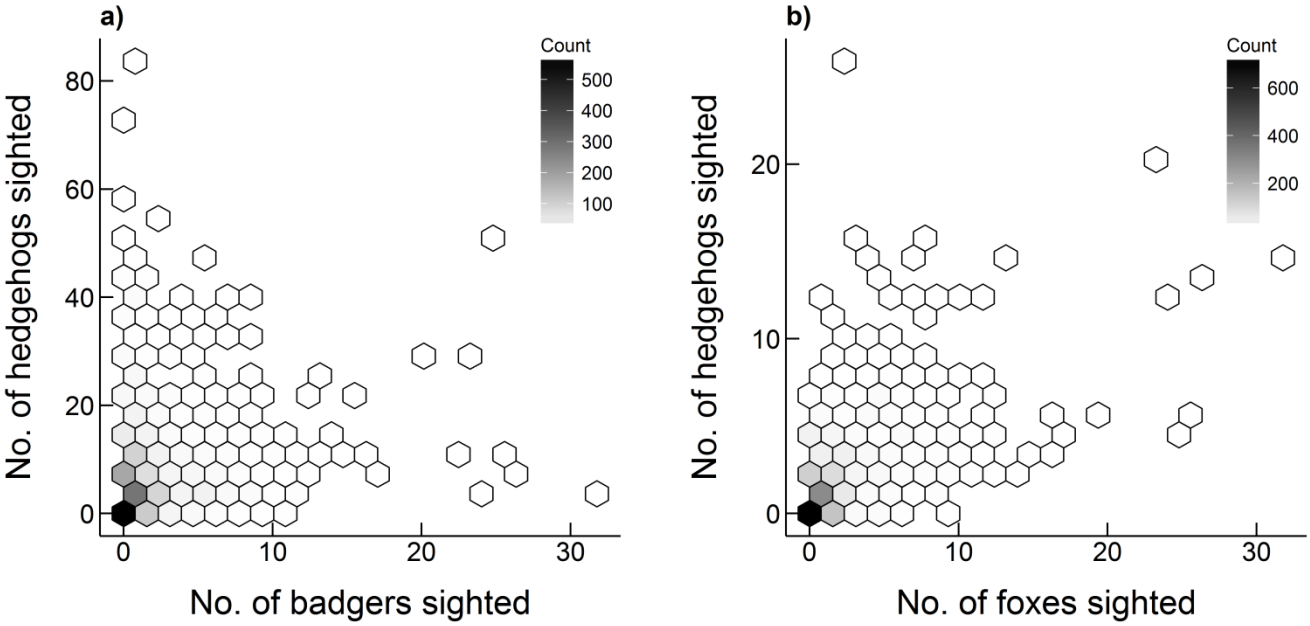
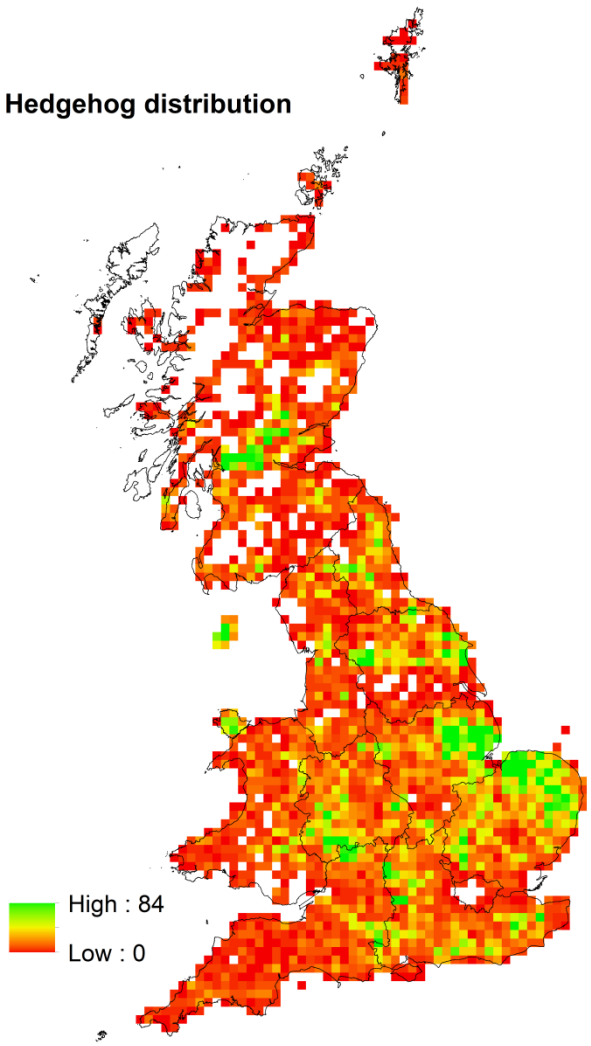
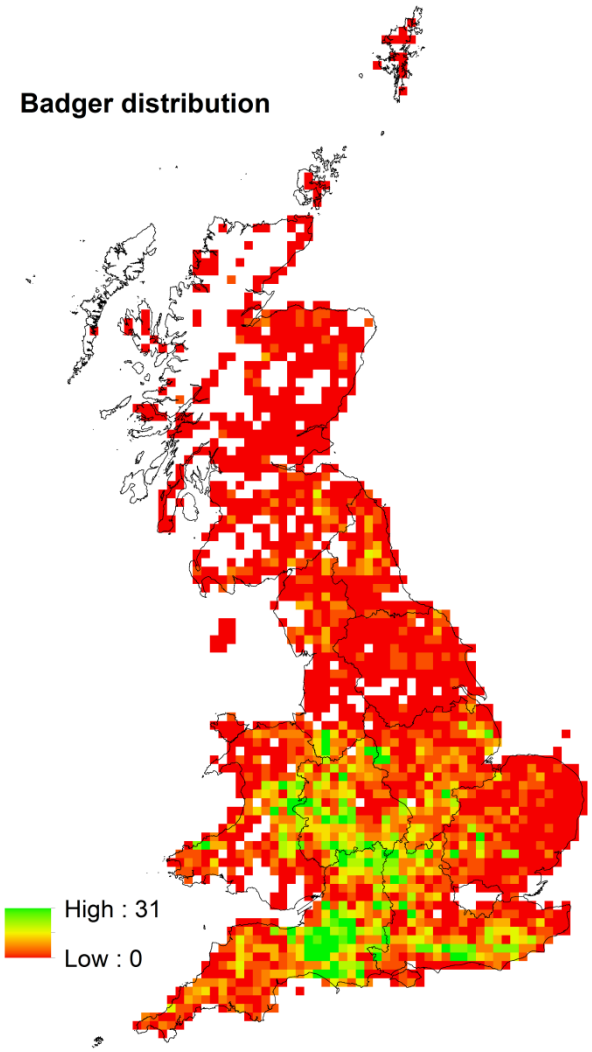


Fig.4 The relationship between the number of predators observed in a 10km^2 grid cell of the UK and the number of hedgehogs observed in the same grid cell during the Mammals on Roads survey 2001-2011





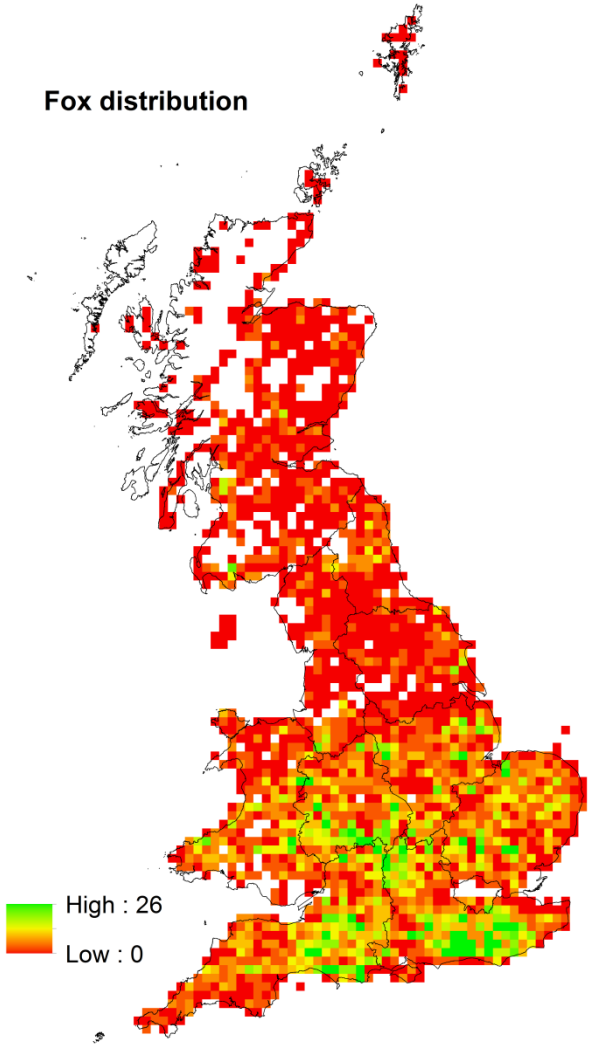


Fig.5 The distribution of hedgehogs, badgers and foxes in the UK at the 10km^2 scale from the annual Mammals on Roads survey 2001-2011

Mammals on Roads: trend analyses

The overall trend analyses found a negative correlation between the quadratic term of year and the number of hedgehogs sighted on a journey (Effect size= -0.003, p=0.0002, 6850d.f, Fig.6). There was also a negative relationship between the number of badgers seen on a journey and the number of hedgehogs sighted (Effect size=-0.46, p<0.0001, 6850d.f, Fig.6). There was a positive relationship between the number of foxes seen on a journey and the number of hedgehogs sighted (Effect size=0.17, p<0.0001, 6850d.f, Fig.6).

