


Factors affecting hedgehog (*Erinaceus europaeus*) attraction to rural villages in arable landscapes

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Abstract Although residential areas are often unfavourable for wildlife, some species can take advantage of the available shelter and anthropogenic sources of food such as supplementary feeding. The European hedgehog (*Erinaceus europaeus*) is increasingly associated with gardens and villages and less so with arable farmland. Suggested drivers for this include the following: hedgehogs' attraction to higher food densities, including natural prey and anthropogenic sources, a greater range of day nest sites and warmer microclimates in rural villages, coupled with decreased risk of predation by badgers (*Meles meles*). We investigated the contribution of these drivers by radio-tracking hedgehogs on four arable sites, two with badgers present. Seventy-eight hedgehogs were tracked, 32 yielding enough data to calculate home range sizes. At the home range and landscape scales, gardens and buildings were the highest ranked habitats compared with their availability. Woodland and arable land were the lowest ranked compared with their availability. Villages were the most selected habitat for nesting. When hedgehogs were found closer to buildings, their ranges were smaller and we speculate this is due to increased food availability in villages. Where badgers were present hedgehogs remained closer to cover and their home ranges were on average 12.2 ha smaller. On badger-occupied sites, 50% fewer radio-tracking fixes were on arable land. We

conclude that resource availability coupled with nest site selection and badger presence drives hedgehogs' selection of rural villages. We found no effect of ambient temperature on habitat use. We recommend focusing conservation efforts on maintaining hedgehog populations in rural villages.

Keywords Arable farmland · Ranging behaviour · Foraging · *Meles meles* · Predation risk · Radio-tracking · Small mammal

Introduction

Built-up areas cover over 16,750 km² 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 built-up areas and intensively managed farmland has resulted in biodiversity losses in both urban and rural areas in the UK (Stoate et al. 2001; Foley et al. 2005; Macdonald and Feber 2015). Urbanisation may be particularly detrimental to wildlife, for example through habitat loss and fragmentation (Dickman 1987; Friesen et al. 1995; Lehtinen et al. 1999), road mortalities and the effect of roads as barriers to movement (Forman and Alexander 1998; Huijser and Bergers 2000; Rondinini and Doncaster 2002; Baker et al. 2004), human-wildlife conflict (Mosillo et al. 1999; Peine 2001; Gompper 2002; Hill et al. 2007; Delahay et al. 2009) and predation of native species by domestic pets (Baker et al. 2003; Woods et al. 2003).

There are also aspects of residential areas that are beneficial for wildlife, for example, low numbers of natural predators (Eden 1985; Gering and Blair 1999; Møller 2012), the availability of supplementary food (Doncaster et al. 1990; Fedriani et al. 2001; Prange et al. 2003; Fuller et al. 2008) and altered physical conditions, such as higher temperatures due to urban warming (Eden 1985; Pickett et al. 2001). There may also be

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higher occurrence of some natural prey species in urban areas allowing predator numbers to increase (e.g. Cooke et al. 2006). These advantageous qualities have allowed some species to thrive in residential areas, particularly omnivorous species, which can take advantage of human food waste (Fedriani et al. 2001; McKinney 2002; Chace and 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 gardens and rural villages, and less so with agricultural land (Hubert et al. 2011; Yarnell et al. 2014; Van De Poel et al. 2015). In the UK, hedgehog numbers are declining, but with more severe declines in rural than urban areas (JNCC 2010; Aebischer et al. 2011; Roos et al. 2012). Even within rural areas, hedgehogs favour rural villages rather than open farmland and arable land is particularly under-selected (Hof and Bright 2010a; Hof et al. 2012). We examine the drivers of hedgehogs' increasing association with villages in rural areas, aiming to establish the causes of their population declines in agricultural areas—and in doing so highlight potential conservation measures.

Several factors might plausibly influence hedgehogs' attraction to rural villages over arable farmland. The hedgehog's diet mainly comprises macroinvertebrates (Yalden 1976; Wroot 1984). Hedgehog abundance is positively correlated with the earthworm abundance of grass fields, and habitats in rural villages such as amenity grassland and garden lawns sustain high numbers of earthworms compared with intensively managed arable fields (Doncaster 1994; Micol et al. 1994; Curry et al. 2002; Young et al. 2006). Hedgehogs also take advantage of waste and pet food left out by humans (Yalden 1976; Morris 1985; Hubert et al. 2011). The availability of nesting habitat may also attract hedgehogs to villages. Although hedgerows are frequently used for nesting in rural areas (Haigh et al. 2012), hedgehogs may also show a preference for nesting close to buildings (Rautio et al. 2014).

