Local variations in small scale movements of hedgehogs in rural areas

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The editing of this report and chapters 1 and 3 are the result of work carried out by Anouschka R. Hof, postdoctoral researcher at Royal Holloway, University of London, under supervision of Paul W. Bright. Chapter 2 forms the Master thesis of Jolanda Snellenberg, Wageningen University, which she carried out under supervision of Anouschka R. Hof (Royal Holloway, University of London) and Frank van Langevelde (Wageningen University). The project was funded jointly by the People's Trust of Endangered Species, the British Hedgehog Preservation Society and by a legacy of Dilys Breece.

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Table of contents

Chapter 1:

The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields

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Abstract

Grassy field margins are thought to be an important feature for a variety of species in arable landscapes. However, it is not well known if the addition of such margins in arable landscapes increases the abundance of macro-invertebrates in arable fields. Therefore, I estimated the abundance of lumbricidae, gastropoda and coleoptera, species important to an array of insectivorous predators, in fields with, and fields without a grassy margin along the edge and further in the arable field.

From the findings it can be concluded that the presence of grassy field margins in arable landscapes leads to an increase in the abundance of coleoptera and lumbricidae but to a decrease in the abundance of gastropoda. These effects were for coleoptera and gastropoda also noticeable further away from the field-edge. The present study has implications regarding the management of arable landscapes to promote the conservation of an array of insectivorous species, and regarding pest management.

1.1. Introduction

In the United Kingdom alone over 70% of the total land area was used for agricultural purposes in 2007 (DEFRA and National Statistics, 2008), area potentially valuable for an array of species (e.g. Chamberlain and Fuller, 2000; Robinson and Sutherland, 2002). However, especially after the Second World War, farm management rapidly changed and intensified resulting in a reduction in diversity of landscapes (Robinson and Sutherland, 2002). Consequently, changes in agricultural management have frequently been mentioned as one of the major causes for the loss of species diversity and abundance (e.g. Krebs *et al.*, 1999; Donald *et al.*, 2001; Robinson and Sutherland, 2002).

Agri-environment schemes were introduced into the agricultural policy of the European Union (EU) in the late 1980s partly with the aim of protecting biodiversity and also in an attempt to reverse some of the negative impacts of agricultural intensification on wildlife and the environment. Many existing agri-environment schemes in Europe have provision for field margins (e.g. Benton 2007; Butler *et al.* 2007). Hence, such margins are present at the edges of many agricultural fields in Western Europe and are an important feature in agricultural landscapes for a variety of species (Vickery *et al.*, 2002; Butet *et al.*, 2006). Many studies focus on the effect of different arable field margin management strategies on invertebrates (Morris and Webb, 1987; Kromp and Steinberger, 1992; Baines *et al.*, 1998; Asteraki *et al.*, 2002; Woodcock *et al.*, 2005, 2007). However few studies investigated the impact of the presence of a grassy field margin in itself in comparison with its absence (Yu *et al.*, 2006), or whether a possible positive effect of grassy field margins on invertebrate abundance extents to surrounding arable fields (Kromp and Steinberger, 1992; Kádár *et al.*, 2004; Smith *et al.*, 2008; Twardowski and Pastuszko, 2008). It is known that undisturbed boundaries such as hedges and beetle banks may act as winter reservoirs for coleoptera in arable landscapes (Sotherton 1984, 1985; Morris and Webb, 1987). Whether the abundance of lumbricidae and gastropoda may be enhanced in arable fields by the presence of an unmanaged boundary is currently not well studied and might be important with respect to the conservation of predators of macro-invertebrates. This paper investigates if the presence of grassy field margins affects the abundance of macro-invertebrates (lumbricidae, gastropoda and coleoptera) in adjacent arable fields.

1.2. Materials and methods

1.2.1. Field selection

A total of 32 arable fields were sampled for invertebrate abundance between June and August 2009. All fields were surrounded by an established hedgerow of at least 2 meters wide. Half of these fields were surrounded by a grassy field margin of 4 or 6 meters wide and managed through an agri-environment scheme (Entry Level Stewardship [Natural England, 2008]). The remaining 16 fields did not have a grassy field margin; they were either harvested until the hedgerow or a fringe (<1m) of scrub and or nettles was still present. In order to minimize impacts of other environmental variables, such as soil type and soil moisture, on invertebrate abundance, fields with and without a grassy field-margin were paired. Paired fields were located on the same farm, had similar soils and were under similar management regimes but for the presence of a grassy field margin. Arable fields held the same crops. Paired field were sampled on the same day to ensure consistent weather conditions. All fields were located in four study sites in The United Kingdom. One study site was located in the area surrounding the village Brancaster in Norfolk (52º, 96'N, 0º, 63'E), one study site was located in the area surrounding the villages Gedney Drove End and Gedney Dawsmere in Lincolnshire (52º, 85'N, 0º, 16'E), another site was located near the village Great Easton in Leicestershire (52º, 53'N, -0º, 75'E), and the remaining site was located near the village Old Windsor in Berkshire (51º, 46'N, -0º, 59'E).

1.2.2. Invertebrate sampling

The abundances of lumbricidae, gastropoda and coleoptera in the fields was estimated. In order to study the abundance of Lumbricidae, a soil sample with a diameter and depth of 15cm was taken with the use of a soil auger. The sample was consecutively weighed and sieved in the field for worms. The total number of lumbricidae (>5mm) and their total biomass were noted. A total of 15 soil samples were taken per field; 5 within 1m distance of the hedgerow, 5 at 10m from the hedgerow and 5 at 20m from the hedgerow. A Graphic representation of the sampling strategy is given in Figure 1.1.

The number and biomass of gastropoda was estimated visually during the night, when they are most active, by spot sampling, using a $0.5m^2$ quadrangle according to the same sampling strategy. The total number and biomass of gastropoda was noted. Pitfall traps were used to get an indication of the species richness and abundance of coleoptera according to the same sampling strategy as in Figure 1.1. Plastic cups (diameter: 8cm, depth: 14cm) were placed in the soil 1cm below the surface as not to impede access to the cup. Traps were filled half with anti-freeze in order to immobilize invertebrates. The traps were left in the field for 72 hours before emptied. Coleoptera in the traps were identified and counted. Statistical analyses were conducted using SPSS (for windows 14th edition, SPSS Inc., Chicago, USA).

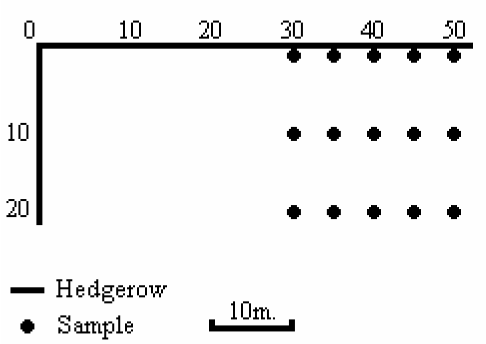

Figure 1.1. Graphic representation of the sampling strategy per field

1.3. Results

1.3.1. Lumbricidae

The mean number of lumbricidae in the soil was significantly higher on fields with a grassy margin than on fields without a grassy margin (Paired Samples T-Test: t=-2.253, df=239, p=0.025). Differences in mean number of lumbricidae between fields with a grassy margin and without a grassy margin were however not significant when distance to the edge was taken into account. At 0m, at 10m and at 20m from the edge, fields with and without a grassy margin had a similar number of worms in the soil (Paired Samples T-Test 0m: t=-1.955, df=79, p=0.054, 10m: t=-1.673, df=79, p=0.098, 20m: t=-0.356, df=79, p=0.723).

The mean biomass of lumbricidae was similar on fields with and without a grassy margin (Paired Samples T-Test: t=-0.863, df=239, p=0.389). At 0m and at 20m from the edge differences between the mean biomass of lumbricidae were not significant between fields with and without a grassy margin either (Paired Samples T-Test 0m: t=-0.325, df=79, p=0.746, 20m: t=0.268, df=79, p=0.790). However, at 10m from the edge the mean biomass of lumbricidae was significantly higher on fields with a grassy margin than on fields without one (Paired Samples T-Test: t=-2.345, df=79, p=0.022).

It was found that on fields with a grassy margin and on fields without a grassy margin both the mean number and the mean biomass of lumbricidae were significantly higher at 0m from the edge than at either 10m or 20m from the edge (ANOVA mean number on fields with a grassy margin: F=17.349, df=2,237, p<0.001, mean biomass on fields with a grassy margin: F=4.281, df=2,237, p=0.015, mean number on fields without a grassy margin: F=7.101, df=2,237, p<0.001, mean biomass on fields without a grassy margin: F=7.187, df=2,237, p<0.001). Differences between 10m and 20m were not significant according to the post-hoc test Bonferroni. Figures 1.2. and 1.3. show the mean number and biomass of lumbricidae.

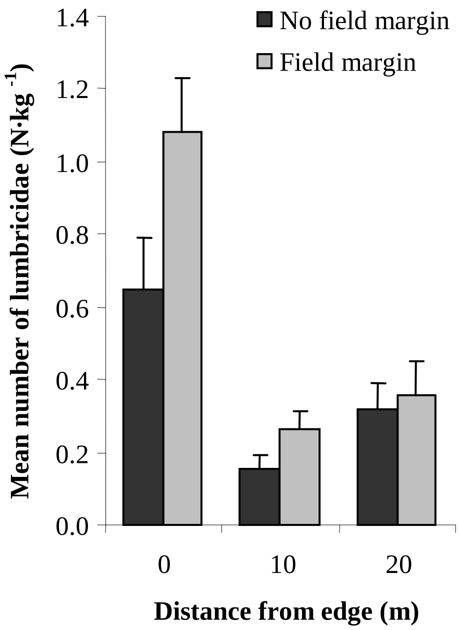

Figure 1.2. Mean number of lumbricidae in the soil in fields with a grassy margin and fields without a grassy margin according to the distance from the edge.

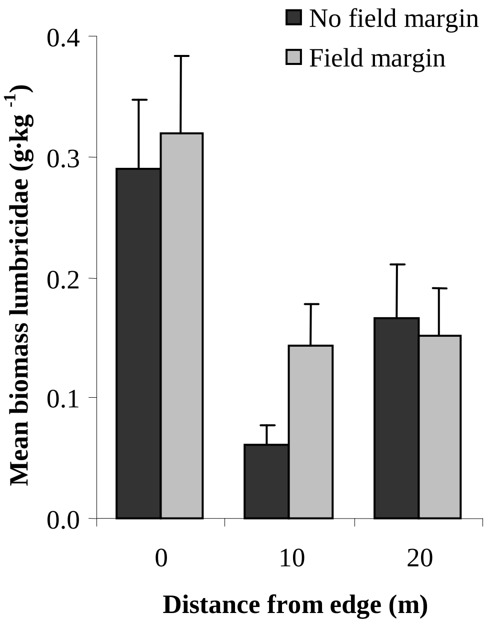

Figure 1.3. Mean biomass of lumbricidae in the soil in fields with a grassy margin and fields without a grassy margin according to the distance from the edge.

1.3.2. Gastropoda

The mean number of gastropoda was significantly lower on fields with a grassy margin than on fields without one (Paired Samples T-Test: t=3.226, df=239, p=0.001). This difference was significant at 0m and at 10m from the edge (Paired Samples T-Test 0m: t=2.625, df=79, p=0.010, 10m: t=2.054, df=79, p=0.043), but not at 20m from the edge (Paired Samples T-Test t=0.000, df=79, p=1.000). Although their mean biomass also seemed to be lower on fields with a grassy margin, this was not significantly so (Paired Samples T-Test all: t=1.606, df=239, p=0.110, 0m: t=1.751, df=79, p=0.084, 10m: t=-0.008, df=79, p=0.994, 20m: t=-0.202, df=79, p=0.840).

On fields with a grassy margin, the mean number and biomass of gastropoda did not significantly differ between edge-distances (ANOVA mean number: F=3.000, df=2,237, p=0.052, mean biomass: F=2.081, df=2,237, p=0.127). However, on fields without a grassy margin the mean number of gastropoda was significantly higher at 0m from the edge than at 20m from the edge (ANOVA: F=8.304, df=2,237, p=0.001). Their mean biomass was significantly higher at 0m from the hedge than at both 10m and 20m from the edge (ANOVA: F=7.315, df=56,117, p=0.001). Differences between 10 and 20m were not significant according to the post-hoc test Bonferroni. The results for the mean number and mean biomass of gastropoda are shown in Figures 1.4. and 1.5.

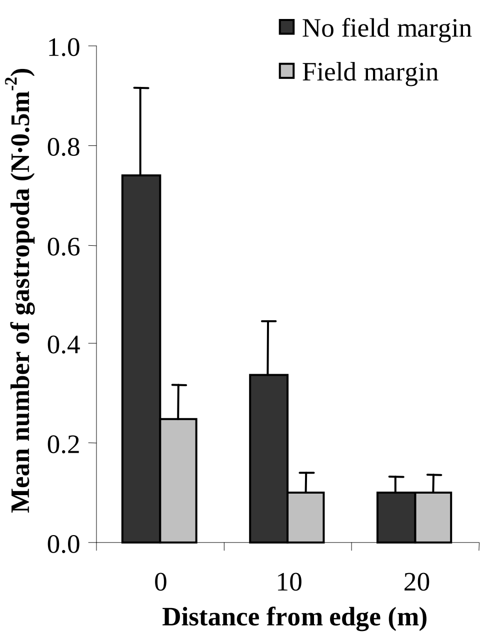

Figure 1.4. Mean number of gastropoda in fields with a grassy margin and fields without a grassy margin according to the distance from the edge.

