The Ecology of the European hedgehog (*Erinaceus europaeus*) in rural Ireland.

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Abstract

This study on the ecology of Irish hedgehogs (*Erinaceus europaeus*) has provided information on detection techniques, home range, habitat selection, potential hedgehog prey, nesting, courtship, genetics, road mortality, parasites, ageing and morphology of this species. Data were obtained from a focal study area in rural Cork, in which 24 radio tagged hedgehogs were monitored from June 2008 to June 2010. Further data were obtained through road kill surveys and the collection of hedgehog carcasses from around Ireland. Hedgehogs of both sexes were found to display philopatry. Habitat was not used in proportion to its availability, but certain habitats were selected and a similar pattern of habitat selection was evident in successive years. Hedgehogs preferred arable land in September and October when prey increased in this habitat and, unlike studies elsewhere, were observed to forage in the centre of fields where prey was most accessible. Badgers were regularly seen at the study site and did not appear to negatively affect hedgehogs' use of the area. Instead the intra and inter-habitat distribution of hedgehogs was closely correlated with that of their potential prey. Male hedgehogs had a mean annual home range of 56 ha and females 16.5 ha, although monthly home ranges were much more conservative. Male home range peaked during the breeding season (April-July) and a peak in road deaths was observed during these months. The majority of road kill (54%) were individuals of one year old or less, however, individuals were found up to eight and nine years of age. Genetic analysis showed a distinct lack of genetic variation amongst Irish hedgehogs when compared to England and France and this suggests colonisation by a small number of individuals in Ireland. The ectoparasites, *Archaeopylla erinacei*, *Ixodes hexagonus* and *Ixodes canisuga* were recorded in addition to the endoparasites *Crenosoma striatum* and *Capillaria erinacei.* In light of the reported decline in many areas of the hedgehogs' range, it is a species of conservation concern, and this is the first study examining the ecology of the hedgehog in Ireland. This study has highlighted the importance of maintaining structures such as hedgerows and the preservation of heterogeneity. This is particularly important in order to ensure the utilisation of habitats such as arable and to prevent suitable habitats becoming isolated.

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Chapter 1-

Introduction

1.1 Genus Erinaceus

There are four genera and 15 species of hedgehog found through Europe, Africa and Asia (Morris 2006) (Fig. 1.1). It has been suggested that the northern limit of the family Erinaceidae, has been determined by climate and particularly by the length of winter during which suitable macro-invertebrate prey is unavailable. A similar limit is also found in another insectivore, the mole (*Talpa europaea*) (Corbet 1988).

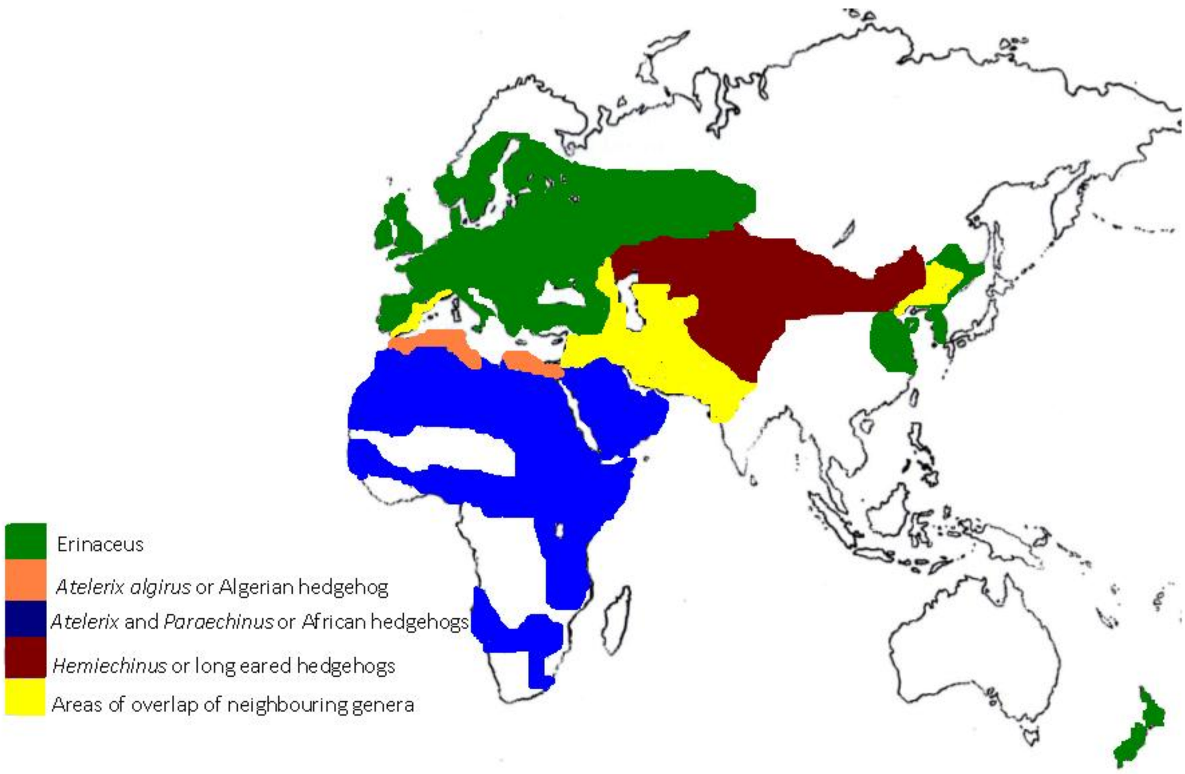

Figure 1.1: The distribution of the four hedgehog genera. (Modified from Morris 2006).

The Western European hedgehog (*Erinaceus europaeus*) is one of four species within the genus *Erinaceus* (Pfäffle 2010). While the Amur hedgehog, *Erinaceus amurensis*, is found in eastern Manchuria, the Korean peninsula, the Amur basin, and the Chinese lowlands (Corbet 1988), the remaining members of this genus are mainly found in Europe (Reeve 1994). A deep divergence both genetically and morphologically in the Eastern European hedgehog, *Erinaceus concolor* has led to its division into two different species: the northern white-breasted *E. roumanicus*, distributed in Eastern

Europe to the Northern Caucasus, and the southern white breasted hedgehog *E. concolor*, distributed in the Middle East (Sommer 2007) (Fig. 1.2 a and b).

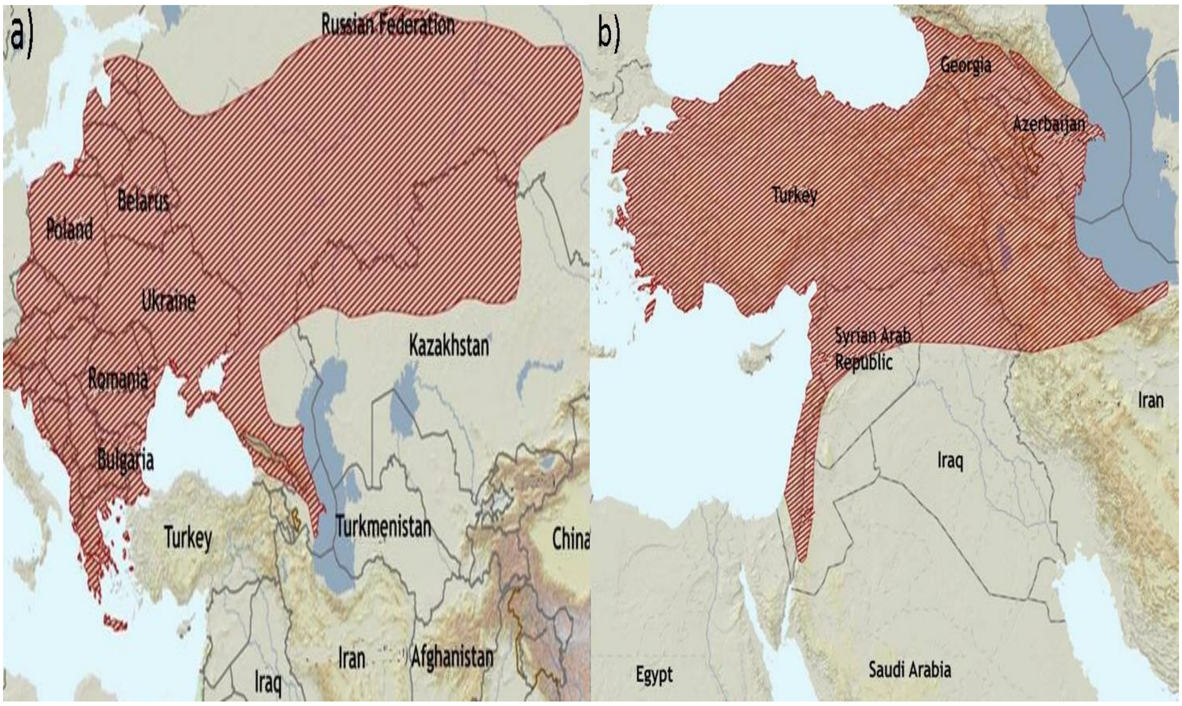

Figure 1.2: The distribution of a) *Erinaceus concolor* and b) *Erinaceus roumanicus*. (Map taken from Pfäffle 2010).

Figure 1.3: The distribution of *Erinaceus europaeus*. Map taken from Pfäffle (2010).

There is an area of overlap, and possible hybridisation between the Eastern European hedgehogs and the Western European hedgehog, existing from the Baltic to the border between

Italy and Slovenia, and from Lithuania east to Kirov, Russia (Santucci *et al.* 2002). The Western European hedgehog while occupying many of the same countries as the Eastern European hedgehogs, is also found further west: in Ireland, England, Portugal, Spain, France, Germany, Italy, The Netherlands, Denmark, Belgium, Switzerland, Austria, Luxembourg and all of the Scandanavian countries (Fig. 1.3) and was introduced to The Outer Hebrides (Jackson & Green 2000) and New Zealand (Jones *et al.* 2005). In the areas where it has been introduced, it is considered to be a pest, due to its feeding on the eggs of ground nesting birds. In New Zealand they are thought to have contributed to the extirpation of 50 bird species (Wodzicki 1950) and in the Hebrides, hedgehogs were found to have accounted for between 36-64% of nest failures in Northern Lapwing (*Vanellus vanellus*), Dunlin (*Calidris alpina*), Common Snipe (*Gallinago gallinago*) and Common Redshank (*Tringa totanus*) (Jackson *et al.* 2004).

1.2 *Fossil record*

In the fossil record of Europe, the hedgehog (*Erinaceus* sp.) is recorded for the first time during the older Pleistocene (>25 Kyrs BP), and during the Pleniglacial (>23000 BP) (Sommer, 2007). During the last Glacial Maximum (23000-16000 BP), *Erinaceus europaeus* was restricted to the Iberian and Italian peninsulas and showed a gradual dispersion out of the glacial refugia (Sommer 2007). According to Sommer (2007), the distribution of both *concolor and europaeus* seems to have been fairly constant since the early Holocene (9600-8600 BC).

Within *europaeus*, three monophyletic clades are seen, termed E1, E2 and E3. The E2 clade is found only in Western Europe, from Spain northwards through France, the Netherlands and into the U.K. and Ireland (Seddon *et al.* 2001). In Ireland the hedgehog was first recorded in the 13th Century in Waterford (Yalden 1999). It is unclear, how the hedgehog arrived in Ireland but there is some suggestion that it was intentionally introduced as a source of food (Savage 1966). In the Republic of Ireland, the hedgehog is strictly protected and is listed in Appendix III of the Bern

Convention as a species requiring protection and under the Irish Wildlife Acts 1976, 2000 (Hayden & Harrington 2001).

1.3 Mammals in Ireland

In Fairley's (1975) *An Irish beast book*, excluding domesticated farm animals and pet mammals, he describes the presence of 21 species of wild land mammal (including human introductions) and seven species of bat in Ireland. Since then the number of identified bat species in Ireland has risen to ten (www.bat conservation Ireland.org) and there has been an introduction of another insectivore, the lesser white toothed shrew (*Crocidura glareolus*) (Tosh *et al.* 2008) and the inclusion of the feral goat (*Capra aegagrus hircus*), bringing the number of land mammals to 23. However, the number of mammalian species in Ireland is still much lower than the U.K. Ireland has half the species of carnivores and one quarter of the species of rodents than in the U.K. (Hayden & Harrington 2001) and just 15% of the 150 mammal species found in continental Europe (Fairley 1975).

The introduction of non-native species continues to cause ecological concern globally (Manchester & Bullock 2000) and is perceived to be one of the leading threats to biodiversity (Wilcove *et al.* 1998). Over half of the mammals that are established in Ireland are believed to be introduced (Hayden & Harrington 2001), either deliberately as is the case with game species such as the Sika deer (*Cervus nippon*), or accidentally as is the case with the pygmy shrew (*Sorex minutus*). While the latter has had no obvious detrimental effects, many of these introductions have threatened the native Irish fauna. This has been seen in the case of the grey squirrel (*Sciurus carolinensis*), the American mink (*Mustela vison*) and the Sika deer. The grey squirrel was introduced when six pairs were brought from the U.K. into Ireland at Castle Forbes Co. Longford in 1911, and subsequently released (Watt 1923). Since then, this species has spread rapidly and is now found in 26 of the 32 counties (Carey *et al.* 2007) leading to a 30% contraction of the range of red squirrels (*Scirus vulgaris*) in the last 10 years (Poole & Lawton 2009). The Sika deer poses a different threat.

Introduced in the 1860s (Lowe & Gardiner 1975), this species hybridises with the native red deer (Bartos & Zirovnicky 1981) with hybrids recorded in areas of Wicklow, Mayo and Galway (McDevitt *et al.* 2009). This hybridisation has put the genetic integrity of the red deer under threat (Abernethy 1994).

Among the mammals found in Ireland, there are some interesting variations to the U.K. The Irish hare (*Lepus timidus hibernicus*) is unique to Ireland, while the stoat (*Mustela erminea hibernicus*) displays differences in size to the stoat found in the U.K. (Moffat 1927). It has been suggested that differences in size is related to variations in prey size (Erlinge 1987) and a reduction in selective pressure in the absence of some potential competitors in Ireland (Dayan & Simberloff 1994).

1.4 Decline of mammal species and farming practices

Population declines have occurred for a number of wild mammalian species in Europe, sometimes drastically so, and changes in farming practice are believed to be significant contributory factors (Macdonald & Tattersall 2007). However, over the last few decades, agricultural changes aimed at making farming more cost-effective have had accelerating adverse effects on wildlife (Kleijn *et al.* 2006). It has been estimated that 50% of all species in Europe currently depend on agricultural habitats (Stoate *et al.* 2009). Donald *et al*. (2001) found that bird population declines and range contractions were significantly greater in countries with more intensive agriculture. During the past 50 years, agricultural intensification has increased crop yields (Asteraki *et al.* 2004), but has been associated with a decrease in biological diversity (Burel *et al.* 2004, Kleijn *et al.* 2006, Bilenca *et al.* 2007, Gelling *et al.* 2007, Vickery *et al.* 2009). Declining populations of U.K. grassland flora and fauna have been attributed to intensification of agricultural management practices, including changes in cutting, fertilizer, grazing and drainage regimes (Woodcock *et al.* 2007).

1.5 Loss of hedgerow

Tapper and Barnes (1986) suggested that modern agriculture has an adverse effect on numbers of hares, something they attributed to the decrease in sheltering areas due to the loss of hedgerow. Hedgerows act as a corridor of movement and dispersal for many forest species, such as carabids, small mammals, and plants (Burel 1996, Bilenca *et al.* 2007, Gelling *et al.* 2007). Therefore, as well as being important nesting sites for a number of mammal species (Morris 1969, Gillings & Fuller 1998, Gelling *et al.* 2007, Burel *et al.* 2004), hedgerows also provide important habitats for their prey (Burel *et al.* 2004). In lowland-farming landscapes in Britain, hedgerows comprise one of the most important surviving elements of semi-natural habitat for birds (Hinsley & Bellamy 2000) and Hegarty and Cooper (1994) found that hedges in more intensively farmed areas were less species-rich. However, there has been a reduction of 50% of the hedgerow stock in the U.K. in the last century(Robinson & Sutherland 2002).

A number of variables are believed to limit the distribution of the European hedgehog in any habitat, with food availability (Kristiansson 1984), the presence of predators (Micol *et al.* 1994) and sufficient nest sites (Jensen 2004) being deemed to be the most important of these. Therefore, the aforementioned reduction in hedgerow and habitat quality is something that would be expected to have a negative impact on a hibernating species like the hedgehog and on their prey, as the retention of hedgerow affects the amount of leaf litter which has a knock-on effect on invertebrate colonisation (Smith *et al.* 2008). According to Hof (2009), although hedgehogs still occur throughout the U.K., the relative abundance had fallen by about 16% in the past 30 to 40 years and the "change in other land used for agriculture" had the mean strongest negative impact on the change in hedgehog abundance. Holsbeek *et al*. (1999) also believed that a similar decline in Belgium was due to habitat loss, fragmentation, traffic mortality, poisoning and other human activities. Doncaster and Krebs (1993) commented on the unpredictable and dramatic changes in resource quality in farmland, to which hedgehogs respond with shifts in their home range. Huijser (2000) observed that during the night hedgerows received greater relative use than other habitats, with hedgehogs spending 30% of their time here, despite hedgerows comprising just 10% of the area. Structures such as hedgerows are valuable for the construction of nest sites for hedgehogs (Morris 1973) but also for their prey. Therefore the absence of sufficient nest sites, particularly hibernacula could result in the absence of hedgehogs in an area. Similarly, Hof (2009) found that the presence of a pile of dead wood, a garden-shed and a hedgehog nest box were positively related to the presence of hedgehogs in an area.

1.6 Ireland's climate and landscape

Ireland's climate is influenced by the Atlantic Ocean and as a result it does not suffer the extremes of temperature experienced by many other countries at similar latitudes (www.met.ie). It has the largest percentage of permanent pasture in the EU, and agriculture is generally less intensive than in most other European countries (Cabot 1999). While agri-schemes in the U.K. have been found to significantly benefit wildlife (Pfiffner & Luka 2000, Kleijn & Sutherland 2003, Asteraki *et al.* 2004, Fuller *et al.* 2005, Kleijn *et al.* 2006) equivalent schemes, such as the Rural Environmental Protection Scheme (REPS) in Ireland have been shown to have less impact, indicating that the contrast between agri- scheme farms and non- scheme farms may be smaller in Ireland. Feehan *et al*. (2005) for instance, found that there was no significant difference between the farm average species richness of REPS and non-REPS grassland farms, or between REPS and non-REPS tillage farms. Species diversity is strongly correlated with spatial heterogeneity (Burel *et al.* 2004) and in Ireland the arable landscape is more heterogeneous than in England (Bracken and Bolger 2006). In Ireland, areas which are predominantly arable still have pockets of grassland mixed in the habitat mosaic, while in England vast areas are devoted almost totally to tillage. In addition, winter stubble is often maintained in Ireland (Bracken & Bolger 2006) which may benefit slug numbers, which are potential hedgehog prey (Glen *et al.* 1989).

1.7 Hedgehog Research

A limited amount of research has been undertaken on the other 14 species of hedgehog, namely on the body temperature (Mouhoub-Sayah *et al.* 2008, Shkolnik & Schmidt-Nielsen 1976) of *Atelerix* and *Hemiechinus*, neurological studies (Gould *et al.* 1978, Ravizza & Diamond 1972) on the genera *Paraechinus* and *Hemiechinus*, and investigations into the origins of the Algerian hedgehog (*Atelerix algirus*) (Morales & Rofes 2008). However, hedgehogs of the genus *Erinaceus* are still the most widely studied. Investigations have taken place into the hibernation of *Erinaceus amurensis* (Yuanjue & Muyan 1989) as well as anatomical studies (Youzhi *et al.* 1999) on this species. Research on *Erinaceus concolor* has mainly focused on investigations into their postglacial expansion and colonisation (Seddon *et al.* 2001, Seddon *et al.* 2002, Santucci *et al.* 2002), while work is currently being undertaken on the movement patterns of an urban population of *Erinaceus roumanicus* in Hungary (Toth *et al.* 2011). However, of this genus, the Western European hedgehog *Erinaceus europaeus* has been studied the most.

In 1969, Morris completed a Ph.D. on the ecology of the European hedgehog in the U.K. Since then there have been a number of doctoral studies on this species, in Sweden (Kristiansson 1984), the U.K. (Reeve 1994), Switzerland (Zingg 1994) Netherlands (Huijser 2000), and Germany (Pfäffle 2010). The main focus of these theses, as well as other research, has been feeding behaviour (Wroot 1984), the effect of roads (Huijser 2000), predators (Ward 1995, Young 2005), heavy metal concentrations (Rautio *et al.* 2010) and parasites (Pfäffle 2010), and more recently possible explanations for the decline of the hedgehog (Dowding 2007, Hof 2009). Other subjects that have been addressed include nesting behaviour and hibernation (Jensen 2004, Walhovd 1978, Walhovd 1979), reproduction (Morris 1966, Reeve & Morris 1986), genetics (Becher & Griffiths 1998), translocation (Warwick *et al.* 2006), dispersal (Doncaster *et al.* 2001) and the effect of the hedgehog on ground nesting birds (Jackson 2001, Jackson & Green 2000, Jackson *et al.* 2004).

However, despite being one of Ireland's most distinctive mammals and for many years being one of only two insectivores in Ireland, the other being the pygmy shrew (*Sorex minutus*), there has been little research on the European hedgehog in Ireland. The exception to this is Mulcahy's (1988) work on the hedgehog flea and the inclusion of the hedgehog in road kill studies (Sleeman *et al.* 1985, Smiddy 2002). Therefore, with the absence of baseline data on the ecology of the European hedgehog in Ireland, habitat use, nesting, hibernation and courtship behaviour of the hedgehogs in Ireland was unknown. Since this a protected species this data could be crucial for its conservation.

1.8 Aims

Hayden and Harrington (2001) reported the hedgehog to be widespread throughout Ireland. However, with no baseline data on this species, we have no idea whether, like the U.K., this species is on the decline (Dowding 2007, Hof 2009), its habitat preferences or any other aspect of its behaviour. While as already stated, Ireland's agricultural landscape is less intensive than in the U.K., agriculture is still the most intensely managed part of the Irish landscape (Cabot 1999) and urbanisation continues to spread (Stapleton *et al.* 2000). It is therefore of paramount importance that as much baseline data are collected on the ecology of the European hedgehog in Ireland, while traditional extensive farmland is still in place and their benefit to species such as the hedgehog can be investigated. Too often species that are considered plentiful in our landscape are overlooked, until a time when the damage cannot be rectified. For example, in the 1840s flocks of passenger pigeons *(Ectopistes migratorius)* were described as being so vast in extent that they darkened the skies for several successive days in areas such as Ohio and Kentucky (Bond 1921). By 1914, this species was extinct (Halliday 1980). In the 1950s the hedgehog population in the U.K. was estimated at about 30 million, by 1995 this had reduced to about 1.5 million (Mac Donald & Burnham 2011). This suggests that the decline in the species is rapid, and road casualty counts carried out between 1990 and 2001 indicate that they have declined by as much as half in that decade alone in the U.K. (Mac Donald & Burnham 2011).

While it could be assumed that the ecology of the hedgehog in Ireland would be similar to its counterparts in the U.K., Ireland's different land-use practices, the milder climate and the different mammal assemblage may result in certain variations in hedgehog behaviour here. This study therefore aimed to gain a greater understanding of the ecology of this species in Ireland and investigate whether differences exist between their behaviour in Ireland in comparison to what is known of this species in other areas of its range. In view of Ireland's less intensive landscape, this study aimed to investigate the role of hedgerow and prey availability in habitat selection in a rural landscape.

1.9 Overview of thesis

The thesis is divided into nine data chapters focusing on different aspects of the ecology of the hedgehog. A single study population was focused on as a model group, so that site philopatry, dispersal and seasonal habitat selection could be thoroughly examined. Chapters two to seven focus on the research from this radio tracked rural population that was monitored from 2008 to 2010, while Chapters eight to ten examine road kill data collected from around Ireland.

- *Chapter 2: A review of techniques for detecting hedgehogs (Erinaceus europaeus) in a rural landscape.* This chapter explores the range of techniques that can be deployed for detecting hedgehogs in an area. It addresses some of the limitations attached to these methods, possible reasons for these limitations and ways in which techniques may be improved. In particular it aimed to explore the following hypotheses and questions:
    - In view of the previous lack of success in previous studies, is trapping successful for detecting hedgehogs in rural Ireland?
    - Can questionnaires, road kill surveys, footprint tunnels or infra red thermal imagery be used as sole methods to detect hedgehogs in an area?
    - Is spotlighting is the most effective method for detecting hedgehogs in an area?
- *Chapter 3: Habitat use by the European hedgehog (Erinaceus europaeus) in an Irish rural landscape.* This chapter deals with a preliminary study completed in the first year of the research. Its main aims were to gather baseline data on the hedgehog population at the study site, and identify

areas that warranted further research, as the study developed in the subsequent two field seasons. It also aimed to test the hypothesis that habitat selection by hedgehogs changed on a seasonal basis and that habitats such as arable land are avoided. Many of the topics dealt with in this chapter act as a baseline and are further explored in later chapters.

- *Chapter 4: Home range and habitat use of hedgehogs (Erinaceus europaeus) in a rural Irish landscape.* This chapter examines some of the information we know from research in the U.K. and other areas of the hedgehogs range. It investigates whether the hedgehogs' behaviour is similar in Ireland to that elsewhere, in light of some of the differences in habitat and climate in Ireland. In particular since a single group including many of the same individuals were monitored, over successive years some of the following hypotheses were examined:
    - Do males have a larger home range than females?
    - Do Individual hedgehogs exhibit site philopatry
    - Do Individual hedgehogs show the same pattern of habitat use in successive years?
    - Is habitat selection related to prey availability?
- *Chapter 5: Intra and inter habitat differences in hedgehog (Erinaceus europaeus) distribution and potential prey availability.* In consideration of some of the findings of chapter four, this chapter further investigates the effect of prey availability on hedgehog distribution, particularly in relation to the hedgehogs' movement within a habitat. Factors such as the presence of predators, e.g. the badger (*Meles meles*), are referred to, to consider the possible impacts that they may have on the presence of hedgehogs in an area. The following hypotheses were investigated:
    - That hedgehogs forage and remain close to hedgerows
    - That the availability of potential prey is the main factor effecting hedgehog habitat selection
    - That potential prey is not distributed equally between and within habitats
    - That hedgehogs forage in areas where prey density is highest
- *Chapter 6: Nesting behaviour and seasonal weight changes of a rural hedgehog (Erinaceus europaeus) population.* As one of the few Irish animals to enter true hibernation, this chapter

focuses on hibernation characteristics of Irish hedgehogs. It firstly investigates nest use during the active period, the location of nests, individual usage and the variation in nest use between males and females. Seasonal variations in weight between the sexes are addressed, particularly in relation to their weight just prior to hibernation and immediately after. The location and number of hibernacula utilised by individuals are examined, as well as winter arousals and weight loss. In particular, in view of the larger home range of males it aimed to test the hypothesis that males utilise a greater number of day nests than females. In relation to hibernation, with Ireland's milder climate, this study aimed to explore the hypotheses that hibernation is shorter, emergence time earlier and weight loss more conservative amongst Irish hedgehogs.