Rural villages may also act as refuges from predation (Hof et al. 2012). The European badger (*Meles meles*) is the main predator of hedgehogs in the UK. Badgers are thought to limit hedgehog numbers in rural areas (Hof and 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). The mechanism for this relationship is unknown, it may be due to direct predation (Doncaster 1994; Hof and Bright 2010a; Trewby et al. 2014), avoidance of badgers (Hof et al. 2012; Pettett et al. 2017) or competition for food (Doncaster 1992). Badgers avoid building setts in residential areas (Neal and Cheeseman 1996) and therefore villages may act as refuge from badger predation (Doncaster 1994), although badgers can become quite abundant on the outskirts of urban areas (Davison et al. 2008). In residential areas, hedgehogs may face attack from domestic dogs (Doncaster 1994), yet 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 (Shkolnik and Schmidt-Nielsen 1976; Wroot 1984; Speakman 1997). Warmer temperatures may also result in higher availability of invertebrate prey for hedgehogs (Crawford-Sidebotham 1972; Edwards and Bohlen 1996; Honek 1997) and increased chances of survival during winter hibernation (Hubert et al. 2011). Villages may offer nest sites with stable temperatures for hibernation, such as in or under buildings (Lausen and Barclay 2006).

We investigate the contribution of four expected drivers of hedgehogs' 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. Hedgehogs that reside in villages, a habitat we speculate has a higher availability of prey and supplementary food (Doncaster 1994; Micol et al. 1994; Curry et al. 2002; Young et al. 2006; Hubert et al. 2011) than the surrounding arable land, will have smaller home ranges than those that utilise arable land.
2. Hedgehogs will show a preference for nesting close to buildings, and villages will have a greater variety of secure nesting habitats than on arable land (Rautio et al. 2014).
3. When badgers are present, hedgehogs will avoid arable land and therefore be found closer to buildings and cover (Doncaster 1994; Hof et al. 2012).
4. 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.

Methods

Study sites

Four sites were selected, 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) (Online Resource 1, Figs. A1–A4). Badgers were present on the farmland on one site in each county; presence was determined by surveys for tracks, active setts and active latrines in October 2013 and April 2014. Sightings by landowners and during radio-tracking studies also confirmed that badgers were active at these sites (Online Resource 1, Figs. A1–A4; Table A1). Sites were all at least 65% arable land, predominately cereal

crops, with some pasture and rough grassland fields (Online Resource 1, Table A1). Rural villages were within 2.5 km of the farm and all contained amenity grassland including parks, playing fields and church yards. Villages were surrounded by small pasture fields and arable land.

Hedgehog tracking

Hedgehogs were captured using red spotlights and anaesthetised using isoflurane (Natural England Licence 2014/SCI/0298, HO PIL 30/10293). A small patch of spines on the rump was clipped and a 10 g radio-tag was glued to the clipped spines using epoxy resin. Hedgehogs were marked using six 1 cm long pieces of coloured heat-shrink tubing glued in a patch at the rear. Hedgehogs were then tracked on the sites from July to October 2013 and April–September 2014. Each site was visited for between four and eight nights at a time in turn over the season, with a mean of 41 nights (s.d. = 8) spent at each site. Whilst on site, hedgehogs were tracked between sunset and 4 am and a radio-tracking fix was obtained for each hedgehog in turn. Hedgehogs were tracked using a hand-held three element yagi directional antenna (Wildlife Materials International, Murphysboro, USA) and a TRX-1000S receiver (Wildlife Materials International, Murphysboro, USA). We recorded the GPS location of the hedgehog to the nearest 5 m, the habitat it was found in (i.e. amenity grassland, arable land, buildings and gardens, hedgerow, pasture, rough grassland and woodland and scrub), 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 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.

Nesting

Radio-tracking was also carried out before sunset on an ad hoc basis, with the aim of recording at least one nest site per hedgehog. The GPS location of the hedgehogs' day nests was recorded, along with the general and specific habitat the nest was found in. General habitat was categorised as follows: 'arable', 'pasture' and 'village' (including amenity grassland, gardens and buildings) and 'woodland' (see Haigh et al. 2012). The specific habitat within each of these general habitats was recorded as 'buildings', 'hedgerows', 'scrub' (including brambles and under bushes) and 'other'. To assess whether particular features of a hedgerow prompted hedgehog selection for day nesting, six hedgerows were randomly selected on each of the farms including two where hedgehogs

had nested at some point during the 2013 and 2014 field seasons. Surveys of these hedgerows were carried out in June 2015 following the DEFRA hedgerow survey handbook methodology (DEFRA 2007).

