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Intra- and interhabitat differences in hedgehog distribution and potential prey availability

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Abstract

With little previous research on the European hedgehog (*Erinaceus europaeus* Linnaeus) in Ireland, 22 hedgehogs (16 females and six males) were tagged at a rural Irish site between June 2008 and November 2009. Transect, surveying surface invertebrates were carried out in the centre and hedgerow in arable and pasture lands distributed throughout the site. In both years, hedgehogs selected arable land and this coincided with a rise in invertebrate density. This and the fact that within the arable field hedgehogs concentrated their activity where there was a greater density of potential prey suggest that hedgehogs learn the spatial location of prospective food. Contrary to other research, in most of the hedgehogs' home range, individuals consistently foraged in the centre of both pasture and arable lands. Potential prey was lower in fields where the hedgerow had no bramble understory, and this suggests that hedgerow with good ground cover acts as an important reserve for invertebrates. Badgers (*Meles meles* Linnaeus) were seen on 12 occasions within the hedgehogs' home range and they did not appear to have a negative effect on the hedgehogs' use of the site. It was concluded that the main factor affecting the hedgehogs' distribution within each habitat was the availability and accessibility of potential prey.

Keywords: arable; hedgerow; predator-prey interactions; spatial learning; surface invertebrates.

Introduction

Agricultural land is an important habitat for many species in Europe (Stoate et al. 2009). Over the past three decades, changes in agricultural management in the UK have resulted in increased crop and grass production (Chamberlain et al. 2000). However, these agricultural changes that aimed at making farming more cost-effective have had an adverse effect on wildlife (Tapper and Barnes 1986, Hinsley and Bellamy 2000, Donald et al. 2001, Thomas et al. 2001). This drive towards larger, more efficient farms has resulted in a reduction of 50% of the hedgerow stock in the UK (Robinson and Sutherland 2002). However, although hedgerows have lost their function as stock barriers (Croxton et al. 2004), as the farm landscape becomes more and more homogenous, their function in maintaining biodiversity and acting as wildlife refuges has never been more important (Chamberlain et al. 2000, Gelling et al. 2007, Bates and Harris 2009).

As their name suggests, hedgehogs (*Erinaceus europaeus* Linnaeus) are generally associated with hedgerow and edge habitat. In the UK, Hof (2009) found that at the landscape level, hedgerow was ranked as the most important habitat preference by hedgehogs. This tendency for hedgehogs to forage and remain close to the borders of fields has been reported in a number of studies in the UK, Denmark and New Zealand (Reeve 1981, Doncaster et al. 2001, Riber 2006, Shanahan et al. 2007). Hof (2009) reported that in 50% of occasions hedgehogs were located less than 1 m from the edge in arable land.

Boitani and Reggiani (1984) stated that hedgehog abundance was influenced by food availability in an Italian hedgehog population, and this was also reported by Kristiansson (1984) in Sweden. The diet of hedgehogs is mainly insectivorous (Reeve 1994) with most of studies noting high incidences of lepidopteran larvae, earwigs, beetles, spiders, harvestmen, caterpillars, slugs, in addition to earthworms (Campbell 1973, Parkes 1975, Yalden 1976, Wroot 1984). As a hibernating species, hedgehogs are under pressure to gain weight quickly during their active period, and Riber (2006) found that foraging was by far the most time-consuming nightly activity for both sexes of hedgehog.

From the above-cited studies, it would be expected that the distribution of hedgehogs is influenced by the location and abundance of their prey within a habitat. This was investigated as part of a larger study on hedgehog home range and habitat use in a mixed agricultural landscape in southwest Ireland. We set out to test the hypothesis that hedgehogs forage along edge habitat and that this is where prey density is highest.

Materials and methods

Study area

The study was carried out between June 2008 and November 2009 in a mixed agricultural area (51°53′59.5″N latitude, 8°29′03.7″W longitude), 37 km from Cork city and 5 km from the nearest town of Bandon. The landscape in this region is predominantly pasture (ca. 60%) and arable (ca. 25%) (Figure 1). The livestock present was mainly horses.