- *Chapter 7, Courtship and the appearance of juveniles in rural Irish hedgehogs (Erinaceus europaeus).* This chapter investigates courtship behaviour. In particular as a polygynous species, it examines pairings amongst the group, peaks in courtship behaviour and the first emergence of juveniles. These data were also supported through the collection of road kill. It aimed to test the following hypotheses:

  - In view of the male bias at the site and the philopatry observed by both sexes, that a high number of repeat pairings occur amongst the study group
  - That a late or second litter occurs amongst Irish hedgehogs and is evident amongst the study group and also through the appearance of juvenile road kill
  - In view of the site philopatry observed at the site and the results of previous research, that little dispersal occurs little amongst juveniles.

- *Chapter 8, Genetics.* In light of the lack of dispersal exhibited by hedgehogs (Chapter 7) and the fact that hedgehogs demonstrate site philopatry (Chapter 4) this chapter examines genetic variation amongst the focal study group. This was to examine the hypothesis that there is a lack of genetic variation amongst both the field site and these clusters in accordance with reduced dispersal amongst localised populations. Additionally, intra and inter-genetic variation was also investigated at other sites through the collection of road kill.

- *Chapter 9, Road mortality of hedgehogs (Erinaceus europaeus) in Ireland.* During the study period, two stretches of road were surveyed for the presence of road kill. This chapter examines seasonal variation in fatalities and through data obtained from carcasses looks at patterns in the occurrence of males and juveniles. It aimed to test the following hypotheses that:
    - The greatest number of hedgehog road fatalities is during the breeding season
    - More males are killed than females
    - A late/second litter is apparent through the appearance of juvenile road kill in autumn
    - Due to Ireland's lower density of national roads there are fewer road casualties than elsewhere
- *Chapter 10 Morphometrics, age and parasite load of an Irish hedgehog population.* This chapter deals with information obtained post-mortem. Variations in the measurements of hedgehogs, particularly between age classes are examined to test the hypothesis that these measurements can be used to separate age classes in the field. The jaw sections of individuals were aged and the age structures of animals killed on the road are discussed. The presence of both ectoparasites and endoparasites are further investigated to assess the following questions:
    - Older hedgehogs have a higher parasite load?
    - Males have a greater parasite load than females?
- *Chapter 11 Conclusions.* This final Chapter addresses some of the main discoveries identified through this research, their implications and ways in which the research started on this species in Ireland can be expanded in the future.

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Chapter 2-

A review of techniques for detecting hedgehogs *(Erinaceus europaeus)* in a rural landscape.

Submitted to The Journal of Negative Results.

Plate 2.1: Spotlighting

Plate 2.2: Footprint tunnel placed in garden

Plate 2.3: Rabbit trap

2.1 Abstract

Various techniques and devices have been developed for the purpose of detecting wildlife but many only provide optimum results in particular habitats, for certain species or under ideal weather conditions. It is therefore advantageous to understand the efficiency and suitability of techniques under different scenarios. The effectiveness of methods for detecting rural Irish hedgehogs was investigated as part of a larger study in April 2008. Road kill sightings and questionnaires were employed to locate possible hedgehog sites. Six sites were subsequently selected, and in these areas trapping, spotlighting and foot print tunnels were employed to investigate whether hedgehogs were indeed in the surrounding landscape. Infrared thermal imagery was examined as a detection device. Trapping and infrared imagery failed to detect hedgehogs in areas where they were known to be present. Footprint tunnels proved to be unsuccessful in providing absolute proof of hedgehogs in an area. No single method of detection technique could be relied upon to conclude the presence of hedgehogs in an area. A combination of methods is therefore recommended. However, spotlighting was the most effective method, taking a mean of 4 nights to detect a hedgehog, in comparison to 48 nights if footprint tunnels were used as a sole method of detection. This was also suggested by rarefaction curves of these two detection techniques, where over a 48 night period hedgehogs were expected to be recorded 27 times through spotlighting and just 5 times in an equivalent period of footprint tunnel nights.

2.2 Introduction

Initial detection of an animal in an area is one of the first major obstacles to any ecological research. Wildlife research projects and management plans depend on accurate estimation of species abundance (St-Laurent & Ferron 2008), for evaluating the effects of habitat manipulations or status of prey bases (Menkens & Anderson 1988) and investigating habitat preferences and home range size (Lemen & Freeman 1985). However, reliable monitoring techniques are often fraught with difficulties, and may only be effective in specific habitat types or for certain species. A number of monitoring methods for a range of mammalian species have been utilised with varying degrees of success. These include mark recapture (Henderson 2003), distance sampling (Anderson *et al.* 1983, Barry & Welsh 2001, Royle *et al.* 2004), spot sampling (Russ & Montgomery 2002, Heikkinen *et al.* 2004), infrared thermal imagery (Boonstra *et al.* 1994, Sabol & Hudson 1995, Butler *et al.* 2006), fluorescent tracers (Frantz 1972, Evans & Griffith 1973, Lemen & Freeman 1985), tracks and signs (Lawrence & Brown 1973), marked baits (Delahay *et al.* 2000), spotlighting (Reynolds & Short 2003, Tannerfeldt *et al.* 2004), road kill surveys (Philcox *et al.* 1999, Baker *et al.* 2004, Seiler *et al.* 2004), questionnaires (Hof 2009) and stable isotope analysis (Peterson & Fry 1987, Alisauskas & Hobson 1993).

Due to their small size, and nocturnal, secretive nature, hedgehogs repeatedly go undetected in an area. Their presence is often only concluded when they appear as road kill or when they are observed in urban gardens This is not surprising as they are one of the most frequently killed animals on, for example, Ireland's roads (Sleeman *et al.* 1985, Smiddy 2002). In many small mammal studies, traps are used as a means of capture (Claassens & O'Gorman 1965, Baker *et al.* 2003). There are no traps specifically designed for hedgehogs, but, in studies by Riber (2006) and Hof (2009) rabbit traps were used. With low capture rates, this method was subsequently abandoned in favour of spotlighting (Riber, 2006, Morris, pers. comm. 2008).

Hedgehogs can run fast, reaching average speeds of 30-40 metres per minute (Morris 2006) but they will often not run when approached and will, instead, roll up, relying on their spines for protection. Therefore many studies (Kristiansson 1981, Reeve 1982, Cassini & Krebs 1994, Dowding 2007, Hof 2009) have adopted capture by hand, having first located animals with a high powered spotlight.

Huijser and Bergers (2000) deployed footprint tunnels to study road avoidance by hedgehogs. They compared the number of hedgehogs using tunnels with the numbers caught when the tunnels were removed and replaced by traps. Harris and Yalden (2004) believed that this method would be the most successful monitoring tool for estimating hedgehog abundance in an area.

As part of a larger study on the ecology of hedgehogs in Ireland, the current study aimed to identify a rural site with a relative high density of hedgehogs to use as the focal study site. It also aimed to test the following hypotheses that:

- In view of the previous lack of success, trapping is unsuccessful for detecting hedgehogs in rural Ireland
- Questionnaires, road kill surveys, footprint tunnels or infra red thermal imagery can be used as sole methods for detecting hedgehogs in an area
- Spotlighting is the most effective method for detecting hedgehogs in an area

2.3 Materials and methods

In total, five methods were employed in order to investigate the presence of hedgehogs in an area. These involved engaging members of the public through completing questionnaires, recording road kill as well as direct searching using trapping and foot print tunnels.

2.3.1 Road kill survey

In April 2008, a road kill survey was launched in Counties Cork and Galway, involving eight volunteers who regularly travelled a specific route (Figs 2.1a and 2.1b). They were supplied with maps of their route and asked to record the date and grid reference for each hedgehog casualty located.

Figure 2.1a: Roads surveyed by five volunteers in County Cork.

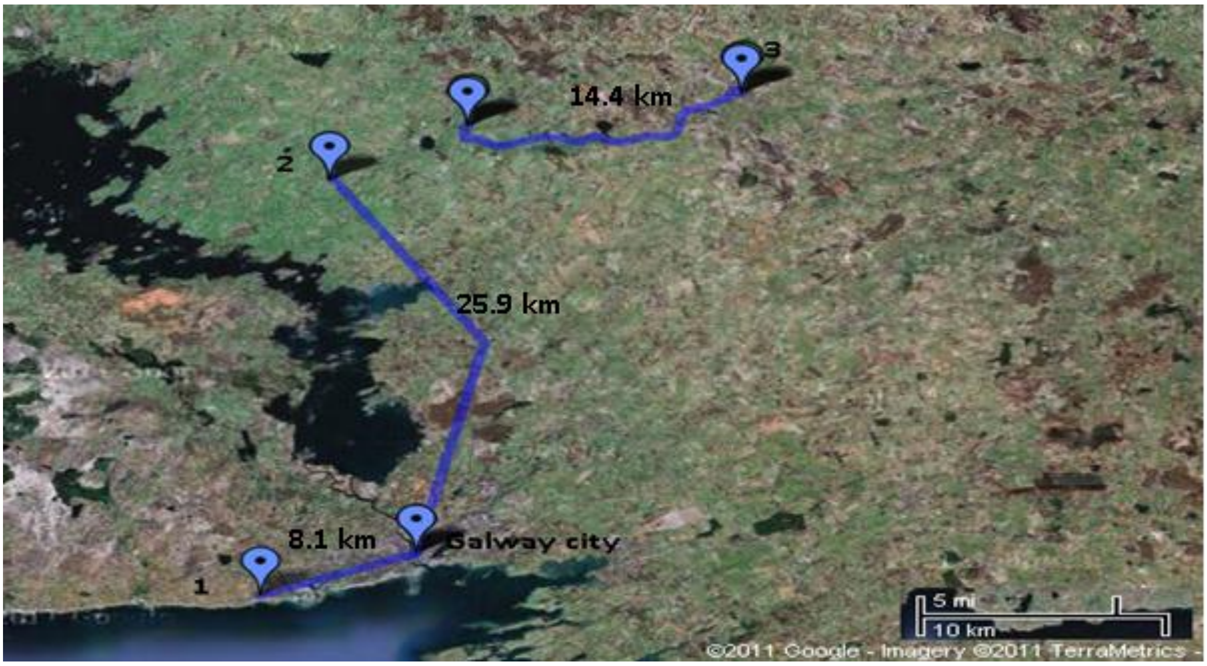

Figure 2.1b: Roads surveyed by three volunteers in County Galway.

2.3.2 Public survey

A questionnaire (Appendix 1) was distributed in June 2008 to agricultural colleges, organic farmers, stud farmers, mart stores and local supply and pet shops in County Cork. Golf courses and households near potential field sites where further searches were being conducted were also visited in order to ask about hedgehog sightings. The survey was also supplied to www.Biology.ie (a website for recording sightings of Irish wildlife), the Irish National Parks and Wildlife Service and Coillte to be placed on their websites. People were asked to indicate any information on habitats, months and times when hedgehogs were sighted, as well as how regularly they were seen i.e. was the sighting a once off or were hedgehogs regularly observed at the site.

Six suitable sites were subsequently selected based on known hedgehog habitat preferences, records of past sightings, and the presence of road kill (Table 2.1). Five of these sites were situated in Munster and one in Connaught.

Table 2.1: The six sites which were monitored for hedgehogs, and method of detection used at each.

Site	Habitat	Presence of hedgehogs	Other mammals recorded	Detection method used
Riverstick, Co. Cork	Mixed farmland with small areas of woodland	Previously seen close to the site	Foxes (*Vulpes vulpes*) Rabbits *(Oryctolagus cuniculus)*	Spotlighting, trapping, footprint tunnels
Ballygarvan, Co. Cork	Organic mixed farmland	Occasional sightings of live hedgehogs	Foxes, rabbits, badgers (*Meles meles*) and Hares (*Lepus timidus hibernicus*)	Spotlighting
Ballinhassig, Co. Cork	Mixed farmland with small areas of woodland	Yearly sightings both alive and as road kill.	Foxes and rabbits	Footprint tunnels and spotlighting
Muskerry, Co. Cork	Golf course- mature woodland, open grassland and farmland	Occasional sightings of live hedgehogs, road kill	Foxes and rabbits	Spotlighting
Ratharoon, Co. Cork	Mixed farmland	Sightings of live hedgehogs	Foxes, badgers, rabbits, hares, stoat (*Mustela erminea hibernicus*) and mink (*Mustela vison*)	Footprint tunnels and spotlighting
Castlehackett, Co. Galway	Mixed farmland with areas of woodland	Yearly sighting of both adults and offspring. Road kill collected nearby	Badgers, pine marten (*Martes martes*), fox and fallow deer (*Dama dama*)	Spotlighting

2.3.3 Footprint Tunnels

Footprint tunnels consisted of a plastic board, 20 x 50 cm (Blarney supplies) on to which heavy grade (140gm) white paper was attached. At each end of the paper a thin layer of graphite powder mixed with paraffin oil (Cork Art Supplies) was placed over around ~10cm of the paper. The tunnels were baited with cat food as an attractant. Corrugated plastic was placed over the boards (29cm high) which were secured to the board with tent pegs (Plate 2.2, Cover page). The tunnels were placed along hedgerows and edge habitat. The tunnels were checked daily and, if used, the paper and bait were changed. In April 2008, 10 tunnels were deployed for 10 nights, 15 for 11 nights and 20 for six nights at Riverstick. In June 2008, 10 were placed at the farm in Ballinhassig for seven nights and 20 for a further four nights (Table 2.2). Five were also placed in a garden in Ratharoon near Bandon for 24 nights, where hedgehogs were seen regularly.

Table 2.2: The sampling effort of each detection technique at each site.

	Riverstick, Co. Cork	Ballygarvan, Co. Cork	Ballinhassig, Co. Cork	Muskerry , Co. Cork	Ratharoon, Co. Cork	Castlehackett, Co. Galway
Spotlighting	24 hours (10 nights)	8 hours (4 nights)	8 hours (4 nights)	5 hours (3 nights)	215 hours (48 nights)	8hours (2 nights)
Tunnels	385 tunnel nights	N/A	150 tunnel nights	N/A	120 tunnel nights	N/A
Traps	176 trap nights	N/A	N/A	N/A	N/A	N/A

2.3.4 Traps

Sixteen rabbit traps (60 x 19x 19 cm) (Plate 2.3) (Animal Care Ltd) were used in Riverstick in May 2008 for 11 nights (Table 2.2). Traps were placed along hedgerows, covered with vegetation and baited with cat food. Traps were checked daily at 5 am and rebaited if necessary.

2.3.5 Spotlighting

At the end of April 2008, direct searching using spotlights began. This consisted of a search of 2 hours after dusk, four nights a week, with a 2 million candle power spotlight (Lightforce). Spotlighting took place at five of these sites over 23 nights for 53 hours (Table 2.2). At the Ratharoon site spotlighting was extended to four hours, with part of this time spent driving around the roads bordering the site.

2.3.6 Tracking

Tagged hedgehogs became useful for detecting other individuals and this was particularly the case during the breeding season, when a number of males (up to 3 were observed, see Chapter 7) were engaged in courtship displays with an individual female. Hedgehogs that were captured between 26 June 2008 and 28 September 2008 were monitored by direct following for a period of 23 nights.

All adult hedgehogs caught after 28 September 2008 were fitted with radio tags. Eight individuals were fitted with 173 MHz, R1-2B transmitters (Holohil) and attached to the animal after the manner of Jackson and Green (2000). The entire tag weighed 10g. Animals were than tracked using a SIKA receiver (BIOTRACK). Data were collected from eight individuals over a total of 33 nights from 28 September 2008 until hibernation in November 2008.

2.3.7 Infrared thermal imagery

When hedgehogs were radiotagged at the site, the use of a handheld infrared thermal imagery camera (Testo 880 range) was tested as a tool for hedgehog detection. Thermal infrared imaging systems which take heat pictures, allow detection of warm blooded animals against a relatively cooler background with or without the presence of visible light (Sabol & Hudson 1995). The camera was tested in three different habitat types at the Ratharoon site: arable, garden and pasture. The camera was first trialled without knowledge of whether any of the tagged hedgehogs were present and later when the hedgehog's location was known to examine the distance of possible detection.

2.3.8 Data Analysis

Means are followed by the ± standard error unless it is stated otherwise. Levels of significance were taken as $p<0.05$ or $p<0.01$. Tests for normality were performed on Brodgar software for univariate and multivariate analysis and multivariate time series analysis version 2.6.3. PASW Statistics Version 17 was used for all further statistical analysis. A comparison of the success of detection techniques was assessed by computing rarefaction curves using the 'estimate S' programme(Colwell 2009). This predicted the expected capture success of each method based on the results obtained when each technique was trialled.

2.4 Results

2.4.1 Road kill survey

One hundred and forty five hedgehogs were recorded as road kill during 2008 by eight volunteers in County Cork. There was a substantial variation in the months hedgehogs were recorded as road kill (χ^2=63.019, df=7, $p<0.01$). The majority (n=126) were recorded between April and August, with only 19 documented after this time (Fig. 2.2).

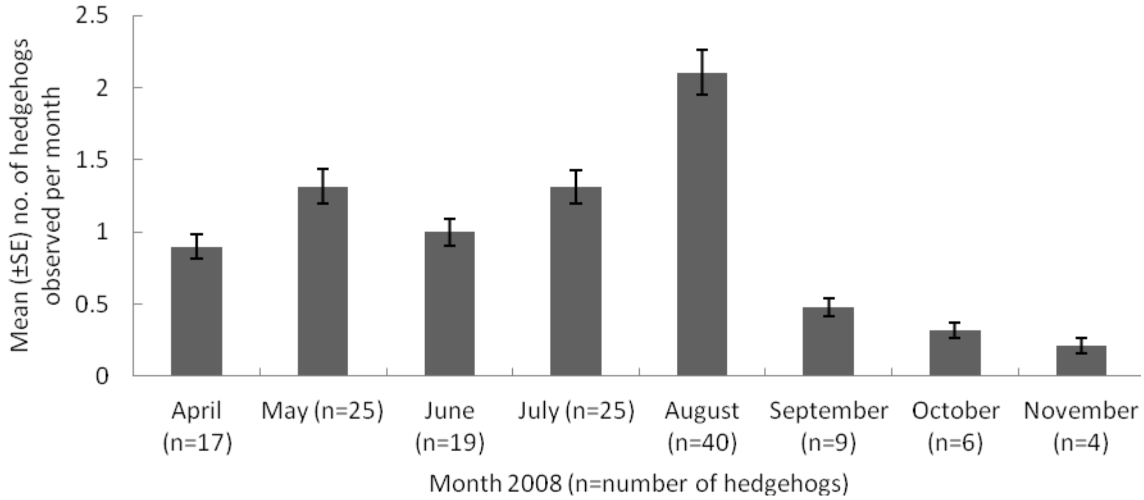

Figure 2.2: The months in which hedgehogs were observed as road kill, on eight routes surveyed weekly, Co. Cork, 2008.

2.4.2 Road kill as a detection method

Hedgehogs were recorded as road kill at Ballinhassig, Muskerry and Castle Hackett on five occasions in total during the study period. They had also been recorded annually by residents at these sites. However, despite this no live hedgehogs were detected at any of these three sites during subsequent surveying.

2.4.3 Public survey

There was a 40% response to the questionnaire survey (88 written + 40 phone replies /320). Hedgehogs were reported in 10 habitats but there was a significant variation in the habitats where hedgehogs were observed (Fig. 2.3) (χ^2=95.088, df=8, $p<0.01$). Of those surveyed, 27% of people had sighted hedgehogs along road verges, and 25% in their garden. A binomial test, established that hedgehogs were observed along road verges, gardens and hedges significantly more than in other habitats ($p<0.01$ (two tailed)).

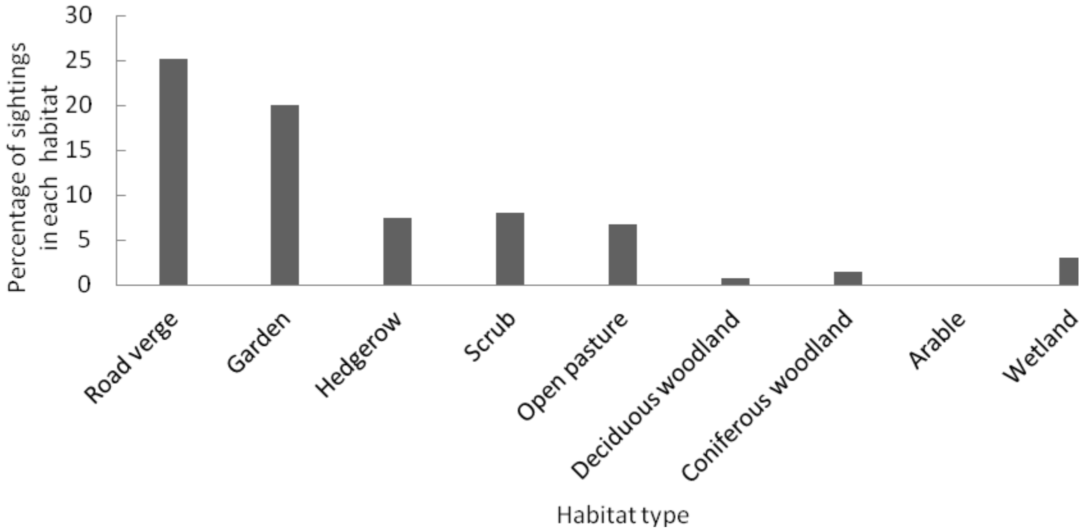

Figure 2.3: Sightings of hedgehogs in habitats from public survey (n=128).

There was a significant variation in the months in which respondents reported seeing hedgehogs (χ^2 = 98.248, df=11, p<0.01). Unsurprisingly, the majority of sightings (57%) of hedgehogs was in the summer months (May-July) (Fig. 2.4) and a binomial test confirmed that hedgehogs were observed significantly more in the summer months than at any other time of the year (p<0.01).

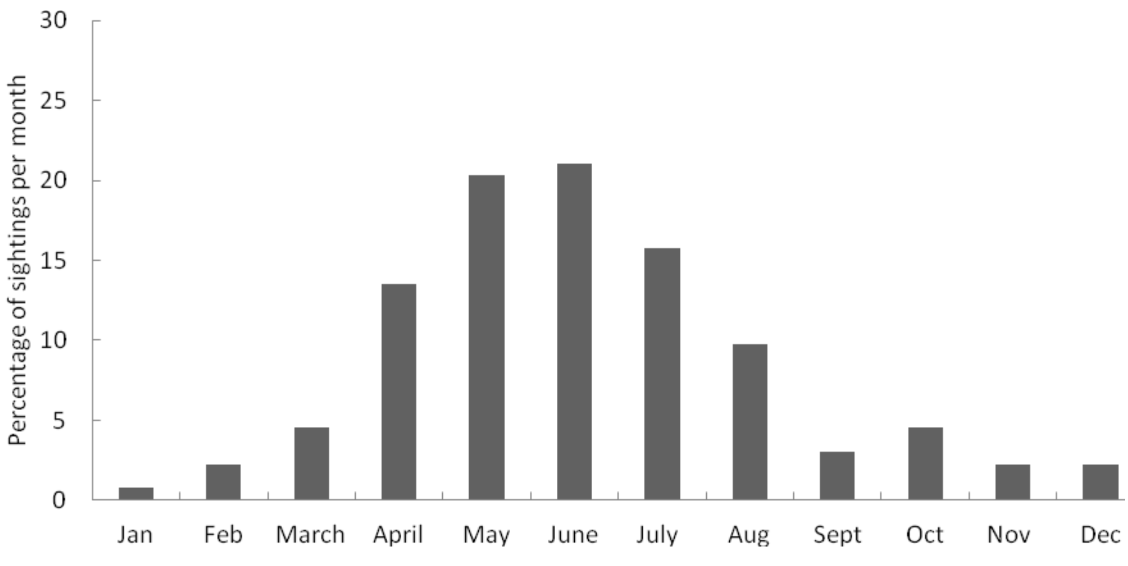

Figure 2.4: Percentage of sightings in each month that respondents had seen hedgehogs (n=128).

Hedgehogs were observed significantly more at particular times of the night (χ^2=12.063, df=5, p<0.01), with the majority (n=44%) of respondents sighting hedgehogs between the hours of midnight and 4 am than at other hours of the day/night (Fig. 2.5). The frequency with which respondents had seen hedgehogs varied greatly: 29% of respondents had seen hedgehogs between 1-5 times, 24% only once, 28% regularly and 13% greater than 5 times. The majority of sightings were of live animals (56%), while 17% were seen as road kill and 27% as both road kill and alive.

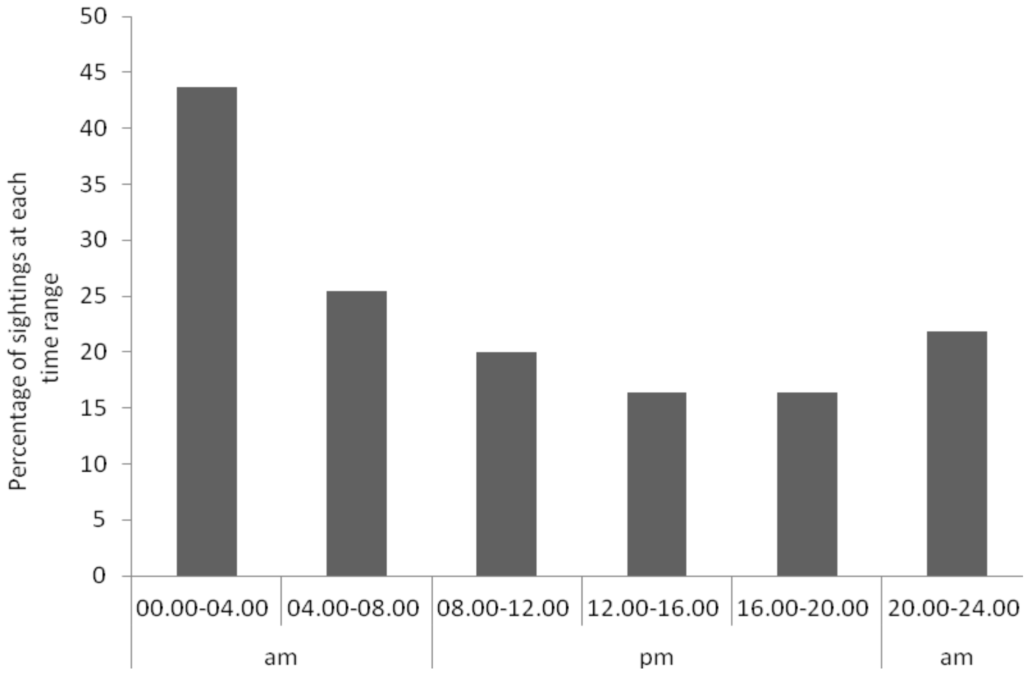

Figure 2.5: The percentage of hedgehog sightings within each time period referred to in the survey.