Temperature

The hourly ambient temperature was recorded using ten data loggers per site during radio-tracking. To measure air temperature close to the ground, each was placed 30 cm off the ground. The loggers were covered with a foil dish in order to mitigate the effect of direct sunlight. Loggers were placed in a variety of habitats: 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 encounter minimal interference, e.g. flower beds in gardens and under isolated trees in the centre of fields. For each radio-tracking fix, the mean ambient temperature from all of the loggers, at the time closest to when the fix was taken, was calculated.

Statistical analysis

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, home range estimates was calculated for each hedgehog over the two seasons, in the program Ranges (Anatrack Ltd., Dorset, UK). Estimates included 100% minimum convex polygons (MCP), which includes all tracking fixes and is frequently used as a home range measure in hedgehogs tracking studies (Riber 2006; Dowding et al. 2010a; Haigh et al. 2013) and, in order to estimate the core range of the hedgehog, 95 and 50% kernel density estimates (Riber 2006). 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) and body mass.

The number of fixes obtained for each hedgehog varied between 1 and 53 fixes over the entire tracking period (mean = 17; s.d. = 12). All tracking fixes were included in the analysis of distance to hedgerows, cover and buildings. For hedgehog home range analysis, accumulation curves were created and it was deemed that only hedgehogs with at least 20 fixes should be included, resulting in 32 hedgehogs in the analyses, with a mean of 29 fixes per hedgehog and a range of 20–53 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 deemed to have enough tracking fixes to be included.

Compositional analysis was performed to examine hedgehogs' habitat selection as this method is comparable to previous studies of hedgehog habitat use (Hof and Bright 2010a;

Haigh et al. 2013). Two analyses were performed following Aebischer et al. (1993). Firstly, at the landscape scale to assess 100% MCP home range selection within the wider landscape, and secondly, to assess the habitats used within a 100% MCP home range compared with their availability in the home range. To examine habitat selection at the landscape scale, an area of 5 km² around each site was digitised and categorised as ‘amenity grassland’, ‘arable land’, ‘buildings’, ‘gardens’, ‘hedgerow’, ‘pasture’ and ‘rough grassland’ and ‘woodland and scrub’. To describe the 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 (1.4 ha) and therefore set-aside was not included in the analysis.

To examine differences in the proportion of radio-tracking fixes that hedgehogs were found 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 at least 10 tracking fixes, where calculating a percentage was deemed reasonable, were included in the analysis.

Compositional analysis was used to examine nest-site 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 the following: hedgerow height, hedgerow width and the height from the ground to the base canopy. The identity of the farm on which the hedgerow was located was included as a fixed blocking factor.

Linear mixed effects models were constructed using the R software (R Core Team 2014) to test whether hedgehogs’ mean distance to buildings, distance to cover and distance to hedgerow varied between those sites—characterised as with or without badgers present, between males and females, and with 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.

All results are stated as mean \pm standard error unless otherwise stated.

Results

Summary

A total of 46 hedgehogs were 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 Online Resource 1, Table A2 for details of study subjects). We wished to capture 20 hedgehogs at each site, but twice as many hedgehogs were found on sites without badgers (site A: 24 and site B: 28), than on sites with badgers (site C: 14 and site D: 12). For the 78 hedgehogs, a total of 1324 GPS fixes was obtained. In the home range analyses, 32 hedgehogs were included (site A: 8, site B: 12, site C: 4 and site D: 8). Sixty-six day nest locations were recorded from 42 individuals. Eight hedgehogs died during the study; three from unknown causes, three road casualties, one electrocuted on electrified chicken wire and one possible badger predation.

Habitat use

Habitat use was statistically significantly non-random (Table 1). At both scales, gardens and buildings were the highest ranked habitats compared with their availability, on sites with and without badgers (Online Resource 1, Figs. A5–A8). Woodland was the least or second least selected habitat in all analyses and at all scales. Arable land was the next least selected habitat after woodland. Other habitats were interchangeably selected depending on the scale. Hedgerow was ranked highly when comparing the proportion available at the landscape scale with the proportion within the home range but became less selected when comparing the availability within home ranges with the proportion of tracking fixes in this habitat. Amenity grassland was ranked highly at the local scale but less so at the landscape scale.

There was a difference in habitat selection at the landscape scale on sites with and without badgers (Table 1). On sites with badgers, buildings were ranked first, and on sites with no badgers gardens and hedgerow were ranked above buildings. The mean proportion of buildings included in the hedgehogs’ home ranges at the landscape scale was $3.16 \pm 0.71\%$ on sites with no badgers, and $6.95 \pm 1.25\%$ on sites with badgers. Additionally, on sites with no badgers, arable land was ranked higher than on sites with badgers and amenity grassland was ranked lower. There was no difference between hedgehog habitat selection at the local scale between sites with and without badgers and on sites where badgers were present. At the local scale on sites with no badgers, the mean percentage of fixes in buildings or gardens was $44.1 \pm 4.2\%$ and on sites with badgers $38.1 \pm 3.4\%$. However, on sites with badgers, habitat use was not significantly different from random, possibly due to low hedgehog numbers on these sites.