Surface invertebrate surveys

Arable Potential invertebrate prey were sampled in habitats where hedgehogs were recorded foraging. Within the arable

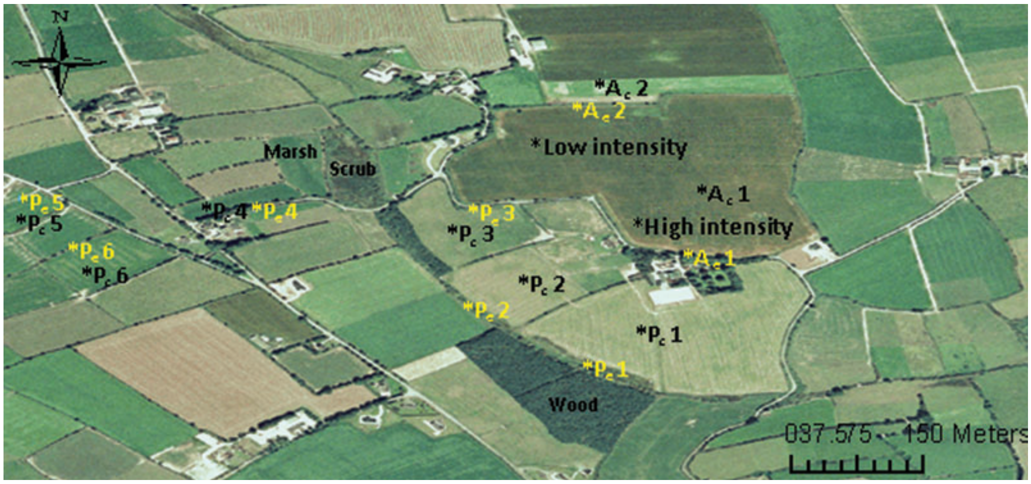

Figure 1 Study area near Bandon, where hedgehogs were active, consisting predominantly of pasture and arable land, with other habitats named. Invertebrates were sampled in areas marked with an *. Surveys carried out along the edge are highlighted in yellow and those in the centre in black.

land, it was noted that hedgehogs consistently foraged in a very small area. Therefore, invertebrates were sampled in areas where a large number of hedgehogs were observed to feed (high-intensity foraging area) and areas where small numbers of hedgehogs foraged (low-intensity foraging area) (Figure 1). In these areas surface prey was counted at weekly intervals, at night, on transects of 60 m×0.46 m. Seventy-two surface transects were sampled in October 2008 and 71 from March to November 2009.

Pasture Weekly invertebrate surveys were carried out from March to November 2009 throughout three areas of pasture land (see P_c1–3 on Figure 1). Three 0.25-m^2 quadrats were placed at random locations along a 60-m transect and the surface invertebrates were quantified. Fifty-four transects were sampled using this method.

Edge/centre During the course of the study, it was observed that the proportion of foraging activity at the centre (>1 m from hedgerow) or edge (<1 m) of a habitat varied across the study area. Therefore, the invertebrate abundance at the edge and centre of habitats was investigated. Three 0.25-m^2 quadrats were placed at random locations along a 60-m transect and the surface invertebrates were quantified as before. Sixteen transects were surveyed on the same night on three occasions in October 2009: six in the centre (P_c1–6) and six along the edge (P_e1–6) of the pasture land; and two in the centre (A_c1–2) and two along the edge (A_e1–2) of the arable land (Figure 1). Identification of molluscs was confirmed by Roy Anderson (Belfast).

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) that 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. The tubes acted as a visual aid and hence minimised the need to recapture the animal each time for individual identification. For permanent identification the animals were also marked using passive integrated transponder tags (MID Fingerprint, Bournemouth, Dorset, UK) inserted into the upper hind leg (Doncaster et al. 2001, Jackson et al. 2004). All procedures were carried out in accordance with current regulations. Licenses were obtained from the Department of Environment, Heritage and Local Government.