At Ratharoon in a door to door survey of people in the immediate vicinity of the site, ten of the 30 respondents had seen hedgehogs in the area. Two of these people had observed them as road kill but not in the previous two years. Of the people who were aware of them in their area, four had been alerted to the presence of hedgehogs by their dogs attacking them in their garden. However, there was a further twenty households who were unaware of hedgehogs in their area**.** Farmers, who were asked, recalled seeing hedgehogs when they worked on the land when young but not in recent years.

2.4.4 Footprint Tunnels

The deployment of tunnels proved surprisingly disappointing (Table 2.3). Tunnels were not used regularly by hedgehogs and in many cases were not used at all. In the Riverstick site hedgehogs were never recorded to use tunnels. In Ballinhassig one of the tunnels that were placed in the garden was used by a hedgehog on one occasion. In Ratharoon, hedgehog prints were believed to be recorded on twelve occasions, successfully indicating their presence at the site, but occurrence was low, with a high incidence of use by non target animals (rodents and domestic cats). Also, as some of the prints had been obscured, some of these records may be dubious. Meanwhile the tunnel use by non target animals represented 67% of records. On the remaining occasions the food either remained in the tunnels the following day (14%) or the bait was gone but there were no footprints (9%). On occasions when hedgehogs were caught by spotlighting in the garden at Ratharoon, the tunnels remained unused by them.

Table 2.3: Use of tunnels over the period that they were baited.

	Riverstick Site (350 tunnel nights)	Ballinhassig Site (150 tunnel nights)	Ratharoon Site (120 tunnel nights)
Rat	34	28	25
Bird	8	16	1
Unknown rodent	186	39	3
Hedgehog	0	1	12
No footprints	88	37	17
Domestic dog/cat	17	2	45
No footprints but food gone	39	31	17

There was a significant variation in the use of the tunnels (χ^2=396.088, df=4, p<0.01) by different taxa, and the tunnels were used by small rodents significantly (p<0.01) more than any other animal (binomial test).

2.4.5 Traps

During the 176 trap nights at Riverstick no hedgehogs or non targets animals were captured.

2.4.6 Spotlighting

Spotlighting efforts were concentrated along edge habitat in each of the six sites. Direct searching using spotlights was carried out for 53 hours over 23 nights, during which hedgehogs were not detected at five of the sites. At the sixth site (Ratharoon) on 17 nights, within the 48 night study period seven hedgehogs were located and caught at the site. However, there was a further 31 nights (120 hours), within the study period, when no hedgehogs were located using this method. Despite this, spotlighting was the most effective detection technique. Hedgehogs were detected on average within 4 nights using this method, while it took an average of 48 nights to identify their presence using footprint tunnels (Fig. 2.6).

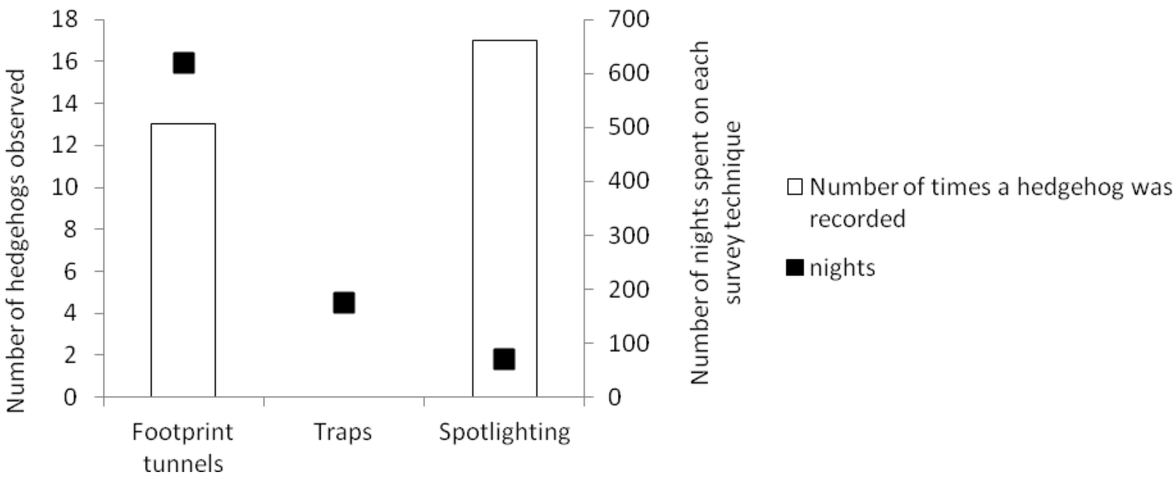

Figure 2.6: The number of nights spent on each detection method and the number of hedgehogs detected in that time.

This was also verified by computing rarefaction curves for spotlighting and footprint tunnels at Ratharoon, where hedgehogs were found to be present. Based on the number of hedgehogs found per night using each method, spotlighting was again found to be more effective than footprint tunnels at this site. For example it was predicted that in a 48 night period, hedgehogs were expected to be recorded on 27 occasions by spotlighting and just five times in 48 footprint tunnel nights (Fig. 2.7).

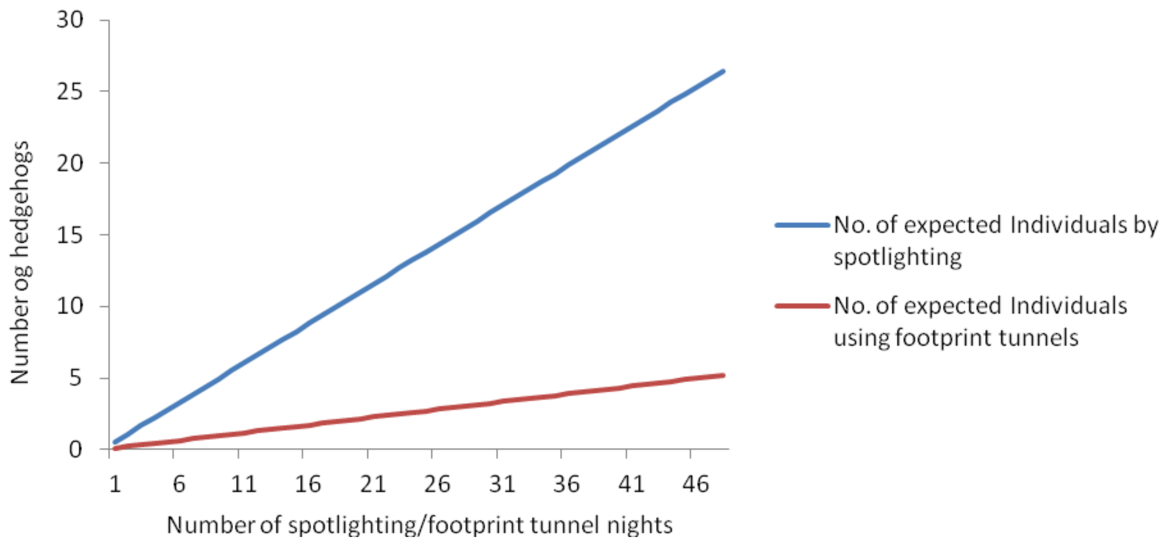

Figure 2.7: Rarefaction curves' showing the number of expected hedgehog records when using spotlighting or footprint tunnels over a 48 night period.

2.4.6 Tracking

Between June 2008 and June 2010, 24 hedgehogs were caught at Ratharoon. Of these 17 (71%) were first caught when spotlighting and 13% while driving around the site. Four males (16%) were first captured during courtship displays and many were also recaptured when tags fell off. This was also a useful time to detect hedgehogs as the loud vocalisations during these displays were good indicators of their presence.

When hedgehogs were directly followed only one individual was followed per night and a mean of 21 (± 0.16) fixes were obtained per individual per night. When hedgehogs were radio tracked up to six were tracked during a night and a mean of 6 (± 0.01) fixes were attained per individual per night.

2.4.7 Infrared thermal imagery

The infrared camera did not detect hedgehogs in garden, pasture or arable land. The detection distance was found to be less than 1 metre and even when the location of the hedgehog was known, the device had to be positioned close (<one metre) to the individual before the hedgehog was detected by the device.

2.5 Discussion

The majority of hedgehog road kill were recorded during the summer months and a peak was observed in August. The longer brighter evenings in August may have influenced the detection of road kill at this time or it may have indicated increased numbers or increased movements of hedgehogs at this time as has been found in other studies (Goransson *et al.* 1976, Kristiansson 1984, Huijser *et al.* 1998, Smiddy 2002).

Road kill counts have often been used as effective indicators of population declines and species abundance (Philcox *et al.* 1999, Baker *et al.* 2004, Seiler *et al.* 2004). In Ballinhassig, Co. Cork, hedgehog road kill had been seen annually for a number of years and during the present study period. This was also the case in the sites at Castlehackett and Muskerry. Road kill had not been witnessed previously at Ballygarvan, but the study site did not border a road. In the site at Ratharoon, road kill had not been recorded at the site by those who responded to the survey (n=30), for the previous two years. The lack of road kill did not reflect the high abundance of the species at the site. Baker *et al.* (2004), when examining fox road kill data, found that short term (i.e. 3 months) counts of road traffic casualties were expected to be variable and less likely to indicate density and that small numbers of casualties are likely to be a limiting factor for the application of such techniques for monitoring populations. Road kill could not therefore be relied upon to indicate the presence of hedgehogs in areas where traffic was minimal and road casualties correspondingly low.

The majority of survey respondents sighted hedgehogs in their gardens or along road verges. This emphasises some of the limitations that such questionnaires can have, due to the biases created by peoples changing lifestyles and the fact that hedgehogs are often only detected when killed on the road or when they enter the public domain. In Ratharoon, where hedgehogs were found at a density of 3.07 per ha (Chapter 3), in a door to door survey of people in the immediate vicinity of the site, ten of the 30 respondents, had seen hedgehogs in the area. However, there was a further twenty households who were unaware of hedgehogs in their area**.** Farmers, who were asked, recalled seeing hedgehogs when they worked on the land when young but not in recent years. This may reflect a genuine reduction in hedgehog numbers. However, it could also be a consequence of peoples changing lifestyles and the reduction in the chance of detection due to the increased use of machinery and subsequent lack of direct contact with the land. Therefore, while questionnaires can be useful to detect the presence of hedgehogs in an area, a lack of detection by respondents cannot be relied upon as a guarantee of their absence. This again highlights the importance of utilising more than one detection method.

In work by Huijser and Bergers (2000) footprint tunnels proved to be successful and the use of the tunnels by hedgehogs was closely correlated with the total number of individual hedgehogs that were caught in traps, immediately after the tunnels were removed. However, in the present study the tunnels were used much more frequently by non target species such as small mammals and birds. In the site in Riverstick, the tunnels were never used by hedgehogs, but neither were hedgehogs detected at this site by extensive trapping or spotlighting. Hedgehogs may simply therefore have not been present. At Ballinhassig one of the tunnels in the garden was used on one occasion but the bait was not taken. The prints were only at the front of the tunnel indicating that the hedgehog had only partially entered. In experiments at the Muskerry site, with a hedgehog that was being rehabilitated in an enclosed garden, it was found not to enter the tunnel if other food was left out for it. It would only walk through the tunnel if given no other option. This lack of success of footprint tunnels and trapping in this study and trapping in studies by Morris (1986), Riber (2006) and Hof (2009) may suggest that hedgehogs may exhibit a form of neophobic behaviour, similar to that displayed by rats (Barnett 1958). Therefore, tunnels may need to be placed at a site for longer, in order to reduce the effects of avoidance behaviour. However, tunnels and traps have been successful in other studies (Huijser & Bergers 2000), which makes the lack of success in the current study surprising and largely unexplained. It may indicate that other factors such as variations in prey availability between the two sites, may have been a contributing factor and this is something that requires further investigation.

At Ratharoon where hedgehogs were caught on a regular basis and recorded at a high density of 3.07/ha (Chapter 3), hedgehogs were found to use the tunnels only occasionally. In total they were believed to have been used on 12 occasions in 120 tunnel nights by hedgehogs. This was despite the fact that hedgehogs were regularly seen in the garden. On many occasions they were observed in close proximity to the tunnels but did not use them.

As hedgehogs often appear at low densities (Egli 2004), particularly in rural areas, a large number of tunnels would have to be utilised to obtain a definite indication of the presence of hedgehogs. Tunnels must be checked regularly in case of the tracks being obscured by non target animals entering later. Also, with Ireland's wet climate the paper is damaged if left out too long. This would take considerable time effort that could be more efficiently spent engaged in other monitoring methods.

Although traps have been used for the control of hedgehogs by game keepers (Yalden 1976), recent research on hedgehogs has reported little capture success (Morris 1986, Riber 2006). In a survey on diet by Yalden (1976) hedgehog carcasses were obtained from game keepers. In spring the estate in question operated 300-500 traps and they caught about 260 hedgehogs per annum (Yalden, 1976). However, these traps were fenn traps and so unsuitable for research such as this and not directly comparable. Riber (2006) caught two hedgehogs in ten rabbit traps over a ten week period. In comparison she caught 29 when searching by spotlight. Low capture success was also reported by Hof (2009), where a total of 2084 effective trap nights in a rural area of approximately 50ha in Kent, resulted in the capture of only one hedgehog. The large number of traps and time period employed by game keepers further emphasises that a greater trapping effort is required in order for trapping to yield a reasonable return. However, due to the effort this requires in checking traps, and other associated labour costs, other methods may prove more successful for the capture of live hedgehogs.

In total 53 hours were spent spotlighting at five of the six sites over a 23 day period. In this time no hedgehogs were observed either alive or as road kill. At the Riverstick site one hedgehog had previously been seen in a garden at the edge of the site. A door to door survey revealed that hedgehogs had been seen occasionally in the previous few years in the area, at a number of neighbouring houses. The deciduous woodland, extensive hedgerow and old buildings at Riverstick indicated that there were plenty of potential nest sites, and in addition there was an abundance of surface invertebrates and no reports of badger activity. It was therefore surprising that over the 24 hours and ten days spent spotlighting in Riverstick, as well as the monitoring of traps and tunnels, that hedgehogs were not encountered. Could it have been that they were concentrating their activity areas not searched or areas where it was difficult to detect their presence? However, it would seem unlikely that not a single sign of hedgehogs would have been recorded during this period. In studies by Micol *et al.* (1994)in the U.K. it took an average of 34.1 ± 1.2 minutes to detect all the hedgehogs in grazed pasture with minimum searcher effort.

At three of the other sites none were detected through spotlighting, despite hedgehogs having been seen annually both alive and as road kill. In Ballinhassig, hedgehog carcasses were observed on three occasions within 0.5 km of the site in 2008. Two hedgehogs were also found drowned in a cattle grid on the farm at Ballinhassig in August 2008, after extensive rainfall. They therefore appeared to regularly use the area, so it is surprising that they were undetected through spotlighting. In Ratharoon, where hedgehogs were eventually found at a density of 3.07 per ha (Chapter 3), spotlighting had been carried out for ten hours over four days before the first hedgehog was caught. Hedgehogs were found on 17 occasions over a period of 48 nights (Chapter 3).However, in this time there were a further 31 nights and 120 hours when hedgehogs were not seen, despite extensive spotlighting. In previous studies in England, Denmark and New Zealand, hedgehogs have been found to forage and remain close to hedgerow (Reeve 1981, Doncaster *et al.* 2001, Riber 2006, Shanahan *et al.* 2007, Hof 2009) and searching was carried out on this assumption. However, when hedgehogs were directly followed in Ratharoon it was discovered that they concentrated their activity in the centre of a field (Chapter 5). Since, before spotlighting started previous published research from the U.K. was used to identify habitat preferences, spotlighting was concentrated along edge habitat which may have further hindered detection. Covering part of the search area by driving along roads proved successful with three of the 24 hedgehogs caught in Ratharoon, first detected by this method.

The infrared thermal imagery was unsuccessful in detecting hedgehogs at the Ratharoon site. Boonstra *et al.* (1994) found the method successful for detecting red squirrel, Arctic ground squirrels, snowshoe hares and meadow jumping mice in Canada, but stipulated that a direct line of sight was necessary, as dense undergrowth could block the image. In the current study even a clump of long grass prevented detection of the hedgehog by the device. Similarly, Sabol and Hudson (1995) reported that although emerging bats appeared bright against a dark cool cave mouth, they disappeared from the thermal imagery view once they flew in front of the warm vegetation surrounding the cave. As well as being restricted to certain times of day when the sun has largely dissipated or not yet heated the ground vegetation (Boonstra *et al.* 1994), a stationary background is also an absolute requirement (Sabol and Hudson, 1995). These limitations were also encountered by Butler *et al.* (2006) who found that ground cover obscured bedded fawns and that fawns were identified only at distances of <1m, when vegetation was not dense. With the high cost of the equipment, restricted ideal conditions that are necessary and the proximity to which one has to be to the individual for detection, it did not prove to be an effective method in this habitat for hedgehog detection.

This study further emphasises some of the limitations involved in the initial detection of a small nocturnal animal, such as the hedgehog. It therefore highlights the importance of long term monitoring of a site before declaring hedgehogs absent. It also stresses the importance of utilising more than one detection device in order to minimise these effects. As has been observed in previous studies, trapping proved unsuccessful for detecting hedgehogs. Questionnaires, road kill surveys and infrared thermal imagery all proved ineffective as sole methods of hedgehog detection. The most successful method of capture proved to be spotlighting. This was particularly the case during the breeding season (April-July), when this usually solitary and quiet mammal, was engaged in courtship displays, and vocalisations facilitated detection.

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Chapter 3 –
A preliminary study to examine habitat use and demographics of a rural population of *Erinaceus europaeus*

Conference proceedings (Aims, November 2009). In press, The Irish Naturalists' Journal (2011).

Plate 3.1: Clockwise from top left, Scrub, wood and pasture, garden and arable

3.1 Abstract

During 2008 an intensive study of the habitat use of hedgehogs took place in a lowland mixed agricultural landscape in Co. Cork. Fourteen animals were tagged; comprising of nine males and five females. These hedgehogs had a density of 3.07 per hectare, which was higher than the densities recorded in other studies. A survey of the ground fauna revealed a variation in invertebrate availability throughout this area. Hedgehog activity was concentrated where potential prey was most abundant. There was a seasonal shift in habitat use with hedgehogs occupying pasture in the early part of the study period, arable land in autumn and scrub once the animals began to enter hibernation.

3.2 Introduction

The Western European Hedgehog was first reported in Ireland in the 13th Century in Waterford (Yalden 1999). With the exception of Mulcahy's (1988) work on the Hedgehog flea (*Archaeopsylla erinacei erinacei)* and road kill surveys (Smiddy 2002) no research has been undertaken on the European Hedgehog in Ireland. Current knowledge is based on research carried out by Morris (1969), Reeve (1981) and Jackson (2001) in the U.K. as well as Kristiansson (1981) in Sweden. Dissimilar landscape, weather conditions, land use practices and a different faunal assemblage in Ireland may result in certain variations in their behaviour here. Ireland's climate is influenced by the Atlantic Ocean and as a result it does not suffer from the extremes of temperature experienced by many other countries at similar latitudes (Met Éireann; www.met.ie). Ireland has the largest percentage of permanent pasture in the EU and agriculture is generally less intensive than in most other European countries (Cabot 1999). Hedgerows are important nest sites for hedgehogs and in Ireland constitute 1.5% of the landscape with a total length of 416,000km (Smal 1995) most of which has remained intact since the 18th Century in contrast to many other European countries where hedgerows have become special features (Cabot 1999).

The nocturnal and secretive behaviour of hedgehogs has made studies of their activity difficult and, while substantial research has been undertaken in urban areas in other countries (Reeve 1981, Micol *et al.* 1994), with the exception of the work of Morris (1988) in English farmland and Riber's (2006) work in Denmark, less is known about rural hedgehogs. In the latter countries, hedgehogs have been found to prefer open pasture with arable, marsh and coniferous woodland representing the lowest rank of habitat preference (Riber 2006, Doncaster *et al.* 2001). A number of variables are believed to limit their distribution in an area most notably nest sites, food availability and the presence of predators. In Denmark, Jensen (2004) found that 55% of nest sites occurred in forested areas with a similar result reported by Riber (2006). Kristiansson (1984) concluded that food availability was a crucial factor regulating the size of a Swedish population while Micol *et al.* (1994) found that the abundance of hedgehogs varied in direct relation to the density of badger (*Meles meles*) setts.

In the early 1900s, Ireland's human population was approximately 2/3 rural and 1/3 urban but, in the 21st Century, it is predominantly urban (Stapleton *et al.* 2000). In areas where farming has persisted, small-scale traditional farms have given way to larger, more intensive enterprises. An increase in efficiency has led to an increase in the use of pesticides, a reduction in hedgerows and a subsequent loss of potential nesting sites for animals like the hedgehog. Farms have become more specialised and productive through the increased use of machinery and this has resulted in a reduction of 50% of the hedgerow stock in the U.K. (Robinson & Sutherland 2002). More than 50% of Europe's most highly valued biotopes occur on low-intensity farmland and yet there is little environmental policy protecting it (Bignal & McCracken 1996). In Ireland, schemes, such as the Rural Environmental Protection Scheme (REPS), have been developed to promote environmentally-friendly farming (Emerson & Gillmor 1999). However, with no baseline data on the ecology of the hedgehog in Ireland, strategies for successfully implementing changes to benefit this species are unclear.

In June 2008, a study began to investigate the ecology of the European Hedgehog in the rural Irish landscape with a view to rectifying some of the gaps in knowledge that we have on the species here. This preliminary study in 2008 aimed to gain baseline data on the study group and identify areas that warranted further investigation in the following two years of the study. It further aimed to examine the effectiveness of monitoring methods and identify patterns in habitat use which would be further investigated in 2009 and 2010. It also aimed to test the hypothesis that habitat selection by hedgehogs changed on a seasonal basis and that habitats such as arable land would be avoided.

3.3 Materials and methods

The study was carried out between June and November 2008 on a site (51˚ 53’ 59.5’’N latitude, 8˚ 29’03.7”W longitude) 36.8km from Cork City and 5.3km from the nearest town of Bandon. The core area searched for hedgehogs was 43ha (Figure 3.1). The area consisted of a mixture of arable (35%) and pasture (41%) with small areas of coniferous woodland (10%) and scrub (6%). The livestock present in the area consisted of horses and dairy cattle. Residential gardens (8%) were clustered throughout the study site, the majority of which were associated with farm yards. During the study period no hedgehogs were recorded dead on the small, relatively quiet roads around the site and a door-to-door survey revealed that none had been observed by residents in the previous two years.

The mean monthly temperature for 2008 ranged from 7.3˚C (November) to 14.6˚C (July). The rainfall in this area ranged from 57mm-193.1mm (June-November) (Met Éireann, www.met.ie).

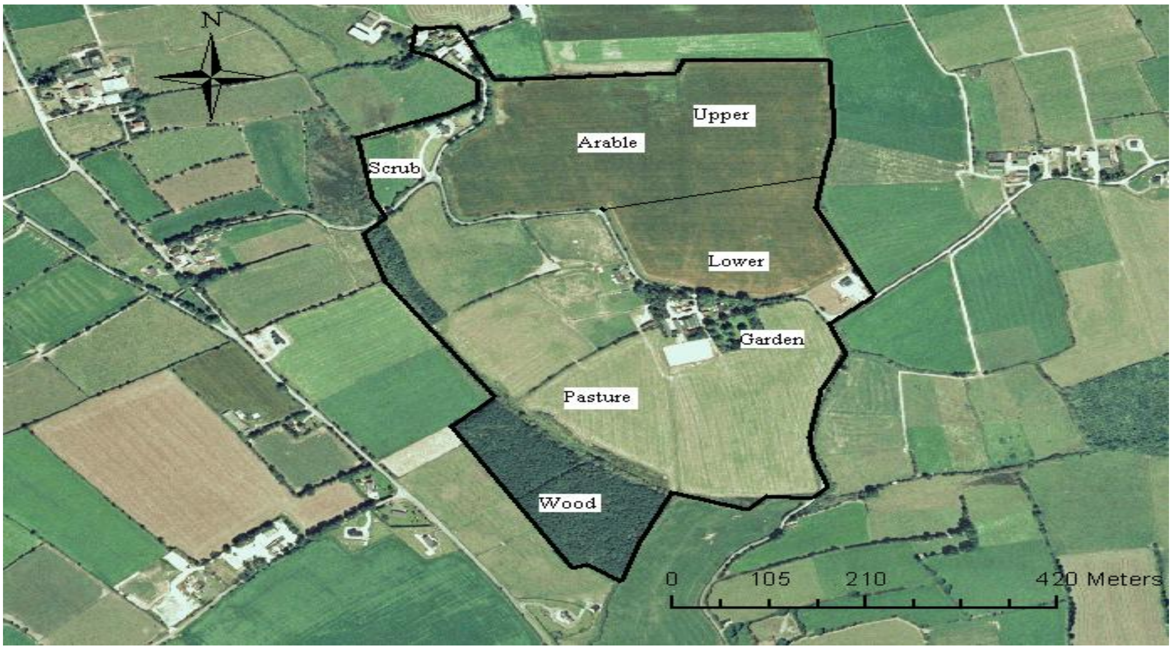

Figure 3.1: Study area, highlighting the 43 hectares that were searched for hedgehog activity.

3.3.1 Capture and marking:

Hedgehogs were captured by hand with the aid of spotlights. The animals were marked using a unique colour combination of 15 heat shrink plastic tubes (R.S. Components) which were attached with glue (Evo-stik) to a number of spines in three specific regions on the animal with glue (left of head, centre and right of head). Reflective tape was also applied to one of the middle markers so that the head region could be identified while tracking. The tubes acted as a visual aid and minimised the need to recapture the animal for individual identification. Animals were fitted with a tip light (MK IV) placed on the back of the animal which aided location in the field. The hedgehogs were also marked using passive integrated transponder (P.I.T.) tags inserted into the upper hind leg (Doncaster *et al.* 2001, Jackson *et al.* 2004). This allowed individuals to be re-identified after hibernation.

All hedgehogs caught were sexed and weighed using digital scales (Harvard apparatus). All procedures were carried out in accordance with current regulations; licenses were obtained from the Department of the Environment, Heritage and Local Government.