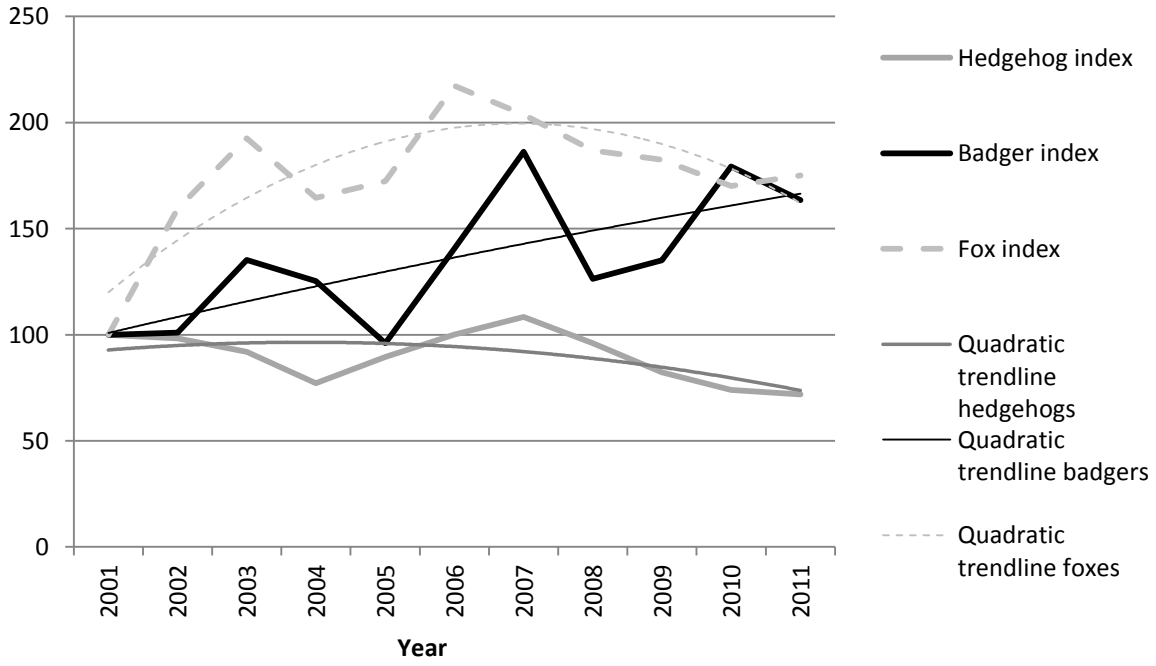


Fig.6 Hedgehog, badger and fox indices calculated from the mean number of hedgehogs, badgers and foxes observed on a journey in each year of the Mammals on Roads survey 2001-2011, with 2001 set as the reference year

At the county level, fewer hedgehogs were seen in 2011 than in 2001, however the confidence intervals of the effect size passed zero (Table 3). There was a significant effect of region, with Northern England, Eastern England and Scotland again having higher numbers of hedgehogs than the South and Wales (Table 3). There was a positive relationship between the proportion of arable land and woodland and the number of hedgehogs seen (Table 3). We found a negative effect of traffic flow on hedgehog numbers, although the effect size was small (Table 3).

Table 2 The results of a linear model to test the effect of badger numbers, fox numbers region, traffic flow, land cover, year and region on the change in hedgehog numbers between 2001 and 2011 at the county level, from the annual Mammals on Roads survey

Variable	**Factor Level**	**Df**	**Residual Deviance**	**P value**	**Effect size**	**95% CI**
Year	*(2001)*	1,118	1252	0.004 **		
	2011				-0.016	-0.378, 0.338
Region	*(EAST MIDLANDS)*	10,118	667.7	<0.0001***		
	East of England				-0.079	-0.227, 0.070
	London				-0.042	-1.230, 0.835
	North East				0.448	0.216, 0.676†
	North West				0.361	0.091, 0.630†
	Scotland				0.436	0.183, 0.690†
	South East				-0.584	-0.813, -0.356
	South West				-0.707	-0.941, -0.475†
	Wales				-0.401	-0.690, -0.115†
	West Midlands				-0.223	-0.422, -0.024
	Yorkshire				0.550	0.384, 0.716
Badger numbers		1,118	666.5	0.275	-0.008	-0.016, 0.000
Fox numbers		1,118	645.3	<0.0001***	0.008	-0.001, 0.018
Arable		1,118	604.2	<0.0001***	0.905	0.536, 1.273†
Woodland		1,118	601.3	0.087**.**	8.308	1.178, 15.454†
Traffic flow		1,118	591.8	0.002**	-1.4e-5	-2.5e-5, -3.7e-6†
Year* Badgers		1,118	588.	0.052**.**	-0.048	-0.075, -0.021†
Year* Foxes		1,118	583.6	0.036*	0.039	0.006, 0.072†
Year* Arable		1,118	566.3	<0.0001***	0.977	0.430, 1.524†
Year*Woodland		1,118	563.8	0.117	-6.716	-15.938, 2.407
Year*Traffic		1,118	563.1	0.387	-8.4e-6	-2.7e-5, 1.1e-5

The model was offset by the number of mammal sighting per county
Words in italics following categorical variables indicate the reference category.
***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 **.**near significance
† 95% confidence interval of the effect size does not contain zero

We found a near-significant interaction between the number of badgers and year and the confidence intervals of the effect size did not pass zero (Table 3). This finding was the result of the negative relationship being stronger in 2011 compared with 2001. This suggests that increases in badger numbers may be a predictor of changes in hedgehog numbers at the county level (Figs.7 and 8). We found a positive interaction between the number of foxes and year on the number of hedgehogs seen in a county and this was stronger in 2011 compared with 2001 (Table 2, Figs.7 and 8). We also found a weak interaction between year and the proportion of arable land in a county on the number of hedgehogs sighted in the county (Table 3). The positive relationship between hedgehogs and the area of arable land in a county was stronger in 2011 than in 2001 (Fig.9). We found no evidence of an interaction between year and traffic flow or area of woodland (Table3).

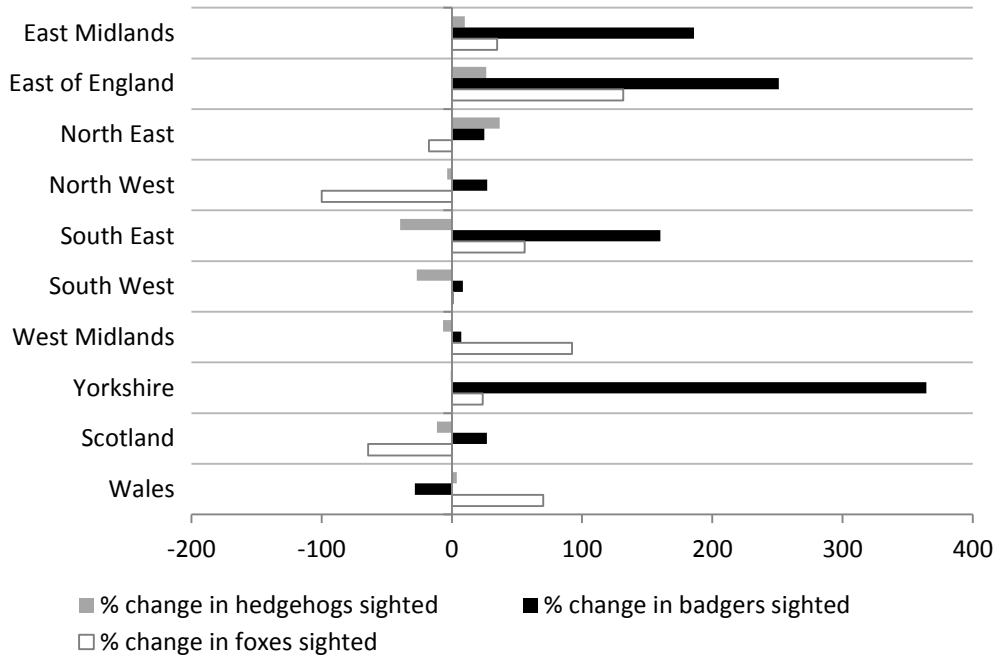


Fig.7 The percentage change by region in hedgehog, badger and fox numbers between years 2001 and 2011 of the Mammals on Roads survey. Numbers were adjusted by the number of journeys in each region each year