Radio-tracking

Hedgehogs were fitted with 173-MHz, R1-2B transmitters (Holohil Systems Ltd, Carp, Ontario, Canada) attached to the animal using the method of Jackson and Green (2000). The entire tag weighed 10 g and was 0.94% of the mean adult hedgehogs' weight and 3.57% of the weight of the smallest juvenile. Continual growth of spines meant that tags fell off and were replaced during the study. No tags remained on the hedgehogs at the end of the study. Hedgehogs were tracked using a SIKA receiver (Biotrack Ltd, Wareham, Dorset, UK). When a hedgehog was located, its position and behaviour were recorded before locating the next tagged animal. During 2008 and 2009, hedgehogs were tracked for a total of 893 h over 160 nights (ca. 6 h per night, 4 nights each week) in the active period (Table 1). Radio-tracking times varied in order that they would occur during the first 6 h after dusk or the 6 h before dawn.

Other mammals

Between June 2008 and June 2010, while spotlighting and monitoring tagged hedgehogs, encounters with, and signs of,

Table 1 The number of hedgehogs (*Erinaceus europaeus*) monitored and sampling effort each year, Co. Cork, Ireland.

Date	Number of hedgehogs	Number of nights	Number of hours	Hours per night
26/6/08–20/11/08	14 (5 females, 9 males)	56	269	5
30/3/09–10/11/09	16 (4 females, 12 males)	104	624	6

other mammals were recorded. Any footprints, faeces and burrows, setts or dens were also recorded and their position plotted on to ortho-photographs (Ordnance Survey of Ireland) of the area using the Geographic Information System software Arc map version 9.2 (ESRI, Redlands, CA, USA).

Data analysis

When means are provided they are followed by the ± standard error, unless otherwise stated. Tests for normality were performed on Brodgar software (Highland Statistics Ltd, Newburgh, UK) 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

Potential prey

Concomitant with the rise in surface invertebrates, in both years, hedgehogs began to concentrate their activity in arable land at the end of September until hibernation (Figure 2). On the arable land there was significantly more potential prey in October 2008 than in 2009 (Z-test: Z=4.513, p<0.01). In October 2008, there was a significantly greater density of molluscs [*Derocerus reticulatum* (Müller), *Derocerus panormitanum* (Lessona and Pollonera), *Milax gagates* (Draparnaud) and *Arion distinctus* (Mabille)] (mean 2.6±0.03 per m^2) than that of earthworms [*Lumbricus terrestris* (Linnaeus)] (mean 0.3±0.01 per m^2) (Z=6.606, p<0.01). Other potential prey in October 2008 consisted of Australian flatworms [*Australoplana sanguine* (Denby)] (mean 0.07±0.005 per m^2) and beetles [*Coleotera* spp. (Linnaeus)] (mean 0.05±0.004 per m^2).

In October 2009, there was a significantly greater density of earthworms (mean 0.6±0.01 per m^2) than that of molluscs (0.02±0.01 per m^2) (Z=2.163, p<0.01). Earthworm density increased from 0.42 per m^2 in July to 0.95 per m^2 in August 2009 (Figure 2). The density of Australian flatworms was reduced (mean 0.02±0.004 per m^2), and beetle density was similar to that in October 2008 (0.04±0.004 per m^2).