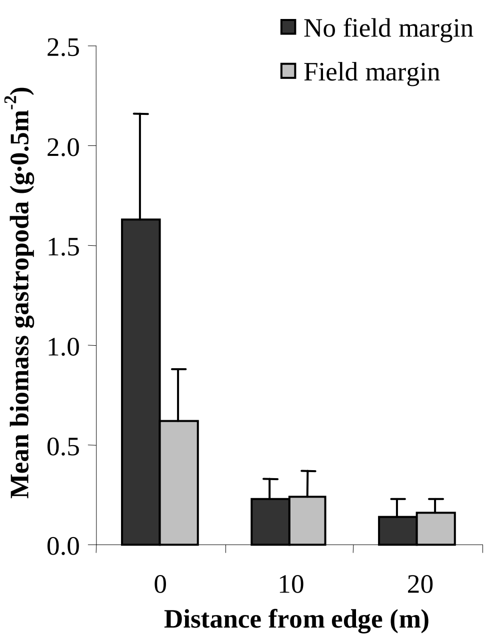

Figure 1.5. Mean biomass of gastropoda in fields with a grassy margin and fields without a grassy margin according to the distance from the edge.

1.3.3. Coleoptera

The mean number of coleoptera in the pitfalls was significantly higher in fields with a grassy margin than in fields without a grassy margin (Paired Samples T-Test: t=-3.582, df=239, p<0.001). This difference was mainly visible at 10m and 20m from the edge. Significantly more coleoptera were found in pitfalls in fields with grassy margins than in pitfalls in fields without grassy margins at 10m and at 20m from the edge (Paired Samples T-Test 10m: t=-2.217, df=79, p=0.029, 20m: t=-2.423, df=79, p=0.018), but not at 0m from the edge (Paired Samples T-Test: t=-1.671, df=79, p=0.099). No significant differences were found in the number of coleoptera between edge-distances (ANOVA fields with a grassy margin: F=0.955, df=2,237, p=0.386, fields without a grassy margin: F=0.861, df=2,237, p=0.424).

There was no difference in the number of species found in the pitfalls between fields with and fields without a grassy margin, regardless of the edge-distances (Paired Samples T-Test all: t=1.454, df=239, p=0.147, 0m: t=0.776, df=79, p=0.440, 10m: t=0.960, df=79, p=0.340, 20m: t=0.816, df=79, p=0.417). There was also no significant difference between the edge-distances (ANOVA fields with a grassy margin: F=1.418, df=2,237, p=0.244, fields without a grassy margin: F=1.039, df=2,237, p=0.355). Figure 1.6. shows the mean number of coleoptera.

In total 18 species of coleoptera were found in the study sites, of which 72% predators, 22% phytophagous species, and 6% detritivores. *Pterostichus madidus* was the most abundant, followed by *Dromius quadrimaculatus* and *Harpalus affinis*. *P. madidus* (Paired Samples T-Test: t=-3.746, df=239, p<0.001) and *P. nigrita* (Paired Samples T-Test: t=-2,152, df=239, p=0.032), were significantly more often present on fields with a grassy margin. *Amara aenea* (Paired Samples T-Test: t=2,883, df=239, p=0.004), and *D. quadrimaculatus* (Paired Samples T-Test: t=2,339, df=239, p=0.020) on the other hand, were significantly more often present on fields without a grassy field margin. Other species did not show a preference. Species from the family nitidulidae (not identified on species level) (ANOVA: F=3.163, df=2,237, p=0.043) and *D. quadrimaculatus* (ANOVA: F=3.007, df=2,237, p=0.050) were the only species significantly more often presence at 0m from the margin than at 10m and 20m from the margin. Other species did not show a preference with regard to edge-distances. Figure 1.7. shows the species richness of coleoptera.

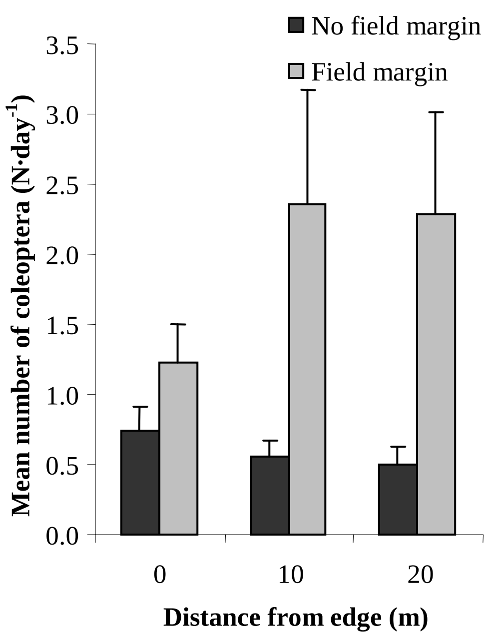

Figure 1.6. Mean number of coleoptera in the pitfalls per day in fields with a grassy margin and fields without a grassy margin according to the distance from the edge.

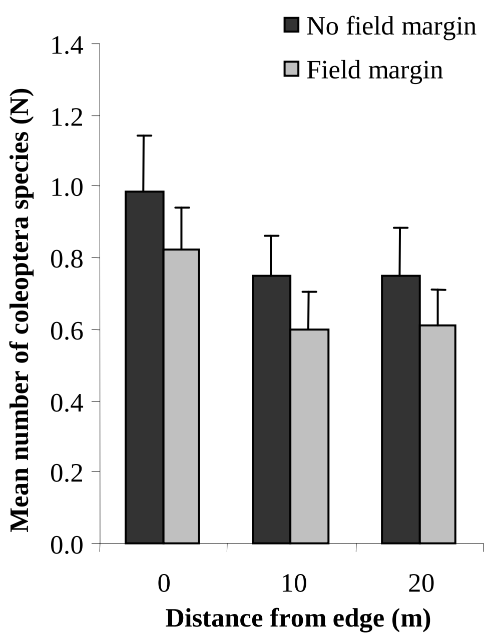

Figure 1.7. Mean number of species of coleoptera in the pitfalls over the catching season in fields with a grassy margin and fields without a grassy margin according to the distance from the edge.

1.4. Discussion

In this study coleoptera were more abundant on arable fields that had grassy margins along the edges, but especially so away from the edge of the field. However, it most be noted that pitfall catches not only depend on the density of populations, but on other factors such as activity and body size of the species as well (Lang, 2000). Nevertheless, it seems that the presence of a grassy margin at the edges of arable fields does not only increase the abundance of coleoptera near the edge of the field (see also Meek *et al.*, 2002), but also in the arable field itself. Indeed, it is known that uncultivated borders may act as winter reservoirs in arable landscapes where coleoptera disperse from to bordering arable fields (Sotherton 1984, 1985; Morris and Webb, 1987). Though, a hedgerow combined with a grassy field margin seems to have a greater effect in general than a hedgerow by itself. Although some species, like the species from the family Nitidulidae and *Dromius quadrimaculatus* were mainly found near the edges, the total species richness between fields with and fields without a grassy margin was not significantly different. Thus, the positive effect of a grassy field margin next to a hedgerow, was limited to the abundance of coleoptera.

The current available literature is ambiguous with regard to the abundance of lumbricidae in arable fields (Curry, 1998; Lagerlöf *et al.*, 2002). From the present study it can be concluded that lumbricidae, like coleoptera, were significantly more numerous on fields with a grassy margin than on fields without one. Nevertheless, the biomass did not differ significantly, thus the mean body mass of the individuals founds in the soil of fields with a grassy margin was lower than that from the individuals found in the soil of fields without a grassy margin. However, both the mean number and the mean biomass of lumbricidae were significantly higher near the edge, regardless the presence of a grassy margin, than further in the field.

Little has been done with respect to the impact of grassy field margins on the presence and abundance of Gastropoda. This study shows that in contrast to coleoptera and lumbricidae, gastropoda were less numerous on fields with a grassy margin than on fields without one, which might be related to the presence of predatory carabids. Though, there was no difference between their mean biomass. In the fields without a grassy margin both the mean number and biomass of gastropoda were higher near the edge. This result shows a clear implication for pest management, where crops in fields that are bothered with a grassy field margin are likely to be less affected by the presence of gastropoda.

It can be conclude that the presence of grassy field margins in arable landscapes is able to increase the abundance of coleoptera and lumbricidae but has a negative effect on gastropoda, and that these effects were seen further away from the field-edge as well with regard to coleoptera and gastropoda. The present study has obvious implications regarding the value of grassy field margins for macro-invertebrates, regarding the management of arable landscapes to promote the conservation of an array of insectivorous species, and regarding pest management. It is evident that grassy field margins promote the abundance of coleoptera and lumbricidae. The addition of such margins in arable landscapes might therefore also benefit predators of macro-invertebrates such as the lapwing (*Vanellus vanellus*) and the hedgehog (*Erinaceus europaeus*). Gastropoda, pests to a variety of crops, on the other hand, were negatively affected by the presence of a grassy field margin. Possibly due to a large amount of carabids in these fields. A variety of existing agri-environment schemes throughout Europe already include grassy field margins (e.g. Benton 2007; Butler *et al.* 2007), further encouragement of implementation is therefore straightforward.

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Chapter 2:

The abundance of badgers (*Meles meles*) as the driver behind the movement of hedgehogs (*Erinaceus europaeus*) at a local scale in a rural landscape

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Jolanda Snellenberg

Abstract

In the last few decades, the numbers of the West-European hedgehog (*Erinaceus europaeus*) are decreasing in Great-Britain. It is very important for the conservation of this animal to understand the mechanisms of this decline. One possible factor could be the abundance of badgers (*Meles meles*), since this species is both a competitor for food, mainly earthworms (*Lumbricus terestris*), and a predator of the hedgehog. The aim of this study was to investigate the relationship between the abundance of badgers and the behaviour of hedgehogs in a rural landscape, with special attention to the edge refuging habit of the hedgehog. This has been done by studying hedgehog movement through radio-telemetry in areas with high and low badger density. At each study-site up to 44 hedgehogs have been equipped with a radio-transmitter and their behaviour has been tracked. We can conclude that hedgehogs do change their location in the landscape under influence of badger presence. Distance kept to edge-habitat and home-range size become smaller when badger density is higher. Furthermore, the amount of habitat with dense vegetation, so vegetation which provides cover, increases when badger density becomes higher. The amount of edge-habitat and urban habitat increases, while the proportion of arable fields decreases. Thus, especially in areas with a high badger density, preservation and/or establishment of edge-habitat and other habitat which provides shelter is very important for the conservation of the hedgehog.

2.1. Introduction

Hedgehogs (*Erinaceidae*) occur in a large part of the world (Reeve, 1994). The last couple of years, the numbers of the West-European hedgehog (*Erinaceus europaeus*), henceforth referred to as hedgehog, are decreasing in Great Britain (Harris *et al*., 1995; Hof, 2009) and probably in more countries in western Europe as well (Personal communication, Anouschka Hof and the Dutch Mammal Society, 2009). In order to explain this phenomenon, a lot of research is currently underway, especially in Great Britain and in The Netherlands. Slowly, it is becoming clear that their decline is caused by a broad range of factors (Dowding, 2007; Hof, 2009; Huijser, 2000). The most well-known cause of mortality is that hedgehogs are frequently run over by cars (Huijser, 2000).

Another factor which probably negatively affects the number of hedgehogs is the change in rural landscapes. During the last century, agriculture has increasingly intensified in Great Britain, which has resulted, amongst others, in a decline of 50% of the amount of hedgerows (Robinson & Sutherland, 2002). Since hedgehogs seem to prefer edge-habitat, like hedgerows and field margins (linear landscape elements), the amount of habitat suitable for hedgehogs has reduced (Hof, 2009; Huijser, 2000; Riber, 2006; Shanahan *et al.,* 2007). Although it is currently not yet known why hedgehogs prefer edge-habitat, this habit has significant implications for conservation of hedgehogs and landscape management.

One of the possible reasons for this preference is the apparent avoidance of the badger (*Meles meles*), which could influence the movement of hedgehogs in two different ways. Badgers are intraguild predators of the hedgehog. This means the diet of both species overlap, with earthworms (*Lumbricus terrestris*) forming a major part of their diet (Goszczynski *et al.*, 2000; Reeve, 1994). Additionally, badgers are also known to predate on hedgehogs (Doncaster, 1994; Young *et al*,. 2006). In a lot of studies in Great Britain, researchers lose some of their hedgehogs to badger predation (for example Doncaster, 1992, 1994; Hof, 2009), an example from Hof (2009) is given in Figure 2.1.

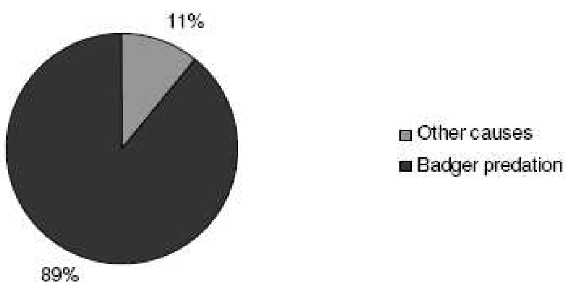

Figure 2.1. Causes of death of eleven hedgehogs equipped with a radio transmitter during two and a half months in 2008 (Hof 2009).