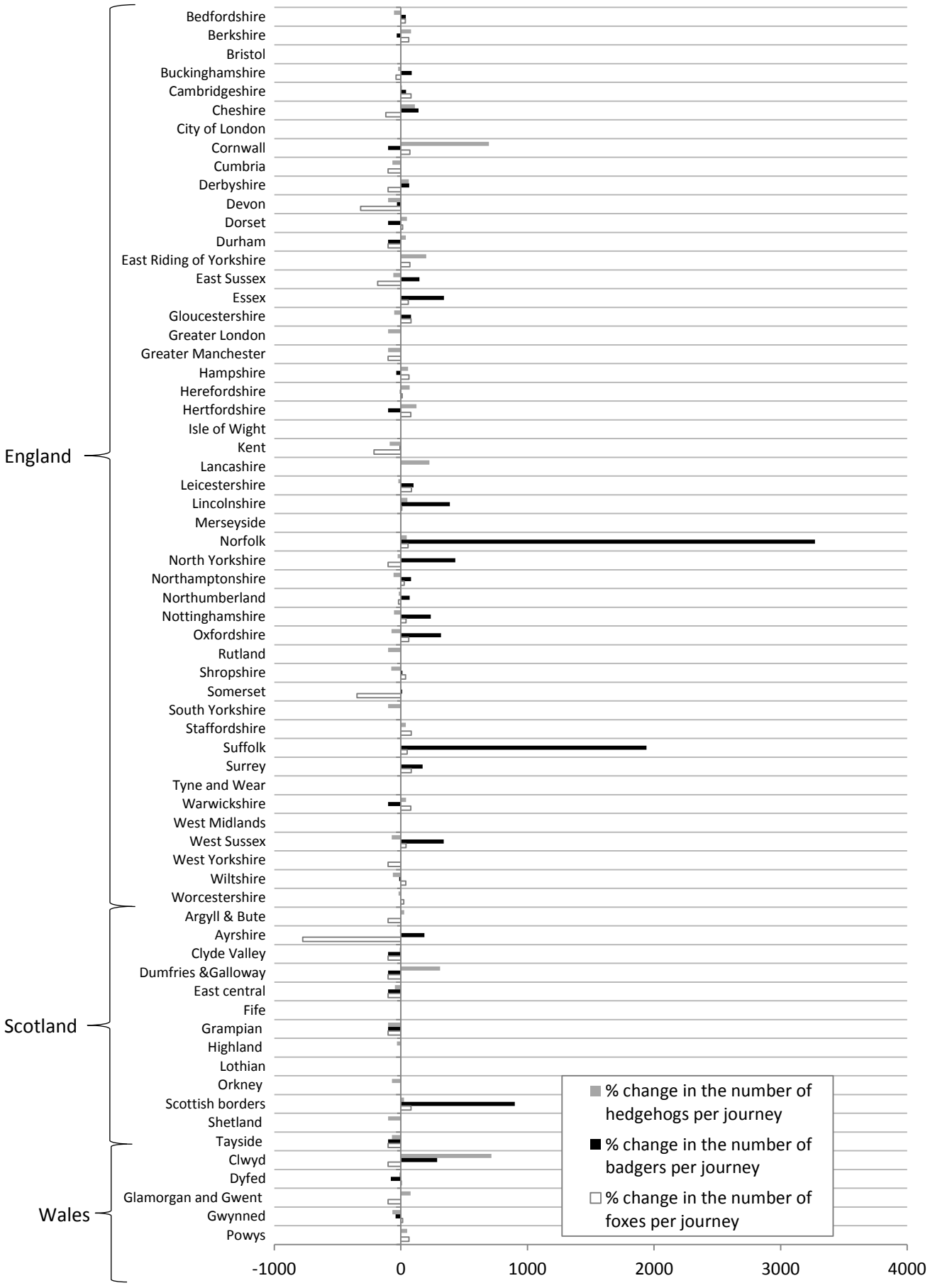


Fig.8 The percentage change by county in hedgehog and badger numbers between years 2001 and 2011 of the Mammals on Roads survey. The number of hedgehogs and badgers was adjusted by the number of journeys in the county. A missing bar indicates no data for the county or no change in numbers

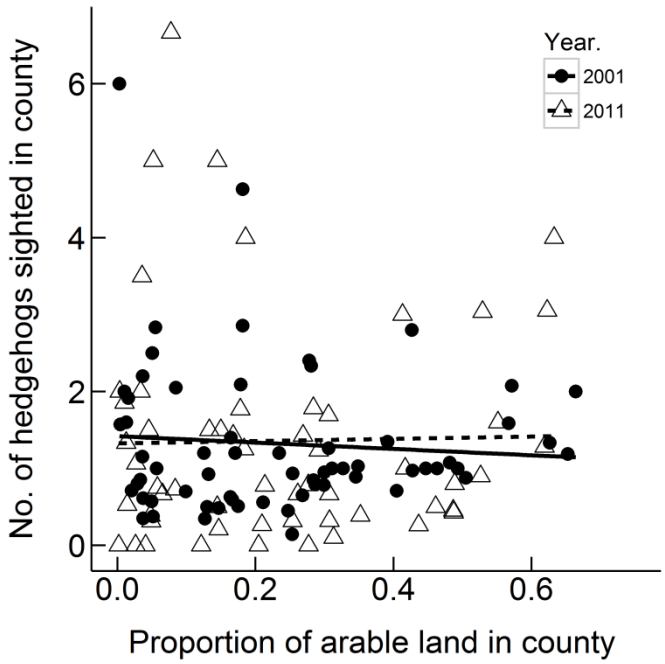


Fig.9 The interaction between the proportion of arable land in a county and the number of hedgehogs observed in the county during the Mammals on Roads survey in 2001 and 2011. Number of hedgehogs was adjusted by the number of journeys in the county

Farmer questionnaire: hedgehog distribution

Of the 644 respondents to the questionnaire in 2012, 47% had seen a hedgehog in the last year. We found an effect of region on hedgehog presence (Table 4). Again hedgehogs were seen more frequently in the East of England, especially in Yorkshire, the North East and the East of England and hedgehogs were seen the least in the South West (Figs. 10 and 11). Hedgehogs were seen most often on dairy and arable farms and least often on livestock farms (Table 4, Fig 12). However, when respondents were questioned on where specifically they usually observed hedgehogs on their farm, they were seen most often in gardens rather than on farmland habitats (Fig. 13).

Table 4 The results of a linear model to test the effect of badger numbers, fox numbers, region, traffic flow, land cover, year and region on hedgehog presence on farmland, from a questionnaire sent to 4000 farmers in the UK in 2012

Variable	Factor Level	Df	Residual Deviance	P value	Effect size	95% CI
Region	*(EAST MIDLANDS)*	10,567	772.13	0.002**		
	East of England				0.517	-0.349, 1.400
	London				0.155	-1.984, 2.095
	North East				1.168	0.216, 2.152†
	North West				0.546	-0.407, 1.507
	Scotland				0.432	-0.329, 1.208
	South East				-0.003	-0.823, 0.825
	South West				-0.480	-1.368, 0.400
	Wales				0.394	-0.618, 1.404
	West Midlands				0.319	-0.553, 1.202
	Yorkshire				1.455	0.502, 2.456†
Badger numbers		1,566	771.47	0.416	0.018	-0.066, 0.101
Fox numbers		1,565	771.11	0.549	0.031	-0.056, 0.122
Farm type	*(ARABLE)*	3,562	755.81	0.001**		
	Dairy				0.214	-0.608, 1.058
	Livestock				-0.825	-1.324, -0.333†
	Mixed				-0.261	-0.733, 0.208
Hedgerow length		1,561	755.59	0.635	-7.8e-7	-5.7e-6, 1.8e-6
Organic status	*(NO)*	1,560	755.19	0.525	-0.424	-1.392, 0.495
	Yes					
Scheme status	*(NO)*	1,559	754.84	0.554	0.065	-0.330, 0.460
	Yes					
HLS status	*(NO)*	1,558	752.62	0.136	0.527	-0.167, 1.236
	Yes					

Words in italics following categorical variables indicate the reference category.

***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 **.**near significance

† 95% confidence interval of the effect size does not contain zero

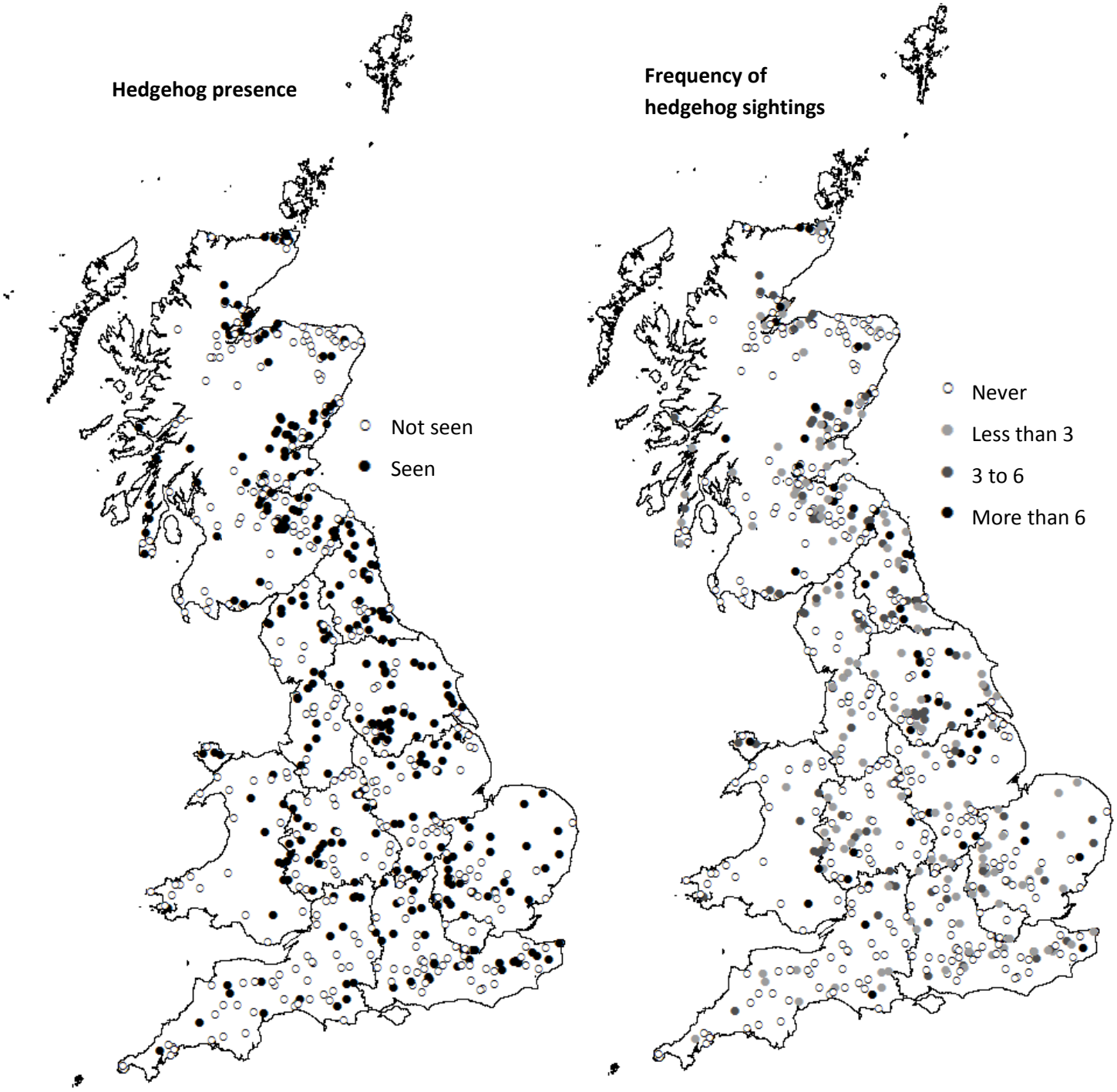


Fig.10 The distribution of respondents to a questionnaire enquiring whether land owners had seen hedgehogs in the past year (on the left) and how frequently they were seen (on the right) in 2012