A further difference in invertebrate density was noted within the arable land. There was a significant variation in the density of potential prey in low-density and high-density foraging areas ($F_{1, 142}$=17.429, p<0.01). The density of surface invertebrates was significantly higher in high-density foraging areas than in the low-density foraging areas

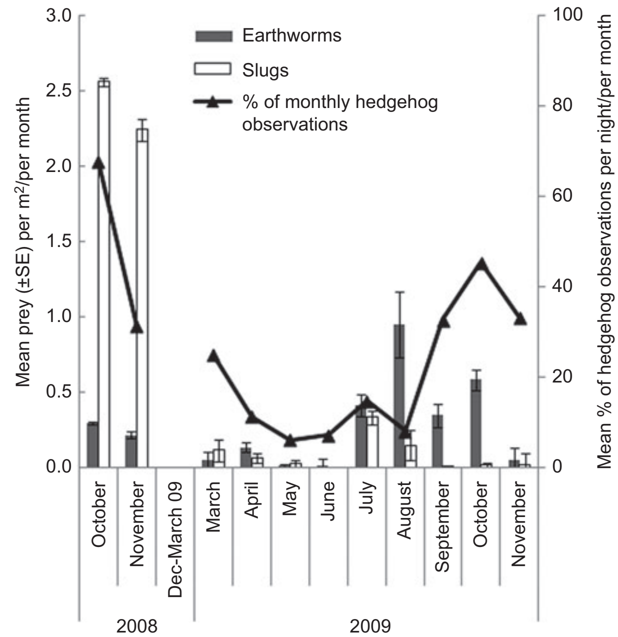

Figure 2 Occurrence of hedgehogs (*Erinaceus europaeus*) on arable land in relation to the density of potential prey. Percentage of all hedgehog observations (n=all hedgehog observations over 6 h per night for 4 nights each week/month) in 2008 and 2009 on arable land (1225 observations) vs. the mean density of earthworms and slugs (no. per sqm) (143 transects).

(Z=3.48, p<0.01). There was a mean of 3.48 invertebrates per m^2 in the high-density foraging areas within the field in 2008 and 0.97 per m^2 in the low-density foraging areas (Figure 3). A lower density of surface invertebrates in the arable field was evident in 2009, but again most were found in the high-density foraging areas (mean number of 0.025 vs. 0.016 per m^2) (Figure 3).

Hedgehog activity coincided with surface invertebrate density. There was significantly more hedgehog activity in

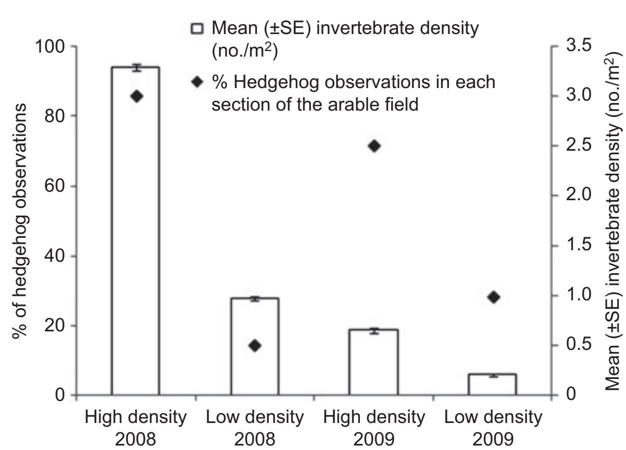

Figure 3 Mean (±S.E.) invertebrates per m^2 (n=143 transects) and the distribution of hedgehog (*Erinaceus europaeus*) activity (%) in the arable field.

the areas of high prey density (Mann-Whitney test: U=23.5, p<0.01) (Figure 3). Only one adult female concentrated her activity in the low-density foraging area of the arable land with 100 observations in this area in comparison to 62 in the high-density foraging zone. The other observed hedgehogs (n=9) concentrated their activity in the high-density foraging area (812 observations), with only 134 observations in the low-density foraging area (Figure 3). This corresponded to the recorded abundance of potential prey (Figure 3).