Table 1 The ranking of habitats selected by radio-tracked hedgehogs when (a) comparing the habitats available at the landscape scale with those in a hedgehog's home range and (b) comparing the habitats hedgehogs were found during radio-tracking with the habitats available within the home range

100% MCP home range selection in the landscape									
Rank	6	5	4	3	2	1	0	<i>p</i>	λ
All	GA >>>	BD >>>	HR >>>	PA >>>	AM >	AB >	WD	0.002**	0.29
Males	GA >>>	BD >>>	HR >>>	PA >	AM >	WD >	AB	0.002**	0.03
Females	GA >	BD >	HR >	PA >	AM >	AB >	WD	0.004**	0.11
Badgers	BD >	GA >	HR >	GA >	AM >	AB >	WD	0.002**	0.10
No badgers	GA >>>	BD >	HR >>>	PA >	AB >	WD >	AM	0.002**	0.09
Habitat selection within 100% MCP home range									
Rank	5	4	3	2	1	0	<i>p</i>	λ	
All	BD & GA >	AM >	PA >	HR >	AB >>>	WD	0.004**	0.39	
Males	BD & GA >>>	PA >>>	AB >	AM >	HR >>>	WD	0.024*	0.26	
Females	BD & GA >	AM >	PA >	HR >	AB >	WD	0.14	0.30	
Badgers	BD & GA >>>	PA >	AM =	AB =	WD =	HR	0.18	0.25	
No badgers	BD & GA >	AM >	HR >	PA >	AB >>>	WD	0.06	0.32	

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. Analysis includes 32 hedgehogs with at least 20 radio-tracking fixes. Ranking was carried out following (Aebischer et al. 1993)

AB arable, AM amenity grass, BD buildings, GA gardens, HR hedgerow, PA pasture, WD woodland

At the landscape scale, males and females selected very similar habitats compared with their availability (Table 1). However, the least selected habitat for females was woodland and for males was arable land. At the local scale, for females amenity grassland was ranked higher than for males and for males arable land was ranked higher than for females.

The percentage of hedgehog tracking fixes recorded on arable land varied with site (ANOVA, $\chi^2 = 49.3$, $p < 0.0001$, 3 *df*, Fig. 1). On sites where badgers were present, a lower percentage of tracking fixes was recorded on arable land: $13.7 \pm 5.1\%$ compared with $27.3 \pm 3.8\%$, on sites without badgers. There was no evidence that the percentage of fixes recorded on arable land differed between males and females (ANOVA, $\chi^2 = 0.26$, $p = 0.61$, 1 *df*).

Home range size

All home range size estimates increased with distance from buildings (Table 2, Fig. 2, Online Resource 1; Figs. A9–12). Home range size also varied between sites and this was statistically significant when home range was measured by 100% MCP (Table 2, Fig. 3). Where badgers were present, hedgehogs had smaller

home ranges when measured by 100% MCP (Table 2, Fig. 3). On sites with badgers, hedgehogs had a mean home range of 9.7 ± 1.9 ha compared with a home

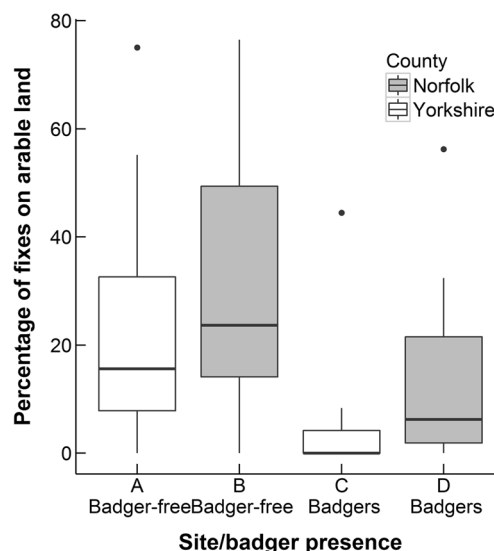


Fig. 1 The significant difference between sites with and without badgers in the percentage of radio-tracking fixes that a hedgehog was found on arable land, in radio-tracking studies carried out on four sites in Norfolk and Yorkshire in July–October 2013 and April–September 2014

Table 2 The results of three 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 by 95 and 50% kernel estimates