3.3.2 Tracking

Animals captured between 26 June 2008 and 28 September 2008 were monitored by direct following. An ultra-violet filter was placed over a spotlight and the animal was observed upon release. Every ten minutes, fixes were taken using a Garmin GPS 60 (CH Marine). The type of habitat and animal location within each habitat was also recorded. Activity along a field verge was defined by the animal being within a metre of the edge. Animals were followed until they returned to the nest site or until they could no longer be located. Ten animals were observed in this way for a total of 23 nights.

All animals caught after 28 September 2008 were fitted with radio tags. Eight animals were fitted with 173 MHz, R1-2B transmitters (Holohil) attached to the animal after the manner of Jackson and Green (2000). The entire tag weighed 10g. Animals were then tracked using a SIKA receiver (BIOTRACK). Data were collected from eight hedgehogs over a total of 33 nights from 28 September 2008 until hibernation in November 2008. Six of these hedgehogs were monitored throughout hibernation.

3.3.3 Surface invertebrate surveys of the arable field

Transects measuring 60m long and 46cm wide were walked and the surface prey counted. In October 2008, six transects were sampled each night in the upper and lower portion of the arable field resulting in a total of 72 transects (Figure 3.1). Mollusc identification was confirmed by Roy Anderson, Belfast.

3.3.4 Data Analysis

All GPS positions were plotted on ortho-photographs (Ordnance Survey of Ireland) of the area using the Geographic Information System (GIS) software Arc Map Version 9.2.

When means are provided they are followed by the ± standard error unless otherwise stated that standard deviation was used. Tests for normality were performed on Brodgar software for univariate and multivariate analysis and multivariate time-series analysis Version 2.6.3. PASW Statistics Version 17 was used for all further statistical analysis. Levels of significance were taken as $p<0.05$ or $p<0.01$.

3.4 Results

3.4.1 Hedgehog demographics

Between 26 June 2008 and 21 October 2008, 14 hedgehogs in total were caught at the site; a density of 3.07 hedgehogs/ha. These consisted of nine adults (six ♂and three ♀) and five juveniles (three ♂ and two♀). Adult males were found to be heavier than adult females and both sexes reached their heaviest weight just prior to hibernation in October (Fig. 3.2).

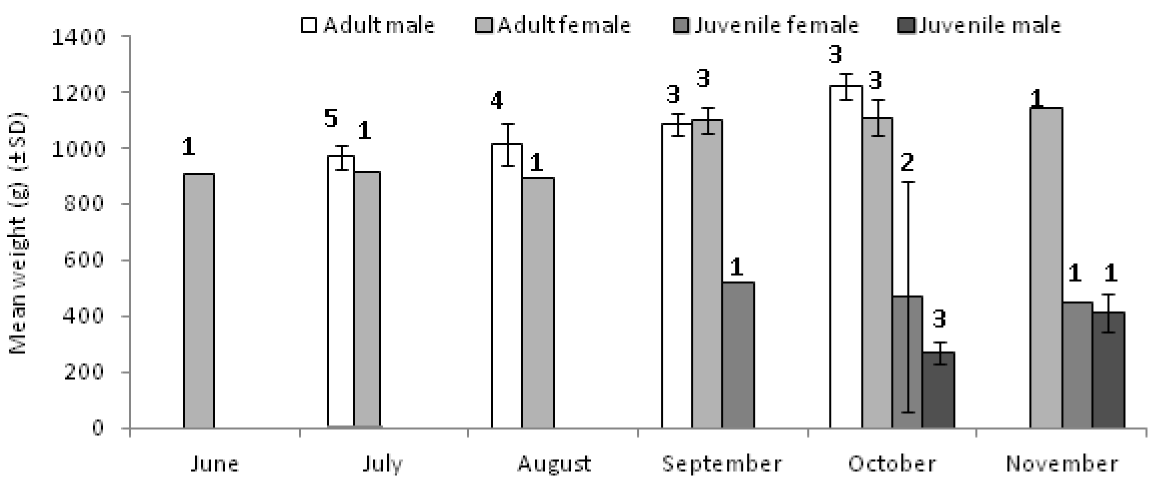

Figure 3.2: Mean monthly weights (±SD) of the 14 hedgehogs from first capture (sample size above bars).

Since the sample size was small, to allow comparison, weights for the six months were grouped into three periods: early (June and July), middle (August and September) and late (the two months just prior to hibernation - October and November). Adult males were heavier than adult females in June/July and October/November (Table 3.1). In August/September, where numbers were sufficient for analysis there was no significant difference between the mean weights of adult males and that of the females (U=6, n_1=6,n_2=3, p<0.05) (Mann Whitney).

Table 3.1: Mean adult weights (± S.D) in the three time periods of the study.

	Adult male	Adult female
June/July	1002g(±43.7) n=5	909g n=1
August/September	1038g (±74.7) n=6	1072g (±91.0) n=3
October/November	1209g(±57.7) n=3	1116g (±14.0) n=3

When males and females were combined there was a significant variation in adult weights between the early, middle and latter part of the study period (one-way anova) (F=10.646, df=2, p<0.05). Adult hedgehogs were found to be significantly heavier (Tukeys post hoc test) (P<0.05) (Table 3.1) in the months just prior to hibernation (October and November) than they were in the rest of the study.

Juveniles were caught at the site on the 18 September (n=1) and the 18 October 2008 (n=4). The juvenile female caught in September weighed 517g when first caught and 856g when she hibernated in October. The four juveniles caught in October had a weight range of 244-272g when first caught (Fig. 3.3). By November, all but two of these juveniles had entered hibernation.

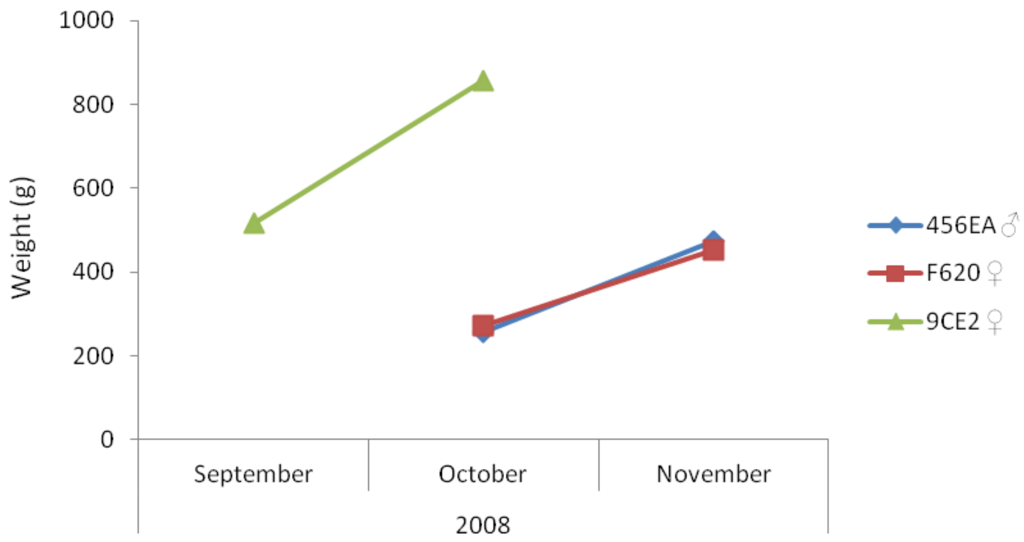

Figure 3.3: The weight range (g) and gain of three juveniles caught at the site in 2008.

3.4.2 Habitat use

Four of the five habitats searched were used by hedgehogs during the study period; none were found in coniferous woodland. Hedgehogs spent a greater amount of time in certain habitats during the study period, completely shifting their range throughout the year. Their monthly locations are illustrated in Figs 3.4a-3.4e.

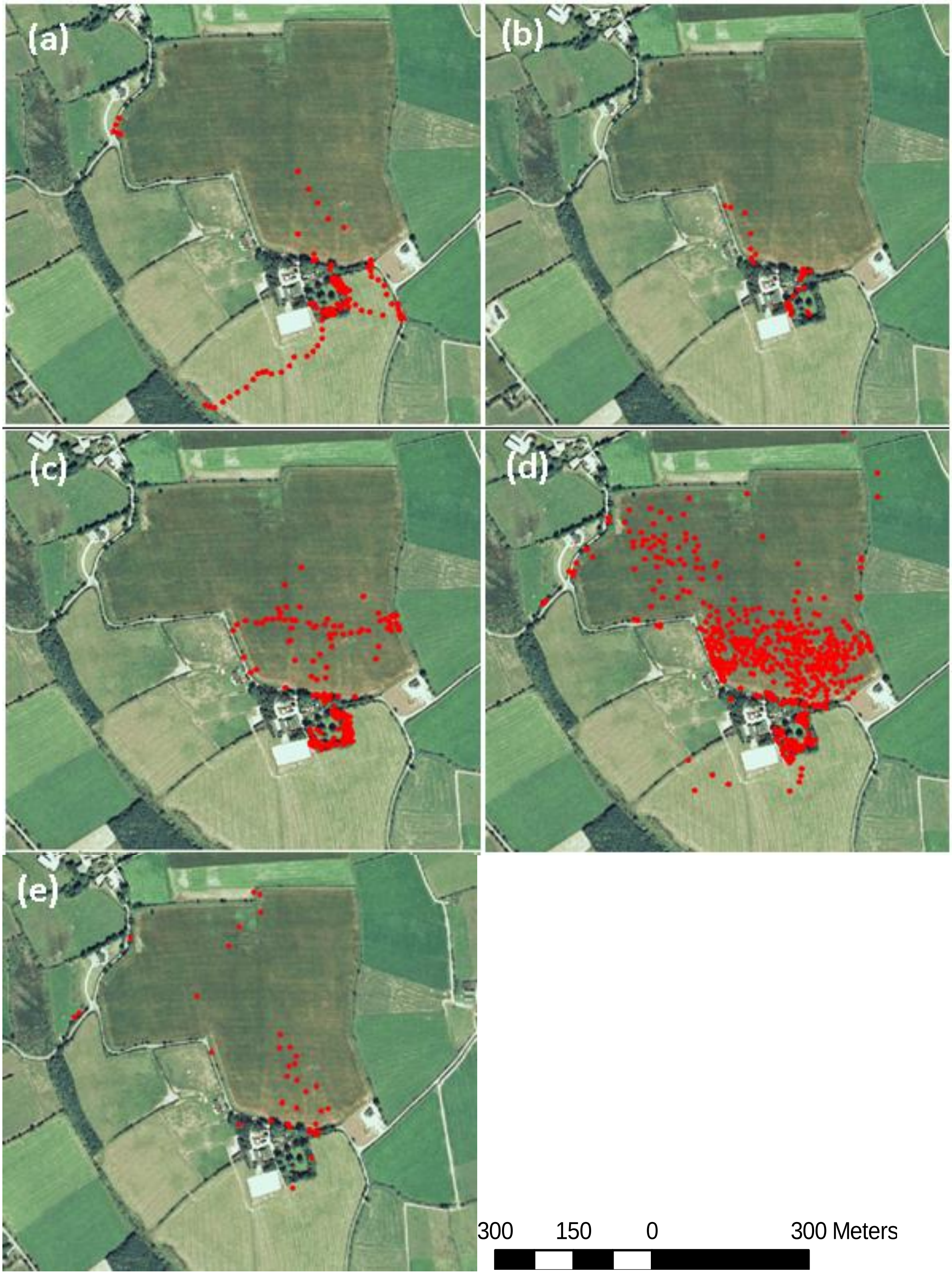

Figure 3.4a-e: Monthly observations of hedgehogs from July (a)-November (e) 2008, in Ratharoon Co. Cork, for all nights and fixes combined.

In July and August 2008 hedgehogs were located in a 0.5 ha garden on 31% and 63% of monthly observations respectively (Figs. 3.4 and 3.5). The crop in the arable field was cut between 8 September and 29 September. At this time, the hedgehogs were seen to move into this habitat (47% observations). In October, 72% of all hedgehog observations were in this arable field and animals that remained active in November continued to feed in this habitat. The hedgehogs began to enter hibernation from the 19 October and at this time the hedgehogs entered areas of scrub, pasture and garden and built hibernacula (see Chapter 6).

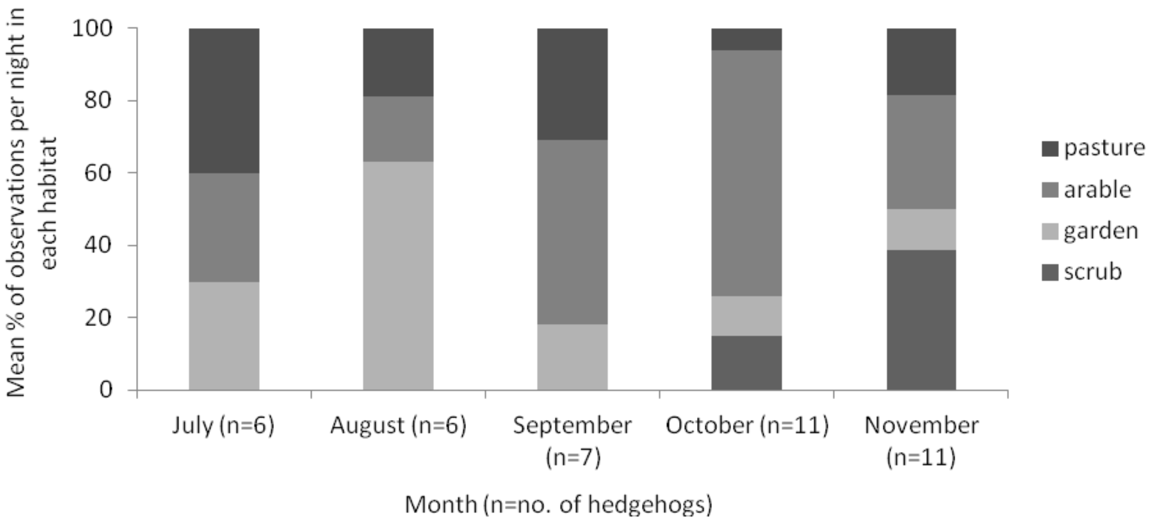

Figure 3.5: Mean percentage of observations per individual per night where the hedgehogs were in a particular habitat

A change in habitat preference over the study period was clearly evident among hedgehogs with hedgehogs selecting pasture in July, garden in August and arable land in September and October (Table 3.2 and Figures 3.4 and 3.5). This variation was found to be significant (one-way anova) (Table 3.3).

Table 3.2: Mean individual nightly habitat use over the study period (observations/individual/night), following Ln (x+1) transformation.

	Pasture	Garden	Arable	Scrub
July	0.50	0.38	0.26	0.00
August	0.21	0.62	0.34	0.00
September	0.35	0.36	0.51	0.00
October	0.06	0.12	0.49	0.13
November	0.08	0.04	0.11	0.12

Table 3.3: One way anova, showing a significant variation in the use of each habitat across the study period.

	df	F-value	p
Pasture	4	4.049	<0.01
Garden	4	4.140	<0.01
Arable	4	5.152	<0.01
Scrub	4	12.144	<0.01

Tukeys post hoc showed that, in July and September, hedgehogs spent significantly more time in pasture than they did in other months (Table 3.4). In August, the garden was used to a significantly greater extent than during the rest of the year. In October, there was a move into arable land and into areas of scrub in November (Table 3.4).

Table 3.4: The habitats in which hedgehogs spent significantly more time on a monthly basis ($p<0.05$).

Month	Pasture	Garden	Arable	Scrub
July	*			
August		*		
September	*			
October			*	
November				*

It was noted that within the arable field adult hedgehogs spent significantly more time in the centre of the field than along the field verge ($U= 5$, $n_1=8$, $n_2=8$, $p<0.01$) (Mann Whitney) (Table 3.5).

It was further noted that hedgehogs were not distributed randomly throughout the arable field. There were significantly more observations in the southern portion of the arable field than in the northern section ($U=8.5$, $n_1=8$, $n_2=8$, $p<0.05$) (Mann Whitney) (Table 3.5).

Table 3.5: Location of individual adult hedgehogs within the arable field (number of observations) from June –November 2008. (a) in relation to the hedgerow and (b) their location within the arable field.

	A		B	
	Field verge	Centre	Southern	Northern
0006D4524A♀	6	42	71	0
0006D2FA56♀	6	87	141	7
0006D47150♀	5	86	36	74
0006D475EC♂	18	53	88	1
0006D3102F♂	0	6	3	3
0006D4A3D6♂	6	41	51	5
0006D48C88♂	0	6	6	0
0006D4AC00♂	0	84	115	0

3.4.3 Surface invertebrate survey

Based on the surface invertebrate surveys, the potential prey in all sections of the arable field was dominated by molluscs, with earthworms constituting less than 10% of available prey (Table 3.6).

Table 3.6: Surface invertebrates found throughout the arable field.

Invertebrates	% Abundance	Range per transect	Mean (±SE) per transect
Molluscs – • *Derocerus panormitanum* • *Derocerus reticulatum* • *Milax gagates* • *Arion distinctus*	90	0-371	68.67±0.12
Earthworms – • *Lumbricus terrestris*	8	0-109	7.64±0.05
Australian flatworms – *Australoplana sanguine*	1	0-10	2.04±0.02
Beetles (Coleoptera spp.)	1	0-6	1.42±0.02

There was a significantly greater density of potential prey at the southern portion of the field than at the northern section (Figure 3.6) (Z=-3.037, P<0.01) (Z test). The majority of hedgehog activity was seen in the southern part of the field where surface invertebrates were significantly more abundant.

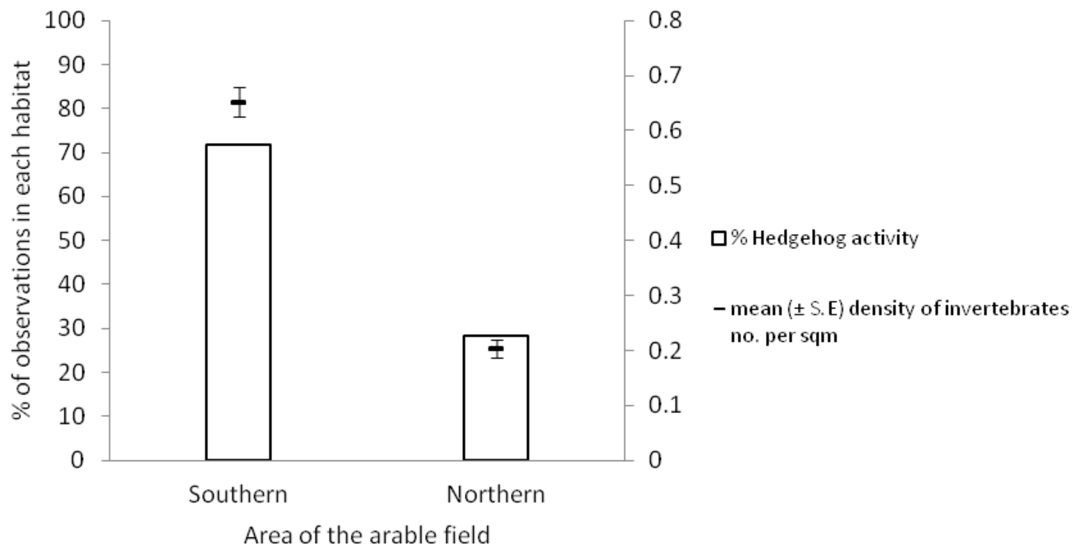

Figure 3.6: Mean (± S.E) number of invertebrates per sqm vs the % of observations that the hedgehogs were recorded in each area of the arable field in October 2008.

3.5 Discussion

Recorded densities for hedgehogs have ranged from 2.5/ha (Parkes 1975) in sand dunes in New Zealand to 0.16/ha (Egli 2004) in a rural area in Switzerland. Hedgehog densities are considered higher in urban than rural areas, with Egli (2004) recording densities of 0.16/ha (rural) and 0.67/ha (urban). This is generally attributed to greater food abundance, availability of nest sites and lower predation pressure in urban areas (Doncaster *et al.* 2001). Densities of 3.07/ha in the current study were high. Micol *et al.* (1994) found that the abundance of hedgehogs varied in direct relation to the density of badgers but, as badgers were regularly seen at the current site, it would indicate that this was not a factor in this study. It is instead suggested that this site offered optimum feeding and nesting sites and this is supported by the rapid increase in the weights of the animals during the study period (see further below).

At weights of between 889-1178g for adult females and adult males weighing between 932-1285g, the hedgehogs in this study were heavier than weights reported in the U.K. Reeve (1981) reported weights of between 600-700g in spring increasing to about 900-1000g in autumn and found that it was relatively uncommon for hedgehogs to weigh more than 1000g. Similarly Dowding *et al.* (2010) recorded average weights of 846 ± 119 for males and 792± 157g for females also in the U.K. In New Zealand, Parkes (1975) recorded a mean weight for males of 706±10.0g and 688±9.9g for females. The site in the present study may have offered very favourable feeding conditions as demonstrated in the arable field where up to six adult hedgehogs foraged in an area of four hectares throughout October. Prey densities were also high with numbers of up to 371 slugs recorded on the surface in one 60m x 46 cm transect. However, this may also be related to Ireland's different faunal assemblage and this will be discussed further in Chapter 7.

In the current study, adult males were generally heavier than adult females. Similarly Morris (1969) reported that, on average, males are heavier than females throughout the year and both sexes are at their maximum weight just before hibernation. It is therefore also not surprising that adults of both sexes were at their heaviest in October. This was the month during which three of the six tagged animals entered hibernation so they would have been accumulating reserves in preparation for hibernation.

The first recorded juvenile at the site was a female on September 18. From her initial capture to her pre-hibernation weight on the 25 October, she had increased from 517g to 856g i.e. an increase of 166% in just over a month. Juveniles are capable of gaining weight quickly and Kristiansson (1984) found that juvenile body weight increased linearly from about 280g in August to about 600g in October i.e. an increase of about 114% in two months.

The late occurrence of the remaining juveniles on the 17 October 2008 would suggest a second litter. In the U.K., Morris (1969) also found that juveniles could be born as late as October showing that fertile matings may occur as late as September. However, in Sweden, the hibernation period is longer than in the U.K. resulting in a breeding season of just two months (Kristiansson 1984). Therefore in Sweden hedgehogs will only have one litter; however in the U.K., a second litter is a common occurrence with Jackson (2006) reporting that 81% of female hedgehogs bred again in the later part of the season particularly if an earlier litter had died. It would appear from the current study that second litters may also occur among Irish hedgehogs (see Chapter 7 for further discussion).

As the four juveniles weighed only between 255-272g when first caught on 18 October it was uncertain whether they could gain enough weight to survive hibernation as the necessary reported pre-hibernation weight has ranged from 450g (Morris 1984) to 650g (Bunnell 2002) in the U.K. to 700g in Sweden (Kristiansson 1990). In New Zealand where hibernation is shorter, Brockie (1990) estimated that even a juvenile of 300g could survive for three months when torpid at 5 ˚C. In the current study one juvenile male reached a pre-hibernation weight of 475g and successfully survived hibernation.

There was a significant shift in the use of habitat on a monthly basis with arable land being utilised to a much greater extent in the latter half of the study period. In farmland in the U.K., Doncaster (1993) attributed the shift in home range to the unpredictable and dramatic changes in resource quality since crops are cut and farm animals are rotated. August was a particularly wet month in 2008 with widespread flooding around 16 August, as mentioned in Chapter 2, this is when two hedgehogs were found drowned in Ballinhassig. Hedgehogs particularly dislike rain so that inclement weather could well reduce the time spent feeding (Morris 1969). In July and August, the hedgehogs spent 31% and 63% of their time in a garden. The garden is dominated by mature trees and bushes and may therefore have provided them with adequate cover allowing them to continue foraging.

The large amount of time that the hedgehogs were found to spend in the arable field of this study was unexpected. In previous studies on hedgehogs in the U.K. and Denmark, it was found to be their least preferred habitat (Doncaster 1994, Doncaster *et al.* 2001). Riber (2006) reported that even though arable land was one of the most common habitat types within the hedgehogs' home range, most of the arable land in her study area was rarely visited by the hedgehogs. Furthermore, Dowie (1987) found no evidence of hedgehogs on 140ha of arable land despite searching for eight weeks and using a variety of methods.

Kruuk *et al.* (1979) attributed the lack of hedgehogs in arable land to be due to the fact that this habitat generally supports fewer earthworms than pasture. In the present study slugs were the dominant prey along surface transects. Wroot (1984) reported that there was a clear tendency to concentrate on only one prey type at a time and to switch from one group to another on a seasonal basis. This move into the arable field in September may therefore have been in response to a change in prey from earthworms to slugs.

The results of the invertebrate surveys showed that there were significantly more invertebrates at the southern portion of the field which corresponded to where the hedgehogs were spending significantly more of their time. The northern portion of the field was occupied by only one adult female (#7150) who foraged and nested there. The other hedgehogs would occasionally move through this area but only to travel to the pasture and scrub that bordered the northern portion of the field.

Although not territorial, Cassini and Foger (1994) found that hedgehogs showed mutual avoidance and suggested that this imposes a limit on the number of animals in an area. In the current study each hedgehog occupied a distinct area of the arable field and was rarely seen to cross the path of another.

Within the arable field, the hedgehogs foraged significantly more in the centre of the field where there was no cover. They returned to the hedgerows only to rest. This was surprising since, in previous studies, hedgehogs had shown a significantly stronger attraction to edge habitat, often moving along hedgerows (Reeve 1981, Doncaster *et al.* 2001, Riber 2006, Hof, 2008 pers. comm.). The hedgerow around the arable field had a lot of thick vegetation and brambles so, although potential prey was available along this edge, it may have been less accessible than in the centre of the field. Badgers were seen on six occasions throughout the area in 2008 and one hedgehog was killed by a badger within the arable field so their presence in the centre of the field does not appear to be a response to an area that was predator free but would appear to have been food driven.

In the present study, the hedgehogs utilised the scrub area in October and November in order to build hibernacula. Half of the tagged hedgehogs (three) built hibernacula in scrub. These areas were overgrown with large areas of bramble (*Rubus* spp.) patches and gorse (*Ulex* spp.). Reeve (1981) reported that of 58 nests, 31 (53.5%) were in prickly vegetation, of those, the majority (24) were in brambles. Morris (1969) also found that hedgehogs showed a marked preference for building nests in brambles. Therefore the hedgehogs' movement into this habitat could have been in response to the need for suitable areas in which to build secure hibernacula.

Previous studies had indicated that hedgehogs were unlikely to use arable land. However, in the present study, hedgehog densities were high and arable land was favourably selected. Arable land should be considered an important habitat for hedgehogs in Ireland and further investigation is therefore warranted in this habitat. This preliminary study provided important baseline data on the study group and highlighted areas which warranted further investigation. In particular it highlighted the following questions:

- Do hedgehogs exhibit site philopatry?
- What is their home range size and does this vary between sexes?
- Is the observed pattern of habitat use and selection seen in successive years?
- Is this related to prey availability and density?
- What is the pattern of weight loss during hibernation?

