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Habitat selection, philopatry and spatial segregation in rural Irish hedgehogs (*Erinaceus europaeus*)

Abstract: As a non-territorial species with no known dispersal period, there are no obvious factors that regulate hedgehog numbers in an area. This study aimed to examine these factors and involved the radio-tracking of rural hedgehogs over a 3-year period. Males had a significantly larger mean annual home range (56 ha) than females (16.5 ha), which was at its maximum during the breeding season. Outside of the breeding season, the home range was relatively small (4–5 ha) in both sexes. The home ranges of males completely overlapped both each other and all of the females. In contrast, females occupied more exclusive areas with little overlap between one another. On a nightly basis, both sexes occupied spatially independent areas with little overlap. Compositional analysis of the data showed that habitats were not used in proportion to their availability but were selected, and this changed seasonally, with the highest preference being for garden and arable land. Hedgehogs tagged for consecutive years exhibited site philopatry and followed the same pattern of habitat selection annually. It is suggested that the spatial separation observed amongst individual hedgehogs could restrict numbers in an area and that female numbers reach a carrying capacity before that of males.

Keywords: carrying capacity; habitat selection; home range; sex differences; spatial separation.

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Introduction

Burt (1943) defined home range in mammals as the area traversed by an individual in its normal activities of food gathering, mating and caring for the young. The importance of these activities changes on a seasonal basis and Kristiansson (1984) noted that, in Sweden, male hedgehogs increased their home range during the breeding season in order to encompass the range of as many females as possible. Hedgehogs [*Erinaceus europaeus* (Linnaeus)] are non-territorial, have a promiscuous mating strategy (Reeve 1994) with reports of multiple paternity (Moran et al. 2009) and a home range overlap has been observed in both sexes in the UK (Reeve 1982). Huijser and Bergers (2000) found that females increased their home range just prior to hibernation, a time when gaining enough weight to survive hibernation became a priority. Home range estimates for hedgehogs have ranged from 2–5 ha in the UK (Morris 1986) to 29.08 ha in Italy (Boitani and Reggiani 1984) for females in rural areas and 32 ha for males in suburban England (Reeve 1982) to 96 ha in rural Denmark (Riber 2006) for males. On a nightly basis, males have been reported to move further than females (Morris 1986, Dowding et al. 2010).

In Ireland, there had been no research into the ecology of the hedgehog. Hof (2009) established that hedgerows and field margins were positively selected by hedgehogs at both the landscape and home range levels. In the study of Boitani and Reggiani (1984) in Italy, the most frequented environments were wet meadows (36.5%). Micol et al. (1994) and Doncaster (1994) reported that hedgehogs tended to be abundant in pasture, whereas Young et al. (2006) observed that hedgehogs were extremely scarce in pasture fields, with only six individuals captured in three of 82 fields sampled. It appears, therefore, that hedgehogs use a variety of rural habitats. However, arable, marsh and coniferous woodland have represented the lowest rank of habitat preference in the majority of studies (Dowie 1987, Doncaster 1994, Huijser 2000, Doncaster et al. 2001, Riber 2006). Wildlife inhabiting farmland, especially arable ecosystems, is in widespread and severe decline throughout much of northern, western and central Europe (Sotherton 1998). This may not be surprising as modern intensively farmed arable land does not provide high-quality habitat for the great majority of invertebrates (Meek et al. 2002), which would also affect their predators. For example, earthworms [*Lumbricus terrestris* (Linnaeus)], which are an important prey item for hedgehogs (Yalden 1976), generally occur at a lower density in arable land than pasture (Kruuk 1979). Hedgerow also persists least well in districts where arable farming prevails (Pollard et al. 1974). As the farming industry in the UK became more specialised during the latter half of the last century, many mixed farms began to specialise in arable production. This change in practice contributed to the loss of approximately half of Britain's hedgerows (Croxton et al. 2004).

Hedgehogs have been reported to be on the decline in the UK (Dowding 2007, Hof 2009), and the intensification of agriculture is considered to be a major contributor to this decline (Hof 2009). This study aimed to examine the home range size and spatial distribution of individual hedgehogs in a mixed agricultural landscape in Ireland, which is lower intensity and has more hedgerows than have been found in previous research. It aimed to identify seasonal habitat selection. By identifying these trends, some of the driving factors that regulate hedgehog numbers could be examined.