Response	Variable	df	F statistic	p value	Effect size	95% CI
100% MCP	Site B NO BADGERS	3, 25	5.75	0.004**	-0.427	-0.968, 0.114
	C BADGERS				-0.452	-1.228, 0.324
	D BADGERS				-0.735	-1.316, -0.154 ^a
	Distance to buildings	1, 25	31.58	<0.0001***	0.028	0.018, 0.038 ^a
	Sex <i>MALE</i>	1, 25	12.20	0.002**	0.699	0.287, 1.110 ^a
	Body mass	1, 25	0.072	0.791	-0.000	-0.002, 0.001
95% Kernel	Site B NO BADGERS	3, 14	2.662	0.088.	-0.608	-1.338, 0.122
	C BADGERS				-0.308	-1.647, 1.032
	D BADGERS				-0.126	-0.871, 0.619
	Distance to buildings	1, 14	20.228	0.0005***	0.030	0.016, 0.044 ^a
	Sex <i>MALE</i>	1, 14	1.800	0.201	0.360	-0.210, 0.931
	Body mass	1, 14	0.391	0.542	-0.001	-0.004, 0.002
50% kernel	Site B NO BADGERS	3, 14	2.999	0.067.	-0.539	-1.205, 0.127
	C BADGERS				-0.150	-1.372, 1.071
	D BADGERS				-0.141	-0.820, 0.538
	Distance to buildings	1, 14	23.732	0.0002***	0.029	0.017, 0.042 ^a
	Sex <i>MALE</i>	1, 14	2.589	0.130	0.391	-0.129, 0.911
	Body mass	1, 14	0.034	0.857	-0.000	-0.003, 0.002

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. Words in *italics* following categorical variables indicate the reference category. Ranges were log transformed before analysis. Site A and female are the reference categories

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

^a Ninety-five percent confidence interval of the effect size does not contain zero

range of 21.9 ± 5 ha at sites without badgers. However as Fig. 3 shows, the site differences in home range size cannot be attributed to badger presence alone; there were also differences between the two sites with

badgers present and the two sites with badgers absent. Males had consistently larger home ranges than females: using 100% MCP, males had a mean range of 21.6 ± 5.8 ha compared with a female range of

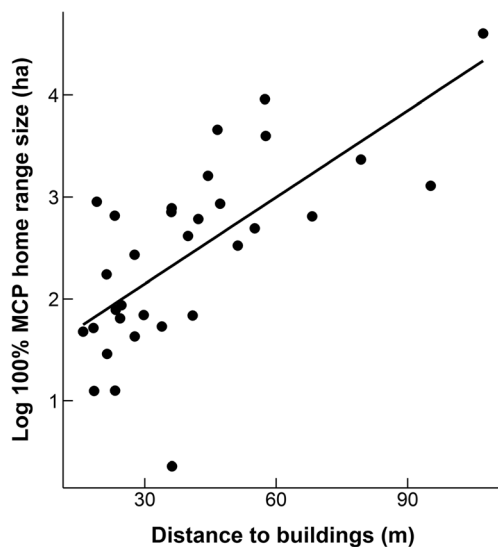


Fig. 2 The significant relationship between the mean distance a hedgehog was found from buildings during radio-tracking and a hedgehog's home range size measured by 100% minimum convex polygons (MCP) on four sites in Norfolk and Yorkshire in July–October 2013 and April–September 2014

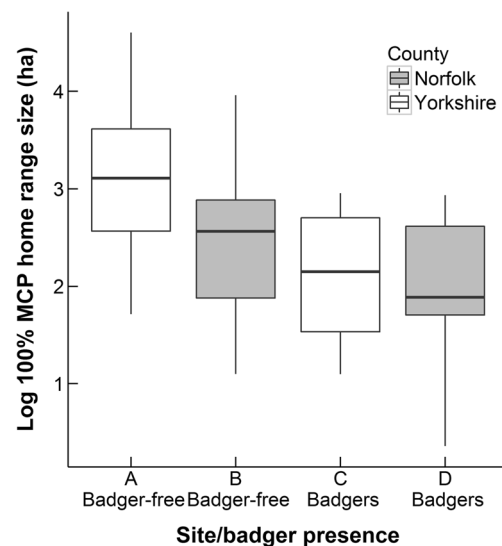


Fig. 3 The significant effect of site, characterised by badger presence, on a hedgehog's home range size measured by 100% minimum convex polygons (MCP) on four sites in Norfolk and Yorkshire in July–October 2013 and April–September 2014

12.4 ± 2.7 ha (Table 2). We found no effect of body mass on home range size (Table 2).