These and other emerging questions are examined in Chapters (4-6).

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Chapter 4-

Rural Irish hedgehogs *(Erinaceus europaeus)* shift their home range to exploit seasonally abundant prey.

Plate 4.1: An adult male foraging in the arable field in autumn.

Plate 4.2: The same adult male foraging in pasture in summer.

4.1 Abstract

In order to further investigate some of the seasonal patterns of habitat selection first detected in 2008 and the factors affecting habitat choice, this focal study group continued to be monitored in 2009 and 2010. Hedgehogs were monitored for the entire active period so that home range could be calculated for the first time for rural Irish hedgehogs. From June 2008 to June 2010, hedgehogs were radio tagged, four nights a week. During this time 24 hedgehogs were caught at the site. A generalised linear model was used to examine factors which affected home range size. Sex and age were significant. Males had a significantly larger annual home range (56 ha) than females (16.5 ha), which was at its maximum during the breeding season (April-July), when individual males encompassed the range of all of the females. However, the monthly home ranges of females remained relatively constant throughout the year. Outside of the breeding season home range was relatively small (4-5 ha) in both sexes and on a nightly basis, individuals occupied small, mutually exclusive, areas. Compositional analysis of the data showed that habitats were not used in proportion to their availability. Hedgehogs concentrated their activity in pasture during the breeding season (April-July) and arable land in September and October. Habitat selection followed the same pattern in both years. This use of arable land by the study group was first observed in 2008 and is contrasting to studies in the U.K. and Denmark, which ranked arable land as the least preferred habitat. However, in the current study arable land was the most preferred habitat in September and October, in successive years, and the second most preferred habitat overall. The increase in hedgehog activity in arable land corresponded with a rise in surface invertebrates in this habitat, and to an increase in the amount of time hedgehogs spent foraging. We suggest that food availability is an important factor influencing hedgehog habitat selection and could be an important indicator of their presence elsewhere.

4.2 Introduction

While much research has been carried out on the European hedgehog in the urban environment (Reeve 1981, Micol *et al.* 1994, Dowding *et al.* 2010), less is known about rural hedgehogs with the exception of Morris's (1988) and Hof's (2009) research in English farmland and Ribers (2006) work in Denmark. Hof (2009) established that hedgerows and field margins were positively selected by hedgehogs at both the landscape and home range levels. In Boitani and Reggiani's (1984) study in Italy the most frequented habitats were wet meadows (36.5%). Micol *et al.* (1994) and Doncaster (1994) reported that hedgehogs were abundant in pasture in the U.K., while Young *et al.* (2006) observed that hedgehogs were extremely scarce in pasture fields, with only six individuals captured in three of 82 fields sampled in the U.K. It appears therefore that hedgehogs use a variety of rural habitats. However, arable, marsh and coniferous woodland have represented the lowest rank of habitat preference in the majority of studies (Dowie 1987, Doncaster 1994, Doncaster *et al.* 2001, Riber 2006). This may not be surprising, as earthworms, which are reported as an important prey item for hedgehogs (Yalden 1976), generally occur at a lower density in arable land than pasture (Kruuk 1979) and in the U.K., hedgerows persist least well in districts where arable farming prevails (Pollard *et al.* 1977).

As mentioned in Chapter 3, Ireland has the largest percentage of permanent pasture in the EU, and agriculture is generally less intensive than in many other European countries (Cabot 1999). In addition, hedgerow constitutes 1.5% of the Irish landscape, with a total length of 416,000km (Smal 1995). Most of Ireland's hedgerow has remained intact since its development in the 18th Century, unlike other European countries where hedgerows have become a special feature restricted to small areas (Cabot, 1999). Hedgehogs have been reported to forage and remain close to the borders of fields in the U.K., Denmark and New Zealand (Reeve 1981, Doncaster *et al.* 2001, Riber 2006, Shanahan *et al.* 2007). Given the different landscape structure it was worth investigating whether this was the case in Ireland too.

Burt (1943) defined home range in mammals “as the area traversed by an individual in its normal activities of food gathering, mating and caring for the young”. The importance of these activities changes on a seasonal basis and Kristiansson (1984) noted that, in Sweden, male hedgehogs increased their home range during the breeding season, in order to encompass the range of as many females as possible. Hedgehogs are non territorial and have a promiscuous mating strategy (Reeve 1994) and a home range overlap has been reported in both sexes in the U.K. (Reeve 1982). Home range estimates for hedgehogs have ranged from 2-5 ha in the U.K. (Morris 1986) to 29.08 ha in Italy (Boitani and Reggiani 1984) for females in rural areas and 32 ha for males in suburban U.K. (Reeve 1982) to 96 ha in rural Denmark (Riber 2006) for males. On a nightly basis males have been reported to move further than females (Morris 1986; Dowding *et al.* 2010).

Kristiansson (1984) concluded that food availability was a crucial factor regulating the size of a Swedish hedgehog population. Hedgehogs in the U.K. have been reported in pasture fields with higher worm counts (Micol *et al.* 1994). In New Zealand the major taxa occurring in both hedgehog stomachs and droppings were lepidopteran larvae, earwigs, unidentified beetles, spiders, harvestmen, slugs and earthworms (Campbell 1973). Yalden (1976) noted that relative to biomass, caterpillars, earthworms and beetles were the most important prey, constituting 55% of the diet in the U.K. An analysis of the spatial distribution and the foraging behaviour of hedgehogs within open meadows in the U.K., in relation to the availability of earthworms, showed that the relative increase in the density of hedgehogs was directly proportional to the relative increase in the density of worms, emphasising the importance of prey in habitat selection(Cassini & Föger 1995). Hedgehogs have also been found to feed on bird’s eggs (Wodzicki 1950, Jackson *et al.* 2004) and vertebrates (Yalden 1976) and therefore, although predominantly insectivorous, their diet is, in many ways, opportunistic. Both Obrtel and Holisova (1981) and Wroot (1984) found a clear tendency for hedgehogs to concentrate on a single type of prey at a time and to switch from one prey group to another according to season.

A preliminary study of this hedgehog group in 2008, indicated that hedgehogs selected habitat and that there was a seasonal shift in habitat use, with hedgehogs responding to variations in prey availability. This aspect of the study aimed to examine this further. In addition to this it aimed to test the following hypotheses that:

a) Males have a larger home range than females
b) Individuals exhibit site philopatry
c) Individual hedgehogs show the same pattern of habitat use in successive years.
d) Habitat selection is related to prey availability

4.3 Materials and Methods

4.3.1 Site

The study was carried out between June 2008 and June 2010 on a site (51˚ 53’ 59.5’’N latitude, 8˚ 29’03.7”W longitude), 36.8km from Cork city and 5.3km from the nearest town of Bandon, Ireland. In 2008, a core area of 43 ha was searched for hedgehogs (Fig. 4.1) comprising of arable (35%) and pasture (41%) with small areas of coniferous woodland (10%) and scrub (6%) (See Chapter 3). The livestock present in the area were horses, dairy cows and cattle. Residences (8%) were associated mainly with farmyards and were clustered throughout the study site.

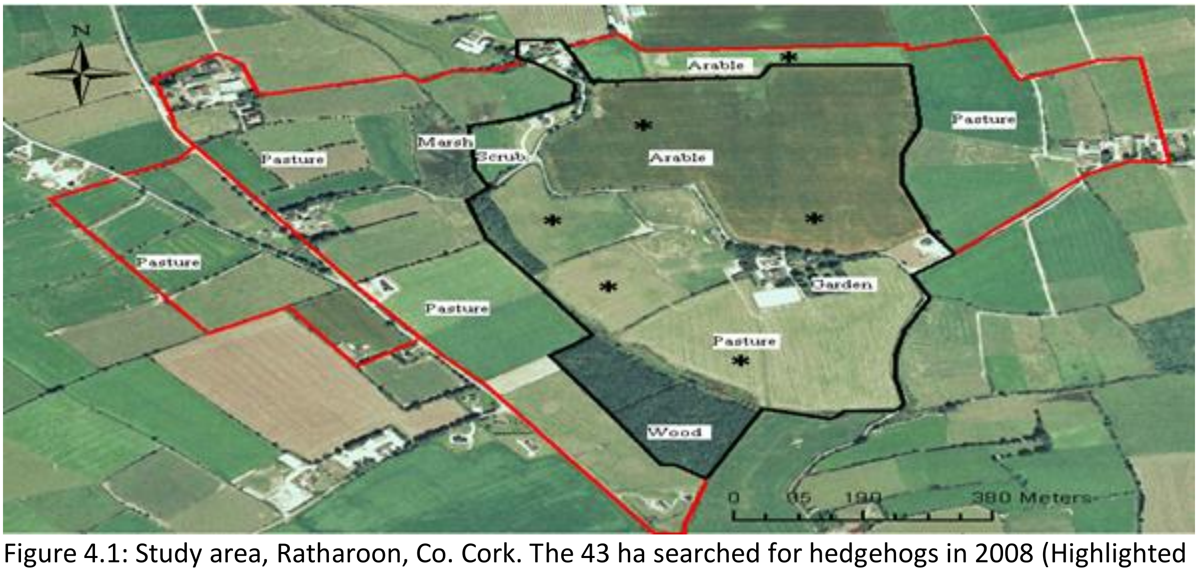

Figure 4.1: Study area, Ratharoon, Co. Cork. The 43 ha searched for hedgehogs in 2008 (Highlighted in black) and in red that covered in 2009 and 2010. Areas marked with an asterisk were surveyed for surface prey.

In 2009 and 2010, the search area was extended to 97 ha (Fig. 4.1). Encompassing the area searched in 2008, this new expanded total area now consisted of 23% arable, 64% pasture, 7% residential garden, 1% scrub, 1% marsh, 4% wood.

4.3.2 Capture and Marking

Hedgehogs were captured by hand with the aid of spotlights. Individuals were marked using a unique colour combination of heat shrink plastic tubes (R.S. Components Ltd, Northants, U.K.) which were attached to the spines. Fifteen were applied to three specific regions (left of head, centre, and right of head) on each animal with glue (Evo-Stik). Reflective tape (CH Marine, Cork) was also attached to one of the middle markers so that the head region could be identified while tracking. The tubes acted as a visual aid and minimised the need to recapture the animal each time for individual identification. Individuals were also marked using passive integrated transponder (P.I.T.) tags (MID Fingerprint, Dorset, U.K.) inserted into the upper hind leg (Doncaster *et al.* 2001; Jackson *et al.* 2004). This allowed individuals to be identified after hibernation.

All procedures were carried out in accordance with current regulations; licenses were obtained from the Department of Environment, Heritage and Local Government.

4.3.3 Direct Observation

From June-September 2008, captured hedgehogs were fitted with a tip light (MK IV) attached to the back of the animal and monitored by direct following (Table 4.1). A UV filter was placed over a spotlight and the animal was observed upon release. Every ten minutes fixes were taken using a Garmin GPS 60 (CH Marine). The type of habitat and the hedgehog's location and behaviour were also recorded. Animals were followed until they returned to the nest site, or until they could no longer be located. In 2010, of the six individuals tagged (Table 4.1), two of these hedgehogs had first been caught in 2008, two in 2009 and two were new individuals.

Table 4.1: Hedgehogs sampled in Ratharoon, Co. Cork from 2008-2010.

Date	Monitoring technique	Number of hedgehogs	Number of nights	Number of hours
26/6/08-28/9/08	Direct observation	7 (2♀,5♂)	17	95
18/10/08-12/11/08	Direct observation	3 (1♀, 2♂)	6	14
28/9/08-20/11/08	Radio tracking	8 (4♀,4♂)	33	160
30/3/09-10/11/09	Radio tracking	16 (4♀,12♂)	104	624
23/3/10-12/7/10	Radio tracking	6 (1♀,5♂)	38	76

4.3.4 Radio Tracking

Animals caught after 28 September 2008 were fitted with radio tags (Plate 4.1, Cover page). The exception to this was three juveniles, who were directly followed between 18th October and 12th November 2008 (Table 1). Eight animals were fitted with 173 MHz, R1-2B transmitters (Holohil Systems Ltd, Ontario, Canada) and attached to the animal after the manner of Jackson and Green (2000). The entire tag weighed 10g. Hedgehogs were tracked using a SIKA receiver (Biotrack Ltd, Dorset, U.K.). When the hedgehog was located its position and behaviour were recorded before locating the next tagged individual. In 2008, this procedure was continued from dusk until the animals returned to their nests at dawn. Six of these hedgehogs were monitored throughout hibernation and again upon emergence. In 2009, Individuals were monitored for either the first six hours of the night after emergence or the six hours before dawn, having first tested that there was no discernable differences in the amount of time individuals spent engaged in previously identified activities between the first six and the last six hours of the night (Mann Whitney U test: U=19.5, n_1=6, n_2=12, p>0.05). Activities were recorded based on an ethogram of activities (See Appendix 2).

4.3.5 Home Range

Home range was calculated from the 2009 fixes only, due to the fact that hedgehogs were tracked for their entire active period in 2009 but not in 2008. Home range was estimated using i) the 100% minimum convex polygon (MCP) and ii) the 95%, 90% and 50% Kernel method, using the Hrt extension for Arc map version 9.2x (Rodgers & Carr 1998). The Kernel calculations were compared to the home range calculated for the 50%, 90%, and 95% MCP. The two methods were used as MCPs alone do not indicate how intensively different parts of an animal's home range are utilised, whereas kernel methods allow the determination of centres of activity (Worton 1995, Seaman & Powell 1996). The 50% Kernel method calculates the core area of animal activity whereas the 95% excludes 5% of the outer most fixes so that occasional excursions out of the area can be separated from the animal's true home range.

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

4.3.6 Data Analysis

GPS positions were plotted on to ortho-photographs (Ordnance Survey of Ireland) of the area using the Geographic Information System (GIS) software Arc map version 9.2.

A General linear model (GLM) using a Gamma distributed response variable was used to examine the effects of age, sex, weight and month on the home range size. Non significant terms were excluded using the drop one procedure (Zuur *et al.* 2007).

Means are followed by the ± standard error unless it is stated otherwise. Tests for normality and the GLM, were performed on Brodgar software for univariate and multivariate analysis and multivariate time series analysis version 2.6.3. PASW Statistics Version 17 was used for all further statistical analysis. Levels of significance were taken as $p<0.05$ or $p<0.01$.

4.3.7 Habitat Selection

Patterns of habitat selection were investigated using compositional analysis, version 6.2 plus (Smith 2005). This technique uses Manova/Mancova type linear models (Aebischer *et al.* 1993). The significance of Wilks lambda and of t-tests is determined by randomisation tests and determines whether the habitat was selected or used in conjunction with its availability (Smith 2005). Minimum convex polygon (MCP) was used to determine the outer limits of an individual hedgehog's home range. The proportion of each habitat available to the hedgehog was determined using ortho-photographs (Ordnance Survey of Ireland) of the site using the Geographic Information System (GIS) software Arc map version 9.2.

4.3.8 Surface Invertebrate Surveys

Surface prey was counted at weekly intervals, at night, on transects of 60m X 0.46 m, in the arable land (Fig. 4.1). Seventy two surface transects were sampled in October 2008 and 71 in March-November 2009. These linear transects were conducted in all areas of the arable field and all surface invertebrates were recorded. Flatworm and Mollusc were collected and identification was confirmed by Roy Anderson, Belfast.

Weekly invertebrate surveys were also carried out from March-November 2009 in three areas of pasture (Fig. 4.1). Fifty four transects, were sampled using a (0.50 x 0.50m) quadrat placed at three random locations along a 60m long transect. These linear transects were conducted in all areas of the field.

4.4 Results

4.4.1 Home Range in 2009

The mean annual home range size (± SE) calculated by the 100% MCP method was 16.5 (±0.5) ha for adult females and 56.0 (± 0.7) ha for adult males (Table 4.2). Males had a significantly larger annual home range than females (U=10.000, n_1=5, n_2=4, $p<0.05$). However, the size of their range changed seasonally and was at its maximum during the breeding season (April to July) (mean ± SE= 17.2 ±0.36 to 22.6 ±0.51 ha) (100% MCP) (Table 4.2, Fig. 4.2). In August, when breeding activity terminated, the mean monthly home range of males was reduced to 5.13 ±0.23 ha (Fig. 4.2). Females were found to maintain a similar monthly home range size throughout the year (Table 4.2) and it increased only marginally during the breeding season, but reached a peak in June (5.8 ±0.75 ha) (Fig. 4.2).

Table 4.2: The mean annual (± SE) home range size (ha) and during and after the breeding season, for adult females, and adult and juvenile males in 2009.

	100% MCP (April-October)	100% MCP (Breeding season only) (April-July)	100% MCP (Outside breeding season)	50% Kernel
Adult Females (n=3)	16.5 ±0.49	4.2 ±0.16	4.05 ±0.19	2.4 ±0.28
Adult Males (n=4)	56.0 ±0.67	15.9 ±0.16	4.50 ±0.12	11.1 ±0.53
Juvenile Males (n=4)	6.4 ±0.28	N/A	2.30 ±0.13	0.8 ±0.20

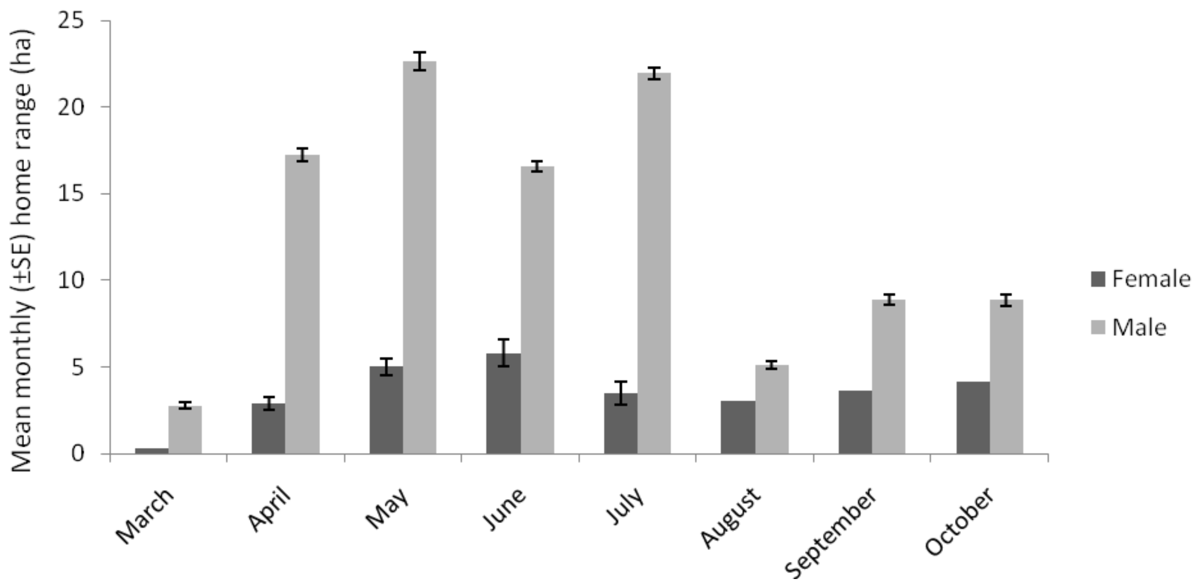

Figure 4.2: The mean monthly home range (±SE) based on 100% MCP of four adult male and four female hedgehogs from March-October 2009.

The significant effect of sex and age on home range size was also verified by the general linear model, which explained 73% of the data (Tables 4.3 and 4.4). Adults had a larger home range than juveniles and the home range of males was larger every month. The month of year did not significantly affect the size of the home range (Table 4.4) but the home range of females varied little on a monthly basis (Fig. 4.2).

Table 4.3: Summary of the general linear model examining the factors significantly affecting the home range size of hedgehogs.
Significance levels *=p<0.05, **=p<0.01, ***=p<0.001

Explanatory variable	Estimate	Standard error	t	P
Intercept	0.2365	0.5224	0.453	0.652316
Sex	-1.1521	0.2665	-4.323	5.49e-05***
Age	-1.5239	0.3968	-3.841	0.000284***
April	2.3533	0.6365	3.697	0.000455***
May	2.7206	0.6381	4.264	6.75e-05***
June	2.6174	0.6513	4.019	0.000157***
July	2.1344	0.5838	3.656	0.000519***
August	1.1405	0.6355	1.795	0.077410
September	2.0663	0.6275	3.293	0.001617**
October	2.3433	0.6059	3.868	0.000260***
November	2.5848	0.9247	2.795	0.006838**

Table 4.4: Summary of the general linear model of the factors significantly affecting the home range size of hedgehogs
Significance factors *=p<0.05, **=p<0.01, ***=p<0.001

Explanatory Variable	df	F value	Pr (F)
Sex	1	7.5937	0.00762**
Age	1	5.0841	0.02758*
Month	8	1.3623	0.23018

The range of males and females overlapped geographically (Figs. 4.3 and 4.4). However, while the home ranges of males overlapped completely with one another and encompassed that of all four adult females (Figs. 4.3 and 4.4) individual females showed little overlap and occupied mutually exclusive areas (Fig. 4.4). Individual males covered the range of all of the tagged females during the breeding season (Fig. 4.3 and 4.4). Overlap was also observed amongst juvenile males (Fig. 4.5).

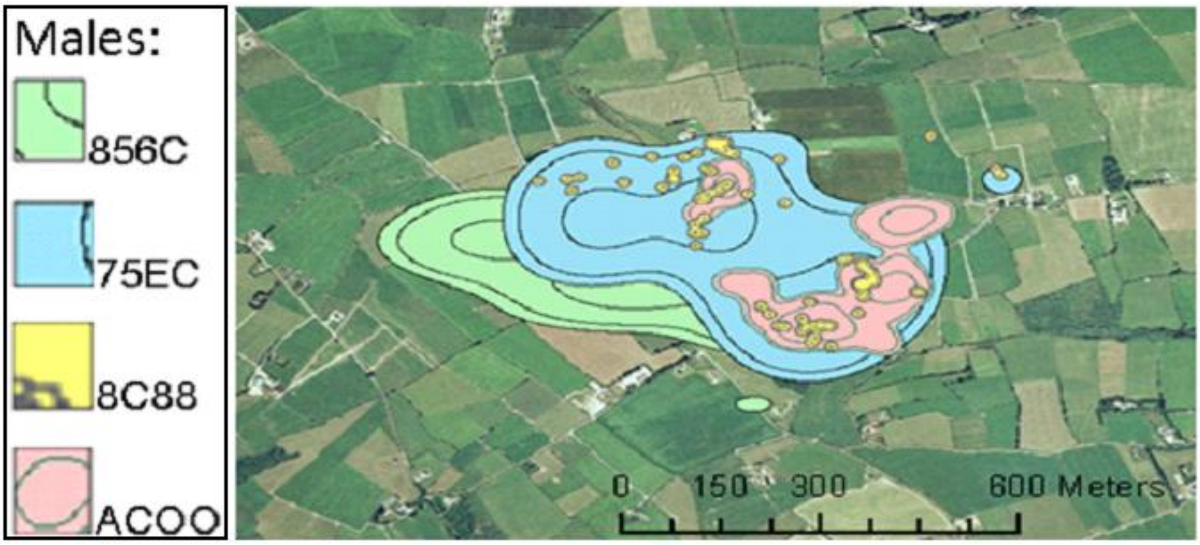

Figure 4.3: 50% (inner circle), 90% and 95% (outer circle) Kernel analysis for four radio tagged adult males, showing annual overlap of home range from March-November 2009 in Ratharoon, Co. Cork.

Figure 4.4: 50% (inner circle), 90%, 95% (outer circle) Kernel analysis for four radio tagged adult females from March-November 2009 in Ratharoon, Co. Cork.

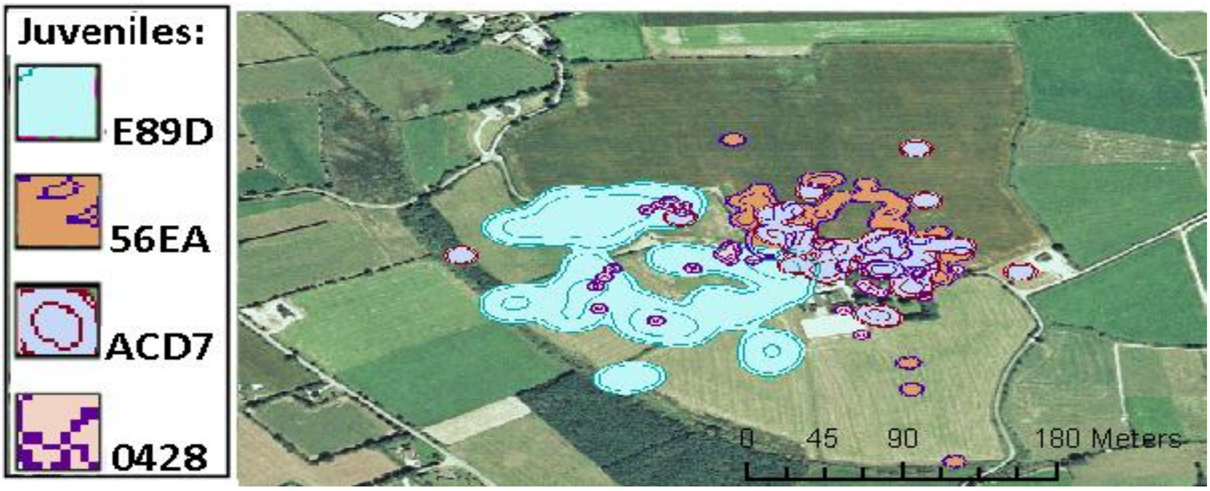

Figure 4.5: 50%, 90% and 95% kernel analysis for 4 male juvenile hedgehogs.

When the breeding period (April-July) ceased home range overlap was less pronounced among males, and mutually exclusive areas were occupied by both sexes. On a nightly basis, individual hedgehogs occupied small specific areas and rarely crossed the path of another individual (Figs. 4.6a and 4.6b).

Figure 4.6 a-b: Fixes from three adult males (blue, black and red) (a) and three adult females (pink, green and turquoise) (b) taken over seven nights from October 5th-October 17th 2008.

Hedgehogs showed philopatry occupying the same areas and following the same pattern of habitat selection in both years. This is illustrated by an adult female (FA56) who was tagged and tracked from June 2008 to March 2010 but failed to emerge from hibernation in 2010 (Fig. 4.7) and an adult male (75EC) who was tracked from July 2008 until July 2010 (Fig. 4.8). This demonstrates that although males remained in the same area they shifted and expanded their home range during the breeding season (Fig. 4.8) while females occupied much smaller areas with a less pronounced seasonal shift (Fig.4.7). In 2008, work at the site did not begin until the end of June, when the breeding season was coming to an end. Therefore, the expansion of the males' home range during the breeding season may have remained undetected in this year.