Materials and methods

Site

The study was performed between September 2008 and June 2010 on a site (51°53'59.5''N latitude, 8°29'03.7"W longitude) 36.8 km from Cork city and 5.3 km from the nearest town of Bandon, Ireland. The site of 97 ha (Figure 1) consisted of 23% arable, 64% pasture, 7% residential garden, 1% scrub, 1% marsh and 4% wood.

Figure 1 Study area in Ratharoon, County Cork, Ireland displaying the habitat types at the site.

Capture and marking

Hedgehogs were captured by hand with the aid of spotlights. All individuals were marked using a unique colour combination of heat-shrink plastic tubes (R.S. Components Ltd., Northants, UK) which were attached to the spines with glue (Evo-Stik, Evode Ltd., Stafford, UK). Fifteen were applied to three specific regions (left of head, centre and right of head) on each animal. Reflective tape (CH Marine, Cork, Ireland) was also attached to one of the middle markers so that the head region could be identified while tracking. The tubes acted as a visual aid and hence minimised the need to recapture the animal each time for individual identification. For permanent identification, individuals were also marked using passive integrated transponder (PIT) tags (MID Fingerprint, Bournemouth, Dorset, UK) inserted into the upper hind leg (Doncaster et al. 2001, Jackson et al. 2004). All procedures were performed in accordance with current regulations; licenses were obtained from the Department of Environment, Heritage and Local Government.

Radio-tracking

From September 28, 2008, hedgehogs were fitted with 173 MHz, R1-2B transmitters (Holohil Systems Ltd., Carp, ON, Canada) attached to the animal in the manner of Jackson and Green (2000), i.e., Velcro was sown around the radio transmitters and attached to a clipped area of spines, to which a corresponding piece of Velcro was glued. The entire tag weighed 10 g and was 0.94% of the mean weight of the adult hedgehogs and 3.57% of the weight of the smallest juvenile. The batteries on these tags lasted for a minimum period of 6 months.

Hedgehogs were tracked using a SIKA receiver (Biotrack Ltd., Wareham, Dorset, UK). When the hedgehog was located, its position, determined using Garmin GPS 60 (CH Marine, Cork, Ireland), and its behaviour were recorded before locating the next tagged individual. Depending on the distance between individuals and the number of hedgehogs being monitored, a mean of between 6 (±0.01) (SE) and 21 (±0.16) fixes were obtained per individual per night. On average, a fix would be obtained at a minimum frequency of once an hour for each individual. In 2008, eight hedgehogs (4♂, 4♀) were monitored continuously throughout the night, i.e., from dusk until the animals returned to their nests at dawn for a period of 33 nights (160 h). Six of these hedgehogs were monitored throughout hibernation and again upon emergence. In 2009, 16 hedgehogs (12♂, 4♀) were monitored for either the first 6 h of the night after emergence or the 6 h before dawn over a period of 104 nights (624 h). In 2010, six hedgehogs (5♂, 1♀) were monitored for 38 nights (76 h). Ten (42%) of the hedgehogs were tracked for periods between 2 and 3 years.

Home range

Due to the fact that hedgehogs were tracked from September in 2008 and from March–November 2009, the home range was calculated from the 2009 fixes only. Home ranges were estimated using the 100% minimum convex polygon (MCP) and the 95%, 90% and 50% kernel method, using the Hrt extension for Arc map version 9.2x (Rodgers and Carr 1998). The two methods were used as MCPs do not indicate how intensively different parts of an animal's home range are utilised, whereas kernel methods allow a better determination of centres of activity (Worton 1995, Seaman and Powell 1996).

Seaman et al. (1999) recommended that home range studies utilising kernel estimates use least squares cross validation to determine the amount of smoothing and obtain a minimum of 30 (but preferably 50) observations per animal. Therefore, in this study, the least squares cross validation was used to select the smoothing parameter, and the home range was calculated for four adult males, three adult females and four juvenile males, all of which had >50 fixes.