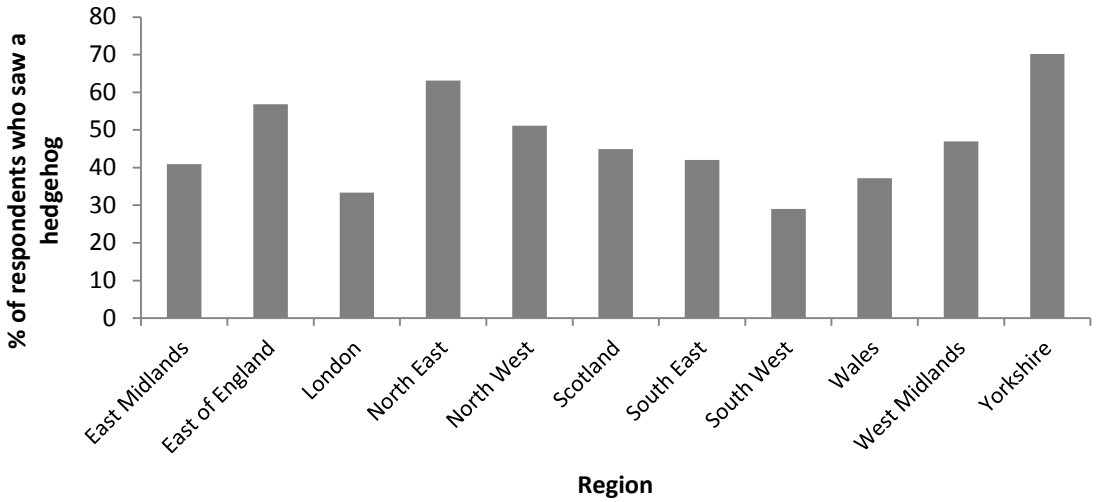


Fig.11 The percentage of respondents of a farmer questionnaire who had seen a hedgehog on their land in 2012 by region

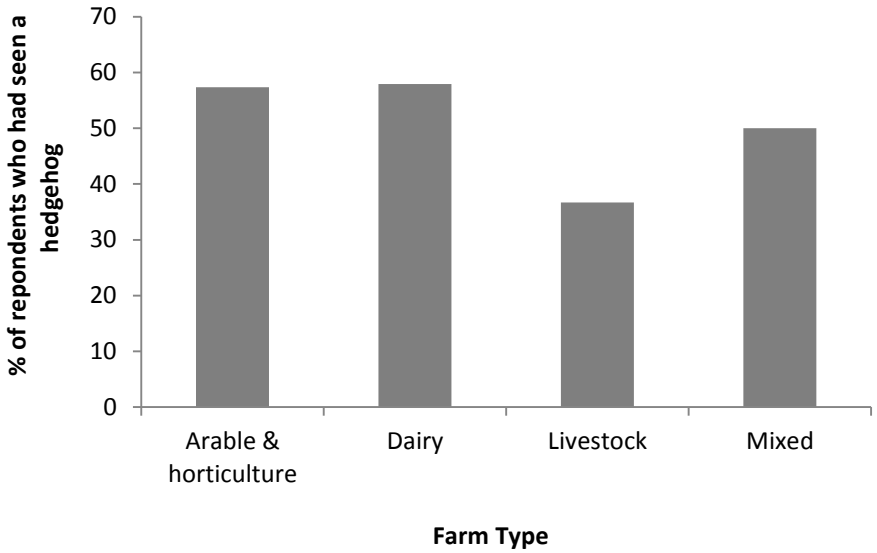


Fig.12 The percentage of respondents of a farmer questionnaire who had seen a hedgehog on their land in 2012 by farm type

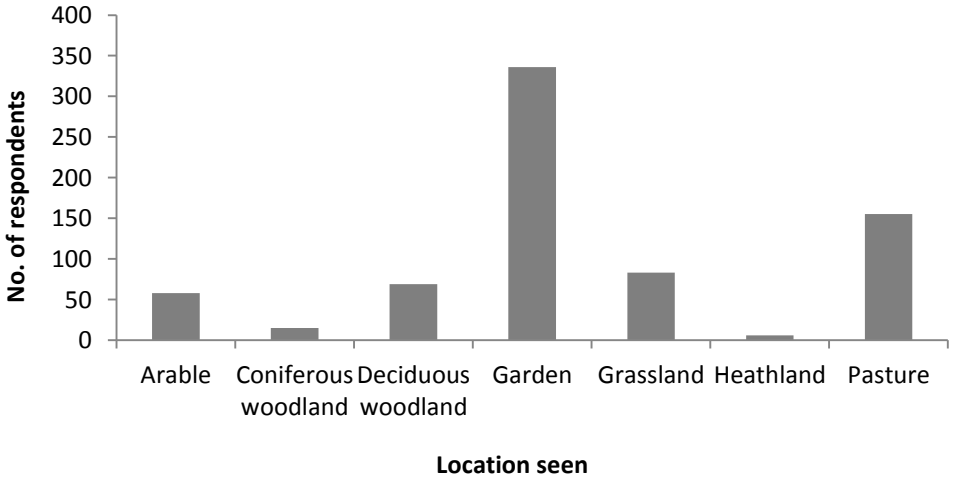


Fig.13 The number of questionnaire respondents who had seen hedgehogs in various habitats on their farm

We found no effect of agri-environment scheme enrolment on hedgehog presence. We found that hedgehogs were seen more often on farms under HLS than on farms without HLS but this was not significant in the model (Table 4, Fig.14a). Of the respondents 7% were from farms enrolled in HLS and 56% of these respondents had seen hedgehogs, compared with 44% of respondents from farms not under HLS. We found no effect of badger numbers, fox numbers, hedgerow length and organic status on reported hedgehog presence in these questionnaires (Table 4).

Farmer questionnaire: trend analyses

When we included data from the 338 land owners who responded both in 2006 and 2012, we again found region and farm type to have an effect on hedgehog presence (Table 5). However, on this data set we also found a significant effect of higher level stewardship enrolment (Table 5). We found a near-significant negative effect of organic status on hedgehog presence (Table 5). Thirty percent of respondent from organic farms had seen a hedgehog in the previous year compared with 50.4% of respondents from non-organic farms. We found no effect of year on hedgehog presence although hedgehogs were seen on more farms in 2006; 52% of respondents saw hedgehogs at least once in 2006 compared with 47% in 2012.

When including interaction terms between year and all explanatory variables, we found that the association of hedgehogs with farms under higher level stewardship (HLS) was stronger in 2012 than in 2006 (Table 5). There were 3% fewer respondents who had seen hedgehogs on farms not enrolled on HLS in 2012 than in 2006 and 15% extra respondents who had seen hedgehogs on HLS farms in 2012 than in 2006 (Fig.14). We found no effect of any other interactions with year (Table 5).

Table 5 The results of a linear model to test the interaction of year with badger numbers, region, traffic flow, land cover and region on hedgehog presence on farmland, from a questionnaire sent to 4000 farmers in the UK in 2006 and 2012

Variable	Factor Level	Df	Residual Deviance	P value	Effect size	95% CI
Year	*(2001)*	1, 649	901.3	0.289		
	2012				-0.067	-0.765, 0.630
Region	*(EAST MIDLANDS)*	10,639	867.4	0.0002***		
	East of England				0.096	-0.683, 0.879
	London				-1.295	-4.333, 0.756
	North East				1.098	0.227, 2.001†
	North West				0.277	-0.600, 1.157
	Scotland				0.583	-0.087, 1.267
	South East				0.212	-0.545, 0.976
	South West				-0.364	-1.147, 0.417
	Wales				-0.650	-1.670, 0.317
	West Midlands				-0.078	-0.975, 0.814
	Yorkshire				1.105	0.193, 2.061†
Badger numbers		1,638	866.4	0.316	0.222	-0.256, 0.741
Fox numbers		1,637	864.4	0.165	0.298	-0.361, 1.004
Farm type	*(ARABLE)*	4,634	853.4	0.011*		
	Dairy				-0.981	-1.973, -0.031†
	Livestock				-0.695	-1.355, -0.049†
	Mixed				-0.353	-1.007, 0.293
Hedgerow length		1,633	853.4	0.942	7.3e-6	-3.6e-6 2.4e-5
Organic status	*(NO)*	1,632	850.0	0.066**.**		
	Yes				-0.944	-2.271, 0.199
HLS status	*(NO)*	1,631	845.8	0.040*		
	Yes				0.007	-0.902, 0.925
Year* Badger numbers		1,629	845.3	0.467	-0.363	-1.224, 0.449
Year* fox numbers		1,626	845.1	0.719	0.187	-0.873, 1.260
Year* Farm type	*(YEAR*ARABLE)*	3,626	841.7	0.331		
	Year*Dairy				0.892	-0.470, 2.284
	Year*Livestock				-0.224	-1.093, 0.645
	Year*Mixed				-0.305	-1.190, 0.579
Year*Hedgerow length		1,625	840.2	0.223	-8.2e-6	-2.5e-5, 3.0e-6
Year*Organic	*(YEAR*NO)*	1,624	840.2	0.793		
	Year*Yes				-0.098	-1.819, 1.640
Year*HLS status	*(YEAR*NO)*	1,623	835.8	0.037*		
	Year*Yes				1.467	0.091, 2.915†