Figure 4.7: Locations of female FA56 for 2008 (black) and 2009 (red)

Figure 4.8: Locations of male 45EC for 2008 (black), 2009 (red) and 2010 (yellow).

4.4.2 Habitat Selection

Using MCP ranges, a comparison of habitat use with habitat availability in the study area indicated that adult hedgehogs did not use the habitat in accordance with its availability (Wilks Lambda: $\lambda=0.18$, $p<0.01$) but selected certain habitats (Table 4.5). Overall, garden and arable land ranked as the most favoured habitat by adult hedgehogs, both habitats being used in a proportion greater than their availability (Table 4.5). Furthermore, the habitats utilised by adult hedgehogs changed on a seasonal basis, with pasture selected in the breeding season, garden in August and arable land in September and October. This corresponded to the shifts in home range referred to in the previous section (Table 4.5 and Figs 4.9a-4.9d).

Table 4.5: Habitat selection by hedgehogs for all years combined. Habitats are ranked in order of greatest to lowest preference.
G=garden, S=scrub, P=pasture, A=arable, M=marsh, W=woodland
>>> refers to a significance of 0.05.

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

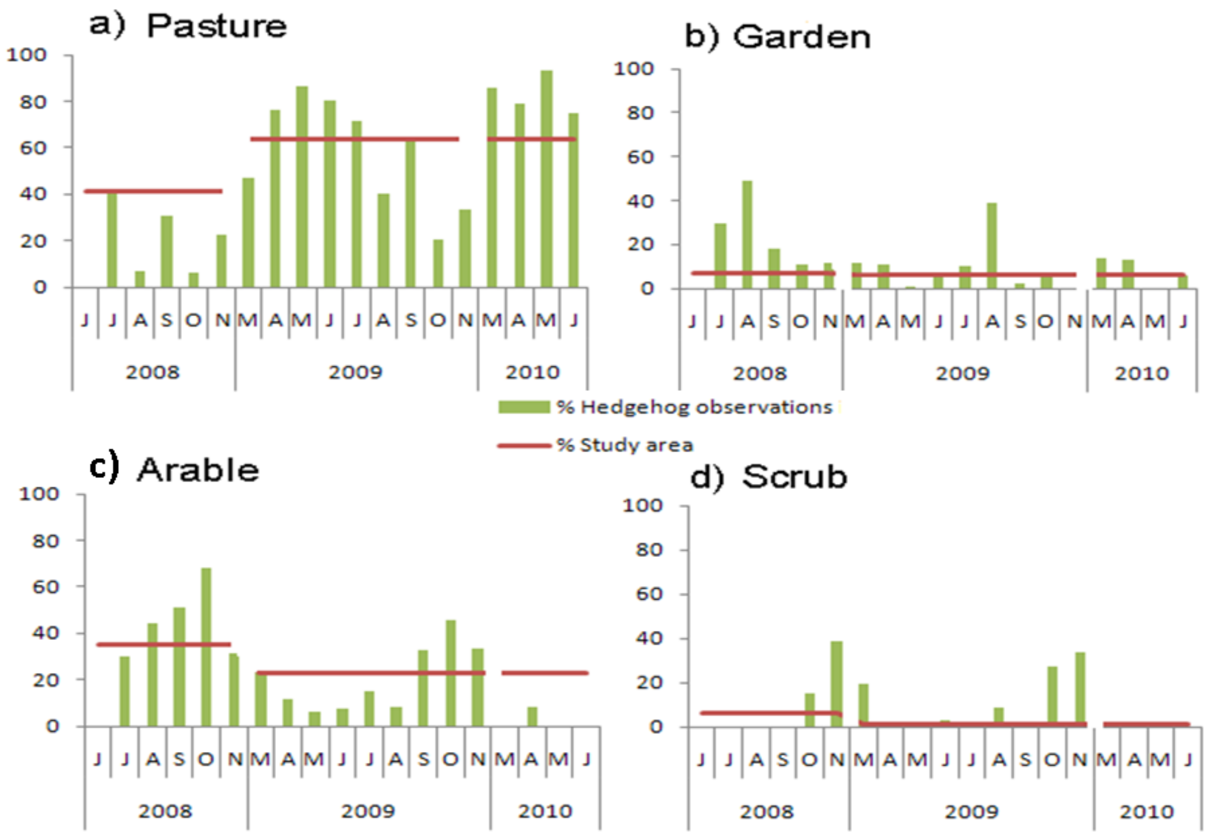

Figure 4.9 a-d: The percentage of nightly observations in 2008 (n=1496), 2009 (n=1629) and 2010 (n=146) where adult hedgehogs were observed in a habitat relative to the percentage of each habitat type within the study area. A bar above the line indicates that habitat was selected, and below the line that it was not used in conjunction with its availability.

4.4.3 Seasonal Variation in Habitat Use

When hedgehogs emerged from hibernation between March and April in both 2009 and 2010, they remained in the areas closest to their hibernacula (garden and scrub) (Figs 4.9b and d). From May-July 2009 and 2010, pasture ranked as the most favoured habitat (Fig. 4.9a) and was used in a proportion greater than its availability (Table 4.5). In August 2008 and 2009, hedgehogs occupied a small (0.5 ha) area of garden which bordered the pasture and made exploratory trips into the adjacent arable land (15ha) (Fig. 4.9c). In September, the hedgehogs moved into the arable land in both 2008 and 2009 (Fig. 4.9c). They remained in this habitat in October foraging and day nesting there (see Chapter 6). Hedgehogs moved into areas of scrub to build hibernacula in late October/November. All but two hedgehogs had entered hibernation by November (Fig. 4.9d).

4.4.4 Potential Prey

The surface invertebrates within the arable field consisted predominantly of molluscs in 2008 and molluscs and earthworms in 2009 (Table 4.6).

Table 4.6: Relative abundance of surface invertebrates found throughout arable and pasture land.

Species	Arable 2008	Arable 2009	Pasture 2009
Molluscs –	90%	45%	78%
• *Derocerus panormitanum*			
• *Derocerus reticulatum*			
• *Milax gagates*			
• *Arion distinctus*			
Earthworms –	8%	48%	12%
• *Lumbricus terrestris*			
Australian flatworms –	1%	1%	0%
• *Australoplana sanguine*			
• Beetles (Coleoptera spp.)	1%	6%	10%

In 2009, when both arable and pasture were examined, the actual abundance of surface invertebrates in pasture was considerably lower than in the arable field throughout the year (Table 4.6 and Figs. 4.10a and b). The maximum invertebrate density recorded in pasture was 0.12 per m^2 (Fig. 4.10) and in arable were 3.12 per m^2 (Fig. 4.11).

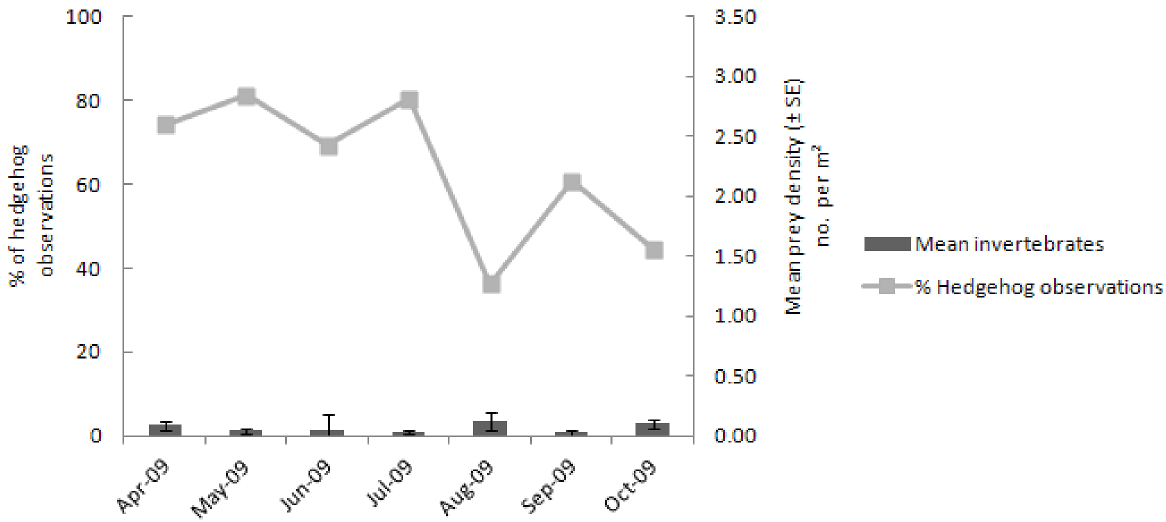

Figure 4.10a: Percentage of all observations where hedgehogs were in the pasture in 2009, (1603 observations) vs the mean prey (±SE) abundance in pasture (54 transects).

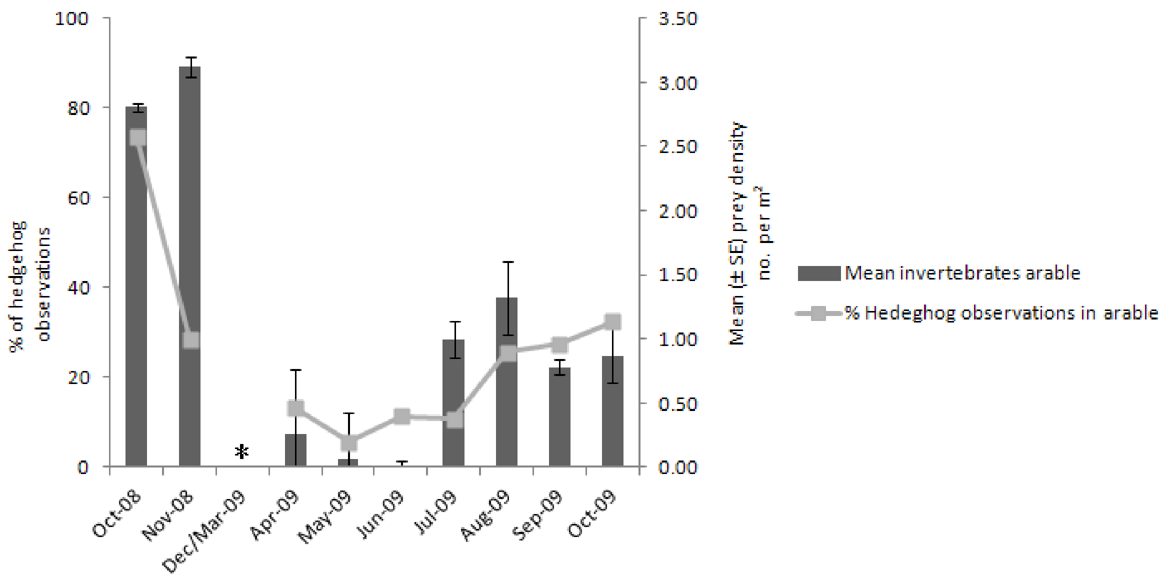

Figure 4.10 b: Percentage of all observations where hedgehogs were in the arable field (1222 observations) in 2008 and (1077 observations) in 2009 vs the mean prey (±SE) abundance in arable (142 transects).
*=hibernation period.

However, during the months that pasture was utilised, hedgehogs spent less time foraging (29%), and up to 35% of their time engaged in courtship behaviour (Fig. 4.11). The density of invertebrates on the surface of the arable land was high in late summer and autumn (Fig. 4.10b). Hedgehogs spent more time in the arable land during these months, when they devoted the majority (66%) of their activity to foraging (Figs. 4.10 and 4.11).

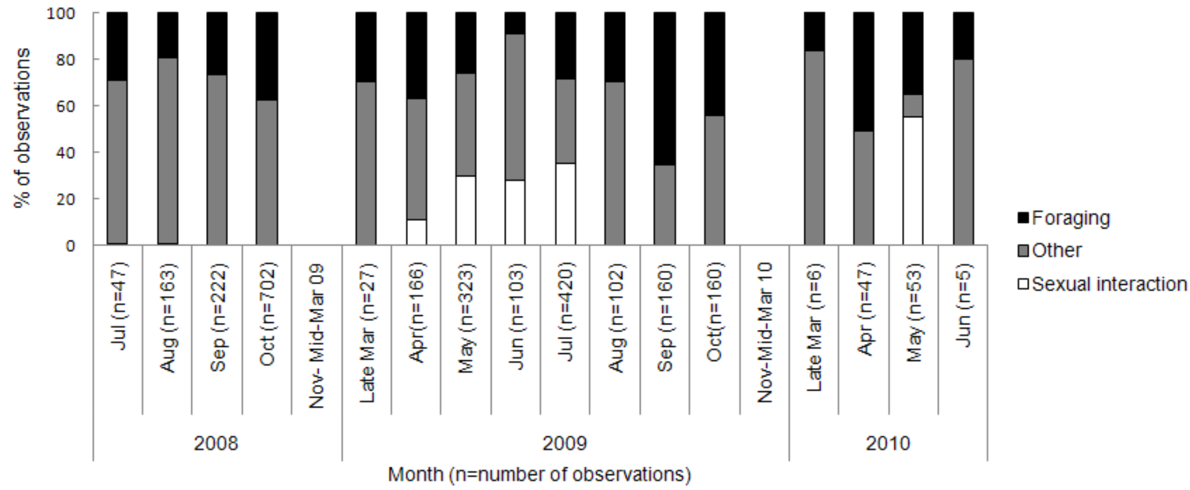

Figure 4.11: The percentage of observations per month when 14 adult hedgehogs were observed to be engaged in a particular activity (n= observations that month; total=2706). "Other" refers to cleaning, walking and stationary activity.

4.4.5 Mortality

Of the 24 hedgehogs caught since 2008, at least 66.7% (n=16) of them were thought to have died by the end of the study. A further 16.7% (n=4) of the individuals were considered transients having been caught just once in the area during the breeding season. Of the 11 cases where the cause of death was known, 91% of them were caused by anthropogenic factors. Of these 55% were due to injuries inflicted by a dog (Table 4.7).

Table 4.7: Causes of death of eleven of the hedgehogs at the site in Ratharoon.

Cause of death	Number (%)
Road	1 (9%)
Dog attack	6 (55%)
Badger	1 (9%)
Other:	
Electric fence	1(9%)
Mowing machine	1(9%)
Wobbly hedgehog syndrome (Graesser *et al.* 2004, Graesser *et al.* 2006)	1(9%)

Five individuals are believed to have died during hibernation; however, unlike the 11 where the cause of death was known, this is unconfirmed. In 2008, four juveniles reached independence on 17th October 2008 (Chapter 3), and only one male (56EA) was recaptured post hibernation. In 2010, an adult female (FA56) who had been monitored since 2008 was never seen again after hibernation, despite maintaining the same home range for the previous two years (Fig. 4.6). A juvenile male (E89D) who was hibernating beside the 9ha pasture was also never seen again.

Following the death of four of the tagged hedgehogs in June 2009 and the loss of signal of the other individual, no further signs of hedgehog activity were recorded at the site up to October 2010.

4.5 Discussion

In the present study hedgehogs showed site philopatry, and maintained the same temporal pattern of habitat use annually in the two years of the study. This is important from a conservation point of view as it demonstrates how vulnerable local populations may be to local extinctions. Males had a mean annual home range (± SE) of 56 ±0.67 ha and females 16.54 ± 0.49 ha. Home range estimates in other studies have ranged from 2-5 ha (Morris 1986) to 29.08ha (Boitani and Reggiani (1984) for females and 32 ha (Reeve 1982) to 96 ha (Riber 2006) for males. Riber's (2006) study took place in a rural area of Denmark with a similar composition of habitat types to the study conducted here. When calculated using a 100% MCP, Riber found that the average home range was 96 (± 24) ha for males and 26 (± 15) ha for females. When the core area was examined using the 50% Kernel, Riber recorded a home range of 12 (± 8) ha for males and 3 (± 0.8) ha for females, a result that is very similar to the core home range in the present study. This implies that a better comparison may be made between studies using kernel estimates. In the current study males were found to have a significantly larger home range than females, with males encompassing the range of all adult females during the breeding season. This has been reported in the majority of studies on hedgehogs (Reeve 1982, Kristiansson 1984, Dowding 2007, Rautio *et al.* 2009), with the exception of Boitani and Reggiani (1984), who found no significant difference in Italy.

The location of the home range in the present study shifted periodically and so was smaller when calculated on a monthly basis. This emphasises the importance of long term studies to avoid underestimation of home range size. When examined on a monthly and individual level, it was found that the home range of males peaked during the mating period (April-July). This is also supported by road kill data, with a peak in hedgehog deaths occurring from April–July (See Chapters 7 and 9). This has previously been seen by Smiddy (2002). Kristiansson (1984) also noted a peak in male home range in the period from April to July in Sweden. Due to their promiscuous mating strategy, during the breeding season(Jackson 2006), it has been suggested that male hedgehogs cover much greater distances on a nightly basis, in order to encompass the range of as many females as possible (Huijser & Bergers 2000). Both Goransson *et al.* (1976) and Huijser *et al.* (1998) reported a preponderance of male hedgehogs as road kill in Sweden and the Netherlands. The males in the current study encompassed the range of all of the females during the breeding season, but when breeding terminated their home range was much reduced and more similar to that of females.

The home range of females was much smaller than males (16.5 ha vs 56 ha) and remained relatively consistent throughout the year, but like males reached a peak in the breeding season. Reeve (1982) found that the ranges overlapped considerably and often completely in both sexes. Unlike Reeve (1982) the ranges of the females in the present study did not overlap completely and instead they occupied mutually exclusive areas, among which the males moved, throughout the breeding season. In the American mink (*Mustela vison*) females maintain their territories and the range of the males overlap with several females (Wolff & Macdonald 2004). A similar situation also occurs in the red squirrel (*Sciurus vulgaris*) where males have much larger home ranges than females and the core-areas of most breeding females are mutually exclusive (Lurz *et al.* 2000). This is discussed further in Chapter 7.

While the home range of both sexes fluctuated and shifted throughout the year, when four adult males (8C88, A3D6, 75EC and ACOO) and three females (7150, FA56 and 524A) were monitored the core area of their home range remained the same for two consecutive years (based on 880 fixes for these individuals in 2008 and 1462 in 2009). Reeve (1982) also found that individuals showed a marked tendency to remain in the same locality from year to year. In Campbell's (1973) study in New Zealand she found that of 100 hedgehogs caught in two and half years, at least 20 were considered resident because they were captured between 10 and 46 times. "Philopatry will favour the evolution of cooperative traits between members of the sedentary sex. Disruptive acts will be a feature of dispersers" (Greenwood 1980). Hedgehogs are non territorial (Reeve, 1994) and have no defined dispersal period (Doncaster 1993), however road kill data would suggest a range expansion amongst males during the breeding season (Chapter 7). On a nightly basis, in the current study, individuals of both sexes occupied specific areas of each habitat and rarely crossed the path of another. In fact, one could successfully predict in which part of the arable field a given individual would be feeding. Although not territorial, Cassini and Krebs (1994) found that hedgehogs showed mutual avoidance and suggested that this could impose a limit on numbers in an area. This also seems to be the case in this rural population.

In the current study, hedgehogs selected certain habitats and their preference changed seasonally with corresponding shifts in activity patterns. Pasture was selected from April-July 2009 and again in 2010. This corresponded with the peak in mating behaviour in both years, with individuals spending between 11% (April 2009) and 35% (May 2010) of their time engaged in courtship during this period. Prey was low in the pasture, in comparison to the adjacent arable land and after the breeding season, hedgehogs moved out of pasture. Similarly, Doncaster (1994) found that hedgehogs showed seasonal variations in dispersal between fields, which he attributed to the use of certain areas during the breeding season and the distribution of earthworm prey.

In the present study, a peak in the use of the garden was recorded in August 2008 and 2009. The hedgehogs used habitat close to their nest sites, at least at the start of the night. They often started their night in the garden while making exploratory trips into the adjacent arable land later in the night, before moving into the arable field completely in September and October 2008 and 2009. In addition, as mentioned in Chapter 3, August was a particularly wet month in both years and the garden's mature trees and bushes may have provided them with significant protection which allowed them to continue foraging.

The hedgehogs' move onto the arable land in September/October in both years coincided not only with an increase in the density of surface invertebrates but also with the increased amount of time hedgehogs spent foraging (26% in May 2009 to 66% in September 2009). The density of hedgehogs has been reported to be directly proportional to the relative increase in the density of earthworms (Doncaster 1994, Cassini and Foger 1995). In the present study hedgehogs were seen feeding on earthworms in both the pasture and arable fields, but earthworm numbers along transects were low in comparison to mollusc numbers, particularly in 2008. Lagerlof *et al.* (2002) recorded that the abundance of earthworms from soil samples from arable land was less than 1 worm per m^2 in Sweden. However, in Ireland, Curry *et al.* (2002) reported earthworm densities of 319 individuals m^2 from soil samples obtained in a conventional wheat plot, and 1160 individuals m^2 in a wheat–clover plot . In the Czech Republic and the U.K., hedgehogs have been shown to concentrate on one prey item at a time and switch from one group to another on a seasonal basis (Obrtel and Holisova 1981, Wroot 1984). Yalden (1976) established that although earthworms were always an important source of prey, their importance changed seasonally with the amount per stomach varying between 0.1g in April and July to 1.9g in June. A change of diet with availability appears to be the case in the current study with hedgehogs responding to a rise in mollusc density in 2008 and earthworms in 2009.

The high level of activity of the hedgehogs on the arable land was first noted in 2008 (Chapter 3) and was unexpected in light of previous research. Previous studies have shown arable land to be their least preferred habitat (Doncaster 1994, Doncaster *et al.* 2001). In Denmark, Riber (2006) recorded that, even though arable land was one of the most common habitat types within the hedgehogs' home range, a large proportion of arable land was rarely visited by the hedgehogs. Comparatively in the U.K., Dowie (1987) found no evidence of hedgehogs on 140 ha of arable land in Hampshire, despite searching for eight weeks and using a variety of methods. However, in the current study arable land ranked as the most preferred habitat in October and was the second most preferred habitat overall. There is increasing evidence that wildlife inhabiting farmland, especially arable ecosystems, are in widespread and severe decline throughout much of northern, western and central Europe (Sotherton 1998). The regular and intensive post-harvest flailing of hedgerows has resulted in some hedges becoming very reduced, and sometimes shorter than the crops that they surround (Croxton *et al.* 2004). Heterogeneity in field margin structure is necessary for the retention of high levels of invertebrate abundance (Sheridan *et al.* 2008). The retention of hedgerow affects the amount of leaf litter, which also has a knock-on effect on invertebrate colonisation (Smith *et al.* 2008). In Ireland, areas which are predominantly arable still have pockets of grassland mixed in the habitat mosaic, while in England vast areas are devoted almost totally to tillage (Bracken & Bolger 2006). As well as maintaining hedgerow in arable areas, winter stubble is often maintained (Bracken and Bolger, 2006) which may also benefit slug numbers (Glen *et al.* 1989). The arable field in the present study was surrounded by a mosaic of pasture and gardens, had a well developed hedgerow network, with good ground cover and a boundary strip. These factors appeared to have had a positive impact on the density of surface invertebrates and subsequently on the hedgehogs who feed on them.

In November of 2008 and 2009, hedgehogs moved out of the arable field and into areas of scrub to build hibernacula. Both earthworms and molluscs are susceptible to changes in soil moisture and temperature (Getz 1959, Whalen *et al.* 1998). According to Crawford-Sidebotham (1972) an increase of 2˚C in temperature at 90 to 100% in relative humidity causes a marked increase in the expected numbers of active slugs, which are more than doubled in many cases. In light of the effects of even small changes in temperature, it is not surprising that a drop in temperature from 9˚ C to -1˚C on the 29th October 2008 resulted in a disappearance in potential prey (Chapter 5), which coincided with the hedgehogs' movement out of the arable field and the onset of hibernation.

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

4.5.1 Conclusion

The hedgehogs in this study exhibited philopatry and maintained the same pattern of temporal habitat use in successive years. The observed seasonal change in habitat selection and range size emphasises the importance of long term study to establish accurate home range estimates and investigate the factors affecting habitat selection. In the current study, seasonal changes in habitat selection corresponded to changes in behaviour. Hedgehogs moved into open pasture in the breeding season, when individuals spent up to 35% of their time engaged in courtship. Arable land was the preferred habitat following a rise in surface invertebrates, at a time when building up fat reserves before hibernation was a priority; while scrub was selected for secure hibernacula. This pattern of habitat use emphasises the importance of mosaic habitats in maintaining biodiversity. The site fidelity shown by hedgehogs highlights the importance of maintaining landscape heterogeneity at the broader scale to ensure genetic diversity and successful recolonisation of other areas.

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Chapter 5-
Intra and interhabitat differences in hedgehog distribution and potential prey availability

Accepted (Mammalia).