Habitat selection

Patterns of habitat selection were investigated using compositional analysis, version 6.2 plus (Smith 2005). This technique uses Manova/Mancova type linear models (Aebischer et al. 1993). The significance of Wilks' λ and of t-tests is determined by randomisation tests and determines whether the habitat was selected or used in conjunction with its availability (Smith 2005). MCP (100%) was used to determine the outer limits of an individual hedgehog's home range. The proportion of each habitat available to the hedgehog within its home range was determined using digitalised ortho-photographs (Ordnance Survey of Ireland) of the site using the geographic information system (GIS) software ArcMap, version 9.2. The habitat type was confirmed by physical inspection of the site, and the proportion calculated in ha using Arc GIS software.

Data analysis

GPS positions were plotted onto ortho-photographs (Ordnance Survey of Ireland) of the area using the geographic information system (GIS) software ArcMap, version 9.2. Means are followed by the ±standard error (± SE) unless it is stated otherwise. Tests for normality were performed on Brodgar software for univariate and multivariate analysis and multivariate time series analysis, version 2.6.3. PASW Statistics, version 17 was used for all further statistical analysis.

Results

Home range in 2009

The mean annual home range size (±SE) calculated by the 100% MCP method was 16.5 (±0.5) ha for adult females and 56.0 (±0.7) ha for adult males (Table 1). Males had a significantly larger annual home range than females (Wilcoxon signed-ranks test: $T=10.000$, $n=8$, $p<0.05$). However, the size of the range of male hedgehogs changed seasonally and was at its maximum during the breeding

Table 1 The mean annual (±SE) home range size (ha) during and after the breeding season for adult females and adult and juvenile males in 2009.

	100% MCP (April–October)	100% MCP (breeding season) (April–July)	100% MCP (outside breeding season)	50% Kernel
Adult females (n=3)	16.5±0.49 (range 0.6–10.8)	4.2±0.16 (range 0.6–10.8)	4.05±0.19 (range 3.1–4.2)	2.4±0.28
Adult males (n=4)	56.0±0.67 (range 3.1–57.4)	15.9±0.16 (range 5.3–57.6)	4.50±0.12 (range 3.1–38.3)	11.1±0.53
Juvenile males (n=4)	6.4±0.28	N/A	2.3±0.13	0.8±0.20

season (April–July) [mean±SE=17.2±0.36 (April) 22.6±0.51 ha (July)] (100% MCP) (Table 1, Figure 2).

In August, when breeding activity terminated, the mean monthly home range of males was reduced to 5.13±0.23 ha (Figure 2). Females were found to maintain a similar monthly home range size throughout the year (Table 1) but also increased during the breeding season, reaching a peak in June (5.8±0.75 ha) (Figure 2).

There was a geographical overlap where both sexes ranged (Figures 3 and 4). However, although the home ranges of males overlapped completely and encompassed the home ranges of all four adult females (Figures 3 and 4), females showed little overlap and occupied mutually exclusive areas (Figure 4). When breeding ceased, the home range overlap was less pronounced, and mutually exclusive areas were occupied by both sexes.

On a nightly basis, individual hedgehogs occupied small specific areas and rarely crossed the path of another individual (Figure 5A and B).

Hedgehogs exhibited philopatry. This is illustrated by an adult female (FA56) who was tracked from June 2008 to March 2010 (Appendix 1) and an adult male (75EC) who was tracked from July 2008 until July 2010 (Appendix 2).

Habitat selection

Using MCP ranges, a comparison of habitat use with habitat availability in the study area indicated that adult hedgehogs did not use the habitat in accordance with its availability (Wilks' lambda: $\lambda=0.18$, $p<0.0001$) but selected certain habitats (Table 2). Overall, garden and arable land ranked as the most favoured habitat by adult hedgehogs, both habitats being used in a proportion greater than their availability. Furthermore, the habitats utilised by adult hedgehogs changed on a seasonal basis (Table 2 and Figure 6A–D).

Figure 3 Fifty per cent (inner circle), 90% and 95% (outer circle) kernel analysis for four radio-tagged adult male hedgehogs (*Erinaceus europaeus*), showing annual overlap of home range from March–November 2009 in Ratharoon, County Cork.