During the course of the study, it was observed that the proportion of foraging activity at the centre or edge ($F_{1, 130}$= 8.738, p<0.01) of a habitat varied across the study area ($F_{1, 130}$=7.701, p<0.01) (two-way ANOVA). Hedgehogs spent significantly more time in the centre of the field than along the edge in pasture land P1–3 (t-test; t=2.859, df=30, p<0.01) and arable land A1–2 (t-test: t=2.770, df=24, p<0.01) (Figures 4 and 5). However, in pasture P4–6, the hedgehogs spent significantly more time along the hedgerow than in the centre of the field (t=1.747, df=12, p<0.01) (Figure 4).

The hedgerow structure was different in the two areas of the study site. In P1–3 and A1–2, the hedgerow was dominated by a bramble (*Rubus fruticosus* aggregate) understory. In contrast, the hedgerow around P4–6 was made up of Hawthorn trees [*Crataegus monogyna* (Jacq.)] with no understory vegetation.

There was a significant variation in the distribution of prey within each habitat ($F_{1, 106}$=22.854, p<0.01). Surface invertebrate density was greater under the hedgerow than in the centre (Z=4.419, p<0.01) in all areas (P1–3, A1–2 and P4–6) (Figure 5). This corresponded to where the hedgehogs spent their time in P4–6 only (Figure 4). In both the arable A1–2 and pasture P1–3, hedgehogs concentrated their activity in the centre (Figure 4) despite greater prey availability at the edge (Figure 5).

The distribution of prey also varied across the site. The relative abundance of surface invertebrates was greatest in arable A1–2 (Figure 5). Both pasture P1–3 and arable A1–2 had a significantly higher abundance of invertebrates in the centre of the field than in the other pasture area (P4–6) (Z=2.438, p<0.01) (Figure 5).

Other mammals

Rabbits (*Oryctolagus cuniculus* Linnaeus) and foxes (*Vulpes vulpes* Linnaeus) were seen on a nightly basis, with burrows and dens located throughout the study site. These rabbit burrows were utilised by hedgehogs on five occasions (Haigh 2011). Hares (*Lepus europaeus* Linnaeus) and stoats (*Mustela erminea* Linnaeus) were also found to utilise the site. Badgers (*Meles meles* Linnaeus) were recorded on 12 occasions from 2008 to 2010, and both species were seen foraging in the same areas of the site. In addition to these visual sightings, badger footprints and faeces were also seen throughout the site.

Discussion

Contrary to the findings of other studies, hedgehogs were observed significantly more often in the open central areas of arable A1–2 and pasture P1–3 in the present study. It has been suggested that hedgehogs forage close to hedgerow as this may offer a refuge from badgers, which are known to forage more in the open (Neal and Cheeseman 1996, Hof 2009). Although areas of cover may represent areas of refuge from predators, cover may also be perceived by prey species as being dangerous because it conceals predators and detection rates are reduced (Cresswell et al. 2010). Although an increased risk of predation at hedgerows may explain the foraging activity of the hedgehogs in the current study, there are only a small number of potential avian predators in Ireland. The eagle owl [*Bubo bubo* (Linnaeus)] is a significant predator of hedgehogs in areas of Europe where the two species coexist (Marchesi et al. 2002, Penteriani et al. 2002). In France, hedgehogs were amongst the most common mammalian prey consumed by