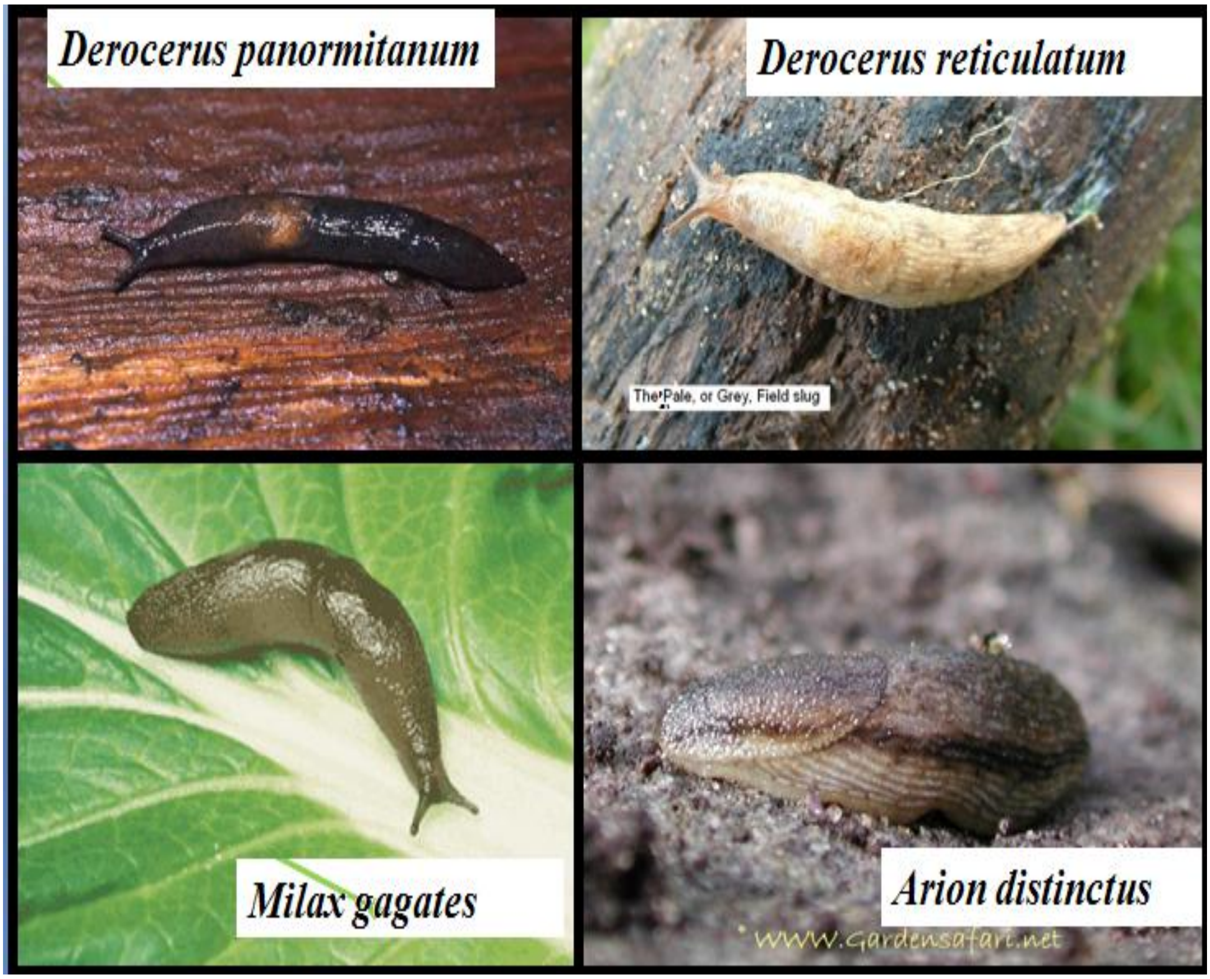

Plate 5.1: Species of slug on which hedgehogs were observed feeding.

5.1 Abstract

Between June 2008 and November 2009, 22 hedgehogs (6♀ and 16♂) were tagged and tracked at Ratharoon, Co. Cork by a combination of direct following and radio tracking and their patterns of movement within each habitat examined. Transects, surveying surface invertebrates were sampled in the centre and hedgerow in arable and pasture land distributed throughout the site. In both years, hedgehogs selected arable land and this coincided with a rise in prey density. This and the fact that within the arable field, hedgehogs concentrated their activity where there was a greater density of potential prey, suggests that hedgehogs learn the spatial location of prospective food. Contrary to other research, in the majority of the hedgehogs' home range, individuals consistently foraged in the centre of both pasture and arable land. Potential prey was lower in fields where the hedgerow had no bramble understory and this suggests that hedgerow with good ground cover acts as important reserves for invertebrates. Badgers (*Meles meles*) were seen on twelve 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.

5.2 Introduction

Agricultural land, due to its historic low intensity land management and resulting high species assemblage, is an important habitat for a number of bird and mammal species in Europe (Stoate *et al.* 2009). Over the past three decades changes in agricultural management in the U.K. have resulted in increased crop and grass production (Chamberlain *et al.* 2000). However, these agricultural changes, aimed at making farming more cost-effective have had an adverse effect on wildlife (Tapper & Barnes 1986, Hinsley & 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 U.K. (Robinson & Sutherland 2002). However, while 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 & Harris 2009). As previously mentioned in Chapters 4 and 5, agriculture in Ireland is generally less intensive than in many other European countries (Cabot 1999). Hedgerow constitutes 1.5% of the Irish landscape, with a total length of 416,000km (Smal 1995) and most of Ireland's hedgerow has remained intact since its development in the 18th Century, unlike other European countries where hedgerows have become a special feature restricted to small areas (Cabot, 1999).

As their name suggests, hedgehogs are generally associated with hedgerow and edge habitat. In the U.K., Hof (2009) found that, at the landscape level, habitat preference by hedgehogs was ranked as follows: hedgerow, village, agri-environment field margins, pasture, amenity grasslands, woodland, set aside and arable. This tendency for hedgehogs to forage and remain close to the borders of fields has been reported in a number of studies in the U.K., Denmark and New Zealand (Reeve 1981, Doncaster *et al.* 2001, Riber 2006, Shanahan *et al.* 2007). Huijser (2000) observed that while 53% of their time was spent on grasslands, more than half of these locations were within five metres distance from a hedgerow or edge. Similarly, Hof (2009) described that on 50% of occasions hedgehogs were located less than a metre from the edge in arable land.

As well as their importance as food sites (Boitani & Reggiani 1984), movement corridors (Doncaster *et al.* 2001) and nest sites (Morris 1969, Reeve 1981) (Chapter 6), it has been suggested that hedgerows may also offer a refuge from badger predation (Hof, 2009). Badgers have been reported as a significant predator of the hedgehog (Pentland 1917, Doncaster 1992, Ward *et al.* 1996, Warwick *et al.* 2006). Hof (2009) illustrated that the abundance of badgers had a strong negative correlation with the current relative hedgehog abundance and with the change in their relative abundance. O'Shea *et al.* (2010) found an increase in hedgehogs killed on the road in areas where badgers had been removed. Similarly Young *et al.* (2006) reported that as sett density increased, both the probability of occurrence of hedgehogs and their abundance decreased. Doncaster (1994) felt that the presence of badgers may hinder the establishment of a population at a site and in Doncaster's (1992) study he found that translocated hedgehogs were most prone to leave woodland areas and its surroundings where badger density was highest. Middleton (1935) found the remains of four hedgehogs in a single badger stomach, however, Del Bove and Isotti (2001) discovered the remains of only two hedgehogs in 69 badger stomachs. Both species are of the same guild, with badgers (Canova & Rosa 1994, Goszczynski *et al.* 2000) and hedgehogs (Campbell 1973, Parkes 1975, Yalden 1976, Wroot 1984) preying on earthworms. Foraging animals can, and do, modify their individual behaviour in response to factors such as density of prey, interference from other foragers and the perceived risk of predators (Ward *et al.* 2000). Janssen (2007) suggested that habitat structure may reduce the effects of intraguild interactions by reducing encounter effects and therefore hedgehogs may encounter badgers less often along hedgerows, as badgers forage more frequently in the open (Neal & Cheeseman 1996, Hof 2009).

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 the majority of studies noting high incidences of lepidopteran larvae, earwigs, beetles, spiders, harvestman, caterpillars, as well as slugs and 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. Therefore it would be expected that the distribution of hedgehogs may be influenced by the location and abundance of their prey within a habitat.

Having examined habitat use and home range over two years (Chapters 3 and 4), this part of the research aimed to test the following hypotheses that:

- Hedgehogs forage along hedgerows
- The availability of potential prey is the main factor effecting hedgehog habitat selection
- Potential prey is not distributed equally between and within habitats
- Hedgehogs forage in areas where prey density is highest

5.3 Materials and Methods

5.3.1 Capturing and monitoring

The study was carried out between June 2008 and November 2009 at Ratharoon, Co. Cork as described in Chapters 3 and 4. Individual hedgehogs were captured by spotlighting and monitored by radio tracking, in the same method described in those Chapters. Data analysis was also as explained in those sections.

5.3.2 Surface invertebrate surveys

Within the arable land it was noted that hedgehogs consistently foraged in a very small area. Therefore invertebrates were sampled in areas where many hedgehogs were observed to feed and areas where low numbers of hedgehogs foraged. As hedgehogs were not observed to dig for prey, transects sampled potential surface prey only. This surface prey was counted at weekly intervals in these areas; along linear transects 60m X 0.46 m, on the arable land at Ratharoon. Seventy two surface transects were sampled in October 2008 and 71 from March-November 2009. All of these transects took place at night while tracking hedgehogs.

Weekly invertebrate surveys were also carried out from March-November 2009 in three areas of pasture in Ratharoon (Fig. 5.1). Sampling was conducted in all areas of the pasture. Fifty four transects, were sampled using a $0.25m^2$ quadrat placed at three random locations along a 60m transect. All surface invertebrates were recorded and flatworm and mollusc identification was confirmed by Roy Anderson, Belfast.

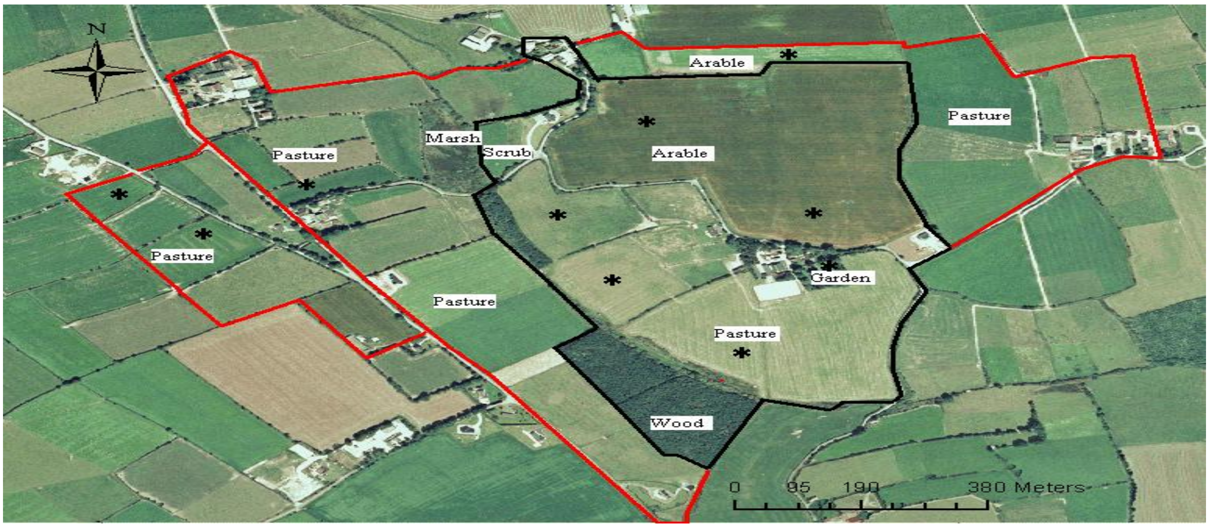

Figure 5.1: Study area, highlighting in black, the 43 ha searched for hedgehogs in 2008 (Ratharoon) and in red that covered in 2009 only (Holland Ivy). Transects were carried out in areas marked with an asterisk.

In October 2009, in order to investigate observed different activity patterns of hedgehogs in Ratharoon and an adjacent area of the site referred to as Holland Ivy, 48 transects were surveyed using the same method as that used in the pasture. In addition to the one arable field and the three areas of pasture already being surveyed, three additional areas of pasture and an arable field, were also surveyed (Fig. 5.1). Transects were selected along the hedgerow and centre of the field in each of these eight areas and these transects were sampled on three occasions (Table 5.1).

Table 5. 1: Details of surface prey surveys at each habitat across the site.

Month/year	Habitat	No. of fields surveyed	Sampling area	Sampling frequency	Position within habitat (site name)
October 2008	Arable	1	60m x 46cm	72	Northern and southern (Ratharoon)
March-Nov 2009	Arable	2	60m x 46cm	71	Northern and southern (Ratharoon)
March-Nov 2009	Pasture	3	3x 50 cm x 50cm along 60m transect	54	All over field (Ratharoon)
October 2009	Pasture Arable	6 2	3x 50 cm x 50cm along 60m transect	48	Centre and hedgerow (Holland Ivy)

5.3.3 Other mammals

Between June 2008 and June 2010, while spotlighting and monitoring tagged hedgehogs, encounters with, and sightings of other mammals were recorded. Any footprints, faeces and burrows, setts or dens were recorded and their position plotted on to ortho-photographs (Ordnance Survey of Ireland) of the area using the Geographic Information System (GIS) software Arc map version 9.2.

5.4 Results

5.4.1 Potential prey

Concomitant with the rise in surface invertebrates, hedgehogs increased their activity in the arable field in September until hibernation (Fig. 5.2). At this time the fluctuation was more pronounced in molluscs' density than earthworms (Fig. 5.2). The majority of the molluscs were juveniles (Anderson, pers. comm.).

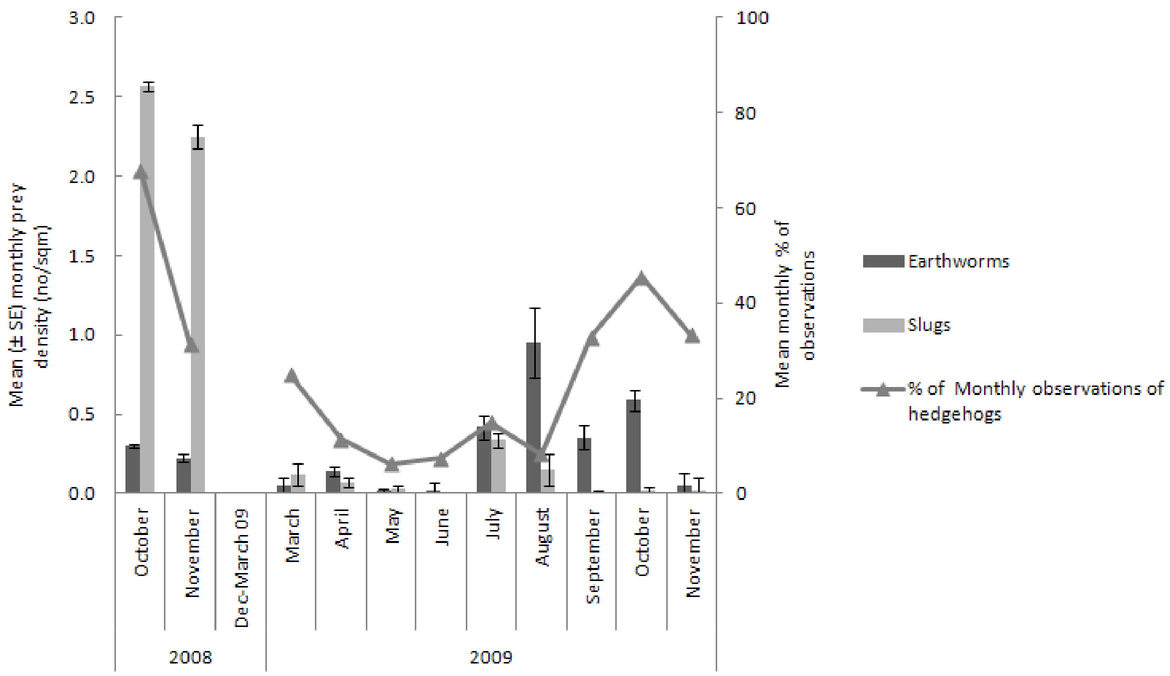

Figure 5.2**:** Percentage of all hedgehog observations on the arable land in 2008 and 2009 (1225 observations) vs the mean density of earthworms and slugs (no. per sqm (143 transects).

The surface invertebrates within the arable field consisted predominantly of molluscs in 2008 and earthworms in 2009, when all samples for that field were combined (Table 5.2). Although the same suite of molluscs species were observed again in 2009, they only represented 45% of the overall available prey in the second year, in comparison to 90% in 2008. There was a large increase in earthworms in the field from 0.42 per m² in July to 0.95 per m² in August 2009. They constituted 48% of the potential prey overall in 2009.

Table 5.2: Relative abundance of surface invertebrates found throughout the arable field.

Species	Arable 2008	Arable 2009
Molluscs (See Plate 6.1, Cover page)–	90%	45%
• *Derocerus panormitanum*		
• *Derocerus reticulatum*		
• *Milax gagates*		
• *Arion distinctus*		
Earthworms –	8%	48%
• *Lumbricus terrestris*		
Australian flatworms –	1%	1%
• *Australoplana sanguine*		
Beetles (Coleoptera spp.)	1%	6%

A further difference in invertebrate density was noted within the arable land. The density of surface invertebrates was significantly higher in the southern portion of the field than in the northern section of the field ($Z= 3.48$, $n_1=52$, $n_2=92$, $p<0.01$). There was a mean of 3.30 ± 0.03 invertebrates per m² in the southern portion of the field in 2008 and 0.97 ± 0.02 per m² at the northern section (Fig. 5.3). A lower density of surface invertebrates in the arable land was evident in 2009 than in 2008, but again the majority were found in the southern section (mean number of 0.025 vs 0.016 per m²) (Fig. 5.3).

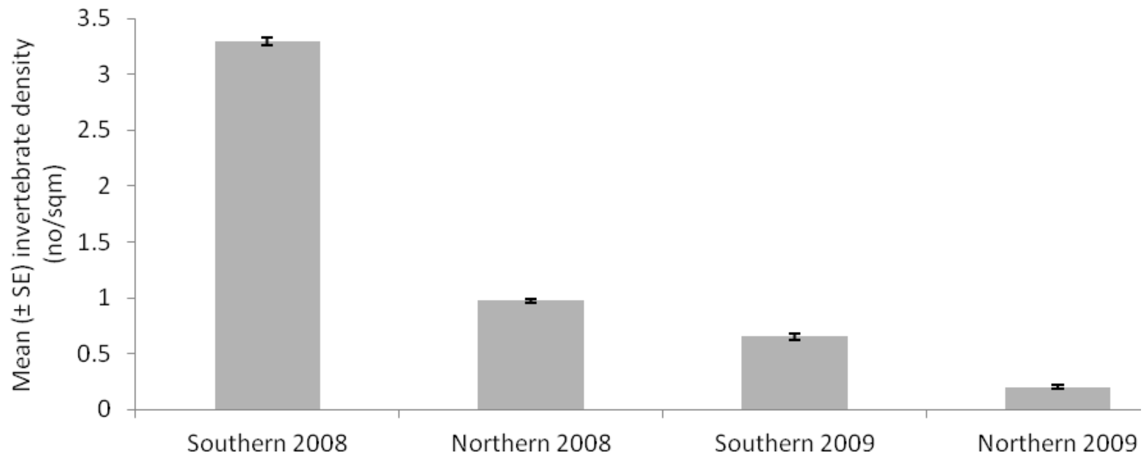

Figure 5.3: Mean (± S.E.) invertebrates per sqm (n=143 transects) in the arable field.

Hedgehog activity coincided with surface invertebrate density. There was significantly more hedgehog activity in the southern portion of the arable land ($U=23.5$, $n_1=12$, $n_2=12$, $p<0.01$) (Mann Whitney) (Fig. 5.4). Only one adult female (#7150) concentrated her activity in the northern portion of the field with 100 observations in the upper section versus 62 in the lower. However, nine hedgehogs, concentrated their activity in the southern section (812 observations), with only 134 observations in the upper zone (Fig. 5.4). This corresponded to the abundance of potential prey (Fig. 5.3).

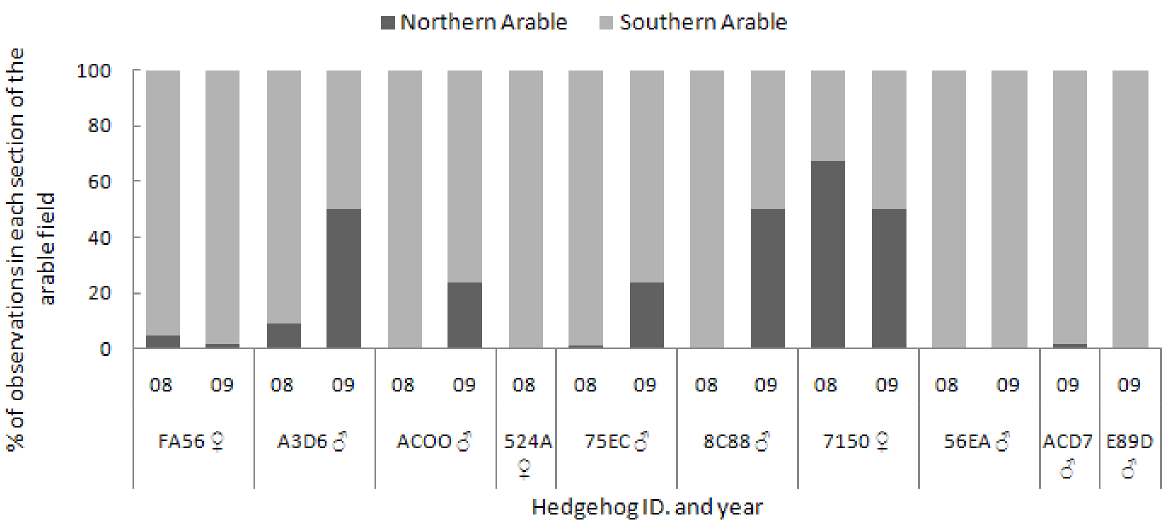

Figure 5.4: Distribution of hedgehog activity (% of observations) in an arable field over two years in Co. Cork.

When the search area was extended in 2009, it was observed that hedgehog behaviour was different in Ratharoon and Holland Ivy. Hedgehogs in the pasture and arable areas of Ratharoon spent significantly more time in the centre of the fields than along the edges (pasture, $U=60.5$, $n_1=16$, $n_2=16$, $p<0.01$); (arable, $U=11.5$, $n_1=13$, $n_2=13$, $p<0.01$) (Mann Whitney) (Figs. 5.5 and 5.6). In Holland Ivy, the hedgehogs spent significantly more time along the hedgerow than in the centre of the pasture field ($U=7.5$, $n_1=7$, $n_2=7$, $p<0.05$) (Mann Whitney) (Figs 5.5 and 5.6).

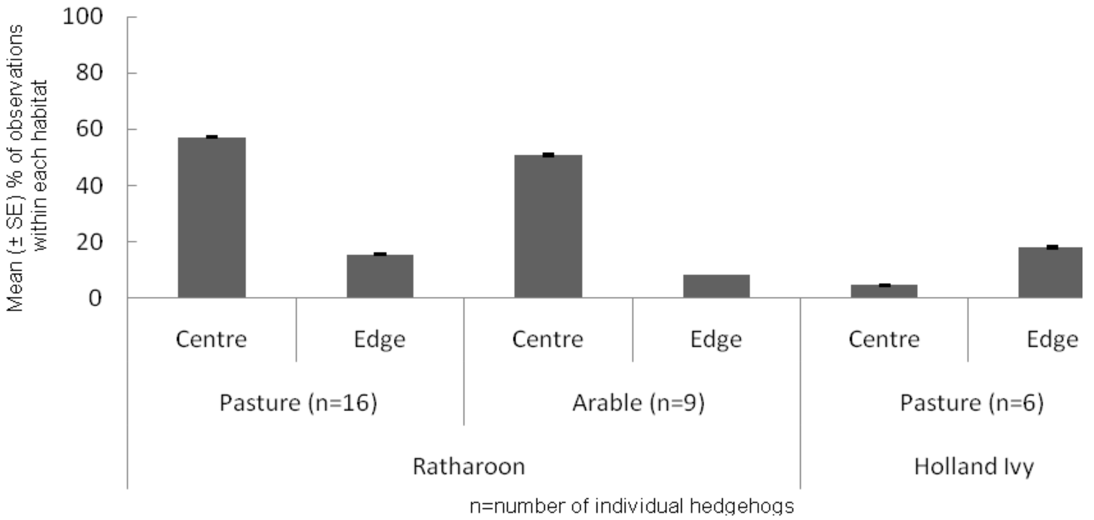

Figure 5.5: The mean (± SE) percentage of hedgehog observations within each habitat in October 2009.

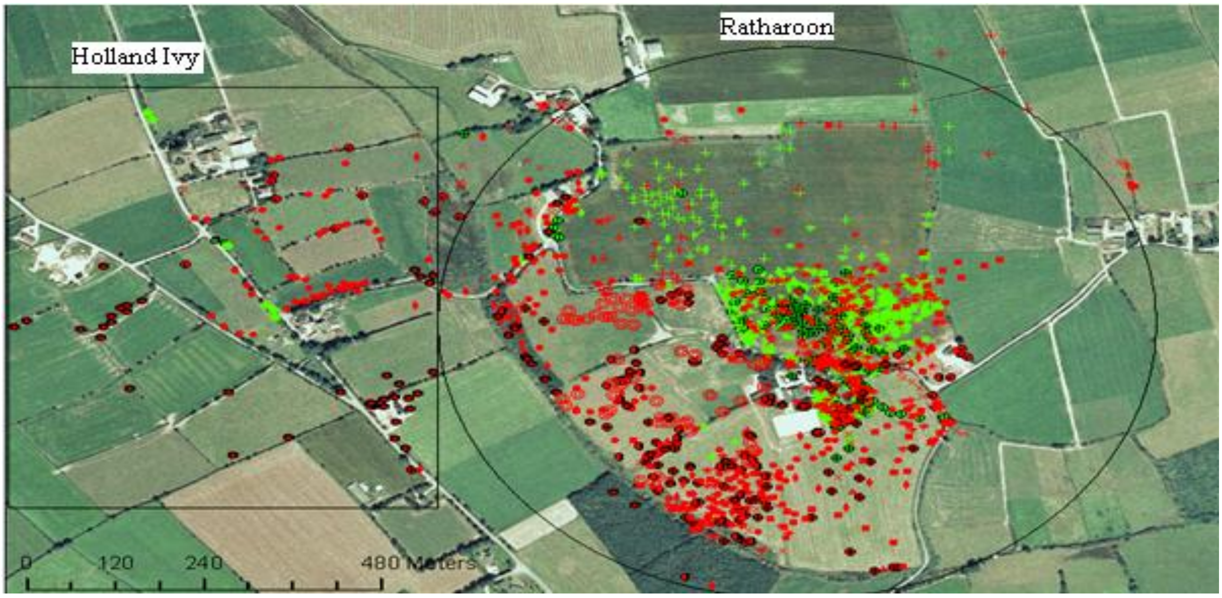

Figure 5.6: The study area highlighting the two areas of the site (Holland Ivy and Ratharoon). The green dots refer to activity in 2008, the red ones to 2009.

The hedgerow structure was different in the two areas. In Ratharoon, the hedgerow was dominated by a bramble (*Rubus fruticosus* agg.) understory. In contrast the hedgerow around Holland Ivy was made up of Hawthorn bushes (*Crataegus monogyna*) with no understory vegetation.

In Holland Ivy, the surface invertebrate density was greater under the hedgerow than in the centre of the field (Figs 5.6 and 5.7). This corresponded to the location of hedgehog observations in this area (Fig. 5.5). However, in both the arable and pasture fields in Ratharoon, prey density was greater at the edge (Fig. 5.7), yet hedgehogs concentrated their activity in the centre (Fig. 5.5 and 5.6).