Nesting

The general habitat used for nesting was non-random ($\lambda = 0.37$, $p = 0.002$). Habitats used were ranked as follows: village >>> woodland > pasture > arable, where >>> indicates a significant difference between habitats. Although the mean percentage of village habitat in the hedgehog home ranges was $35.35 \pm 3.41\%$, 60% of the 66 nests studied were within villages. Forty-eight percent of these were constructed in scrub, 25% in buildings (e.g. under garden sheds or in hay barns) and 23% in hedgerows. Nests in hedgerows in villages were in the hedgerows of amenity grassland or garden hedgerows. Across the four villages, 28% of hedgerows were predominately conifer species, 19% privet (*Ligustrum* sp.) and 19% hawthorn (*Crataegus monogyna*). Only eight nests were constructed in arable fields and eight in pasture fields. When farmland was used, hedgerows were by far the most chosen habitat, 75% of nests, and were predominately hawthorn (*C. monogyna*) and blackthorn (*Prunus spinosa*) with brambles (*Rubus fruticosus*). Day nest sites were frequently observed to be situated towards the centre of home ranges (Online Resource 1, Fig. A13).

The mean total width of the hedgerow was wider in farmland hedgerows in which hedgehogs nested than hedgerows hedgehogs were not observed nesting in, but this was only near significance in a logistic regression (Fig. 4, $z = 7.13$, $p = 0.08$). 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.

Distance to habitat features

On the two sites where badgers were present, hedgehogs were found a mean distance of 4.7 ± 1.1 m closer to cover, 13 ± 1.7 m closer to hedgerows and 7.2 ± 3.5 m closer to buildings (Fig. 5, Table 3), than on the sites without badgers, although the analysis of distance to buildings was not statistically significant. When ambient temperature was lower, hedgehogs were found further from cover (Table 3). There was no evidence for a difference in the distance found to any of these features between males and females (Table 3).

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 ($t_{1,246} = 36.6$, $p < 0.0001$). The actual fixes were found



Fig. 4 The width of hedgerows selected or not by nesting hedgehogs on four sites in Norfolk and Yorkshire. Hedgerow width was near statistical significance in determining whether hedgehogs nested in a hedgerow or not (logistic regression, $z = 7.13$, $p = 0.08$)

a mean of 728 ± 16 m to badger activity compared with 473 ± 23 m for the randomly generated points (Online Resource 1, Figs. A14 and A15).

Discussion

Our aim was to examine the contribution of four expected drivers of hedgehogs' selection of rural villages in arable landscapes. Firstly, we confirmed that hedgehogs selected rural villages over the surrounding predominantly arable farmland. Buildings and gardens were most the selected habitat

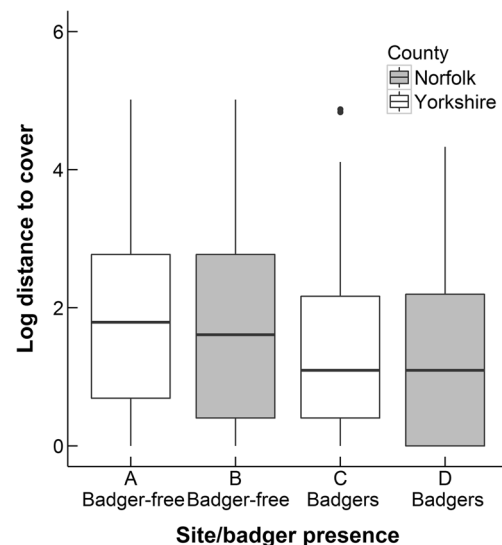


Fig. 5 The significant difference between sites with and without badgers in the distance hedgehogs were found to cover, including hedgerows, scrub and shrubs, during radio-tracking studies carried out on four sites in Norfolk and Yorkshire in July–October 2013 and April–September 2014

Table 3 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	3, 55	3.088	0.034*	0.443	−0.290, 1.195
	BADGER-FREE				−0.025	−1.006, 0.975
	C BADGERS				−0.860	−1.725, 0.007
	D BADGERS				−0.011	−0.061, 0.039
Distance to cover	Ambient temperature	1, 9–14	0.180	0.672	0.137	−0.475, 0.760
	Sex <i>MALE</i>	1, 50	0.196	0.660	0.137	−0.475, 0.760
	Site B	3, 53	3.428	0.023*	−0.216	−0.562, 0.127
	BADGER-FREE				−0.652	−1.122, −0.191 ^a
Distance to building	C BADGERS				−0.462	−0.864, −0.064 ^a
	D BADGERS				−0.039	−0.066, −0.012 ^a
	Ambient temperature	1, 8–86	7.908	0.005**	0.128	−0.155, 0.414
	Sex <i>MALE</i>	1, 48	0.804	0.374	0.246	−0.207, 0.702
Distance to building	Site B	3, 59	2.536	0.065	−0.508	−1.104, 0.098
	BADGER-FREE				−0.199	−0.738, 0.332
	C BADGERS				−0.012	−0.039, 0.015
	D BADGERS				0.233	−0.144, 0.616
Distance to building	Ambient temperature	1, 9–04	0.757	0.384	0.233	−0.144, 0.616
	Sex <i>MALE</i>	1, 55	1.498	0.226	0.233	−0.144, 0.616