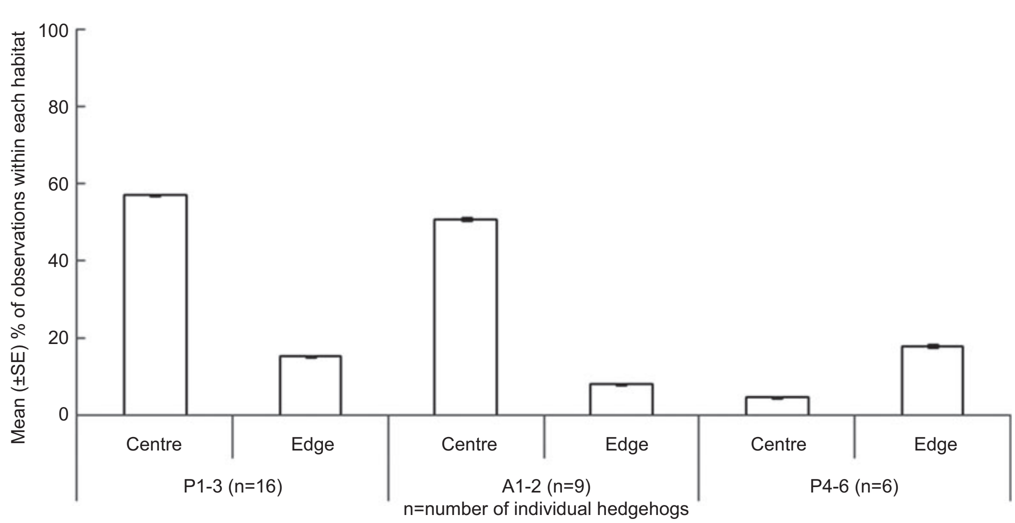

Figure 4 The mean (±S.E.) percentage of hedgehog (*Erinaceus europaeus*) observations within each habitat.

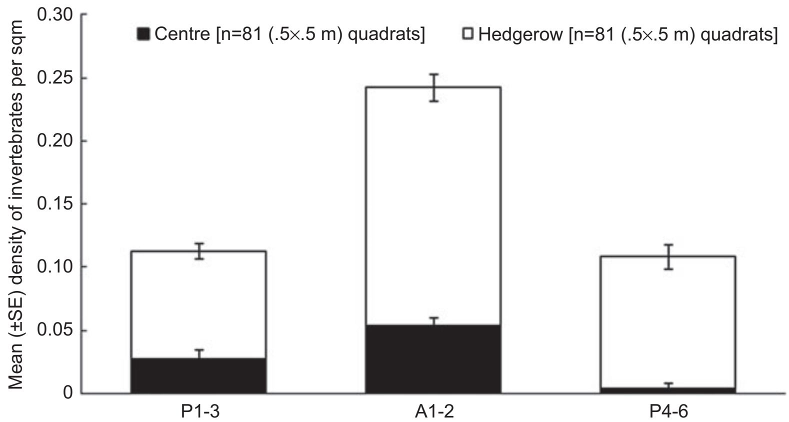

Figure 5 Mean invertebrates (±S.E.) per m^2 in hedgerow vs. the centre of the field in four areas in 2009.

eagle owls (Penteriani et al. 2002) and hedgehogs also dominated their prey in Italy (Marchesi et al. 2002). The eagle owl is absent in Ireland; and while the golden eagle [*Aquila chrysaetos* (Linnaeus)], which feeds predominantly on hedgehogs in Sweden (Tjernberg 1981), was reintroduced to Ireland in 2001 (O'Toole et al. 2002), this is currently restricted to small areas to the north and southwest of Ireland. Of the other possible avian predators in Ireland, the hedgehog is probably too large for the barn owl [*Tyto alba* (Scopoli)] (Yom-Tov and Wool 1997). Furthermore, hedgehogs have shown a significantly stronger attraction to edge habitat, moving along hedgerows in studies where large avian predators are present, e.g., Denmark (Riber 2006), as well as areas where they are not, e.g., UK (Reeve 1981, Doncaster et al. 2001, Shanahan et al. 2007, Hof 2009).