It has already been shown that the behaviour of hedgehogs can be influenced by the density of badgers at landscape level. Several studies show that the density of hedgehogs is lower in areas with higher badger density (Doncaster, 1992; Micol *et al.,* 1994; Young *et al.,* 2006). Furthermore, hedgehogs which are newly introduced in an area with a high badger density tend to migrate away from that area (Doncaster, 1992). It is however not known to which extent the movements of a local hedgehog population are determined by the abundance of badgers and whether the threat of badger predation causes the edge refuging habit in hedgehogs.

There are some general studies that hypothesize about this behaviour. A new term has been introduced for the adaptation of behaviour in relation to predation risk, namely "ecology (or landscape) of fear". The most well-known example deals with large herbivores in Yellow Stone National Park, where it has been shown that animals which were used to live in a predator-free environment adapted their (movement-) behaviour after the reintroduction of wolves (Laundré *et al,.* 2001). Similar effects of predators on movement of prey have been shown in other species (e.g. Hilton *et al.,* 1999; Sweitzer, 1996; Van Der Merwe & Brown, 2008). In the case of the hedgehog, Ward *et al.* (1996) showed that foraging hedgehogs tend to avoid badger faeces, both in captivity and in the wild. Furthermore, Hof (2009) found that a female hedgehog which lived further away from badger activity tended to cross fields more often and generally walked further away from the safety of the edge-habitat than the hedgehogs in fields which were much more frequented by badgers.

The aim of the study was to investigate the impact of badgers (*Meles meles*) on the edge refuging habit of hedgehogs (*Erinaceus europaeus*) in a rural landscape. Knowledge about this impact could help future conservation of the hedgehog. The focus of this study was on the distance hedgehogs keep to edge-habitat, but also habitat selection and home-range size will be taken into account. It was expected that with a higher badger density, hedgehogs would stay closer to edge-habitat and so have more edge-habitat in their home-range. Furthermore, hedgehogs will use more habitat with a dense vegetation, so a high amount of cover, when badger density is high than in areas with a low density. It was reasoned that the animals would have a smaller home-range when badgers are present, because the animals would try to avoid contact with badgers. Differences between males and females were taken into account, since it has already been shown that they maintain a different distance from edge-habitat and have a different home-range size (Hof, 2009; Huijser, 2000; Reeve, 1994). The sex of juveniles is hard to establish, since they cannot be unrolled easily, so they were treated as a separate category (Burton, 1969).

2.2. Materials and methods

2.2.1. Areas

In this study, data from three different sites were collected during the summer of 2009. Data collected from one site in 2008 by Anouschka Hof will be used in the analyses as well. Schematic drawings of all sites are presented in Appendix 2.1 (Figure 2.6.-2.9.).

The 609ha site of the study in 2008 is located on the northern coast of Norfolk, UK (52º, 58'N, 0º, 40'E). Habitat and vegetation characteristics are described by Hof (2009). The area consists mostly of arable fields with 6m wide field margins around them. Furthermore, 33km of hedgerow were present (approximately 54m of hedgerow per hectare) and some extensively managed pasture fields. Badgers were present at the site as confirmed by sightings and by other signs of badger activity (predations on hedgehogs). No badger setts were found due to access restrictions (Hof 2009). Regarding the high level of badger predation (8 deaths out of 44 hedgehogs in a two and a half months time span), this site was classified as 'high badger density site'.

The first site (99ha) that was surveyed in 2009, The Crown Estate, is located near Old Windsor, Berkshire, Middlesex, UK (51º, 46'N, -0º, 59'E). The site mainly consisted of arable fields (27ha; wheat or rapeseed) with field margins (6m wide) and pasture grazed by horses or cattle (33ha), all surrounded by hedgerows or tree lines. A lot of goosegrass (*Galium aparine*) grew in the arable fields. Hedgerows (2-3m high, 2-3m wide; 9km in total) consisted mostly of common hawthorn (*Crataegus monogyna*) overgrown with bramble (*Rubus fruticosus*) and bordered by grasses, thistles (*Circium* spp) and nettles (*Urtica* spp), which were also the most common species in the field margins (5-100cm high, 6m wide). The set aside areas (0.4ha) were either mostly bare soil, with predominantly chamomile (*Matricaria recutita*) growing in patches of 20-50cm high or completely overgrown with nettles (*Urtica* spp). The hedgehogs also frequented the village of Old Windsor. Data collection took place between 22nd of June and 16th of July 2009, for a total of 20 non-consecutive nights. Badgers have been present in the area, but were not present at the time of this study as determined after intensive searching for badgers and signs of badger presence (marks, hairs, latrines, setts), and by consulting the park manager and game keeper Andrew Stanley and Steve Searle. This site was thus classified as 'Low badger density site'. In total 29 hedgehogs were seen, of which 23 animals were large enough (>400g, see below) to receive a transmitter (10 females, 13 males).

The second, 647 ha large site was located on a farm near Gedney Dawsmere, South Lincolnshire, UK (52º, 51'N, 0º, 9'E). It consisted mainly of arable fields (483ha) with either wheat (most dominant), peas, lettuce, potato, tomato or cabbage. Some fields were being harvested during the time of data-collection. Most fields were surrounded by a 2-6m wide field margin, consisting of various weeds and grasses, of which the main weed species were species of thistles (*Circium* spp), dock (*Rumex* spp) and nettles (*Urtica* spp). Also a few sea specific species were found, such as sea holly (*Eryngium maritimum*). A lot of fields were surrounded by hedgerows (2-3m high, 16km in total) or tree lines (up to 14m high) of which some were fairly recently planted. The dominant species in the hedgerows was common hawthorn (*Crataegus monogyna*) with hedge bindweed (*Calystegia sepium*) growing in it. The tree lines consisted of many different tree species, but species of maple (*Acer* spp) were the dominant species, which were also the most abundant species in the 10ha of woodlands. There were only 4ha of pasture present. The hedgehogs also visited gardens in Gedney Dawsmere. Data were collected from 19th of July to 13th of August on 19 non-consecutive nights. The area did not have a badger population, no signs of badgers have been found during the fieldwork period (see below; low badger density). In total 24 hedgehogs were encountered, of which 15 received a transmitter (7 females, 8 males).

The last site was located on a farm between the villages of Caldecott and Great Easton, Leicestershire, UK (52º, 31’N, -0º, 44’E). The hedgehogs only used a 39ha area in and between Great Easton and Bringhurst. The whole site (195ha) consisted of arable fields with wheat, which were all surrounded by a hedgerow (2-4m high, 12km in total) and some surrounded by a field margin, 2-6m wide, in which grasses were most common. Hedgerows consisted of either common hawthorn (*Crataegus monogyna*) or elder (*Sambucus nigra*) and blackthorn (*Prunus spinoza*), surrounded by weeds and grasses. The most common weeds were thistles (*Circium* spp), willowherbs (*Epilobium* spp) and nettles (*Urtica* spp). The fields were being harvested and ploughed at the time of data-collection, which took place between the 17th of August and the 10th of September on 19 non-consecutive nights. An occupied badger sett was present, along with a number of empty (main and transitory) setts. The occupied sett is estimated to house between 6 and 10 individuals (see below; high badger density). In total 8 hedgehogs were encountered and all animals were equipped with a transmitter (2 females, 6 males).

2.2.2. Hedgehogs

Hedgehogs were located by walking through the study site with a spotlight of a million candlepower and whilst tracking already caught individuals. When an animal was found, it could easily be picked up. All animals were weighed, sexed, marked with water based paint (Crown Paints, UK). Animals that weighed more than 400g were equipped with a radio transmitter (Biotrack Ltd, Dorset) as described by Hof (2009). The 400g limit was kept to comply with the ethic guidelines as set by The American Society of Mammologists, which recommends that the weight of the radio transmitter should not exceed 5% of the animal's bodyweight (The American Society of Mammologists, 1998). A beta-light was attached to the transmitter to enhance visibility, so the observers could keep a greater distance, thus reducing disturbance of the animals. The transmitters were tracked using receivers from Telonics Inc. (Arizona, USA) together with Yagi antennae (Biotrack Ltd, Dorset, UK). The transmitters were removed when sufficient data were collected; the hedgehogs were then weighed again.

When hedgehogs were equipped with a radio transmitter, animals were tracked from dusk until dawn. It was attempted to track them for at least ten different nights, obtaining fixes between once per half hour and once per hour. Animals were located either by sight or by triangulation when sight or access was impeded (like in gardens). For each fix, habitat, distance to edge-habitat and behaviour was recorded. Habitat was defined by one of the following categories: arable field (plus species and height of the crop), ditch, field margin, garden, pasture (grazed grass), hedgerow, lawn (mown grass), road (-verge), set aside, shrubbery and woodland. When behaviour could be observed, the following categories were used, after Reeve (1994): courtship, foraging, grooming, locomotion, meeting or stationary. Grooming was observed only once, so this category was left out of the analyses. Animals which were encountered whilst the observer was not actively tracking these animals were also noted to aid density estimation. All fixes obtained are presented in Appendix 2.1.

During the studies in 2009, only one animal died. This one female from Old Windsor was run over by a car. One male from Great Easton had to be taken to the RSPCA because it was in bad health. In 2008, 9 animals died (mostly due to badgers) as described by Hof (2009).

2.2.3. Badgers

The abundance of badgers was estimated using baited camera-traps, active searching for setts, latrines and other signs during the day (Sadlier *et al.* 2003), and interviews or letters to inhabitants in or around the site. When a sett was found, it was checked for signs of activity like digging and tracks. If a sett was deemed inhabited, people were posted near the sett for a few evenings, during dusk, to make sure that the sett was indeed inhabited by badgers and to count the number of animals seen emerging. Also camera traps were placed near potentially active setts. Camera traps were baited with dog food or unpeeled peanuts (Cagnacci *et al.*

2007; Wilson *et al.* 2003). Only once did a camera register a badger, on the Great Easton site, when baited with peanuts.

2.2.4. Analyses

Habitat and vegetation was recorded in the field and digitized in ArcMap (ArcGIS 9.2, ESRI, USA). Hedgehog locations were displayed on this map. Home-range size and location was calculated in RANGES 6 (Anatrack Ltd., Dorset, UK) as described by Hof (2009). Home-ranges were only calculated for animals with a minimum of 25 fixes, to ensure that there were enough fixes to represent the home-range of the animal. To ensure that this minimum was correct, an asymptote was established using a 95% incremental analysis (Kenward *et al.*, 2001). When 25 fixes were not enough, animals with less fixes than necessary were excluded. A second method, used to estimate the core area of the home-ranges, was cluster analyses. The objective cores were estimated using nearest neighbour distribution. The habitat per home-range was established by making an intersect in ArcMap.

To calculate hedgehog density, strip transects were used. Visibility was standardized as 100% to 10m each side, after Hof (2009), except in Great Easton, where visibility was less good and gardens were inaccessible. Therefore, in Great Easton, the size of the area is taken as the total area size minus the gardens (7.5ha), with only 5m 100% visibility to each side. Total length of the transects per person per night was estimated (using 7 nights) to be 10km in Great Easton and Old Windsor and 11km in Gedney Dawsmere.

Statistical analyses, for which no specific programme is mentioned above, were done in SPSS for Windows 15.0 (SPSS Inc, Chicago, USA). The difference in distance from edge-habitat between the different badger densities was compared with a Generalized Linear Model (GLM), using a Gamma-distribution. Two measures were taken to equalize the amount of data between hedgehogs and thus prevent a bias, since non-parametric tests are sensitive to differences in sample size. Animals which were not seen, due to their presence in gardens, were given the value 4m. This was estimated to be the maximum distance animals could be from other habitat in the gardens, since gardens were generally not longer than 8 m., or contained a lot of shrubbery. Furthermore, random fixes were deleted from individuals with more than 10% more fixes than average, until they had as many fixes as the animal with the one but most fixes.

The four areas were treated as two groups, one with high badger density (Brancaster and Great Easton) and one with low badger density (Old Windsor and Gedney Dawsmere). Site was used as a factor nested within badger density. Habitat and behaviour were also used as factors. For behaviour, meeting and courting were taken as one group, since otherwise the sample size of these two categories would be too small. The influence of habitat on location was tested with a Kruskal-Wallis test, with a Scheffe post-hoc test. Ditches were not taken into account, since these were not available for all hedgehogs. The analyses for distance were also done with just the habitat-types which were surrounded by edge-habitat, arable field and pasture, since that is the core of this research.

Correlation in home-range size and sex was tested with a Pearson correlation test. Home-ranges are not linked in hedgehogs, since they do not display territorial behaviour (Reeve, 1994). This means that all home-ranges can be treated as separate measurements. Difference in home-range size between sexes was tested with a Mann-Whitney U test. Difference between home-range analyses methods was tested with a Wilcoxon test. The influences on size of home-range were tested with a Generalized Linear Model, using a Normal-distribution and home-range size as the dependent variable. Habitat preference was tested both within the habitat of the total study area and within home-range with a Kruskal-Wallis test and a Scheffe post-hoc test. The total study area was defined by the outer most hedgehog locations found, except in Great Easton. Here, the home-ranges found overlapped so much, that when using the outer most fixes, it did not yield a good representation of the whole area available. Therefore, in Great Easton, the study area was defined as the (larger) area in which was searched for hedgehogs during the nights (195ha), since this area was also available for the animals in Great Easton and we can be sure to a high degree that there could be no additional animals found in the 'added' area.