Seasonal variation in habitat use

Hedgehogs followed the same pattern of habitat selection annually. When hedgehogs emerged from hibernation between March and April, they remained in the areas closest to their hibernacula (garden and scrub). From May–July, pasture ranked as the most favoured habitat (Figure 6B) (Table 2). During these months, hedgehogs spent up to 35% of their time engaged in courtship behaviour (29% foraging) (Figure 7). In August, hedgehogs showed a strong preference for garden land (0.5 ha) and made exploratory trips into the adjacent arable land (15 ha) (Figure 6A). In September, when the crop was

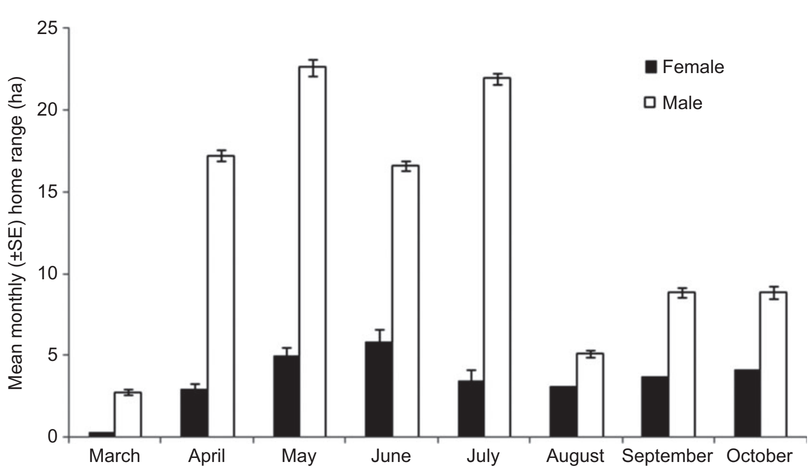


Figure 2 The mean monthly home range (±SE) based on 100% MCP of four adult male hedgehogs (*Erinaceus europaeus*) and four females from March to October 2009.

Figure 4 Fifty per cent (inner circle), 90%, 95% (outer circle) kernel analysis for four radio-tagged adult female hedgehogs (*Erinaceus europaeus*) from March to November 2009 in Ratharoon, County Cork.

harvested, the hedgehogs moved into this arable land permanently (Figure 6A). Hedgehogs remained in this habitat in October, both foraging and day-nesting there (Haigh et al. 2012b). This corresponded to an increase in invertebrates in this habitat (Haigh et al. 2012a). At this time, they devoted the majority (66%) of their activity to foraging (Figures 6C and 7). In late October/November, the hedgehogs moved into areas of scrub to build hibernacula (Figure 6D).

Discussion

In the present study, hedgehogs showed site philopatry and maintained the same temporal pattern of habitat use annually. Males had a mean annual home range (±SE) of 56±0.67 ha and females 16.54±0.49 ha, which is consistent with other research (Reeve 1981, Reeve and Morris 1986, Riber 2006). In the current study, males were found to have a significantly larger home range than females, with males encompassing the range of all adult females during the breeding season. This result has been reported in the majority of studies on hedgehogs (Reeve 1982, Kristiansson 1984, Dowding 2007, Rautio et al. 2009), with the exception of Boitani and Reggiani (1984), who found no significant difference in Italy.

The location of the home range in the present study shifted periodically and so was smaller when calculated on a monthly basis. This emphasises the importance of long-term studies to avoid underestimation. When examined on a monthly and individual level, it was found that the home range of males peaked during the mating period (April–July). This is also supported by road kill data, with a peak in hedgehog deaths occurring from April–July (Kristiansson 1984, Huijser et al. 1998, Smiddy 2002, Haigh et al. unpublished data). Due to their promiscuous mating strategy during the breeding season, it has been suggested that male hedgehogs cover much greater distances on a nightly basis in order to encompass the range of as many females as possible. Both Goransson et al. (1976) and Huijser et al. (1998) reported a preponderance of male hedgehogs as road kill in Sweden and the Netherlands. The males in the current study encompassed the range of all of the females during the breeding season, but when breeding terminated, their home range was much reduced and more similar to females.