In the current study, pasture P1–3 was grazed by horses. As observed in the present study, horses in pastures are known to establish a pattern of shortly grazed patches, relatively free of faecal droppings, and ungrazed taller patches, where horses preferably defecate and urinate (Lamoot et al. 2004). As a result, vegetation is longer in these latrines (Loucougaray et al. 2004). Meek et al. (2002) reported that grazed swards were generally more impoverished than tall swards. The horse manure may have caused higher nutrients in these areas and a consequential greater number of earthworms that subsequently attracted hedgehogs to these areas, and both hedgehogs and badgers were observed feeding on earthworms in these taller patches. However, hedgehogs were also found to spend significantly more time in the centre of the arable field than along the hedgerows. Although this was clearly not a result of variation in nutrients due to horses, the hedgehogs again appear to have been affected by the distribution of potential prey. The fact that hedgehogs utilised the arable field at all was surprising, as in previous studies this habitat has been found to be avoided by hedgehogs (Dowie 1987, Doncaster 1994, Doncaster et al. 2001, Riber 2006). Hof (2009) reported that hedgehogs rarely selected arable land in the UK, but when they did the distance to the hedgerow was less than 1 m on 50% of occasions. In Ireland, Curry et al. (2002) reported earthworm populations of up to 1160 individuals per m^2 in soil samples from a wheat clover plot. However, in Sweden, although only one earthworm per m^2 was recorded in arable land, the density was found to be higher in soil samples from the centre of fields (Lagerlöf et al. 2002). Earthworms disperse along the soil surface over significant distances at night (Valckx et al. 2009), and these nightly movements along the surface make them particularly susceptible to hedgehog predation (Yalden 1976).

In the present study, slugs, particularly *Derocerus reticulatum*, were the most common invertebrate found along the surface transects in the arable field. *Derocerus reticulatum* is a serious pest of crops (Cook et al. 1996), feeding on fresh green plant material in arable habitats (Cook et al. 1997). It is therefore not surprising that in the current study, they were one of the dominant surface invertebrates found along transects, as the arable field had a well-established hedgerow with good ground cover, an uncultivated boundary strip and winter stubble, factors that are reported to increase slug abundance (Glen et al. 1989, Hegarty and Cooper 1994). However, their nightly location in the centre of the field is surprising, as although Cook et al. (1997) found that *D. reticulatum* may travel a few metres during a night's foraging, spending the following day in a refuge, the centre of the field offers little daytime protection and allows little time to travel back to the hedgerow. Most of the slugs found were juvenile (Anderson, pers. comm.). *Derocerus reticulatum* is an annual species, with only a few individuals surviving the winter. Eggs laid in the spring hatch to form the summer and autumn populations (Getz 1959), and the abundance of slugs in the arable field may be a result of these juveniles.

Molluscs reached their highest density in the arable field in October 2008. This was in contrast to other studies that reported mollusc species such as *Derocerus reticulatum* declined substantially between July and October (Bohan et al. 2000). In the present study, there was a greater density of molluscs (2.6 per m^2) than earthworms (0.30 per m^2) in October 2008, but the opposite occurred in 2009 (slugs 0.02 per m^2, earthworms 0.59 per m^2). The breeding season of molluscs can take place at any time of year and is largely related to the moisture in the soil (Carrick 1942). August 2008 was a month of exceptionally heavy rain over most of Ireland, bringing flooding in many areas (www.met.ie). The large number of slugs in 2008 may have resulted from the increased rainfall. However, six hedgehogs, monitored in 2008 and 2009, followed the same pattern of habitat selection and increased their activity in the arable land as prey density increased, despite the change in prey species.

The results of the invertebrate sampling showed that there were significantly more invertebrates in the arable land in areas where many hedgehogs foraged. Invertebrates such as earthworms and slugs are particularly sensitive to environmental factors, such as temperature and humidity (Crawford-Sidebotham 1972, Young et al. 1993, Griffiths et al. 1998, Whalen et al. 1998), and the increased soil moisture of this section of the field is likely to be beneficial to the distribution of these species. Cassini and Krebs (1994) found that hedgehogs learned the spatial location of food patches and engaged in area-restricted searching. This is also suggested by the current study, as not only did hedgehogs enter arable land when a peak was observed in invertebrate density, but also hedgehogs restricted their activity within the arable land to where there was the greatest density of potential prey.