Habitat density was measured in the field by estimating the amount of horizontal cover at ground level (hedgehog level). Habitats with high density were field margins, hedgerows, road verges and woodlands. The other habitat types (mentioned above) were judged to be not so dense that they could provide cover for the hedgehogs.

To estimate the difference in net displacement, a linear regression analysis had to be used, due to the large effect of the time between fixes. The less fixes, the smaller the found displacement. This was solved by taking interval time also into account, besides badger density. Displacement data was transformed to "ln (displacement+1)" to make the data normally distributed. Fixes which were further apart than 90 minutes were not taken into account, since the accuracy will probably be to low when fixes are further apart. Only 400 (out of 2833) fixes from Brancaster were used to equalize sample size. Fixes were randomly chosen and the randomization had no effect on significance.

2.3. Results

2.3.1. Density

In total, 88 hedgehogs were tracked for this study, 50 males and 38 females. The ratio between males and females seen differs per area, but not much: 6:5 in Brancaster, 4:3 in Old Windsor, 8:7 in Gedney Dawsmere, 3:1 in Great Easton. This predominance of males has been found in more studies and seems to be normal in the UK (Reeve, 1994).

Hedgehog density in Brancaster was estimated to be about 7.3 km$^-$2, as described by Hof (2009). In Old Windsor, on average 3.8 animals per night were encountered whilst tracking other hedgehogs, resulting in a density of 10 km^{-2}. In Gedney Dawsmere, 4.7 animals were seen on average per night, which gives a density of 8.6 km^{-2}. In Great Easton, no animals were seen outside the villages. The density there is thus very low. In the villages, on average 0.9 animals were seen each night, which gives a density of 3.7 km^{-2}. There is no difference in hedgehog density between the different badger densities (t-test; t=1.968, df=2, p=0.188).

2.3.2. Distance from Edge-Habitat

Badger density did have a significant negative influence on the distance hedgehogs kept from the edge of a habitat (GLM; χ^2=108.518, df=1, p<0.001). Site, used as a nested variable within badger density, also had an influence (GLM; χ^2=367.380, df=3, p<0.001). Hedgehogs in Great Easton kept the smallest distance to edge-habitat, 4m smaller than Brancaster. The then smallest was Brancaster, followed by Old Windsor (12m bigger) and Gedney Dawsmere with the largest distance (13m bigger). Juveniles were significantly closer to edge-habitat than adult females (-13m; GLM; χ^2=45.256, df=1, p<0.001). Adult males were slightly further away than adult females, but this was not significant (0m; GLM; χ^2=0.237, df=1, p=0.627). The behaviour of a hedgehog was also significant for its location (GLM; χ2=62.187, df=4, p<0.001). Both foraging and resting were localized further away from edges than meeting (3m/4m; GLM; χ^2= 11.053/14.668, df=1, p<0.001). Walking behaviour has been seen throughout the distances (GLM; $\chi^{2=}$0.906; df=1; p=0.341). Habitat did have a significant effect on the distance hedgehogs kept from the edge. The mean distance per habitat was classified with a Kruskall-Wallis test and a Scheffe Post-Hoc (see Figure 2.2.; GLM; Low badger density: χ^2=479.277, df=10, p<0.001; High badger density: χ^2=295.841, df=10, p<0.001).

When only taking arable fields and pasture into account in the GLM, animals did show a significant difference in distance between sex (χ^2=112.253, df=2, p<0.001). Also badger density, with site as a nested variable, had an effect (χ^2=183.784, df=3, $p<0.001$). The distance of animals to edge-habitat in sites with low badger density was higher than in sites with high badger density, with males being further away than females and juveniles even further away in both densities (see Figure 2.3.). Also, habitat still has an effect, the mean distance of hedgehogs on pasture is further away than on arable fields (χ^2=59.433, df=1, $p<0.001$).

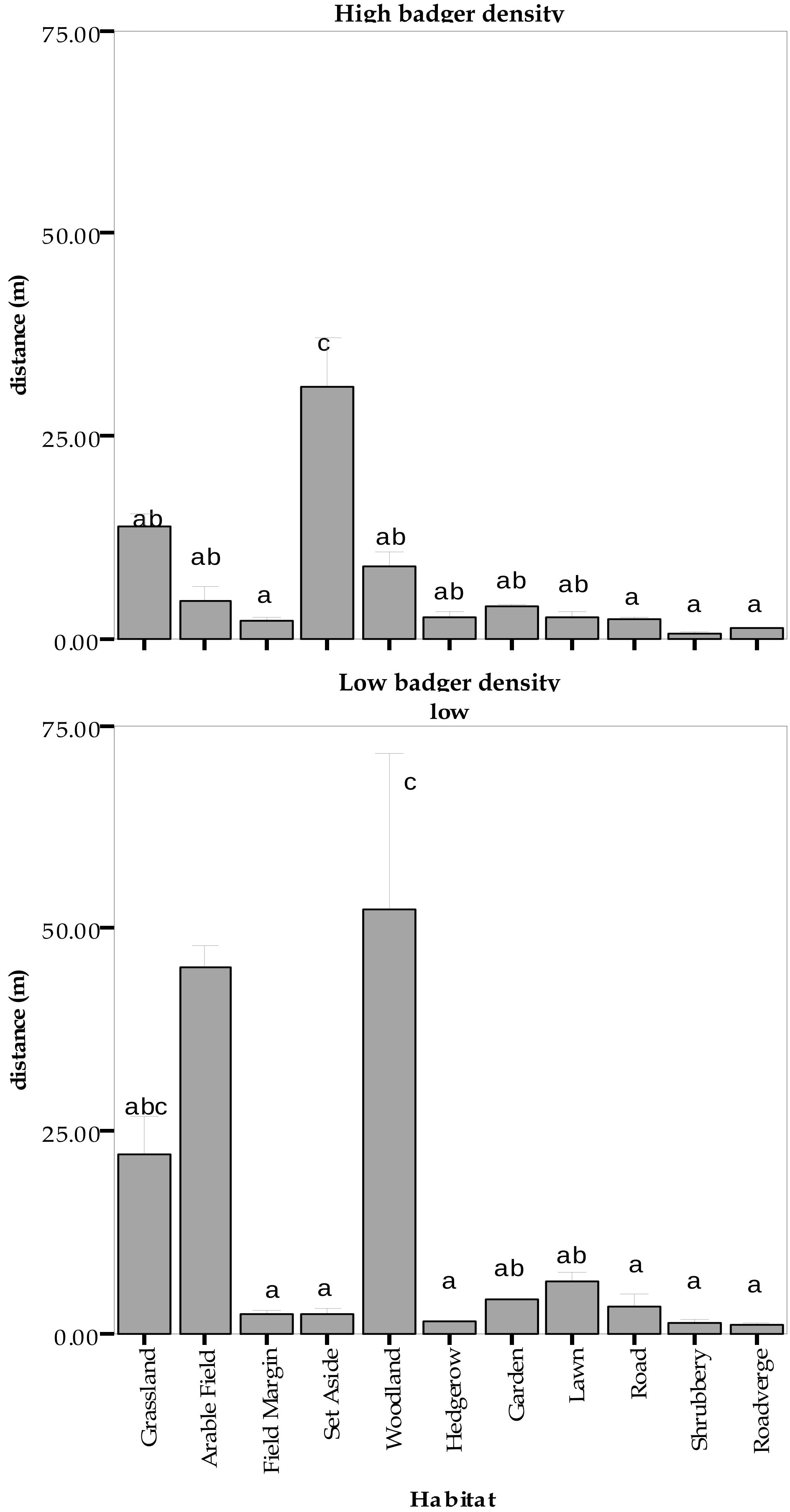

Figure 2.2. The mean distance of hedgehogs to the edge of the habitat type, per habitat per badger density. The letters a-c signify significantly different groups, with the smallest distances in group a. Error bars display s.e.

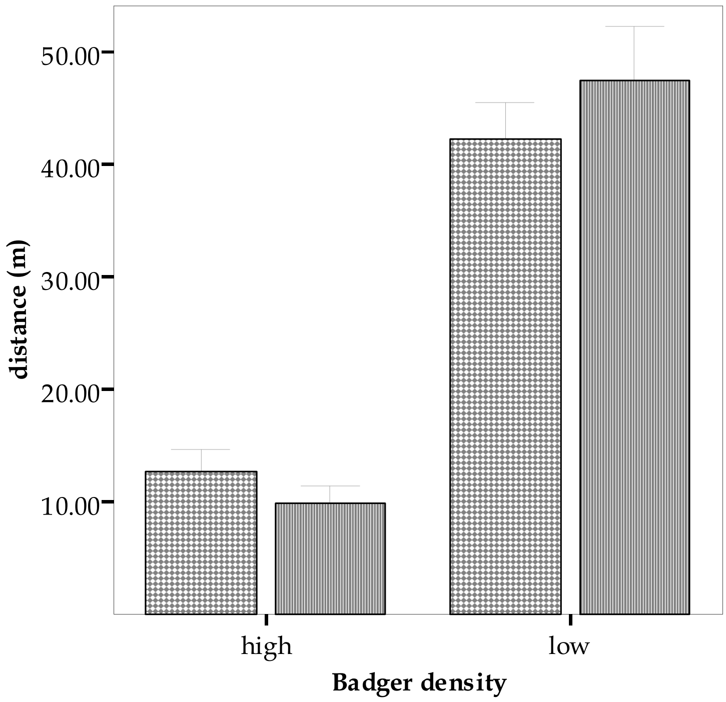

Figure 2.3. The mean distance to edge-habitat in arable fields and pastures per sex per badger density. Error bars show s.e. Juveniles are not taken into account. Dotted are males (High badger density N=107, Low N=216), striped are females (High badger density N=107. Low N=115).

Table 2.1. Home-range size per sex per site calculated with different methods.

Site	*Sex*	*Minimum Convex Polygon*			*Cluster Analyses*		
		Mean	*N*	*S.E.*	*Mean*	*N*	*S.E.*
Brancaster	f	4.43	17	1.03	3.21	17	0.75
	m	24.92	16	3.70	19.33	16	3.21
	Total	*14.37*	*33*	*2.58*	*11.02*	*33*	*2.124*
Old Windsor	f	6.73	3	1.62	4.21	3	1.69
	m	10.59	9	1.12	8.03	9	0.85
	Total	*9.63*	*12*	*1.03*	*7.07*	*12*	*0.88*
Gedney Dawsmere	f	13.55	7	4.04	10.25	7	4.11
	m	84.89	8	29.35	64.51	8	26.03
	Total	*51.59*	*15*	*17.99*	*39.19*	*15*	*15.38*
Great Easton	f	6.11	2	4.16	3.79	2	2.93
	m	7.31	6	4.29	6.64	6	4.32
	Total	*7.01*	*8*	*3.24*	*5.93*	*8*	*3.24*
Total	f	6.99	29	1.33	5.05	29	1.19
	m	31.21	39	7.49	24.03	39	6.29
	Total	*20.88*	*68*	*4.55*	*15.94*	*68*	*3.80*

2.3.3. Home-Range

There was a significant difference between the weight of males and females (t-test; t=9.7, df=67, p<0.001), with males being heavier, but there was no significant relationship between home-range size and weight in both males and females (Pearson; males: r=0.166, N=39, p=0.313; females: r=0.105, N=29, p=0.589).

Incremental analyses showed that an a-asymptote was reached in Brancaster at 45 fixes for males and 38 for females, in Great Easton at 25 for both males and females, in Gedney Dawsmere at 29 for both males and females and in Old Windsor at 26 for males and at 23 for females. Individuals with less fixes were left out of further analyses.

The means of both MCP and cluster analyses for all sites are shown in Table 2.1. Home-ranges tended to overlap at least partly with home-ranges of other individuals, both in males and females. Cluster analyses gave significantly smaller home-range sizes than MCP analyses (t-test; t=3.418, df=65, p<0.001).

The difference between cluster analyses and MCP is probably due to the fact that hedgehogs do not really stick to a small area, but tend to roam and explore the area around the area they know well (Reeve, 1994). A cluster analysis determines the core area, where hedgehogs are seen the most and base their 95% limit on those data and not the outermost 5% like MCP analyses. Since hedgehogs roam a lot, it is probably better to use MCP analyses, which shows the total area where the animals goes and not only the active core, like cluster analyses does. Therefore, the rest of the analyses are only done with the MCP outcomes.

Sex and site have a significant influence on home-range size determined with MCP analyses (GLM; Site: χ^2=24.768, df=3, p<0.001; Sex: χ^2=14.872, df=1, p<0.001). Hedgehogs in Brancaster had significantly smaller home-ranges than in Gedney Dawsmere (GLM; χ^2=16.048, df=1, p<0.001), but differed not significant from the home-ranges in Old Windsor and Great Easton (GLM; χ^2=1.222, df=3, p=0.269 resp. χ^2=1.579, df=1, p=0.209). Average field size in all habitat types did not differ significantly between the areas (GLM; χ^2=7.702, df=3, p=0.053) and was therefore not taken into account. The hedgehogs in the grouped areas with a high badger density (Great Easton and Brancaster) had a significantly smaller home-range than in the areas with no badgers (Old Windsor and Gedney Dawsmere) (GLM; χ^2=24.768, df=3, p<0.001).