Figure 5 Fixes from three adult male (A) and three adult female hedgehogs (*Erinaceus europaeus*) (B) taken over 7 nights from October 5–17, 2008.

Table 2 Habitat selection by hedgehogs for all years combined.

	λ	χ^2	df	p		Rank
March	0.37	8.90	3	0.03	p<0.05	G>S>P>A
April	0.38	10.58	3	0.01	p<0.05	P>G>S>A
May	0.02	49.03	5	0.00	p<0.0001	P>M>W>S>>>G>A
June	0.17	17.56	5	0.00	p<0.01	P>S>W>M>G>A
July	0.34	15.21	4	0.00	p<0.01	P>G>A>W>S
Aug	0.10	27.90	5	0.00	p<0.0001	G>>>P>A>S>>>W>M
Sept	0.45	6.46	2	0.04	p<0.0001	G>A>P
Oct	0.20	11.20	3	0.01	p<0.05	A>G>S>>>P
Nov	0.24	9.94	3	0.02	p<0.05	S>A>G>P
Total	0.18	36.30	5	0.00	p<0.0001	G>A>P>S>>>W>M

Habitats are ranked in order of greatest to lowest preference.
G, garden; S, scrub; P, pasture; A, arable; M, marsh; W, woodland.
>>> refers to a significance of 0.05.

The home range of females remained relatively consistent throughout the year but, like males, reached a peak in the breeding season. Reeve (1982) found that the ranges overlapped considerably and often completely in both sexes. Unlike Reeve (1982), the ranges of the females in the present study did not overlap completely, and instead they occupied mutually exclusive areas among which the males moved throughout the breeding season. However, this may have also been apparent in Reeve (1982) study if statistical analysis had been conducted on core areas, as was the case in the present study.

Although the home range of both sexes fluctuated and shifted throughout the year, when four of the same adult males and three of the females were monitored, the core area of their home range remained the same for 2 consecutive years. Reeve (1982) also found that individuals showed a marked tendency to remain in the same locality from year to year. Greenwood (1980) stated that philopatry will favour the evolution of cooperative traits between members of the sedentary sex and that disruptive acts will be a feature of dispersers. Hedgehogs are non-territorial (Reeve 1994) and have no defined dispersal period (Doncaster 1993). On a nightly basis in the current study, individuals of both sexes occupied specific areas of the habitat and rarely crossed the path of another. Reeve (1982) asserted that, although not territorial, hedgehogs maintained areas through mutual avoidance. This was also apparent in the study of Cassini and Krebs (1994), and they suggested that it could impose a limit on numbers in an area. We also suggest this to be the case.

In the current study, hedgehogs selected certain habitats, and their preference changed seasonally with corresponding shifts in activity patterns. Pasture was selected from April–July 2009 and April–July 2010. This corresponded with a peak in mating behaviour in both years, with individuals spending between 11% (April 2009) and 35% (May 2010) of their time engaged in courtship during