Words in italics following categorical variables indicate the reference category. The reference site, site A, was badger-free

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

^a Ninety-five percent confidence interval of the effect size does not contain zero

compared with their availability at the landscape and local scale, and arable land, along with woodland, was under-selected compared to its availability.

Hedgerow was ranked highly when comparing the proportion available at the landscape scale with the proportion within the home range but became less selected when comparing the availability within home ranges with the proportion of tracking fixes in this habitat, unlike in previous studies (Hof and Bright 2010b). It may be that hedgerows are only heavily used when hedgehogs are on arable land, as cover from predation (Hof et al. 2012), whereas 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 the centre of hedgerows during nightly tracking (mean percentage of area that was hedgerow at the landscape scale on the four sites: $1.83 \pm 0.05\%$, mean percentage of hedgerow at the home range scale: $3.36 \pm 0.22\%$). 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.

Amenity grassland was ranked highly at the local scale compared with its availability in the home range, but less so at the landscape scale. Hedgehogs were frequently observed foraging on football pitches, playparks and cricket pitches in the villages. On one site (site C), the most frequently used foraging habitat was a mowed grass strip in the centre of an arable field used for flying model aircraft. These findings indicate that amenity grassland is a valuable foraging habitat for hedgehogs and could explain why hedgehogs select villages. Hedgehogs were also frequently located at food left out specifically for hedgehogs or for pets, indicating that supplementary food availability is also important in determining hedgehog habitat use (Hubert et al. 2011; Pettett 2016).

At the local scale, for females amenity, grassland was ranked higher than for males and for males arable land was ranked higher than for females. Females tend to be more

sedentary than males and focus on foraging and raising young, whereas the strategy of male hedgehogs is to move around trying to locate females to mate with (Reeve 1994). This idea explains why females selected amenity grassland to a higher degree compared to its availability as this appears to be a key foraging habitat for hedgehogs. This is supported by the larger home range sizes of males. Also, males were observed to cross arable land more frequently, e.g. to move between villages.

The first of our four hypotheses asserted that hedgehogs residing in villages would have smaller home ranges than those that selected arable land. 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. We speculate that this finding may be due to a lower availability of resources, i.e. lower earthworm abundance, on arable land than on mowed grass habitats in rural villages (Doncaster 1992; Doncaster 1994; Doncaster et al. 2001), and the availability of supplementary food, which might require hedgehogs to forage further on arable land. Increased locomotion may be energetically costly (Kenagy and Hoyt 1989; Covell et al. 1996) and this could be a driver of hedgehogs' preference of villages (Pettett et al. 2017). However, further study of prey availability in rural villages compared with arable land is needed to substantiate this. Home range size may also be negatively correlated to the density of a population (Wolff 1985; Trehwella et al. 1988; Moorhouse and Macdonald 2008). In this study, the sites where hedgehogs had the largest home ranges (sites A and B) had the highest densities of hedgehogs. It could be that hedgehogs in villages with higher numbers of hedgehogs spill out onto the surrounding arable land in search of food.

This study also provides support for our second hypothesis; that hedgehogs prefer to build day nests in villages rather than on arable land. Village habitats were ranked as the most selected habitat for nesting. 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 provides evidence that nest sites may be more secure in villages, although human disturbance of nests in villages is potentially problematic. These results indicate that nest site choice may be a factor in determining hedgehogs' selection of rural villages. However, we did not measure nest site availability in this study and so it is not clear whether hedgehogs nested in villages due to the variety and structure of available nest sites or whether they were simply nesting close to good foraging habitat. Nest sites tended to be reasonably central within the home range (Online Resource 1, Fig. A13) and therefore it is likely that food availability plays a part in their selection. However, it could be argued that hedgehogs simply forage close to good nesting sites.

Hedgerows were still selected for nesting 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. There was a relationship between increasing hedgerow width and increasing likelihood of hedgehogs nesting in it, but this relationship was not statistically significant, possibly because the number of hedgerows utilised on arable farmland was low compared with those not utilised (20 not used, 8 used). The UK Biodiversity Action Plan hedgerow 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 $3.18 \pm \text{SE } 0.33$ m compared with $2.78 \pm \text{SE } 0.25$ 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 investigate this further.