There is a significant relation between the net displacement of hedgehogs and sex, interval time and badger density (regression; n=2, t=-4.822, p<0.001; n=90, t=-13.986, p<0.001; n=2, t=-18.554, p<0.001). Males have a larger net displacement than females (see Figure 2.4.). When the interval between fixes obtained becomes larger, the displacement seems to become smaller. Also, when there is a higher badger density, the net displacement of hedgehogs goes down.

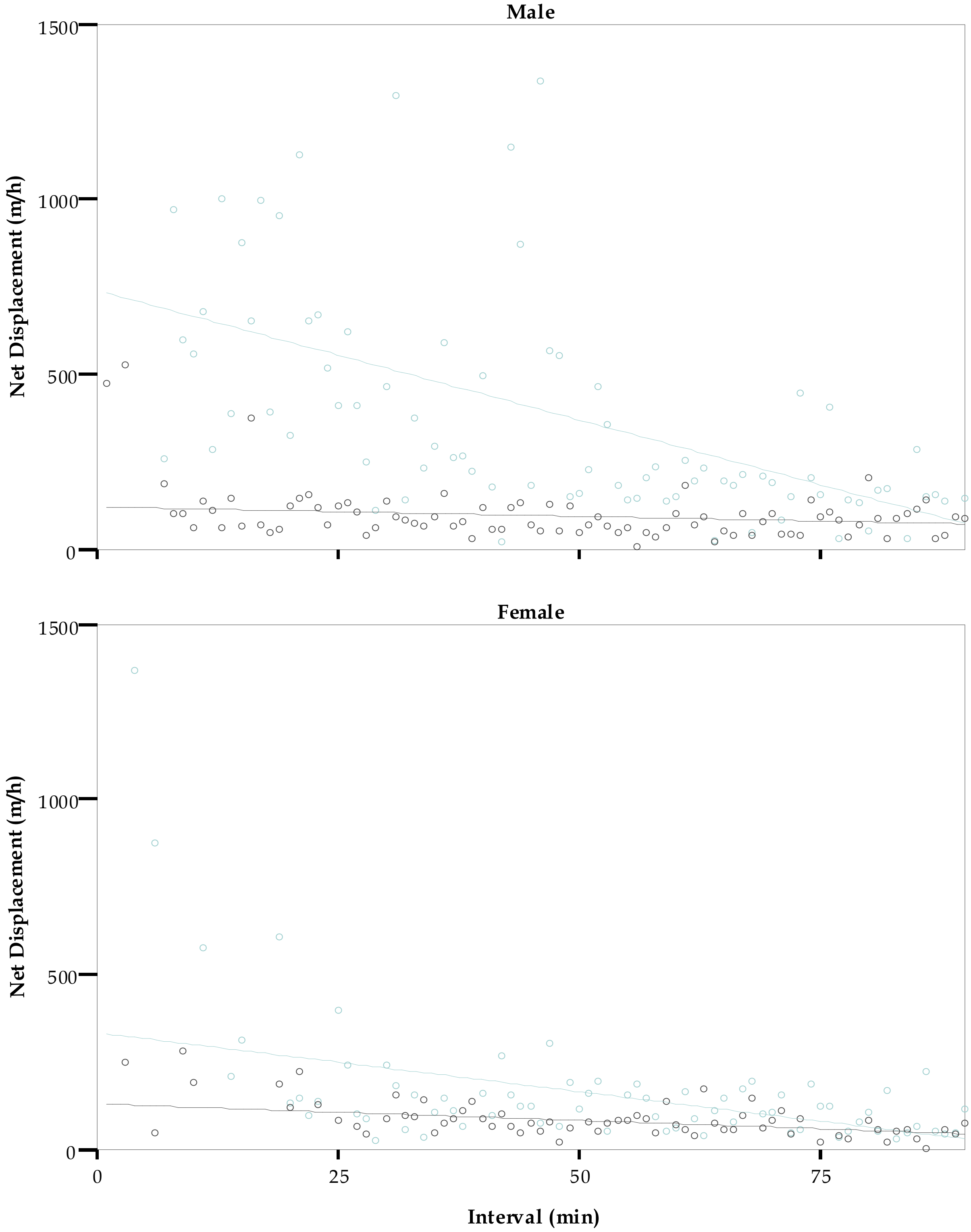

Figure 2.4. Regression between the interval and net displacement for high badger density (dark; n=665) and low badger density (light; n=578) for both sexes.

2.3.4. Habitat Selection

The habitat selection of hedgehogs on both a landscape level and home-range level in Brancaster has been described in Hof (2009). When looking at where fixes were obtained, the density of vegetation did not have a significant effect in areas with a low badger density (ANOVA; $F_{1,6}$=1.273, p=0.302), but with a high badger density, density of the habitat types did become significant (ANOVA; $F_{1.6}$=47.888, p<0.001). When badger density was high, hedgehogs were fixed more in habitats with a higher density (see Figure 2.5.; see Table 2.3., Appendix 2.2. for absolute amount). There was no difference between the sexes at both badger densities (ANOVA; high: $F_{1,6}$=0.000, p=0.990; low: $F_{1,6}$=0.099, p=0.764)

Of all hedgehogs which were encountered whilst not tracking these animals, in all areas, most were found on a lawn (28 out of 106) and the road verge (23 out of 106). Fixes from males and females were obtained in different habitat types and had to be split up. Since juveniles were only encountered by accident, they were not taken into account.

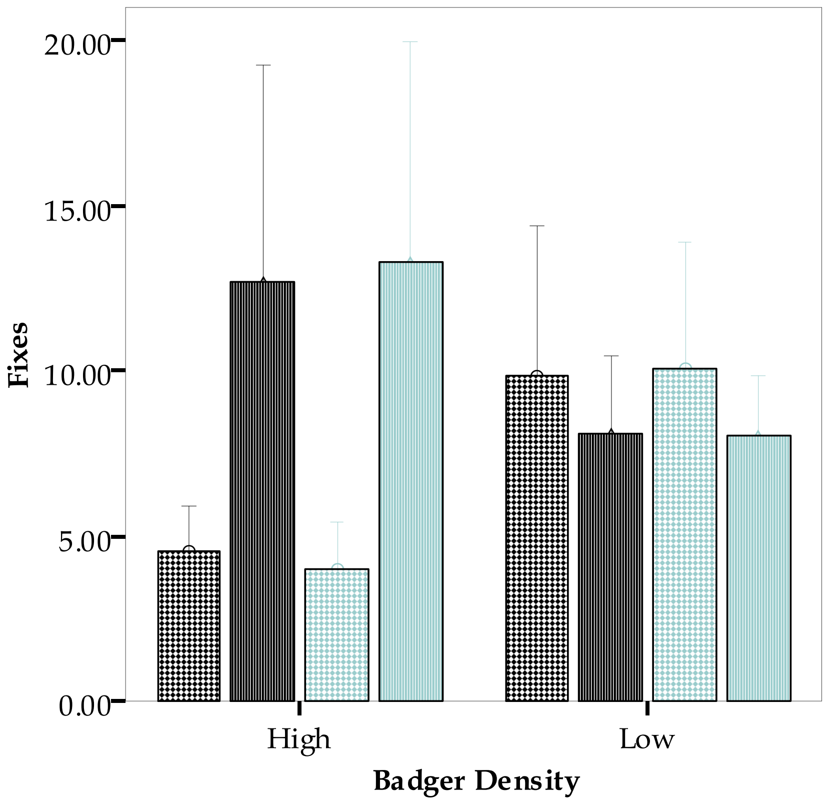

Figure 2.5. The percentage of fixes obtained per badger density in habitats with high and low badger density per sex. Dotted bars are habitats with high vegetation density (N=10), striped bars are habitats with low vegetation density (N=12). Dark bars are males, light bars are females. Error bars show s.e.

Table 2.2. gives an overview of the ranking of habitat present in the home-range of the animals in the areas surveyed in 2009. It shows that males and females selected different habitats. The hedgehog in Great Easton which travelled to the next village is left out of the analyses, since the habitat he travelled through is unknown, which made up a large part of its home-range. Animals in all areas have a high ranking of urban habitat, namely gardens, lawn and roads.

The proportion of habitat in a home-range relative to the proportion of habitat in the total study area is not significantly different between males and females in both badger density groups (Table 2.5., Appendix 2.2; ANOVA; $F_{1,66}$=1.032, p=0.313; percentages shown in Table 2.4., Appendix 2.2). Therefore, males and females were not separated in this analysis. When looking at the amount of vegetation that offers shelter within home-ranges, there is no significant difference for both areas with a high badger density and areas with a low badger density (ANOVA; Low: $F_{1,34}$=0.681, p=0.415; High: $F_{1,34}$=0.671, p=0.419).

Table 2.2. Ranked habitat selection at a landscape level. Italic means that there was no significant difference between the habitats. – means that the habitat type was not available for the animals or there was no data. The higher the rank, the more present in home-range.

Site	***Sex***	***Pasture***	***Arable field***	***Field margin***	***Set aside***	***Wood-land***	***Garden***	***Lawn***	***Road***	***Ditch***
Brancaster	All	*3*	*7*	*2*	*6*	*5*	*1*	*4*	-	-
	f	*5*	*7*	*4*	*6*	*3*	*1*	*2*	-	-
	m	*2*	*7*	*1*	*6*	*4*	*3*	*5*	-	-
Old Windsor	All	*8*	*4*	*2*	*5*	*7*	*6*	*1*	*3*	-
	f	*8*	*7*	*5*	*1*	*4*	*6*	*2*	*2*	-
	m	*8*	*4*	*2*	*6*	*7*	*5*	*1*	*3*	-
Gedney Dawsmere	*All*	*6*	*5*	*8*	*9*	*7*	*1*	*4*	*3*	*2*
	f	*4*	*5*	*7*	*9*	*6*	*1*	*8*	*2*	*3*
	m	*6*	*5*	*4*	*9*	*8*	*2*	*1*	*7*	*3*
Great Easton	All	*3*	*5*	*5*	-	-	*1*	*4*	*2*	-
	f	*3*	*4*	*4*	-	-	*1*	*4*	*2*	-
	m	*3*	*5*	*5*	-	-	*1*	*4*	*2*	-

2.4. Discussion

2.4.1. Distance from Edge-Habitat

The distance hedgehogs keep from edge-habitat was negatively influenced by the amount of badgers present in the study sites. This could be because edge-habitat gives more shelter for predation, since the vegetation there is generally denser than in arable fields and pastures. Another very distinct phenomenon is that the hedgehogs in Great Easton did not leave the village. Again, this habit might be because gardens are thought to offer more shelter than arable fields, outside of the villages. Furthermore, no badgers were observed in the village Great Easton, so it might also be a way to avoid all contact with them. Hedgehogs in Gedney Dawsmere were sometimes even seen 200m into a bare fallow field, where there was no cover at all, but also no badgers.

These observations show a high correspondence to the “landscape of fear” theory, in which is stated that animals can adapt their behaviour and their location in the landscape in a predator-prone environment (Laundré *et al.*, 2001; Van Der Merwe & Brown, 2008). Another finding that supports this theory is that hedgehogs were resting relatively more, further away from edge-habitat than close-by, which could mean that hedgehogs do have a higher vigilance further away from shelter. Reeve (1994) described that hedgehogs often pause between foraging to smell and listen for possible danger, which from a distance will look like resting to the observer. It could also be that the animals were scared of the observer, but this was prevented by keeping enough distance from the animals. Due to the beta-light, a minimum distance of 20m could be kept, which was deemed enough by Reeve (1994). Therefore, the observer probably had a negligible effect on the behaviour of the animals.

Even though there were no badgers present in the areas where hedgehogs were further away from the edge-habitat, there were foxes seen, animals who may also be predators of hedgehogs (Burton, 1969). Foxes were thought to have no significant influence since it is generally assumed that they cannot uncurl healthy hedgehogs and therefore do not pose a great threat to most hedgehogs (Reeve, 1994). However, it could be that the presence of this other predator does influence the vigilance, since foxes do eat animals which do not curl op quickly enough (Burton, 1969). This effect of predators on vigilance has also been shown in other small mammals (for example Dickman & Doncaster, 1984).

It is remarkable that juveniles stay closer to edge-habitat in all areas. This could be a bias, since juvenile hedgehogs did not get a transmitter, because the animals were too small and therefore could not be tracked on a regular basis. Data from juvenile hedgehogs only came from accidental encounters. Since visibility in arable fields was generally not very good, the chance of encountering a juvenile in an arable field and thus further away from edge-habitat was smaller than obtaining a fix from a radio-tracked adult in an arable field. This is also shown by accidental encounters in general, which were mostly in the ‘narrower’ habitats with high visibility, like lawns and road verges, where the maximum distance animals can be from the edge is smaller than for example in an arable field.

There could also be other additional reasons for the distance kept from edge-habitat, like food abundance (see chapter 3) or navigation (Huijser, 2000). This means that for now it is not possible to conclude that badger density is the only reason for this behaviour, but judging by the amount of differences found, it is possible to conclude that badger density forms at least part of the reason for hedgehogs to show edge-refuging behaviour.