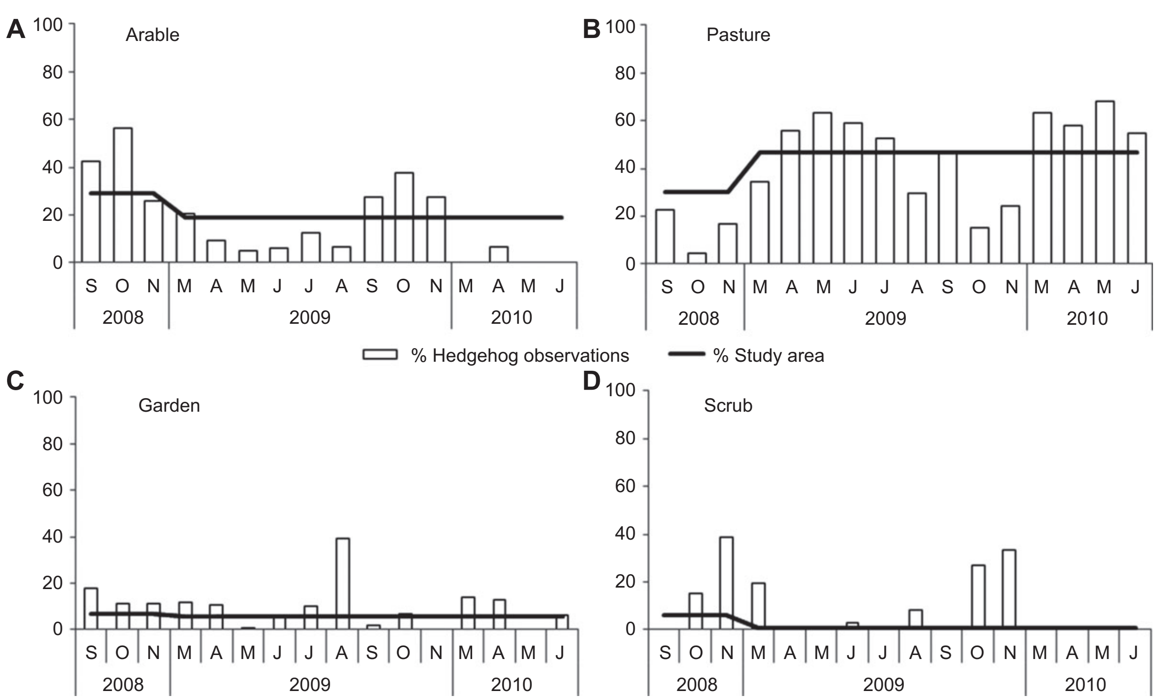
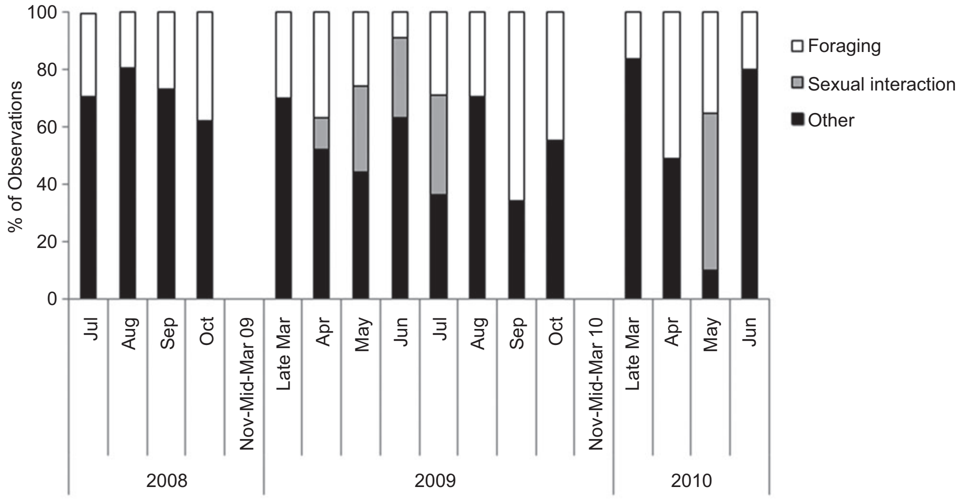


Figure 6 (A–D) Percentage of nightly observations in 2008 (n=1496), 2009 (n=1629) and 2010 (n=146) where adult hedgehogs (*Erinaceus europaeus*) were observed in a habitat relative to the percentage of each habitat type within the study area.



Total number of observations

	2008					2009									2010			
	J	A	S	O	N-M	M	A	M	J	J	A	S	O	N-M	M	A	M	J
Total	47	163	222	702	0	27	166	323	103	420	102	160	160	0	6	47	53	5
Foraging	14	31	60	267	0	8	61	84	9	122	30	106	70	0	1	24	19	1
S.interaction	0	2	0	0	0	0	18	97	29	147	0	0	0	0	0	0	29	0
Other	33	130	162	435	0	19	86	142	65	151	72	54	90	0	5	23	5	4

Figure 7 The percentage of observations per month when 14 adult hedgehogs (*Erinaceus europaeus*) were observed to be engaged in a particular activity (n=observations that month; total=2706). "Other" refers to cleaning, walking and stationary activity.

this period. Prey was low in the pasture in comparison to the adjacent arable land (Haigh et al. 2012a) and after the breeding season, hedgehogs moved out of pasture. Similarly, Doncaster (1994) found that hedgehogs showed seasonal variations in dispersal between fields, which he attributed to the use of certain areas during the breeding season and the distribution of earthworm prey.