Hedgehog activity within each habitat was not consistent throughout the site. In pasture P4–6, activity was predominantly along the hedgerow. The hedgerow structure was different in this area of pasture and in all areas of the site; prey was more abundant along the hedgerows. However, the hedgerow in pasture P1–3 and arable A1–2 had a lot of thick vegetation and brambles, so although prey was also more abundant in the hedgerows of these areas, it may have been less accessible than in the centre of the field. In contrast, the hedgerow around pasture P4–6 had little ground vegetation and the prey was freely accessible. Prey within the centre of the pasture at P4–5 was also very low, with 0.004 surface invertebrates per m^2 in comparison to 0.05 m^2 in the centre of arable A1–2. Hedgerows with good ground cover, like that of A1–2 and P1–3, are easily the best kind of hedgerow to support biodiversity, with leaf litter providing suitable shelter for invertebrates (Pollard et al. 1977). Lagerlof et al. (2002) found that when earthworm populations in a field decline, the field boundaries may serve as sources from where re-immigration can take place.

Badgers have been reported as a significant predator of the hedgehog (Pentland 1917, Doncaster 1992, Ward et al. 1996, Warwick et al. 2006), yet Del Bove and Isotti (2001) discovered the remains of only two hedgehogs in 69 badger stomachs. In the present study, hedgehogs and badgers were found to occupy the same areas within each habitat and both were seen foraging on earthworms in the centre of pastures (P1–3). Hedgehogs foraged freely in the centre of the fields, showing no signs of predator avoidance. Within habitats where activity was confined to the edge there was little or no ground cover to act as refugia for hedgehogs. It is therefore suggested that badger predation is not a common occurrence at this site and that badgers had little impact on the habitat choice of hedgehogs. This is surprising because in the UK, Hof (2009) established that hedgehogs were seen at a greater distance from hedgerow when their home range was located away from badger activity. Micol et al. (1994) also reported that farms that had hedgehogs were those where there were no badger setts. However, as the UK and Ireland have been established to host about one third of all of Europe's badgers (Delahay et al. 2009), it seems unlikely that hedgehogs would be able to completely avoid this potential predator. As a competitor for prey, such as earthworms, hedgehogs may only prove a threat when other food sources are scarce. Ward et al. (1997) found that although hedgehogs initially avoided areas tainted with badger odour, this behaviour did not persist. This they felt was probably due to the cost of predator avoidance, which was negligible in the enclosure because of the presence of a superabundant food source. Therefore, although Hof (2009) found that hedgehogs were only seen at 21% of the sites where badgers were present, as opposed to at 32% of the sites where badgers were not seen, both species may coexist if abundant food is available. According to Frid and Dill (2002), habitat choice is the outcome of decisions that balance the trade-off between predation risk and resource richness. In both years of this study, hedgehogs selected the arable land in October and their move into this area coincided with an increase in surface invertebrates. Both species have a varied diet, and although earthworms were found to be a stable food for badgers (Canova and Rosa 1994) and hedgehogs (Yalden 1976), Muldowney et al. (2003) did not find a strong relationship between earthworms and badger abundance. Similarly, in this study, hedgehogs appeared to respond to fluctuations in the density of invertebrates, regardless of whether they were molluscs or earthworms.

In conclusion, contrary to the findings of other studies carried out in the UK, the distribution of badgers did not appear to adversely affect this population of hedgehog's use of a habitat. Instead, the density of surface invertebrates appeared to be the main contributory factor of those examined, influencing hedgehogs' use of a habitat in both years. It is suggested, from the present study, that hedgehogs learn the spatial location of potential prey and respond to seasonal fluctuations in their density. This, therefore, emphasises the importance of maintaining hedgerow, particularly in arable areas where hedgehogs have previously been considered scarce. Modern intensively farmed arable land does not provide high-quality habitat for most of the invertebrates (Morris and Webb 1987). This is mainly because hedgerow survives least well in these areas (Pollard et al. 1977). However, as shown in the present study, this habitat can support high species richness, if hedgerow with good ground cover is preserved, to provide nest sites not only for mammalian and avian species but also for their potential prey.

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