2.4.2. Home-Range

It was observed that hedgehogs in the areas with high badger density had on average a smaller home-range than hedgehogs in the areas with low badger density, as also found in the net displacement. The negative influence of a predator on home-range size has also been shown in other small mammals (Beaudoin *et al.*, 2004). Home-range size in small mammals does not seem to be influenced by inter-specific competition for resources (Barta *et al.*, 1989), but not much research has been done on this subject. Nevertheless, the result of this study signals that the change in behaviour of hedgehogs will be mostly related to the predation pressure by badgers and probably less to competition over food with badgers.

The fact that home-range size was linked to sex is seen in most studies (for example Reeve, 1994), especially because this study mostly took place during the mating season, when males are known to walk large distances to search for females (Reeve, 1994). This is something that also comes forth in the net displacement, where males have a larger displacement.

The significant relation between interval and net displacement can be explained by a high amount of ‘turning’ by the hedgehogs. When time between fixes becomes longer, the net displacement becomes shorter. When animals mainly walk in a straight line, this displacement should not become much smaller. In this case, displacement decreased quite rapidly with increasing interval time. That hedgehogs do not tend to move in a straight line has also been seen in New Zealand (Shanahan *et al.* 2007).

2.4.3. Habitat Selection

Hedgehogs utilized habitats with dense vegetation more than open vegetation, only when there was a high badger density. This was not seen when looking at the amount of habitat within home-range. This could be explained with the way home-range was specified. In this study, an animal's home-range is the area where most fixes were found. This means that if an animal, for example, uses only the field margin around a field, the field itself will be a part of the home-range, even though the animal has not used it. To overcome this problem, it is best to concentrate on where animals were seen when looking at habitat selection and less at habitat within home-range. When looking at fixes, the animals do show a correspondence to the hypotheses stated in this research, namely that animals in areas with high badger density seek out habitat with a high amount of cover. Hedgehogs were seen often in urban areas in all sites, but in sites with low badger density, animals were also seen a lot on arable fields. As said above, the most striking observation was that the hedgehogs in Great Easton greatly preferred urban areas, even though rural habitat was available.

Furthermore, this habitat utilization found in this study supports the "landscape of fear" theory. Animals in a predator-prone environment selected habitats with a high amount of cover more often than animals in areas without badgers. This is also seen in other animals, even when there is a trade-off between food abundance and amount of cover (for example Beaudoin *et al.*, 2004; Laundré *et al.*, 2001). If there was also a trade-off between food and shelter in this study is dealt with in chapter 3.

Habitat selection found in other publications is very diverse (Bunner, 2004; Hof, 2009; Huijser, 2000; Morris, 1988; Riber, 2006; Zingg, 1994). All these studies see relatively more use of hedgerows than available in the study-area, which is also found in this study. Also the preference for urban areas is often found (Bunner, 2004; Hof, 2009; Riber, 2006; Zingg, 1994). Bunner (2004) found a much lower amount of field margin in the home-ranges of hedgehogs, while that study was done in almost the same area around Old Windsor. This difference is probably due to the fact that the managers of the Crown Estate have established a lot of new field margins the last few years (personal communication, Paul Bright, 2009). These differences in habitat selection prove the generalist habit of hedgehogs and the ability to survive in a very broad range of habitats.

2.5. Conclusion

Hedgehogs do indeed adapt their behaviour when badgers are present. The results found show great resemblance with the "landscape of fear" theory. In areas with a high badger density, the animals stay closer to edge-habitat or do not even leave the village. Furthermore, in areas with high badger density, hedgehogs prefer habitat which provides more shelter, while this phenomenon is not observed in areas with a low badger density. As said above, all those conclusions have also been drawn for other species whilst testing for this theory.

Future research is needed to understand if this influence of badgers is only due to their predatory role or that their competition over food also has an influence, since that cannot be clearly stated from these results. Also in other countries is research needed, where it is not yet known if badgers also influence the behaviour of hedgehogs.

The results of this research make clear that the conservation and recovery of field margins and hedgerows (habitat with a high amount of shelter) in areas with a high badger density is very important in future conservation of the hedgehog. It is also important, even in areas without badgers, to make the general public aware of the fact that hedgehogs spent a lot of time in gardens and people can help these animals by making their gardens hedgehogs friendly.

Acknowledgements

I have learned a lot during the course of this research and this could not have happened without the help of a lot of people. First and foremost, I’d like to thank the British Hedgehog Preservation Society and The People’s Trust for Endangered Species for providing funding for this project. Furthermore, my supervisors, Frank van Langevelde and Anouschka Hof, for their time, comments and providing the opportunity for me to learn an invaluable lesson about research. Anousckhka Hof, also thank you for providing me access to the data obtained in 2008. Thanks also to Henjo de Knegt for his help with the home-range analyses. The study would have been impossible without the farmers and game-keepers who gave us permission to do our study on their land and without the dozens of member of the public who granted us access to their gardens or tips about the badgers and hedgehogs in their area.

Emily Throgmorton, Simon Thompson, Michael Bennett, Jeremy Smith and Nathaniël Severs, you all really showed that more hands make lighter work. Thank you for your time, enthusiasm and friendship. Another thanks to Simon, who also helped me with my English. Another big thank you to my boyfriend, Tim Hofmeester, who helped with thinking, writing, tracking and gave me his unconditional support during this study. And of course thanks to everybody who asked how it was going and showed an almost unstoppable interest in what I was doing. It really kept me going.

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Appendix 2.1. Study Sites with the Obtained Fixes

Figure 2.6. The study site in Norfolk used in the study of 2008 by Hof (2009). The areas pictured as village are Brancaster, Burnham Deepdale and Brancaster Staithe.

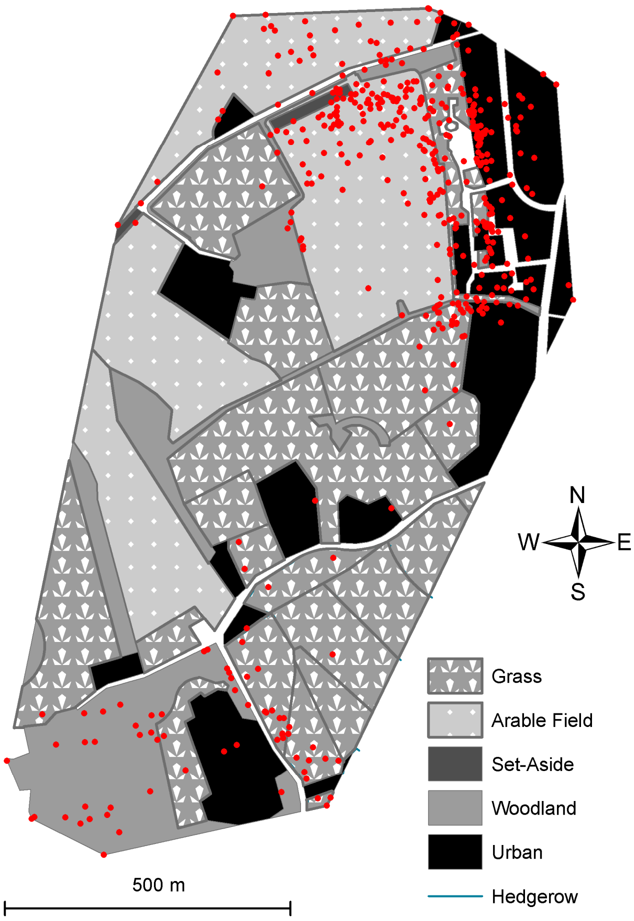

Figure 2.7. The study site around Old Windsor of 2009. The depicted village is Old Windsor.

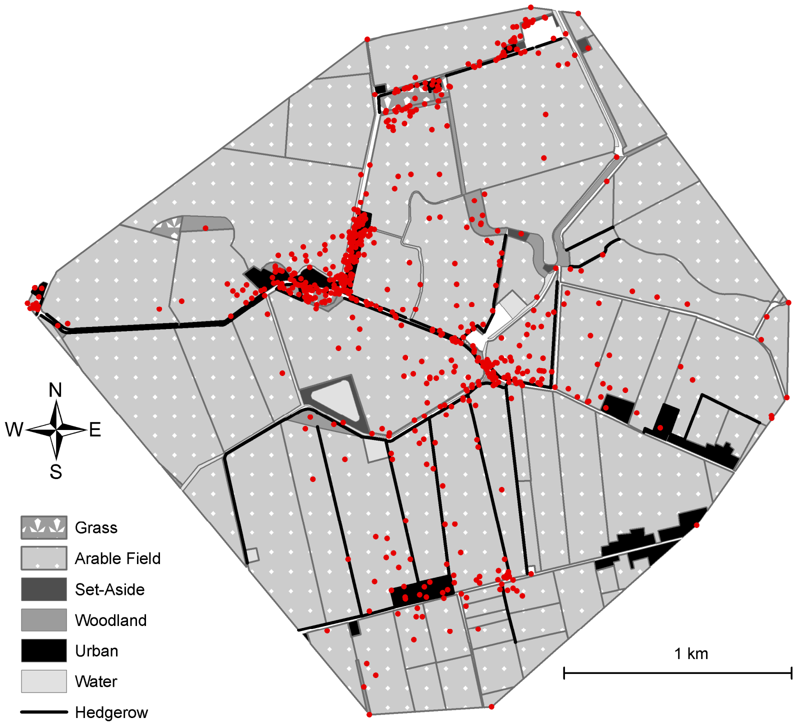

Figure 2.8. The Gedney Dawsmere site, studied in 2009. The villages shown are Gedney Drove End and Gedney Dawsmere.

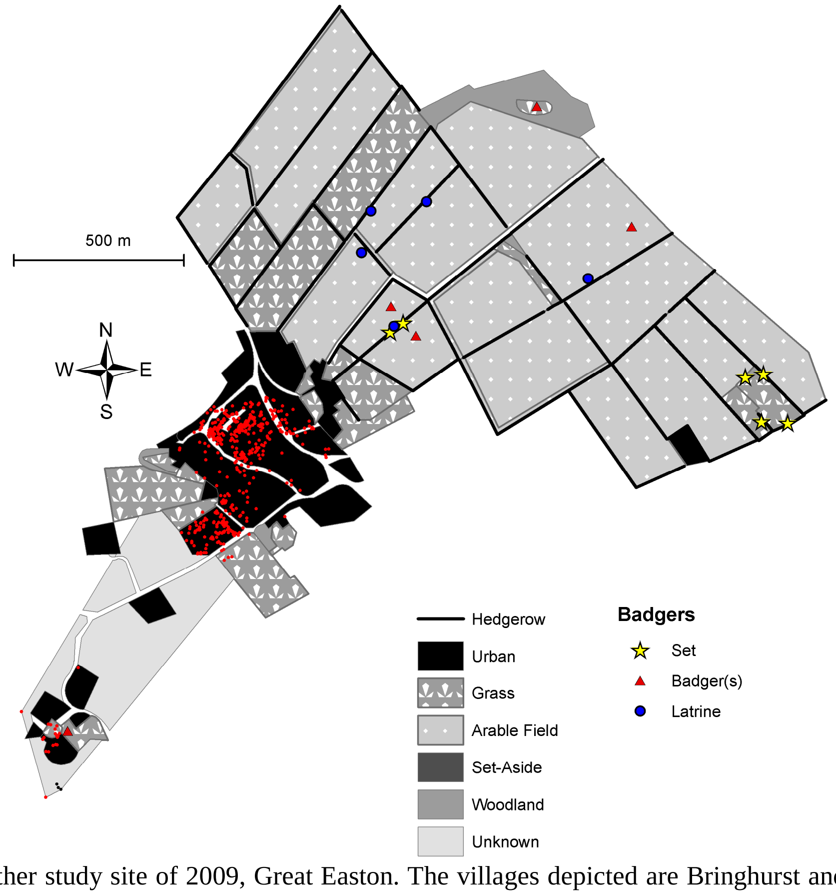

Figure 2.9. Another study site of 2009, Great Easton. The villages depicted are Bringhurst and Great Easton. A part of the agricultural landscape is also shown, because of the badger sightings and the different determination of the total study area.

Appendix 2.2. Habitat Selection

Table 2.3. The amount of fixes per habitat per site per sex for both years. Juveniles are not taken into account.

	Brancaster		*Old Windsor*		*Gedney Dawsmere*		*Great Easton*	
	Male	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*	*Female*
Pasture	166	95	49	6	2	0	10	1
Arable Fields	88	66	84	57	165	76	0	0
Field Margin	231	127	21	10	43	23	0	0
Hedgerow	122	108	27	13	57	24	6	2
Woodland	42	114	6	23	15	7	4	4
Set-Aside	45	1	2	4	1	4	1	0
Garden	294	448	99	28	34	31	319	92
Lawn	64	169	23	17	17	37	22	7
Shrubbery	37	28	11	2	0	0	14	4
Road	10	10	4	2	1	14	15	5
Road-verge	6	19	2	1	29	49	9	1
Other	2	6	0	1	10	5	1	0
Not Seen	15	6	5	0	1	1	2	0

Table 2.4. The percentages of habitat within home-range (average) per sex and within the total study area. "Other" habitat is water and ditches.