Words in italics following categorical variables indicate the reference category

***Significant at p<0.001 level, **Significant at p<0.01 level, *significant at p<0.05 **.**near significance

† 95% confidence interval of the effect size does not contain zero

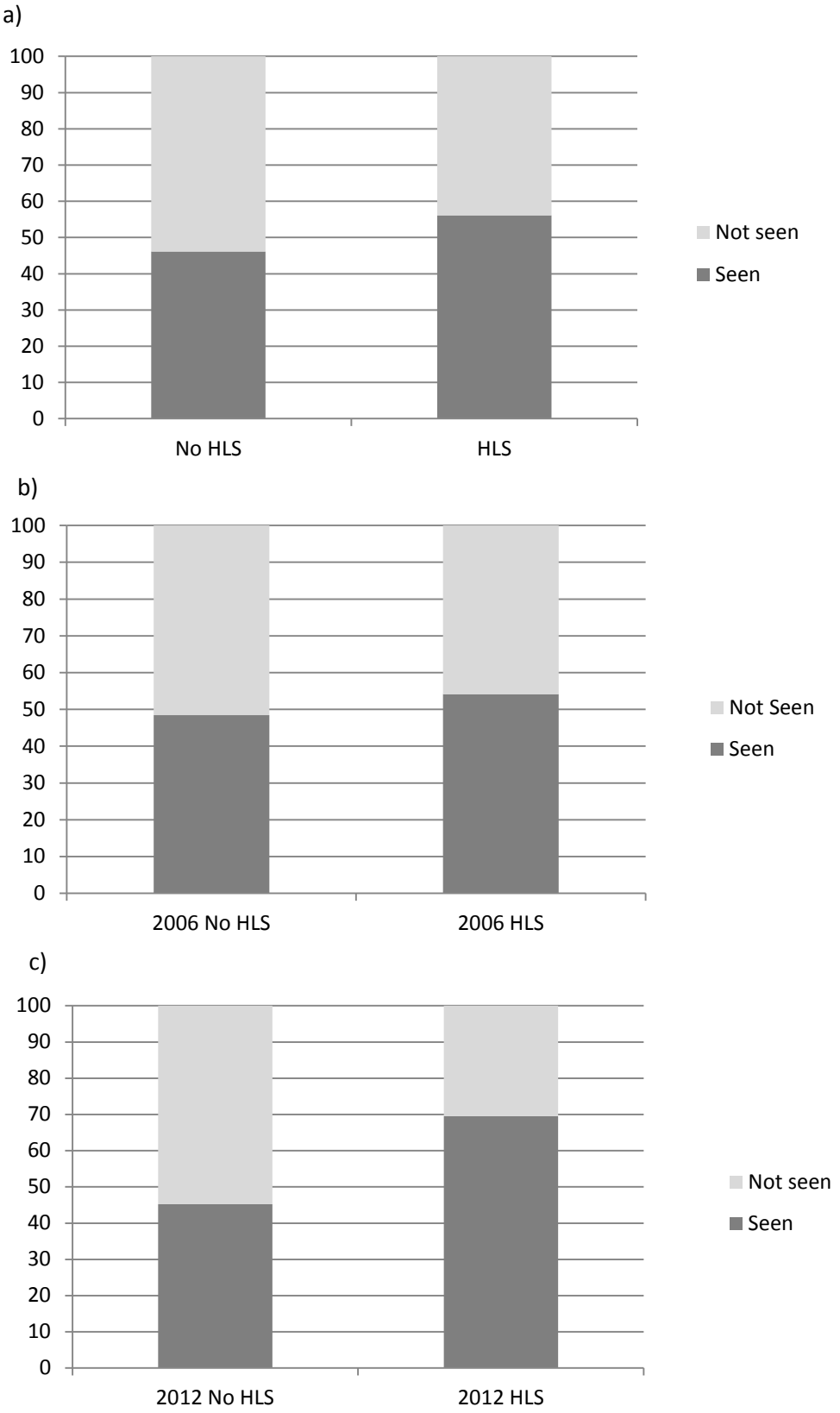


Fig.14 The percentage of respondents of a farmer questionnaire who had seen a hedgehog on their land in the previous year on farms under higher level environmental stewardship (HLS) and farms not enrolled in HLS. a) is the results of the 2012 farmer questionnaire, b) and c) are results from landowners who responded to the questionnaire in 2012 and 2006

Spotlight survey

We saw at least one hedgehog on 46% of the thirteen farms surveyed and therefore did not see hedgehogs on 54% of the farms, despite only surveying farms where respondents had seen a hedgehog in the past year. Hedgehogs were observed at six farms down the east of the country (Fig.15).



Fig.15 Results of a spotlight survey across 13 predominately arable farms in England in April-June 2013

Discussion

Mammals on Roads: hedgehog distribution

The decline in hedgehogs and current distribution of hedgehogs in the North and North East of England and Scotland presented here has been shown in previous national surveys of the hedgehog in Britain (Hof 2009; Hof & Bright 2012). Our study confirms these previous findings and indicates that one probable cause of the hedgehog's association with the East of England, North East of England and Scotland is the distribution of predators. We found that badgers were at higher density in South and South West England and foxes were found at higher density in South and South East England. This finding adds to a wealth of evidence that badger presence affects hedgehog distribution both at the field scale (Doncaster 1992, 1994; Micol, Doncaster & Mackinlay 1994; Ward, Macdonald & Doncaster 1997; Ward, Austin & Macdonald 2000; Doncaster, Rondinini & Johnson 2001; Young *et al.* 2006; Hof *et al.* 2012) and at the national scale (Hof 2009; Hof & Bright 2009, 2012; Van De Poel *et al.* 2015). However, these results also show that predation by the red fox may be equally responsible for hedgehog distribution in Britain.

Hedgehogs were seen most frequently on arable land in the Mammals on Roads survey and this habitat class had the highest selection ratio. This result may be due to the higher abundance of hedgehogs in the arable dominated east of England, rather than a preference for arable land, which is avoided at the field scale (Doncaster 1992, 1994; Doncaster *et al.* 2001; Hof & Bright 2010). Also, the observation of hedgehogs on a road in an arable area does not tell us which part of the arable field hedgehogs were utilising- indeed hedgehogs often avoid the centre of arable fields in favour of hedgerows and edge habitat (Hof & Bright 2010, 2012). The land class with the second highest number of hedgehog sightings was improved grassland and this habitat had a selection ratio of 1.06. Hedgehogs have previously been shown to avoid improved grassland in national surveys (Hof 2009), but do select short grass habitats at the field scale due to high earthworm abundance (Doncaster 1992, 1994).

Over a thousand of the 11,000 hedgehogs sighted during the MoR survey were observed in urban areas and this habitat class had the second highest selection ratio, despite the public being asked not to record in built-up areas during the survey. Hedgehogs have been found to select urban areas at the field scale (Doncaster 1992, 1994; Reeve 1998; Doncaster *et al.* 2001) and there may be several reasons for this, including high abundance of prey, particularly earthworms on garden lawns and amenity grassland (Micol *et al.* 1994; Young *et al.* 2006; Dowding *et al.* 2010), hedgehogs' attraction to supplementary food (Hubert *et al.* 2011) and avoidance of badgers (Hof *et al.* 2012) Other speculative suggestions include attraction to a warmer microclimate in urban areas (Hubert *et al.* 2011) and a higher availability of nest sites and conspecifics (Reeve 1998).

Mammals on Roads: trend analyses

The results from the overall trend analysis showed that hedgehogs declined overall in the study but that there was a spike in numbers in 2007. It is typical for small mammal populations to fluctuate annually (Harris *et al.* 1995) and the hedgehog's population variability may be associated with survival of hibernation, which is linked to winter temperatures and fat reserves (Morris 1984; Jensen 2004). We found that at the journey level, fox numbers were positively correlated with hedgehog numbers. This finding may be a result of hedgehogs and foxes sharing similar habitat preferences. For example, they both prey on earthworms and also scavenge for human food waste (Yalden 1976; Macdonald 1980; Wroot 1984; Doncaster, Dickman & Macdonald 1990). Badgers also prey on earthworms (Neal & Cheeseman 1996) and therefore also overlap in niche with hedgehogs (Doncaster 1992). However, it is thought that only badgers have the dexterity to unroll a hedgehog from its defensive position (Neal 1986) and thus may have a greater impact on hedgehog numbers.

At the county level, we also found that the number of foxes seen was positively correlated with the number of hedgehogs seen, the opposite to our finding at the 10km^2 level. This finding again may be due to an unidentified aspect of habitat availability at the county level which is preferential for both hedgehogs and foxes. We found evidence that the effect of badger presence on hedgehog numbers

was more pronounced in 2011 than in 2001. One potential cause of this interaction could be changes in the number of badgers in the UK (Fig.6). The density of main badger setts has increased by 88% since 1985 in England (Judge *et al.* 2014). This finding is also reflected at a local scale, for example in Wytham Woods, where badgers numbers have almost trebled since 1987, seemingly due to climate change (Macdonald & Newman 2002; Macdonald, Newman & Buesching 2015). Hof (2009) also found the national increase in badger numbers had a negative effect on hedgehog numbers.

We found an interaction between year and the proportion of arable land per county on hedgehog sightings in a county. The positive relationship between hedgehogs and the proportion of arable land in a county was stronger in 2011 than in 2001 (effect size 2001= 0.91, 2011= 1.62). This finding could be a result of hedgehogs declining to a greater degree in the South West (a region characterised by pastoral farmland (Carey *et al.* 2008) and high badger numbers (Judge *et al.* 2014)), and therefore hedgehogs appearing to select arable land, which dominates the East of England. We also found a positive relationship between the proportion of farm woodland in a county and hedgehog numbers. Hedgehogs have been shown to avoid woodland at the field scale (Doncaster 1992; Reeve 1998; Haigh, O'Riordan & Butler 2013), possibly to avoid badgers which often excavate setts in woodland (Neal & Cheeseman 1996). However, previous national studies have shown hedgehogs to be associated with coniferous woodland (Hof 2009) or deciduous woodland (Hof & Bright 2012). It may be that the proportion of farm woodland in a county is a proxy for the intensity of management of farms in the county or the level of urbanisation. For example the lowest proportion of farm woodland in a county was in Greater London, Greater Manchester and the West Midlands and the greatest proportion of farm woodland was in three Scottish regions; Grampian, Argyll & Bute and Scottish Borders.

At the county level, we found a negative relationship between mean traffic flow on the roads and the number of hedgehog sightings. It is likely that this finding is a result of fewer hedgehogs being present in counties with high traffic flow and urbanisation such as in London (Hof 2009). There is a

concern that road kill data are simply related to traffic density rather than population changes (Baker *et al.* 2004; Van Langevelde & Jaarsma 2004), however we found no interaction between year and traffic flow in the model.

Farmer questionnaire: hedgehog distribution

Results from the farmer questionnaire found that hedgehog distribution across Britain matched the distribution found from the Mammals on Roads survey; hedgehogs were seen more frequently in the North and East of the country and in Scotland. A higher number of respondents had seen hedgehogs on arable and dairy farms than on livestock and mixed farms. The number of respondents who had seen hedgehogs on livestock farms was particularly lower than all other farm types, which was also found by Hof & Bright in their analysis of the 2006 dataset (2012). The selection of dairy farms may be due to the high percentage of grazed pasture on these farms, a habitat higher in earthworm abundance than intensively managed arable land (Curry 1994; Curry, Byrne & Schmidt 2002; Curry *et al.* 2008), and therefore a preferred foraging habitat of hedgehogs (Doncaster 1992, 1993). Again the preference for arable farms may be a result of hedgehog association with the east of the country, where predator numbers are lower, rather than hedgehog preference for arable land itself, which is supported by the finding that hedgehogs were most frequently seen in gardens rather than on farmland. Studies have shown short grass habitats, such as garden lawns, to be utilised by hedgehogs for foraging due to the easy accessibility and abundance of earthworms (Doncaster 1992; Dowding *et al.* 2010; Hubert *et al.* 2011).