The third of our four hypotheses asserted that when badgers are present hedgehogs will avoid arable land and therefore be found closer to buildings and cover. This study demonstrated that on sites with badgers, hedgehogs stayed closer to buildings and had a lower percentage of radio-tracking fixes on arable land than hedgehogs on sites without badgers. Hedgehogs have previously been shown to stay closer to cover in the presence of badgers on four further sites in England by Hof et al. (2012) and studies of other small mammals also show a trade-off between prey availability and distance to cover in the presence of predators (Lima and Dill 1990; Kotler et al. 1991; Hughes and Ward 1993; Orrock 2004). We can conclude that hedgehogs may perceive a greater threat from badger presence further from cover, on sites where badgers are present.

Hedgehogs on sites with badgers had smaller home ranges (when calculated by 100% MCP) than hedgehogs on sites without badgers, regardless of the number of radio-tracking fixes they were observed to be on arable land, suggesting that hedgehogs have restricted movement when badgers are present, even in village habitats. Furthermore, on the two badger-occupied sites, buildings were ranked before gardens and hedgerows at the landscape scale and vice versa when badgers were absent. Finally, the hedgehogs tracked in this study were found further from badger activity than a randomly generated set of tracking fixes. These results support the notion that predator avoidance is one possible cause of hedgehogs' selection of rural villages (Micol et al. 1994; Laundre et al. 2010; Hof et al. 2012). However, badger presence was not the only cause of the site differences in home range size, there were differences between the two sites with badgers and the two sites without, plausibly due to other differences between the sites such as resource availability. Additionally, on sites without badgers, buildings and gardens were still the most selected habitat.

There were no confirmed predation events by badgers during this study as in previous studies of hedgehogs on arable land (Hof and Bright 2010a). Therefore research into the

mechanism behind the effect of the negative relationship between badgers and hedgehogs is needed, such as following badger and hedgehog movements at the same time to assess the frequency of predation events and how often hedgehogs and badgers come into contact. Resource availability will play a key role in this relationship. For example, hedgehogs on site D did move away from the village to forage on the grassy model plane airstrip even though this was closer to badger activity. Road deaths were the highest cause of mortality in the study and could potentially impact on rural hedgehog populations (Wembridge et al. 2016).

We found no evidence for our final hypothesis; that hedgehogs may be attracted to the warmer microclimate in rural villages than on the surrounding farmland. Hedgehogs were in fact found further from cover when it was colder. The reason for this finding is unclear; it may be a result of hedgehogs travelling further from cover to find macroinvertebrates, which are scarce in colder weather (Crawford-Sidebotham 1972; Edwards and Bohlen 1996; Honek 1997). 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. Future study should include the effect of humidity and rainfall on ranging behaviour.

Summary

Our evidence indicates that hedgehogs preferentially select rural villages rather than open farmland, particularly arable land. We speculate that the availability of natural and supplementary prey may be one reason hedgehogs are attracted to rural villages. This is supported by the finding that hedgehogs that spent more time closer to buildings had smaller home range sizes. Further research into prey availability 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 the surrounding arable farmland. We also found some evidence that badger presence alters hedgehog habitat use, increasing their association with buildings and cover, suggesting that badgers may be another potential cause of hedgehogs' preference for rural villages. However, on sites with no badgers, hedgehogs also selected buildings and gardens over any other habitat type.

Our research confirms 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, for example by improving garden management and preserving green spaces and secondly, improving the

surrounding arable land, chiefly in respect to cover from predation and connectivity between rural villages. Although this research shows that residential areas are selected by hedgehogs, hedgehogs are also in decline in urban areas (PTES and BHPS 2015) and villages and face a suite of problems which were beyond the scope of this study including the following: poisoning from molluscicides and rodenticides (Keymer et al. 1991; Dowding et al. 2010b), a lack of habitat connectivity due to enclosed gardens (Hof and Bright 2009) and deaths on roads (Huijser and Bergers 2000; Rondinini and Doncaster 2002). Wildlife friendly gardening and the consideration of habitat connectivity in urban planning may reduce some of these threats to hedgehogs (Hof and Bright 2009). On arable land, increasing hedgerow length and quality will offer cover from badger predation (Hof et al. 2012; this study), and provide nest sites (Haigh et al. 2012) 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, for example small mammals (Fitzgibbon 1997; Kotzageorgis and Mason 1997; Baker and Harris 2007; Gelling et al. 2007), birds (Green et al. 1994; MacDonald and Johnson 1995; Cornulier et al. 2011) and amphibians and reptiles (Ficetola and De Bernardi 2004; Salazar et al. 2016).

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