Area	*Sex*	*Pasture*	*Arable Field*	*Field margin*	*Set aside*	*Wood-land*	*Garden*	*Lawn*	*Road*	*Other*
Brancaster	m	12.09	47.76	4.18	6.53	5.12	21.40	1.90	-	-
	f	12.19	42.00	4.23	0.00	9.33	27.53	3.93	-	-
	Total	7.74	57.55	4.70	5.40	4.74	16.02	2.57	-	-
Old Windsor	m	10.50	38.85	3.59	0.47	3.68	20.70	12.82	9.38	-
	f	0.35	40.99	2.86	2.24	26.85	13.67	7.71	5.34	-
	Total	33.01	27.78	1.42	0.37	13.71	16.99	3.88	4.08	-
Gedney Dawsmere	m	2.07	81.93	0.63	0.43	2.02	5.01	0.68	5.15	2.10
	f	7.83	54.27	0.72	0.69	1.53	19.23	0.43	12.74	2.55
	Total	0.65	89.03	0.54	0.47	1.56	1.47	0.11	2.71	1.44
Great Easton	m	0.28	0.00	0.00	-	0.00	87.36	-	12.36	-
	f	9.37	0.00	0.00	-	0.00	80.95	-	9.68	-
	Total	16.10	54.30	1.77	-	2.56	12.61	0.28	3.95	-

Table 2.5. Habitat selection in home-ranges from total habitat available. <1 means a smaller proportion in home-range than in total area; >1 means a bigger proportion in home-range than in total area. – indicates that the habitat was not available or there was no data, while 0,00 means that the habitat available, but was not used.

Habitat type	*Brancaster*		*Old Windsor*		*Gedney Dawsmere*		*Great Easton*	
	Male	*Female*	*Male*	*Female*	*Male*	*Female*	*Male*	*Female*
Pasture	1.57	1.56	0.32	0.01	3.19	12.09	0.02	0.58
Arable Field	0.83	0.73	1.40	1.48	0.92	0.61	0.00	0.00
Field Margin	0.90	0.89	2.53	2.01	1.15	1.32	0.00	0.00
Hedgerow	0.80	0.61	0.47	0.02	0.29	0.26	0.00	0.00
Set-Aside	1.21	0.00	1.27	6.05	0.92	1.47	-	-
Woodland	1.08	1.97	0.27	1.96	1.29	0.99	0.00	0.00
Garden	1.56	1.72	1.22	0.80	3.40	13.08	6.93	6.42
Lawn	1.53	1.53	3.31	1.99	6.02	3.86	0.00	0.00
Road	-	-	2.30	1.31	1.90	4.70	3.13	2.45
Other	-	-	-	-	2.79	3.16	-	-

Chapter 3:

The relation between food availability, predator presence and small scale movements of hedgehogs (Erinaceus europaeus) in arable dominated landscapes

Anouschka R. Hof

Abstract

Understanding the movement of animals plays a significant role in a variety of ecological fields of study; an insight into the how and why of animal movements may aid the conservation of the species investigated. The West European hedgehog (*Erinaceus europaeus*) is a relatively mobile species, and adapted to a wide range of habitat types. However, they are frequently associated with edge habitat and, in arable landscapes, mainly utilized field margins. This edge-refuging habit is not well understood and may be the result of fear of predators, food availability or other factors.

The results thus suggest that arable land may be a 'landscape of fear' for hedgehogs in the presence of a high amount of badgers. It however does appear that in areas with lower numbers of badgers hedgehogs do not stay close to edge habitat on arable fields because they seek cover from badgers, but because they are in search of food.

It can be concluded that it is especially beneficial for the conservation of hedgehogs in areas with a high badger abundance to increase the complexity of the structure of the landscape by amongst others establishing more and denser hedgerows in rural areas.

3.1. Introduction

Understanding the movement of animals, such as seasonal migration, immigration, emigration and local redistribution, plays a significant role in a variety of ecological fields of study like meta-population ecology, epidemiology and spatial ecology. Additionally, an insight into the how and why of animal movements may aid the conservation of the species investigated. Animal movements are affected by a range of biotic and abiotic factors. Climatic variations, quality of the habitat, availability of resources, and presence of competitors and/ or predators all may affect movement patterns of species to a high or low extent.

Although the hedgehog (*Erinaceus europaeus*) is adapted to a wide range of habitat types, and is a relatively mobile species, they are able to cover distances of over 1000m a night (Reeve, 1994), they are frequently associated with edge habitat (e.g. Morris, 1986; Dowie, 1993; Huijser, 2000). As has been found by Hof (2009) hedgehogs mainly utilized field margins in arable landscapes. This edge-refuging habit is not well understood and may be the result of fear of predators such has, for instance, been shown for the elk (*Cervus elaphus*) (Hernández & Laundré, 2005). Availability of food might also be the main cause as has, for instance, been shown for several warblers (Johnson & Sherry, 2001). Availability of other resources such as nest material (Hof, 2009) has also been mentioned.

In chapter 2, the impact of badgers on small scale movements of hedgehogs in agricultural landscapes has been studied. However, as it has been estimated that hedgehogs spend up to 84% of their active time foraging (Wroot, 1984), their movements might be largely dictated by the distribution and abundance of prey items such as lumbricidae, coleoptera and gastropoda (Reeve, 1994). Food availability has been shown to be the main decisive factor in movement patterns of various species (Sherman, 1984; Johnson & Sherry, 2001 e.a.) and may well be the main cause of the edge refuging habit of hedgehogs. To be able to understand which factors drive small scale movements of hedgehogs in agricultural landscapes this chapter aims to combine the results found in chapter 2 with part of the results found in chapter 1.

3.2. Materials and methods

The invertebrate (lumbricidae, gastropoda, coleoptera) abundance was estimated in fields that were utilised by hedgehogs in the four study sites described in chapter 2: Brancaster, Gedney Dawsmere, Great Easton and Old Windsor. Since hedgehogs in the Great Easton site hardly left the village and were not seen on fields where access was allowed, random fields were chosen for invertebrate sampling as to get an idea of the food availability in this site in comparison to the other sites. In addition to the arable fields with a grassy field margin sampled in chapter 1, several other arable fields with a grassy field margin, pasture fields and set aside fields were sampled, provided that they were utilised by hedgehogs and that access was allowed. Arable fields without a grassy field margin were not utilised by hedgehogs and therefore left out of the analyses. Table 3.1. shows the number of samples obtained per habitat type per site. The sampling method for lumbricidae, gastropoda, and coleoptera was as described in chapter 1.

The radio-tracking data obtained in chapter 2 was used to relate the abundance of lumbricidae, gastropoda and coleoptera to hedgehog movements. Badgers were absent in Gedney Dawsmere and in Old Windsor. They were present in Brancaster and in Great Easton (see chapter 2 and Hof, 2009). Since the presence of badgers was only recorded as present or absent, it was decided to classify food availability in two classes as well: low availability and high availability. In this way comparison between the impact of badgers and food availability on the distance with which hedgehogs were found in agricultural fields was deemed less biased towards one of the variables. The cut point between high and low food availability was based on two equal groups. Statistical analyses were conducted using SPSS (for windows 14^{th} edition, SPSS Inc., Chicago, USA).

Table 3.1. Number of samples obtained from invertebrates per habitat type per site.

Site	*Habitat*	*Number of Samples*
Brancaster	Arable	30
	Field margin	15
	Pasture	45
	Set aside	45
Gedney Dawsmere	Arable	100
	Field margin	50
Great Easton	Arable	40
	Field margin	20
Old Windsor	Arable	20
	Field margin	10
	Set aside	15

3.3. Results

3.3.1 Food availability

The mean invertebrate abundance was significantly the highest in Old Windsor, followed by Gedney Dawsmere, Brancaster and Great Easton (Kruskal-Wallis Test, χ^2=96.007, df=3, p<0.001). However, the differences between the latter three were not significant (Kruskal-Wallis Test, χ^2=3.111, df=2, p=0.211). In each habitat type the mean invertebrate abundance was remarkably higher at Old Windsor than at the other sites (Figure 3.1.). Differences between the mean abundance of invertebrates between the sites were significant for arable fields (Kruskal-Wallis Test, χ^2=61.119, df=3, p<0.001), field margins (Kruskal-Wallis Test, χ^2=31.009, df=3, p<0.001) and set aside (Kruskal-Wallis Test, χ^2=32.642, df=1, p<0.001). Differences between the sites without Old Windsor included were also significant for arable fields (Kruskal-Wallis Test, χ^2=16.546, df=1, p<0.001) and for field margins (Kruskal-Wallis Test, χ^2=23.405, df=1, p<0.001).

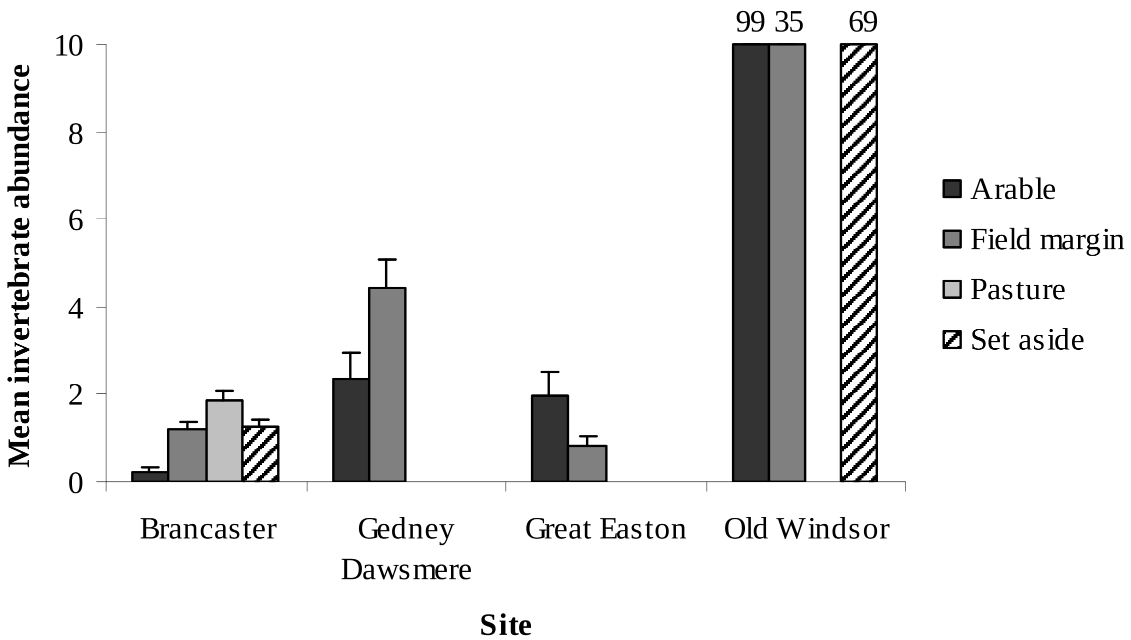

Figure 3.1. Mean invertebrate abundance per habitat type per site. Invertebrate abundances were summed: mean abundance of coleoptera per pitfall, mean abundance of gastropoda per 0.5m^2, mean abundance of lumbricidae per kg soil.

The high mean abundance of invertebrates at Old Windsor was mainly due to the large amount of coleoptera found at this site (Figure 3.2.). Coleoptera were significantly most abundant at Old Windsor and least abundant at Brancaster (ANOVA, F=103.364, df=3, p<0.001). Gastropoda were also significantly most abundant at Old Windsor but least abundant at Great Easton (ANOVA, F=8.894, df=3, p<0.001). Lumbricidae on the other hand were significant present in a higher abundance at Brancaster, whilst they were least abundant at Old Windsor (ANOVA, F=11.345, df=3, p<0.001).

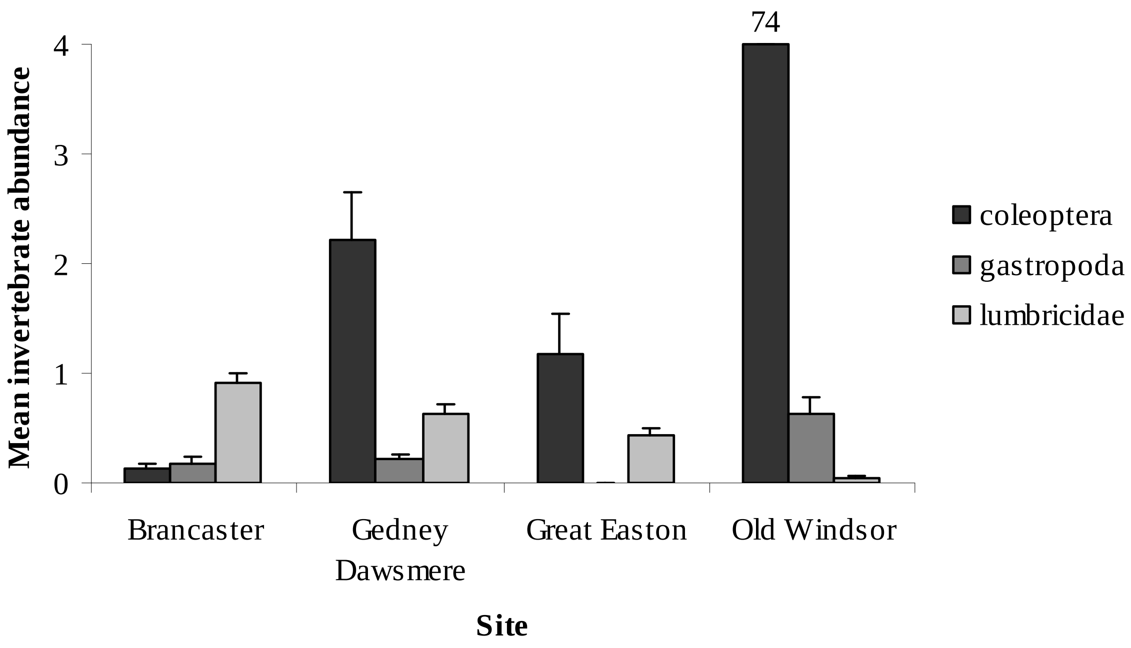

Figure 3.2. Mean number of coleoptera (·pitfall^{-1}), gastropoda (·0.5m^{-2}), and lumbricidae (·kg soil^{-1}) per site.