A higher number of respondents from farms enrolled in higher level stewardship had seen hedgehogs in the past year than those from farms under other agri-environment schemes or without any scheme. Unlike entry-level environment schemes, HLS schemes are negotiated with the land owner and entail a greater level of management for wildlife (Natural England 2013). Higher level agri-environment schemes may be beneficial to hedgehogs due to increased hedgerow quality, hedgerows being important to hedgehogs for refuge from predators (Hof & Bright 2012), nesting

habitat (Haigh, O'Riordan & Butler 2012b) and as dispersal corridors (Moorhouse *et al.* 2014). Farms enrolled in HLS may also have a greater number of habitats rich in invertebrates, such as conservation headlands and buffer strips, which may be beneficial for foraging (Hof & Bright 2010). It could be argued that land owners on HLS farms are more interested in wildlife and therefore more likely to spot hedgehogs. However, no effect of agri-environment scheme was found on hedgehog presence in the analysis of the 2006 responses (Hof 2009).

Farmer questionnaire: trend analyses

When we included data from land owners who responded in both 2006 and 2012, we found no effect of year on hedgehog presence. This outcome may be as there was only six years in between the two questionnaire studies, rather than the ten years available for the MoR analysis and this length of time was not long enough to detect the downward trend in hedgehog numbers. We found that the association of hedgehogs with farms under higher level stewardship was stronger in 2012 than in 2006. This result was more likely to reflect an increase in the number of hedgehogs seen on HLS farms than a decrease in the number of landowners from farms not enrolled on HLS (Fig.14). This finding suggests that hedgehog numbers have increased on HLS farms during the six years between the surveys. Again, this could reflect the increased level of wildlife management practices on HLS farms.

Interestingly, when carrying out the trend analysis, we found that fewer respondents from organic farms had seen hedgehogs in the previous year than respondents from non-organic farms. A larger sample size is needed to substantiate this finding as only 4% of respondents farmed organically.

Spotlight survey

We saw at least one hedgehog on just under half of the surveyed farms. On discussion with land owners we found, on more than one occasion, that the land owner thought they had hedgehogs on their farm but the agronomist or contractor working the farm had not seen hedgehogs in the previous year, which could explain why we found no hedgehogs on some of the farms. However,

farmers carry out most of their work in daylight hours. We surveyed a small number of farms, only arable farms, and only for two-three nights each, which may also explain our low detection rates. In spite of the small sample size, hedgehogs were only observed at farms down the east of the country, which supports the distribution of hedgehogs found in the analysis of the 2012 farmer questionnaire results and the results of the Mammals on Roads survey.

Study limitations

One drawback of the MoR dataset was the decrease in the numbers of participants each year, and therefore the number of journeys each year, which fell from 2077 in 2001 to 551 journeys in 2011. Although we were able to offset the models by the number of journeys, the measures of hedgehog and predator abundance would be less reliable in 2011 than in 2001. Furthermore, there were far fewer badger and fox sightings in the study, especially in 2011, than hedgehog sightings resulting in the observed predator distributions being less reliable than the hedgehog distribution. However, we were still able to detect the near statistically significant effect of changes in predator numbers on hedgehog numbers.

Our site visits indicated that farmers were often over-optimistic about the number of hedgehogs on their farms. Also, farmers may have been more likely to respond to the survey if they take an interest in wildlife and have seen hedgehogs. Therefore, the proportion of farms with respondents who had seen hedgehogs may be an over-estimation of the proportion of farms with hedgehogs present in the country. Nevertheless, the questionnaire offered a quick and easily repeatable method to obtain information on changes in hedgehog numbers which are difficult to survey for on farmland (Haigh, Butler & Riordan 2012a).

Summary

We provide evidence from three surveys - MoR, a farmer questionnaire and a spotlight survey - that hedgehogs are distributed in the North and East of England rather than the South West. We found that badger and fox abundance was negatively correlated with hedgehog abundance at the $10km^2$

scale and therefore predator presence is one probable cause of hedgehog distribution in Britain. We detected an overall downwards trend in hedgehog numbers from the MoR survey and the analysis found one potential cause was an increasing negative correlation between badger numbers and hedgehog numbers between 2001 and 2011. Although the number of respondents who saw hedgehogs in 2006 and 2012 decreased, we found no significant effect of year from analysis of the farmer questionnaire results. We found a positive effect of HLS on hedgehog presence from the farmer questionnaires, which was stronger in 2012 than in 2006. These findings indicated that predator numbers and entry into higher tier agri-environment schemes affect hedgehog numbers nationally.

Over fourteen thousand farms in England fall under HLS, covering 1,348 thousand hectares of land compared with 6,389 thousand hectares covered by entry level schemes (DEFRA 2015). Thus, the area in which hedgehogs benefit from increased management is relatively small. Furthermore, in 2015 agri-environment schemes were changed in the UK to schemes which are now competitive to enter (Natural England 2015). The benefits of these new schemes for hedgehogs, which still include a higher tier version, need to be investigated as this study has indicated the potential for the schemes in sustaining hedgehog numbers locally. The higher tier schemes may also offer improved environmental complexity (Macdonald & Feber 2015), which increases the habitats in which hedgehogs can take refuge from predators and therefore possibly mitigate the effect of badgers and foxes on hedgehog numbers (Janssen *et al.* 2007).

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Appendix

HEDGEHOG QUESTIONNAIRE

1. How often did you see hedgehogs on your farm during last year?

❑ None seen
❑ Seen less than 3 times
❑ Seen 3-6 times
❑ Seen more than 6 times

2. In comparison to ten years ago, do you currently see (Please tick only ONE box):

❑ About the same number of hedgehogs on your farm?

❑ More hedgehogs on your farm, because of (Please circle ALL the relevant options):

- Increase of suitable habitat (e.g. hedgerows, pasture)
- Increase of available food (e.g. slugs, worms, beetles)
- Less intensive farm management (Please specify): ……
- Decreasing numbers of badgers
- Other (Please specify): ……

❑ Fewer hedgehogs on your farm, because of (Please circle ALL the relevant options):

- Decrease of suitable habitat (e.g. hedgerows, pasture)
- Decrease of available food (e.g. slugs, worms, beetles)
- Intensification of farm management (Please specify): ……
- Increasing numbers of badgers
- Other (Please specify): ……

3. Where do you usually see hedgehogs on your farm? (Please tick ALL the relevant boxes)

❑ Garden
❑ Rough (unfarmed) grassland/ downland/ moorland
❑ Lowland heathland e.g. with gorse, heather
❑ Arable farmland
❑ Pastoral farmland i.e. grazing
❑ Predominantly deciduous woodland
❑ Predominantly coniferous woodland
❑ Other (Please specify): ……..

4. Is your farm MAINLY concerned with (Please tick ALL that apply):

❑ Rearing livestock ❑ Dairy ❑ Arable ❑ Poultry/eggs
❑ Market garden or horticulture ❑ Other (Please specify):……

5. How many hectares does your farm cover? ……hectares

6. What percentage of your farm is arable land, grassland (including pasture and set aside), woodland? (Please tick only ONE box per line)

Arable land:	❑ 0%	❑ 1 - 25%	❑ 26 - 50%	❑ 51 - 75%	❑ over 75%
Grassland:	❑ 0%	❑ 1 - 25%	❑ 26 - 50%	❑ 51 - 75%	❑ over 75%
Woodland:	❑ 0%	❑ 1 - 25%	❑ 26 - 50%	❑ 51 - 75%	❑ over 75%

7. What is the approximate total length of hedgerows on your farm? ……..metres

8. Is your farm certified as organic by a DEFRA approved body?

❑ Yes ❑ No

9. Is your farm, or part of your farm, in any agri-environment scheme(s)? (Please tick ALL that apply)

- ❑ I do not have any agri-environment scheme(s) on my farm
- ❑ Entry Level Stewardship
- ❑ Higher Level Stewardship
- ❑ Organic Entry Level Stewardship
- ❑ Other (Please specify): ……

10. If your farm has been in ANY agri-environment scheme(s), how long in total has it been in such scheme(s)?

- ❑ Just started
- ❑ Less then 5 years
- ❑ Between 5 and 10 years
- ❑ More then 10 years

If you would be happy for us to contact you with regard to carrying out research on your farm, please fill in your details below:

Name:…….

Address:…….

……

Telephone:…….. Email:…….

Thank you very much for completing this questionnaire. Your input is greatly appreciated.

Please send the questionnaire back using the enclosed pre-paid envelope to:

People's Trust for Endangered Species
15 Cloisters House
8 Battersea Park Road
London
SW8 4BG

www.ptes.org
enquiries@ptes.org
020 7498 4533

Discussion

Overview

This thesis was planned as an investigation of why hedgehogs favour rural villages over arable land, with the aim of finding practical methods for improving arable land for hedgehogs and curtailing hedgehog declines in rural areas. In the introduction to this thesis I discussed the specific factors that were thought to be the most plausible explanations for hedgehogs' avoidance of arable land and preference for villages. These included: prey availability, badger presence, microclimate and nest site availability.

The findings reported here indicate that rural villages offer denser forage availability, particularly in the form of supplementary food, a greater availability of secure nesting sites and shelter from predation by badgers, and therefore support higher numbers of hedgehogs than the surrounding arable farmland. In contrast, arable farmlands were associated with larger home range sizes and higher energetic costs for hedgehogs- which I interpret as deriving from their supporting a lower density of prey- and therefore require hedgehogs to travel further to fulfil their energetic requirements. The higher badger numbers and relative lack of cover on arable land, also increases predation risk. The presence of badgers may also limit hedgehogs' ability to forage, as evidenced by the lower daily energy expenditure and smaller home range sizes observed for hedgehogs occupying habitats in which badgers were present. In the absence of badgers, hedgehogs still preferentially selected villages, potentially due to the greater availability forage and nesting sites, but also used farmland for foraging. In the presence of badgers, hedgehogs stayed closer to buildings and edge habitats and spent a significantly lower proportion of their time on farmland. These observations accord with the findings from the Mammals on Roads survey which showed that hedgehog presence and abundance at a national scale, was negatively correlated with badger presence and abundance. Also at a national scale, a farmer questionnaire demonstrated that a higher number of respondents from farmland under Higher Level Stewardship (HLS) had observed hedgehogs in the preceding year than respondents from non HLS farms.