In the present study, a peak in the use of the garden was recorded in August. The hedgehogs used habitat close to their nest sites, at least at the start of the night. They often started their night in the garden and made exploratory trips into the adjacent arable land later in the night, before moving into the arable field completely in September and October of 2008 and 2009.

The hedgehog's move onto the arable land in September/October in both years coincided not only with an increase in the density of surface invertebrates (Haigh et al. 2012a) but also to the increased amount of time hedgehogs spent foraging (26% in May 2009 to 66% in September 2009). The high level of activity of the hedgehogs on the arable land was particularly unexpected. Previous studies have shown arable land to be their least preferred habitat (Doncaster 1994, Doncaster et al. 2001, Riber 2006). Comparatively, in the UK, Dowie (1987) found no evidence of hedgehogs on 140 ha of arable land, despite searching for 8 weeks and using a variety of methods. However, in the current study, arable land ranked as the most preferred habitat in October and was the second most preferred habitat overall. Intensively managed arable monocultures have been described as manmade deserts for wildlife (Sotherton 1998). The regular and intensive post-harvest flailing of hedgerows has resulted in some hedges becoming very reduced and sometimes shorter than the crops that they surround (Croxton et al. 2004). Heterogeneity in field margin structure is necessary for the retention of high levels of invertebrate abundance (Sheridan et al. 2008). The retention of hedgerows affects leaf litter, which also has a knock-on effect on invertebrate colonisation (Smith et al. 2008). In Ireland, areas that are predominantly arable still have pockets of grassland mixed in the habitat mosaic, whereas in England, vast areas are devoted almost totally to tillage (Bracken and Bolger 2006). As well as maintaining hedgerows in arable areas, winter stubble is often maintained (Bracken and Bolger 2006), which may also benefit slug numbers (Glen et al. 1989). The arable field in the present study was surrounded by a mosaic of pasture and gardens and had a well-developed hedgerow network, with good ground cover and a boundary strip. These factors appear to have had a positive impact on the density of surface invertebrates (Haigh et al. 2012a) and, subsequently, on the hedgehogs who feed on them.

In November of 2008 and 2009, hedgehogs moved out of the arable field and into areas of scrub to build hibernacula. Both earthworms and molluscs are susceptible to soil moisture and temperature (Getz 1959, Whalen et al. 1998). According to Crawford-Sidebotham (1972), an increase of 2°C in temperature at 90% to 100% in relative humidity causes a marked increase in the expected numbers of active slugs, which are more than doubled in many cases. In light of the effects of even small changes in temperature, it is not surprising that a drop in temperature from 9°C to -1°C on October 29, 2008 resulted in a disappearance in potential prey (Haigh et al. 2012a), which coincided with the movement of hedgehogs out of the arable field and the onset of hibernation.

With the exception of five males caught just once during the breeding season, the remaining 19 hedgehogs were recaptured regularly at the site and were considered resident, maintaining the same area from one season to the next. Casagrandi and Gatto (2002) found that fragmented populations, characterised by a small number of conspecifics inhabiting each patch, are heavily affected by natural and human disturbance, which may lead to local extinctions. Following the deaths of four of the tagged individuals in June 2010, there was no further evidence of hedgehogs at the Irish site, despite regular searching until October 2010. Holt and Keitt (2000) considered that the likelihood of a species being found in a habitat does not just depend upon the local qualities of that habitat, but also upon the overall level of occupancy of habitats at broader spatial scales, which defines a regional pool of source populations available for colonising suitable empty sites. There were a small number of females encountered during the study, and in 2010, the only known female at the site was killed before she successfully reared young. With no known females at the site, males may move out of the area in search of other females and populations may build up elsewhere as a result. We suggest that hedgehogs in the rural Irish landscape exist at the metapopulation level, characterised by subpopulations dependent on small numbers of females.

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Appendix

Appendix 1 Locations of female FA56 for 2008 (black) and 2009 (red).

Appendix 2 Locations of male 45EC for 2008 (black), 2009 (red) and 2010 (yellow).

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