Coleoptera were significantly most abundant on set aside and least abundant on pasture (ANOVA, F=2.920, df=3, p=0.034). In contrast, gastropoda were significantly most abundant on pasture and least abundant on set aside (ANOVA, F=5.504, df=3, p=0.001). Lumbricidae were also significantly most abundant on pasture, but least abundant on arable fields (ANOVA, F=26.502, df=3, p<0.001) (Figure 3.3.).

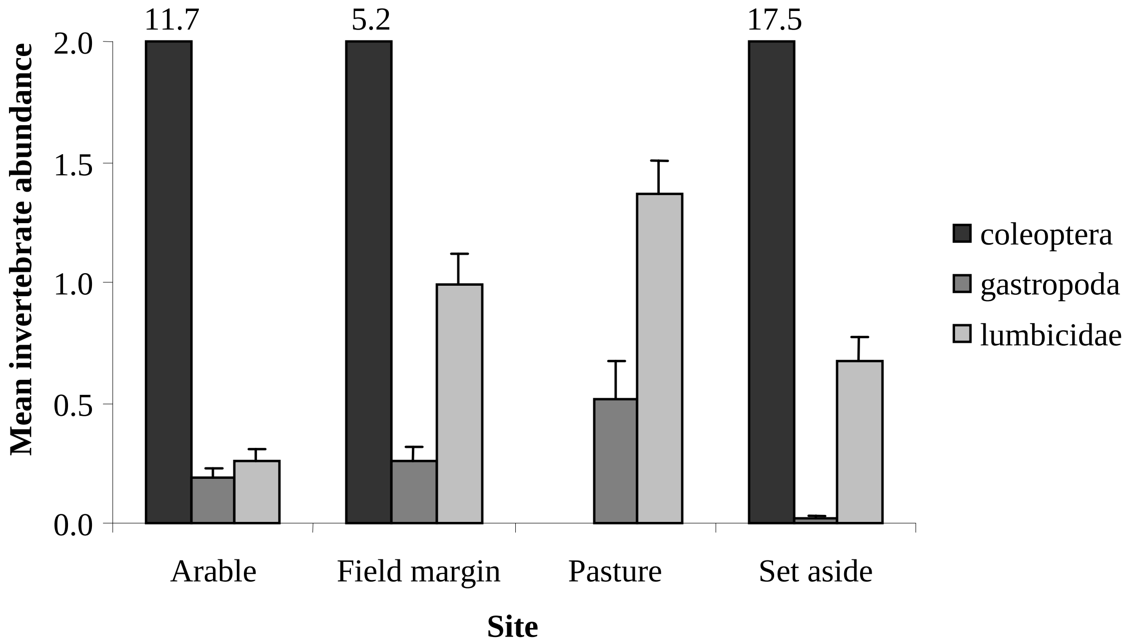

Figure 3.3. Mean abundance of coleoptera (·pitfall^{-1}), gastropoda (·0.5m^{-2}), and lumbricidae (·kg soil^{-1}) per habitat type.

3.3.2 Habitat selection of hedgehogs in relation to food availability

In chapter 2 the habitat selection of hedgehogs was determined per site; it was seen that hedgehogs did not significantly prefer habitat types that offer cover in sites where badgers were present. Table 3.2. Shows the habitat selection ranked according to preference, and invertebrate abundance ranked according to availability per habitat type per site. The ranking of habitat selection was significantly related to the ranking of the availability of lumbricidae (Pearson Correlation Test, $r=0.742$, $n=11$, $p=0.009$), but not to gastropoda, coleoptera or all invertebrates combined. This means that habitats that were preferred by hedgehogs significantly more often held a high than a low abundance of lumbricidae.

Table 3.2. The habitat selection ranked according to preference, and invertebrate abundance ranked according to availability per habitat type per site. The higher the rank the higher the preference of the habitat and the higher the availability of invertebrates.

Area	*Habitat*	*Habitat selection*	*Total invertebrate abundance*	*Gastropoda abundance*	*Lumbricidae abundance*	*Coleoptera abundance*
Brancaster	Arable	4	4	2	4	3
	Field margin	1	3	3	2	2
	Pasture	2	1	1	1	3
	Set aside	3	2	3	3	1
Gedney Dawsmere	Arable	1	2	2	2	2
	Field margin	2	1	1	1	1
Great Easton	Arable	1	1	1	1	1
	Field margin	2	2	1	2	2
Windsor	Arable	2	1	1	2	1
	Field margin	1	3	2	1	3
	Set aside	3	2	3	2	2

3.3.3 Food availability and badger presence in relation to hedgehog movements

A GLM (Table 3.2) showed that badger presence, and the combined impact of food availability and badger presence, were related to the distance with which hedgehogs were situated to cover on agricultural land. However, the impact of habitat type was larger. The height of the crop and food availability by itself did not have a significant impact and were not included in the model. Figure 3.4. shows the combined effect of food availability and badger presence in relation to the mean distance to cover with which hedgehogs were found on agricultural land.

Table 3.3. The result of the GLM with dependent variable ‘distance to cover (m)’.

Source	*Sum of Squares*	*df*	*Mean Square*	*F*	*Sig.*
Corrected Model	309927	11	28175	32.671	<0.001
Intercept	14810	1	14810	17.173	<0.001
Habitat	126450	3	42150	48.876	<0.001
Food availability * badger presence	49142	2	24571	28.492	<0.001
Badger presence	9926	1	9926	11.510	0.001
Behaviour	14621	5	2924	3.391	0.005

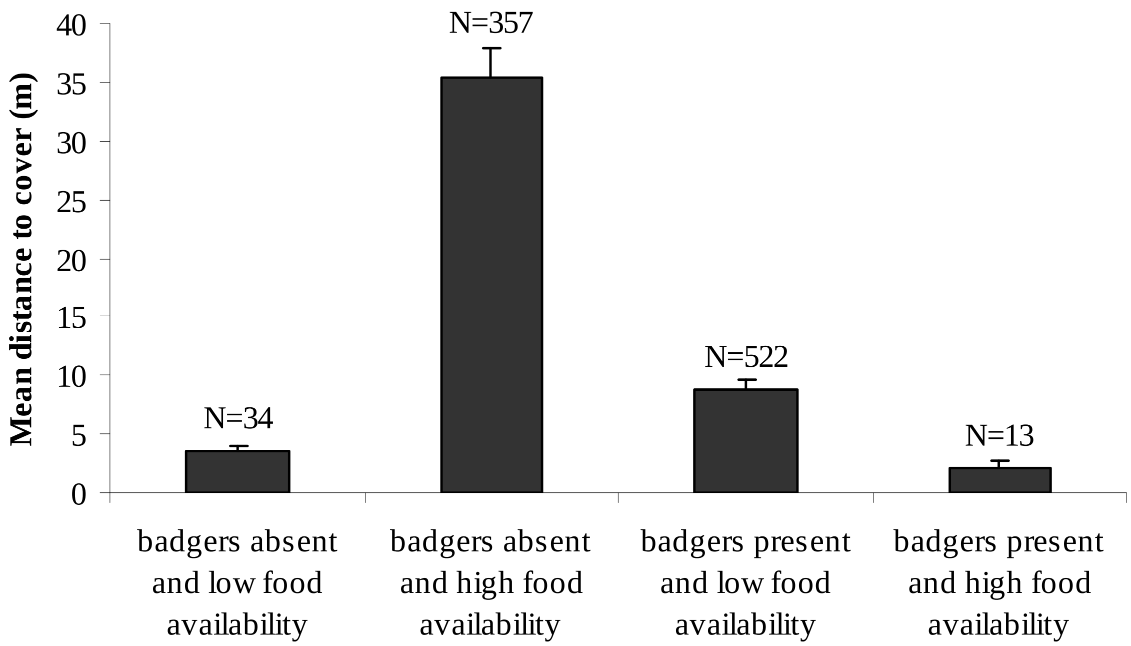

Figure 3.4. Mean distance to cover at which hedgehogs were found on agricultural land in relation to the combined effect of food availability and badger presence.

Since the variable habitat had the largest impact on the distance with which hedgehogs were situated from cover habitat, a GLM was built for ‘arable’. No significant GLM could be obtained for ‘field margin’. Too few data points from too few sites were thought to be obtained for pasture (N=82, 1 site) and set aside (N=44, 2 sites). GLM models were therefore not built for these habitat types. The GLM for ‘arable’ (Table 3.3.) showed that the presence of badgers did not have a significant impact on the distance with which hedgehogs were situated to cover on arable fields. The food availability though, had the main significant impact.

Table 3.4. The result of the GLM for habitat type ‘arable’ with dependent variable ‘distance to cover (m)’.

Source	*Sum of Squares*	*df*	*Mean Square*	*F*	*Sig.*
Corrected Model	215298	6	35883	23.990	<0.001
Intercept	59477	1	59477	39.764	<0.001
Food availability	162572	1	162572	108.689	<0.001
Behaviour	20999	5	4200	2.808	0.017

3.4. Discussion

3.4.1 Food availability

The high number of coleoptera found in Old Windsor, in comparison to the other sites, is remarkable. The composition of the vegetation was comparable to the other sites (see chapter 2), and therefore does not offer an explanation. Pitfall catches however, do not only depend on the density of the insect population. Factors like body size of the species and activity also play a role (Lang, 2000) and may offer a possible explanation since the timing of sampling did differ between the sites (sampling occurred between June and August 2009). Nevertheless since it was attempted to sample sites under similar climatic conditions, and the difference was in such an order of magnitude, it seems likely that actual abundances of coleoptera were higher at Old Windsor than at the other sites as well. Differences in the number of predators present were not studied and might form part of the explanation.

Since predatory carabids were most dominant amongst the coleoptera found, it is not surprising that the abundance of gastropoda was low on those habitat types where the abundance of coleoptera was high. Differences between the abundance of Lumbricidae or most likely related to soil type and moisture content (Curry, 1998).

3.4.2 Habitat selection of hedgehogs in relation to food availability

Hedgehogs preferred to utilise habitat types with a high availability of lumbricidae. Indeed, lumbricidae can form an important part of their diet (Reeve, 1994), but are also an important staple food for badgers (Neal & Cheeseman 1996). In sites with a low food availability the pressure of intraguild predation may increase (Polis *et al.*, 1989). Theoretically, a low availability of lumbricidae might thus enhance badger predation on hedgehogs. No evidence has been found for this statement since lumbricidae were most abundant in Brancaster, the only site where hedgehogs were predated by badgers.

3.4.3 Food availability and badger presence in relation to hedgehog movements

Although it was seen from the results in chapter 2 that hedgehogs were situated less far from the edge in sites with a high badger density , it was also found that hedgehogs wandered further in the field on pasture fields than on arable fields irrespective of badger presence. In combination with the results from chapter 3 it can thus be concluded that on arable fields food availability is the main driver behind the movements of hedgehogs. It must however be noted that hedgehogs did not utilise arable fields at all in one of the sites with badger presence

(Great Easton). It is therefore advised to study the movement of hedgehogs on arable fields on more sites with confirmed badger presence.

However, at the Great Easton site several badger setts were established, and no badger setts were seen at the other site with confirmed badger presence (Brancaster). Based on the former and on the fact that more badgers were seen in the Great Easton site, it was thought that Great Easton held a higher number of badgers. The results thus suggest that a high number of badgers may drive hedgehogs from agricultural land they otherwise occupy or may cause the elimination of hedgehog populations in landscapes with a high badger density, as has been suggested by Micol *et al.* (1994). Arable land may therefore be a 'landscape of fear' (Laundré *et al.*, 2001) for hedgehogs in the presence of a high amount of badgers. Indeed, hedgehogs were seen more often in habitat types that provide cover from badgers (see chapter 2). It however does appear (see above) that in areas with lower numbers of badgers hedgehogs do not stay close to edge habitat on arable fields solely because they seek cover from badgers, but also, and more so, because they are in search of food.

Unfortunately it was not possible to obtain a model for other habitat types, since the focus of this study was on arable land, but it adds weight that hedgehogs were on average situated further in the field on pasture (where invertebrate abundance was higher) than on arable fields irrespective of the presence of badgers. Nevertheless, the ideal situation for hedgehogs seems clear: no badgers and a high food availability. This indicates that hedgehogs indeed do not stay near edge habitat because of other possible factors such as proximity to nest sites or visual orientation as has been suggested by Huijser (2000).

The results imply that it is especially beneficial for the conservation of hedgehogs in areas with a high badger abundance to increase the complexity of the structure of the landscape, which has also been shown to diminish intraguild predation in other taxa (Finke & Denno, 2002; Janssen *et al.*, 2007). This can be done by establishing more and denser hedgerows in rural areas, dense shrubbery and undergrowth in urban areas, and by increasing the connectivity between suitable habitats. Additionally, the availability of macro-invertebrate food important to hedgehogs, especially lumbricidae, might be enhanced in arable dominated landscapes by introducing grassy field margins on arable fields (see chapter 1).

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