Below I detail the evidence from my thesis underpinning the above conclusions, and discuss its implications for conservation action, in terms of mitigating the negative attributes of arable land for hedgehogs, and consider the most promising options for further research.

Evidence for higher forage availability in rural villages

Chapter 3 demonstrated a positive correlation between a hedgehog's mean distance to buildings over a season, which was interpreted to be a metric of its 'village' preference, and the size of its home range. I speculated this was due to denser prey availability in rural villages than on the surrounding arable farmland and that hedgehogs foraging on arable farmland had to travel further to find prey. This idea is supported by the results of the energetic experiments in Chapter 4, which showed that hedgehogs had higher daily energy expenditures (DEE) further from buildings, and the most likely explanation is increased locomotion necessary to achieve an adequate food intake.

The results reported in Chapter 5 indicated hedgehogs generally consumed similar prey types along the gradient from buildings to open arable land. I found Bovidae DNA in 93% of samples and Suidae in 89% of samples and laboratory trials indicated that the Bovidae and Suidae DNA was likely to be from pet food consumed by hedgehogs. Evidence from sightings of hedgehogs radio-tracked to food bowls in gardens, and discussion with inhabitants of local villages, supports the conclusion that hedgehogs frequently consumed pet food across all four sites. Pet food has previously been linked to hedgehog attraction to urban areas in France (Hubert *et al.* 2011), and in this study the presence of DNA surmised to be from pet food in all faecal samples suggests this is at least partly responsible for the hedgehog's preference for gardens in Britain.

It could be argued that home range size is linked to population density as well as food density (Wolff 1985; Ostfeld & Canham 1995; Fortier & Tamarin 1998; Moorhouse & Macdonald 2008). Chapters 3 and 4 showed that hedgehog numbers were higher in rural villages than on the surrounding arable land and it may be that hedgehogs in rural villages had smaller home ranges in response to greater intraspecific competition, even though hedgehogs are not territorial and have overlapping ranges

(Reeve 1981, 1994). Alternatively, hedgehogs may simply have had smaller home ranges in villages as they are restricted to the bounds of the village. These two arguments do not explain why there is high density of hedgehogs in villages and it is likely that this is down to a combination of food density and lower predation risk in villages than on arable land.

No relationship was found between hedgehog condition and a hedgehog's mean distance to buildings in a season, suggesting that hedgehogs that use arable land are able to forage sufficiently. Hedgehogs may have two behavioural strategies in arable landscapes; residing in villages where food density is high but where competition for mates and food is high, or using arable land where food is less dense but competition is lower. However, all hedgehogs radio-tracked during this research used habitats associated with humans and an alternative hypothesis is that hedgehogs that spent more time further from buildings may simply be crossing arable land to reach different gardens. Finally, hedgehogs may have always preferentially selected rural villages rather than their traditional association with farmland and, previous to their decline, some individuals were forced to occupy the less productive farmland habitat surrounding the village. Now hedgehogs are in lower numbers, there may be reduced competition for the preferable village habitat and fewer hedgehogs on the farmland surrounding rural villages.

Risk of badger predation on arable land

The presence of badgers appears to have both direct impacts on hedgehog numbers and indirect impacts on hedgehog behaviour. On sites with badgers, hedgehogs stayed closer to edge habitats and buildings than hedgehogs on sites without badgers, potentially to minimise the risk of badger predation (Chapter 3). Hedgehogs on sites with badgers also had smaller home ranges (Chapter 3) and a lower DEE (Chapter 4) than hedgehogs on sites without badgers, regardless of the amount of time they spent on arable land, suggesting that hedgehogs have restricted movement when badgers are present, even in villages, and this may impact on foraging ability. There was no effect of badger presence on the prey families present in the hedgehog's diet (Chapter 5), yet in this thesis I did not

study the volume of prey consumed. Further study is required to test if badger presence affects the quantity but not quality of hedgehog diet, for example by using feeding trials to equate the abundance of DNA in hedgehog faecal samples to the biomass of prey consumed.

Fewer hedgehogs were captured and encountered on sites with badgers, both in rural villages and on the surrounding farmland, than on sites without badgers, indicating that badger presence also affects hedgehog numbers within rural villages as well as on arable land (Chapters 3 and 4). This finding is in agreement with a study of hedgehog abundance on amenity grassland by Young *et al*. (2006), which found hedgehog numbers were negatively correlated with badger sett abundance in the surrounding area. On sites with badgers, the hedgehogs that were captured and subsequently radio-tracked, spent less time on arable land than hedgehogs on sites without badgers (Chapter 3), again probably due to a perceived risk of predation on arable land facilitated by the hedgehog's keen sense of smell (Ward, Macdonald & Doncaster 1997; Ward, Austin & Macdonald 2000). Although the scope of this thesis meant I was limited to radio-tracking hedgehogs on four sites in two counties, Hof *et al.* (2012) also radio-tracked hedgehogs on four predominately arable sites in Lincolnshire, Berkshire, Norfolk and Leicestershire, and found similarly that hedgehogs on sites with badgers were observed closer to edge habitats and spent more time in rural villages, demonstrating the behavioural responses of hedgehogs to badgers seem to be widespread in England.

Nationally, badger presence and abundance were negatively associated with hedgehog presence and abundance, based on the Mammals on Roads (MoR) survey (Chapter 6). Hedgehogs were in higher abundance in the arable dominated lowlands of the East and North East of the country than in the pasture dominated South and South West, where badgers were in highest abundance (Chapter 6). At the county level, the negative relationship between hedgehog numbers and badger numbers was more pronounced in 2011 than in 2001 (Chapter 6), suggesting that the increases in badger numbers observed during the MoR survey has exacerbated a negative effect on hedgehog

numbers nationally. Chapter 6 also highlighted that fox abundance may also have an effect on hedgehog distribution, particularly at the 10km^2 scale.

Unlike in previous radio-tracking studies (Doncaster 1992, 1994; Warwick, Morris & Walker 2006; Hof & Bright 2010a), there was only one suspected hedgehog death from badger predation throughout the course of radio-tracking for this thesis and this occurred on arable farmland. Many of the responses of hedgehogs to badger presence presented here, are likely to be indirect non-lethal effects of predation rather than direct predation, for example, a reduction in movement and energy expenditure when badgers are present. If badger numbers continue to increase, these impacts may be exacerbated, for instance, through reduced encounters with conspecifics for mating and reduced foraging opportunities, which may impact on hedgehog survival and reproductive success, thus increasing the likelihood that rural hedgehog populations will fall below the minimum viable population sizes required for persistence.

These findings add to the wealth of evidence that badger presence affects hedgehog distribution and behaviour at the field scale (Doncaster 1992, 1994; Micol, Doncaster & Mackinlay 1994; Ward *et al.* 1996, 1997, 2000; Doncaster, Rondinini & Johnson 2001; Young *et al.* 2006; Hof *et al.* 2012), and distribution at the national scale (Hof 2009; Hof & Bright 2009, 2012; Van De Poel, Dekker & Van Langevelde 2015). The presence of badgers is highly likely to be a key cause of hedgehog distribution in the countryside in Britain, and a trigger for hedgehogs' avoidance of arable land and selection of rural villages, where badgers are in lower density. Nonetheless, this thesis also provides evidence that badgers alone do not account for the hedgehog's preference for villages: hedgehogs on sites without badgers also selected villages, although they did spend more time on arable land. Where badgers are present, rural villages may facilitate hedgehog survival in Britain, yet in lower numbers than in villages with no badgers on the surrounding farmland.

Availability of nesting habitat in rural villages

In Chapter 3, I reported evidence that villages offer a wide range of day nesting habitats for hedgehogs, in corroboration with previous study in Finland, where over half of day nests in urban areas were constructed in built-up areas (Rautio *et al.* 2014). During my research, villages were ranked as the most selected habitat for nesting and within villages scrub was the most used habitat. In this study scrub included bushes and areas of brambles and weeds, which were plentiful in gardens. A variety of man-made structures were used for nesting in villages including garden sheds, hay barns, compost heaps and under tarpaulin. Nest sites in villages were often inaccessible, such as under garden sheds, which supports the hypothesis that nest sites may be more secure in villages. Hedgerows were still selected in villages and were the most common habitat used for nesting on farmland, as in a study by Haigh *et al.* (2012b).

There was some evidence that hedgerow quality was an indicator of whether it was used for nesting or not. Hedgerows that hedgehogs nested in were shorter and wider than those never used. Short, wide, compact hedgerows are arguably more dense than tall, slim hedgerows and it has previously been suggested that hedgehogs will not nest in hedgerows that are particularly sparse at the base (Hof & Bright 2010b). Maintaining hedgerows in good structural condition, particularly at the base, may therefore increase nest site availability for hedgehogs.

The effect of microclimate on hedgehog distribution

Temperature appeared to have a mixed and often ambiguous effect on hedgehog attraction to villages. Hedgehogs were found further from cover when it was colder (Chapter 3). The reason for this finding is unclear. There was no evidence that the relationship was due to hedgehogs using the centre of arable fields after harvesting in September and October when temperatures are colder. An effect of time in the evening was examined, as temperatures are warmer earlier on in the evening when hedgehogs may be closer to edge habitats because they have just emerged from the nest, but no effect was found.

There were significant differences in temperature between arable land and village gardens. Arable fields were a mean of 1^{o}C colder than gardens (Chapter 4), which may result in higher energetic costs the further hedgehogs are from buildings, due to a higher cost of maintaining endothermy. In spite of this, day in the season, a proxy for temperature, was positively correlated with DEE. This relationship has been found in previous studies of intraspecific DEE (Bryce *et al.* 2001; Fletcher *et al.* 2012) and Dowding *et al*. (2010) found that hedgehog activity, and therefore energy expenditure, increased with temperature, which they proposed was due to increased prey activity. Consistent with the hypothesis that temperature is important, hedgehog condition was particularly poor on the most northerly site (Chapter 4), where the coldest night temperatures were recorded.

Conservation implications

I have shown that rural villages are selected by hedgehogs over arable farmland, especially in the presence of badgers. However, when hedgehogs did use arable farmland they nested in hedgerows and we can speculate that hedgehogs require hedgerows with dense vegetation at the base to nest in. Only 10% of hedgerows on arable land have been judged to be in good structural condition (Carey *et al.* 2008). Consequently, hedgerow quality on arable land should be increased. Furthermore hedgehogs may have to cross open arable land to move between villages, which may promote gene flow between populations. In the landscapes modelled by Moorhouse *et al*. (2014), a doubling in hedgerow length facilitated an additional 51% of model hedgehogs to travel over 2000m, via increased permeability for hedgehogs, and thus hedgerow quantity should be maintained or increased to allow movement between villages. Altering the model landscape in relation to badger presence did not change the distance hedgehogs travelled in the study (Moorhouse *et al.* 2014).

Chapter 5 reports evidence that Lumbricid earthworms, Carabid beetles and Lepidopteran larvae were likely to be important food sources for hedgehogs. Thus, hedgehog conservation is expected to depend on the maintenance of habitats on farmland that support these prey items, such as grassy field margins which increase invertebrate abundance (Meek *et al.* 2002; Woodcock *et al.* 2007;

Smith *et al.* 2008; Hof & Bright 2010b; Macdonald & Feber 2015). Hedgehogs on one site frequently foraged in predominately white clover set-aside; hedgehogs on this site had more Lepidoptera DNA in their faeces (Chapter 5). Set-aside fields are beneficial in maintaining invertebrate abundance and habitat heterogeneity on farmland and therefore may be beneficial for hedgehogs (Van Buskirk & Willi 2004; Macdonald *et al.* 2007).

Hedgehogs also foraged on rough grassland areas on farmland and, as found in previous studies, selected short grass habitats such as amenity grassland and garden lawns (Micol *et al.* 1994; Young *et al.* 2006; Dowding *et al.* 2010a). The greatest density of hedgehogs observed on arable land during this study was on a mowed grass strip in the centre of an arable field used for flying model aeroplanes. Sections of short grass in arable fields such as field margins could emulate these resource patches and should also be encouraged. Currently agri-environment scheme grassy field margins are mowed once a year in the UK (Natural England 2015). The findings of my research suggest that having areas mowed more frequently may improve earthworm availability for hedgehogs.

A questionnaire sent to 644 farmers in 2012 found that on farms under Higher Level Stewardship (HLS), 56% of respondents had seen hedgehogs, compared with 44% of respondents from farms not under HLS (Chapter 6). Unlike entry-level environment schemes, HLS schemes are negotiated with the land owner and entail a greater level of management for wildlife (Natural England 2013). Higher level agri-environment schemes may be valuable for hedgehogs due to increased hedgerow maintenance and a greater number of habitats rich in invertebrates, such as conservation headlands, buffer strips and grassy field margins, which may be beneficial for foraging (Hof & Bright 2010a). Higher tier schemes should continue to promote these in-field enhancements in order to ensure suitable habitat and habitat connectivity for hedgehogs.

Badger numbers are increasing in the UK (Chapter 6; Judge *et al.* 2014), most likely due to warmer winters and a lack of natural predators (Macdonald & Newman 2002; Macdonald, Newman &

Buesching 2015). There is a worry that badgers will increasingly populate villages and suburban areas, removing the predator free space selected by hedgehogs (Davison *et al.* 2008). The current increase in badger numbers in the UK countryside is a highly politicised as badgers are a reservoir of bovine tuberculosis (bTB) and are known to damage crops (Macdonald *et al.* 2015). There have been calls to cull badgers to save hedgehogs and a study in England over the five years of the Randomised Badger Culling Trial (RBCT) found that hedgehog numbers doubled on amenity grassland in areas where badger culls were taking place (Trewby *et al.* 2014). Additionally, O'Shea *et al.* (2010) found higher numbers of hedgehog roadkill on a transect in a badger removal area than in a control non-removal area in the Republic of Ireland. However, these studies are localised and do not address the effect of badger culling on hedgehog numbers on arable land. Therefore, the current evidence is not sufficient to demonstrate that culling badgers would increase hedgehog numbers on arable land. Furthermore, badger removal during the RBCT resulted in an increase in numbers of another predator of hedgehogs, the red fox (*Vulpes vulpes*) (Trewby *et al.* 2008).

Badgers are well-loved and protected in the UK (Badger Act 1973; Wildlife and Countryside Act 1981; Protection of Badgers Act 1992) and thus calls to carry out widespread culls in attempts to control bTB have been met with strong opposition. Mitigating the negative effects of badgers on hedgehogs though other means than the removal of badgers is therefore desirable. Hedgehogs and badgers have co-existed since the Mesolithic in the UK (Maroo & Yalden 2000; Yalden 2010), one possible cause of the increasingly negative impact of badgers on hedgehog numbers on arable land, aside from increases in badger numbers, is changes in farming practices in the past 60 years (Robinson & Sutherland 2002). Increases in the application of pesticides has caused a decrease in invertebrate prey abundance (Moreby & Southway 1999; Wilson *et al.* 1999), thus removing prey for badgers and potentially increasing predation pressure on hedgehogs. Furthermore, since 1945, 50% of the hedgerows in Britain have been removed (Robinson & Sutherland 2002). Loss of edge habitat removes vital shelter for hedgehogs from badger predation, hedgehogs stayed closer to hedgerows when badgers were present both in this study (Chapter 3) and a study by Hof *et al.* (2012), and a

decrease in habitat structure in this fashion potentially exacerbates the effects of intraguild predation on hedgehogs (Janssen *et al.* 2007). Therefore, increasing habitat complexity, structure and food availability may increase the chance that intra-guild prey and predators can co-exist (Polis & Holt 1992; Morin 1999; Finke & Denno 2002; Janssen *et al.* 2007). Enhancing habitat structure and complexity could be accomplished by planting and restoring existing hedgerows and increases in invertebrate abundance could be accomplished by maintaining grassy field margins and increasing areas of set-aside. These aims could theoretically be achieved through the promotion of higher tier agri-environment schemes.

The work described in this thesis has shown that rural villages are selected by hedgehogs over arable farmland. Nevertheless, hedgehogs are also declining in residential areas; a third of the UK's urban population has been lost in in the last ten years (PTES & BHPS 2015). Hedgehogs may therefore also face a suit of threats in rural villages. Causes of the hedgehog decline in urban areas may differ from that in rural areas and includes poisoning from molluscicides and rodenticides (Keymer, Gibson & Reynolds 1991; Dowding *et al.* 2010b), a lack of habitat connectivity due to enclosed gardens (Hof & Bright 2009), and deaths on roads (Huijser & Bergers 2000; Rondinini & Doncaster 2002). Wildlife friendly gardening and the consideration of habitat connectivity in urban planning may reduce some of these threats to hedgehogs (Hof & Bright 2009), including encouraging homeowners to feed hedgehogs suitable foods, which were important for hedgehogs in this study.

Further research

In scoping methods for improving arable land for hedgehogs, a national footprint tunnel or spotlight survey would be valuable for ground-truthing the results of the farmer questionnaire survey, especially for establishing which aspects of HLS farms are beneficial to hedgehogs. As higher tier schemes are in the minority compared with entry level schemes, work must also be done at the landscape scale to connect farmland with extant hedgehog populations.

Further study which can aid in the examination of the relationship between badgers and hedgehogs includes: analysis of badger diet, closer radio-tracking of hedgehog and badger movements in combination and assessing if increasing hedgerows successfully diminishes the effect of badgers. A study from Poland found hedgehog remains in fewer than 1% of 271 badger faecal samples (Myslajek *et al.* 2013), suggestive of a low number of predation events, but not easy to interpret without knowledge of hedgehog density in the study area and the impact of predation events on hedgehog numbers. A similar study in the UK, using the molecular methods developed in Chapter 5 and in areas of known hedgehog abundance, would indicate how frequently hedgehogs are eaten by badgers in varying habitats, and aid in disentangling the effects of direct predation and the non-lethal impacts of badger presence. Radio-tracking hedgehogs and badgers simultaneously would also help to establish the dynamics of the hedgehog-badger relationship. For example, investigating how frequently hedgehogs and badgers come in to contact on sites where they are both present, and how often contact results in a predation event. Tracking could be aided by recent technologies such as proximity loggers used in the study of bTB transmission between cattle and badgers (Böhm, Hutchings & White 2009; Drewe *et al.* 2012).

Although it is speculated that increasing hedgerow availability will lessen the effect of badgers on hedgehogs, this is yet to be tested in the field. Improvements would have to go beyond the current quantity and quality of agri-environment scheme hedgerows, as these have not been enough to stem the hedgehog decline. Experimental manipulation of hedgerows would need to be carried out and would be costly and incredibly difficult to implement. For example, in the year 2000 it was estimated to cost £3000 to restore one kilometre of hedgerow (Pretty *et al.* 2000). Also added to these initial costs are the ongoing maintenance costs, a potential change in crop yields and the time needed for new hedgerows to become established (Forman & Baudry 1984; Semple, Bishop & Morris 1994). On a larger scale, a study of the costs involved in restoring hedgerows to meet Biodiversity Action Plan (BAP) targets in Devon found that an input of one million pounds a year for five years would only achieve favourable management of 2.5% of hedgerows in Devon (Mills 2002).

Summary

To survive hedgehogs must achieve balance between dietary intake and energetic output, avoid predation and find secure nest sites. Rural villages offer an environment in which this can be achieved and are a key habitat for hedgehog preservation in the countryside. To increase the chance of hedgehog persistence, we must not only conserve rural village hedgehog populations, but enhance the intensively managed farmland surrounding villages to increase the connectivity between these island populations and mitigate the negative impacts of badgers. Improving arable land for hedgehogs should include increases in hedgerow quantity and quality, provision of short grass foraging patches and increased habitat heterogeneity. These improvements can be made through the implementation of agri-environment schemes, particularly higher tier schemes. These recommendations are relevant to many species struggling to survive in landscapes dominated by human habitation and intensively managed farmland.

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