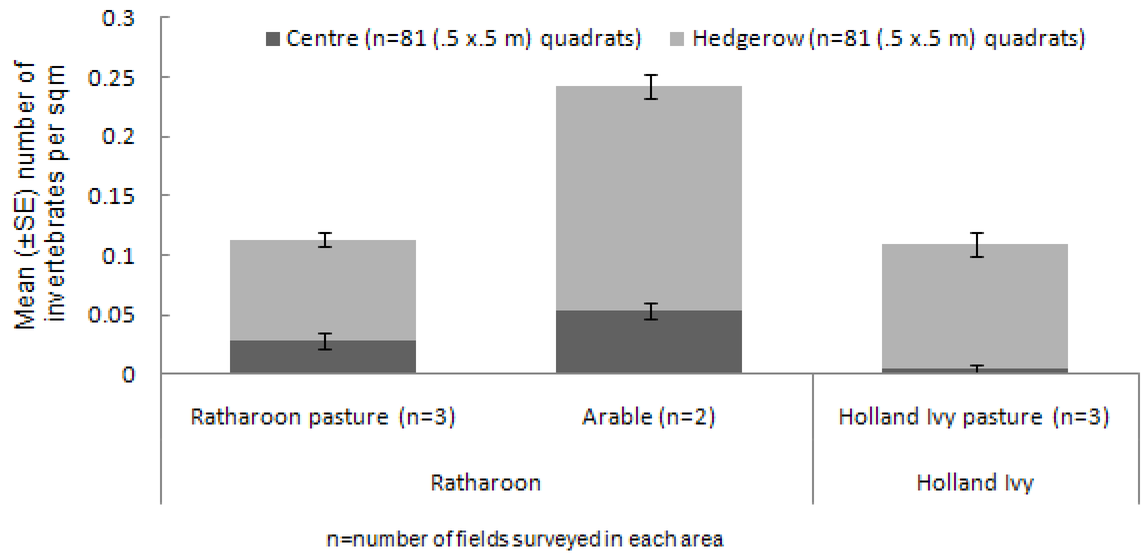

Figure 5.7: Mean invertebrates (±S.E.) per m² in hedgerow vs the centre of the field in four areas in 2009.

The relative abundance of surface invertebrates was higher in the arable field than in pasture at Ratharoon (Fig. 5.7). The pasture around Ratharoon had a higher abundance of invertebrates in the centre of the field than in Holland Ivy pasture.

5.4.2 Other Mammals

Rabbits (*Oryctolagus cuniculus*) and foxes (*Vulpes vulpes*) 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 (Chapter 6). Hares (*Lepus timidus hibernicuss*) and stoats (*Mustela erminea hibernica*) were also found to utilise the site. Badgers were recorded on twelve occasions from 2008-2010. These sightings occurred while spotlighting or tracking hedgehogs and both hedgehogs and badgers were seen foraging in the same areas of the site. In addition to these visual sightings (Fig. 5.8), badger footprints and faeces were also seen throughout the site.

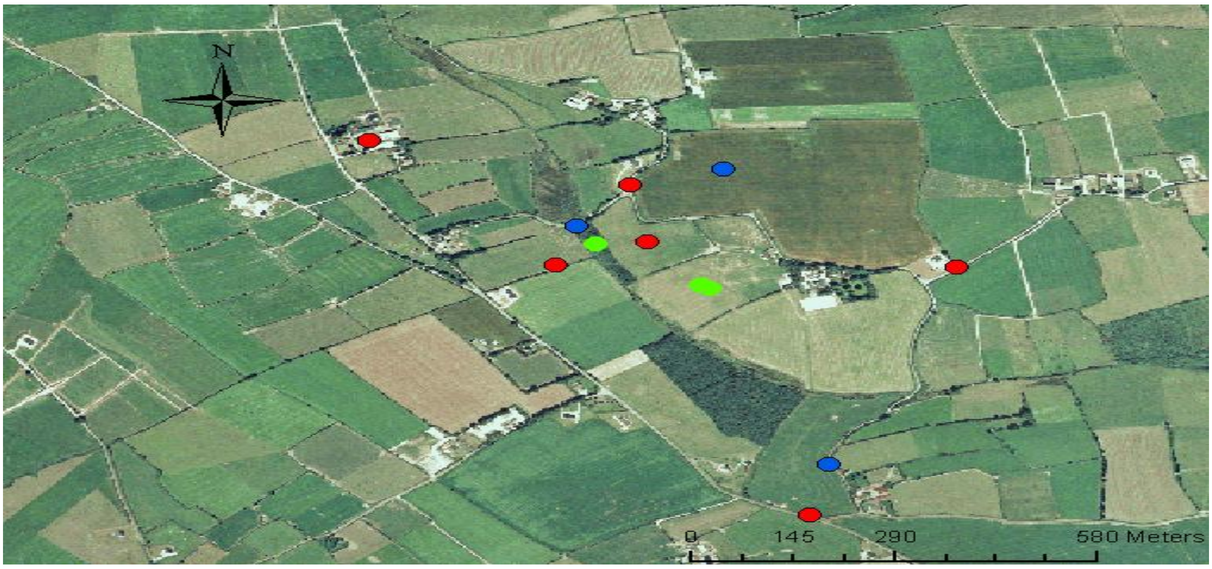

Figure 5.8: Badger sightings during the study period (blue=2008, red=2009 and green=2010).

5.5 Discussion

Contrary to the findings of other studies, in the present study within the Ratharoon area, hedgehogs were observed significantly more often in the very centre of the field. This was surprising as in previous studies hedgehogs have shown a significantly stronger attraction to edge habitat, moving along hedgerows (Reeve 1981, Doncaster *et al*. 2001, Riber 2006, Shanahan *et al*. 2007, Hof 2009). In the current study, pasture at Ratharoon was grazed by horses. 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 had fewer invertebrate species than tall swards. In the present study these latrines were located in the centre of the pasture. The horse manure may have caused higher nutrients in these areas, than elsewhere in the field and a consequential greater number of earthworms that subsequently attracted hedgehogs to these areas. 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. While 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, since, as mentioned in Chapters 3 and 4, 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 U.K., but when they did the distance to the hedgerow was less than one metre on 50% of occasions. In Ireland, Curry *et al.* (2002) reported earthworm populations of up to 1160 individuals m^2 in soil samples from a wheat clover plot. However, while in Sweden 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, all factors that are reported to increase slug abundance (Glen *et al.* 1989, Hegarty & Cooper 1994). However, their nightly location in the centre of the field is surprising, as although Cook *et al*. (1997) found that *Derocerus 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 day-time protection and allows little time to travel back to the hedgerow. The majority of 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 dispersing.

Beetles were located only in small numbers along the transects, but were found to be a significant prey item of hedgehogs in the U.K. and New Zealand (Campbell 1973, Parkes 1975, Yalden 1976). Thomas *et al.* (2001) discovered when looking at arable fields that predatory beetles were found mainly in the centre and beetles are a predator of slugs, with Symondson *et al.* (1996) finding slug remains in 84% of beetles. 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 the arable field when a peak was observed in mollusc density, but within the arable field hedgehogs restricted their activity to where there was the greatest density of these molluscs. Furthermore, as mentioned in Chapter 4, individual hedgehogs fed in the same patches on a nightly basis.

Hedgehog activity within each habitat was not consistent throughout the study area. At Holland Ivy, activity was predominantly along the hedgerow. The hedgerow here consisted of hawthorn trees and in contrast to Ratharoon there was no bramble understory. When surface transects were carried out it was found that, in all areas of the site, prey was more abundant along the hedgerows. However, in Ratharoon, 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. Prey within the centre of the pasture at Holland Ivy was also very low, with 0.004 surface invertebrates per m² in comparison to 0.05 per m² in the centre of the arable field in Ratharoon. Hedgerows with a complex structure, like that of Ratharoon, are easily the best kind of hedgerow to support biodiversity, with the leaf litter providing suitable shelter for invertebrates (Pollard *et al.* 1977). Lagerlof *et al*. (2002) found that when the earthworm populations in a field declined, the boundaries may serve as sources from where re-immigration can take place.

Despite the fact that badgers were seen regularly at the site (n=12 occasions), only one hedgehog was known to have been killed by a badger in the two year study period. The hedgehogs and badgers were found to occupy the same areas within each habitat and both were seen foraging on earthworms in the centre of the pasture in Ratharoon. 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 in this area and that badgers had little impact on the habitat choice of hedgehogs. This is surprising, as in the U.K., 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 U.K. 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. Ward *et al.* (1997) found that although hedgehogs initially avoided areas tainted with badger odour this did not persist. This, they felt was probably due to the costs of predator avoidance, which was negligible in their enclosure due to the presence of a superabundant food source. Therefore, although Hof (2009) found that hedgehogs were only seen on 21% of the sites where badgers were present, opposed to on 32% of the sites where badgers were not seen, both species may co-exist if abundant food is available. The hedgehog killed in the current study was predated in October. Although potential prey was abundant at the site at this time, with winter approaching there would be increasing pressure on resources, due to the effects of decreasing temperature on invertebrate activity (Young *et al.* 1993). 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 (Chapter 3 and 4) and their move into this area coincided with an increase in surface invertebrates. Hedgehogs and badgers 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 available prey, whether that was molluscs (2008) or earthworms (2009).

5.5.1 Conclusions

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, influencing habitat selection in both years. Hedgehogs fed on molluscs and their activity increased in areas with high surface invertebrates. This suggests that hedgehogs learn the spatial location of potential prey and respond to seasonal fluctuations in their density. In contrast to other studies hedgehogs foraged away from cover, in the very centre of the majority of fields at the site. Potential prey was more abundant in the centre of fields that had a complex hedgerow with a thick bramble understory than in areas where it had been removed. This, therefore, emphasises the importance of maintaining hedgerow, particularly in arable areas where hedgehogs have previously been considered scarce. Modern intensively farmed arable land, without hedgerow, does not provide high quality habitat for the majority of invertebrates (Asteraki *et al.* 2004). This is mainly due to the fact that hedgerow survives least well in these areas (Pollard *et al.* 1977). However, as shown in the present study, this habitat can support both hedgehogs and their potential prey, if hedgerow with good ground cover is preserved, not only to provide nest sites for mammalian and avian species but also for their potential prey.

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Chapter 6-

Nesting behaviour and seasonal weight changes of a rural hedgehog *(Erinaceus europaeus)* population

Accepted (Acta Theriologica).

Plate 6.1: Three of the sites where both day nests and hibernacula were located.

6.1 Abstract

Apart from the 10 spp. of bat, the European hedgehog is the only Irish mammal that undergoes true hibernation. As of yet we have no information on nesting, seasonal weight changes or the hibernation behaviour of this species in Ireland. Between 2008 and 2009, hedgehogs were caught and monitored by radio tracking at a rural Irish site. Hedgehogs were weighed on a weekly basis while day nests were recorded in the active period and hibernacula thereafter. Males occupied significantly more day nests than females. Both day nests and hibernacula were constructed in the hedgerow of arable land, a habitat that has been reported to be poorly utilised by hedgehogs in the U.K. and Denmark. Hedgehogs were found to be larger than the recorded weights for hedgehogs in the U.K., and New Zealand. Adult males, with the exception of their weight immediately post hibernation, were at their lowest weight during the breeding season. With the first emergence of young in July, females were at their lowest weight in August. Individuals that were weighed over the two years showed little fluctuation from one year to the next. Over the two years, individuals were found to occupy a mean of 1.8 (±0.9) (SD) hibernacula (maximum of 3) and they rotated between nests up to five times (mean of 2.5 ±1.6). When hedgehogs occupied multiple hibernacula, those occupied in mid winter (December-January) were occupied for significantly longer than those occupied at the start (October-December) and end (January-March) of hibernation. With southern Ireland's milder winters, it was expected that hedgehogs in Ireland would have a shorter hibernation period, earlier emergence, lower weight loss and the ability to survive hibernation at a lower weight. This proved to be the case with a mean hibernation period (±SE) of 148.9 (± 0.5) days, a mean weight loss of 17.0 (± 0.53) %, emergence in March and the ability of late juveniles to survive at a pre-hibernation weight of 475 grammes.

6.2 Introduction

A number of variables are believed to limit the distribution of the European hedgehog in an area, with nest sites (Jensen 2004), food availability (Kristiansson 1984) and the presence of predators (Micol *et al.* 1994) deemed to be the most important of these. For a hibernating species, like a hedgehog, adequate nest sites are essential if a habitat is to meet the animal's basic requirements. In Denmark, Jensen (2004) recorded that 55% of hibernacula occurred in forested areas, with a similar result found by Riber (2006) for day nests in Denmark. In Ireland only 9.6% of the land area is currently covered by forest (Rudel *et al.* 2005). However, while Ireland has the lowest percentage of forest cover by land area of all European countries (EPA 2008), Ireland has extensive hedgerow networks, which have been recognised as important habitats for conservation on a European level (Pithon *et al*. 2005). Pollard *et al.* (1977) suggested that this network of hedgerows can provide a suitable substitute for woodland species of trees, so what has been taken away by felling may, to some extent, have been restored by planting hedges. Unfortunately, as farms have become more specialised and efficient, and with the growing need for larger fields, this has had a knock-on effect on hedgerows, with a reduction of 50% of the hedgerow stock in the U.K. (Robinson & Sutherland 2002). However, while farmland is the most intensively managed part of the Irish landscape, it is still generally less intensive than in other European countries (Cabot 1999) and small field sizes have been maintained in many areas (Pithon *et al.* 2005).

Unlike other mammal species who build a secure permanent nest site, the day nests of hedgehogs are often flimsy structures designed for short term occupancy (Morris 1973). Despite this, in the U.K. hedgehogs have been shown to exhibit philopatry, returning to a particular nest throughout the year but usually occupying multiple nests (Morris 1969). In the U.K. this was found to be generally dependent on the size of the individual's home range and Reeves (1981) noted a tendency for males to move nests more often than females. Individuals may use the same nest but simultaneous occupancy has not been recorded (Riber 2006).

In Britain adult hedgehogs usually weigh between 600-700g increasing to about 900-1000g in autumn (Reeve 1982). In New Zealand, Parkes (1975) reported a mean weight for males of 706 ± 10g and for females 688 ± 9.9g. In previous studies, males, in contrast to females, showed a fairly constant weight throughout the year, but with a tendency to increase weight just prior to hibernation, having reduced their weight during the breeding season (Reeve, 1981).

Juveniles are capable of putting on weight quickly and Reeve (1981) stated that new juveniles that appeared in early August in the U.K. increased their weight to exceed 500g by October. According to Morris (1969), some individuals can achieve 800-900g within a year of their birth and Jackson (2006) observed that sub adults were on average nearly a third heavier one year later.

In Denmark, Jensen (2004) described how the average duration of hibernation was 178.8 ± 13.1 (SE) days for juveniles and 197.7 ± 2.2 days for adults. In the U.K. Morris (1969) reported a duration of ~ 180 nights, while in Sweden, hibernation was observed to last ~210 nights (Kristiansson 1984). The only record of hibernation in Ireland was recorded by a Mrs Kenny in Tipperary who noted the hibernation period of an individual hedgehog in her garden over four years as 139 days in 1980 and 1982 and 150 in 1983 (Fairley 1984).

The necessary weight required to survive hibernation varies depending on the country's climate. In the U.K. hedgehogs have been reported to hibernate from October or November through to April (Morris 1969, Jackson 2001). According to Reeve (1982) British hedgehogs are smaller than continental hedgehogs and are able to survive winter with a lower body mass. Estimates in the U.K. for the minimum hibernation weight range from 450g (Morris 1984) to 650g (Bunnell 2002). In Denmark, a minimum weight of 513g was deemed necessary for survival (Jensen 2004). Brockie (1990) estimated that hedgehogs in New Zealand needed to weigh at least 300g to survive hibernation. In Sweden, Kristiansson (1984) found that hedgehogs tended to have a larger pre-hibernation weight than British hedgehogs, something which he suggested could be due to the harsher Swedish winters. What is the weight required for an Irish hedgehog to survive hibernation?

Grass continues growing for longer in Ireland than any other European country (Cabot, 1999), and the winters are generally milder in Ireland. Does this allow for a shorter hibernation period?

With this milder climate the current study hypothesised that variations would be apparent in the hibernation activity of hedgehogs in Ireland, in comparison to elsewhere. In particular, the study aimed to test the hypotheses that hedgehogs could survive hibernation at a lower weight, hibernation is shorter, weight loss more conservative and emergence earlier than what has been previously observed elsewhere in Europe. With Ireland’s less intensive agricultural practices and greater density of hedgerows, the current study also aimed to investigate the location of day nests and hibernacula and the impact of this, on habitat selection.

6.3 Materials and Methods

The study was carried out between June 2008 and March 2010 at Ratharoon, Co. Cork, as described in chapters 3 and 4. Individuals were captured by spotlighting and monitored by radio tracking in the same manner that was described in these chapters. Data analysis was also as explained in these sections.

Daily minimum and maximum temperatures were measured at around approximately midday at the site. The mean minimum temperature was in the range of 2.1˚C (February 2009) to 13.6˚C (April 2008) (Fig. 6.1). The mean maximum temperature was in the range of 4.8˚C (February 2010) to 15.9˚C (June and July 2009) (Fig. 6.1). The rainfall data were obtained from Met Eireann and was in the range of 17 mm (February 2009) to 232.8 mm (November 2009) (www.met.ie) (Fig. 6.1).

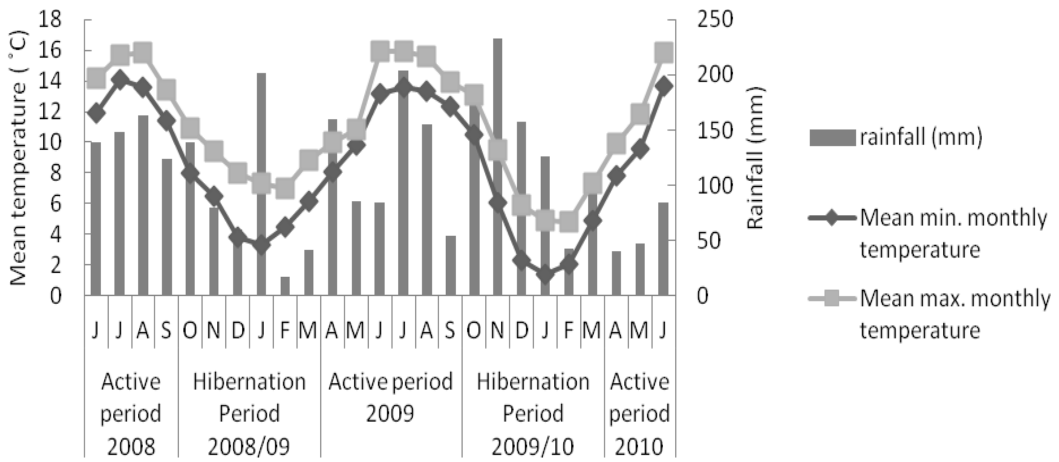


Figure 6.1: Minimum and maximum monthly temperature (degrees Celsius) and rainfall (mm) over the study period.

All hedgehogs caught were classified as adult or juvenile, sexed, weighed using digital scales (Harvard apparatus, Kent, U.K.), hind foot measurements taken and growing and broken spines noted. Tagged individuals were weighed at weekly intervals during their nights foraging. They were weighed up until they entered hibernation and immediately following re-emergence. The animal was considered to be a juvenile if it satisfied all of the following criteria: weight less than 600g when first caught; hind foot length of less than 3.6cm (Fig. 6.2); and presence of growing spines.

The hind foot length of hedgehogs at the study site was significantly correlated with the weight of the animal (R_S= 0.93, n=24 p<0.01) (Spearman rank) (Fig. 6.2).

When the hind foot of an individual adult was measured during the active period in both 2008 and 2009, no change in hind foot length was observed where there was no significant weight change. However, when the hind foot of a juvenile was measured in 2008 and remeasured during the active period in the following year, the hindfoot length showed a significant increase in size, indicating that hind foot length is a good parameter for separating age classes.

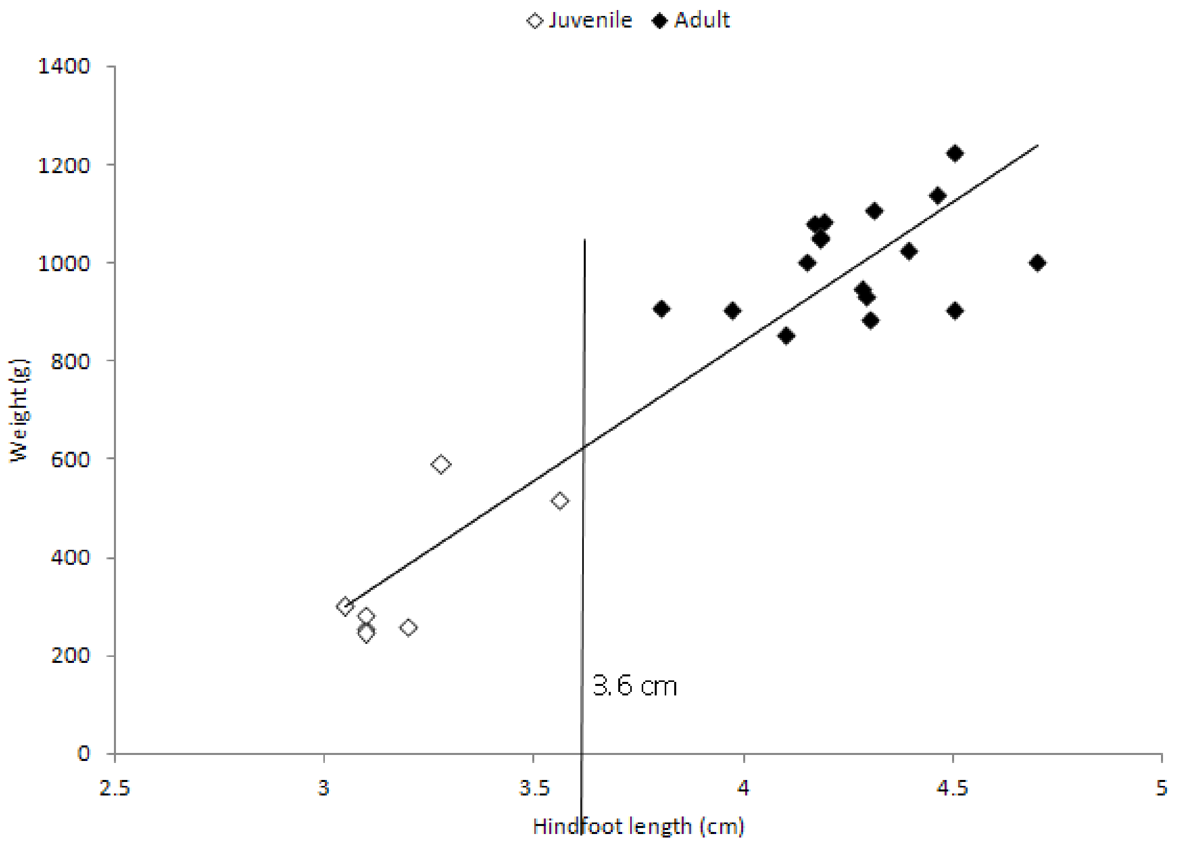


Figure 6.2: Hindfoot length vs weight for all hedeghogs caught at the site between June 2008 and 2010.

Day nests were either identified at the end of the night or during the following day. In 2008/09 six hedgehogs were monitored throughout hibernation and upon emergence and in 2009/10, five hedgehogs were studied (Table 6.1). Individuals were considered to be hibernating if they did not leave their nest for seven consecutive nights. Hibernacula were identified in accordance with Morris's (1973) description of winter nests i.e. "compact structures 30-60 cm in diameter, commonly sited below a small bramble bush or pile of logs. The nest walls were of dead leaves closely packed to form a laminated mass up to 20 cms thick. This flat packing, rather than random arrangement of the leaf litter was often the only external indication of a nest."

Once the animals were considered to have entered hibernation their location was checked at weekly intervals.

Table 6.1: Details of hedgehogs caught and tracked each year and the duration of each observation technique.

Date	Monitoring technique	Number of hedgehogs	Number of nights	Number of hours
26/6/08-28/9/08	Spotlighting	0	31	120
26/6/08-28/9/08	Direct following	8 (2♀,6♂)	17	95
18/10/08-12/11/08	Direct following	3 (1♀,2♂)	6	14
28/9/08-20/11/08	Radio tracking	8 (4♀,4♂)	33	160
Hibernation	Radio tracking	6 (3♀,3♂)	N/A	N/A
30/3/09-10/11/09	Radio tracking	16 (4♀,12♂)	104	624
Hibernation	Radio tracking	5 (1♀, 4♂)	N/A	N/A

6.4 Results

6.4.1 Day nests

Day nests of radio tagged hedgehogs were located 260 times between June 2008-November 2009, during which 117 different nest locations were identified (Figs 6.3a and 6.3b).

Figure 6.3a: Day nests 2008 (n=122)

Figure 6.3b: Day nests 2009 (n=138)

Day nests were recorded 122 times in 2008 and 138 times in 2009. A total of 117 individual day nests were utilised by hedgehogs, 53% of these were located in pasture and 30% in arable land (Table 6.2). However, while the majority were located in hedgerow of pasture, those nests were only returned to these on 37% of occasions. In contrast, day nests in the hedgerow of the arable field were used by hedgehogs on 45% of occasions during the study period (Table 6.2). This was significantly more than any other location (Kruskall Wallis: H= 8.536, df = 2, $p<0.05$, followed by Dunn's comparison test) (Table 6.2). In general these nests were situated amongst thick bramble. However, in warm weather (13-14.5˚C) hedgehogs were observed on three out of 100 occasions to nest amongst long grass in pasture (Table 6.2). No nests were located in the marsh habitat.

Table 6.2: The number and percentage of times day nests were recorded in each habitat and the number and percentage of each individual nest in each habitat in 2008 and 2009.

	Pasture				Arable	Garden		Scrub	Wood	Marsh	
	Hedgerow	Silage bale	Burrow	Grass	Hedgerow	Hedgerow	Shed	Bramble patch	Bramble patch		Total
No. of observations	97	15	5	3	117	11	3	5	4	0	260
% of all observations	37	6	2	1	45	4	1	2	2	0	100
No. of different nest locations	62	1	2	3	35	6	1	4	3	0	117
% of total nest locations	53	1	2	3	30	5	1	3	3	0	100

Hedgehogs were recorded returning to a nest a maximum of seven times during the study period (Fig. 6.4). However, each hedgehog also had several day nests which they used only once. Individual nests were utilised by a number of different hedgehogs but never simultaneously. For example, one day nest that was made in an abandoned silage bale (See Plate 6.1, Cover page) was used by two different adult females (524A and FA56) and an adult male (ACOO) in 2008. In 2008/09 this nest was utilised as a hibernaculum by the adult male (ACOO) and female (524A), but not at the same time. This nest was used as a day nest in 2009 by the same two adult females (524A and FA56) as in 2008, but the adult male did not return to it. It was not utilised again as a hibernacula in 2009/10. However, it continued to be used as a day nest in 2010 by another adult male (75EC).

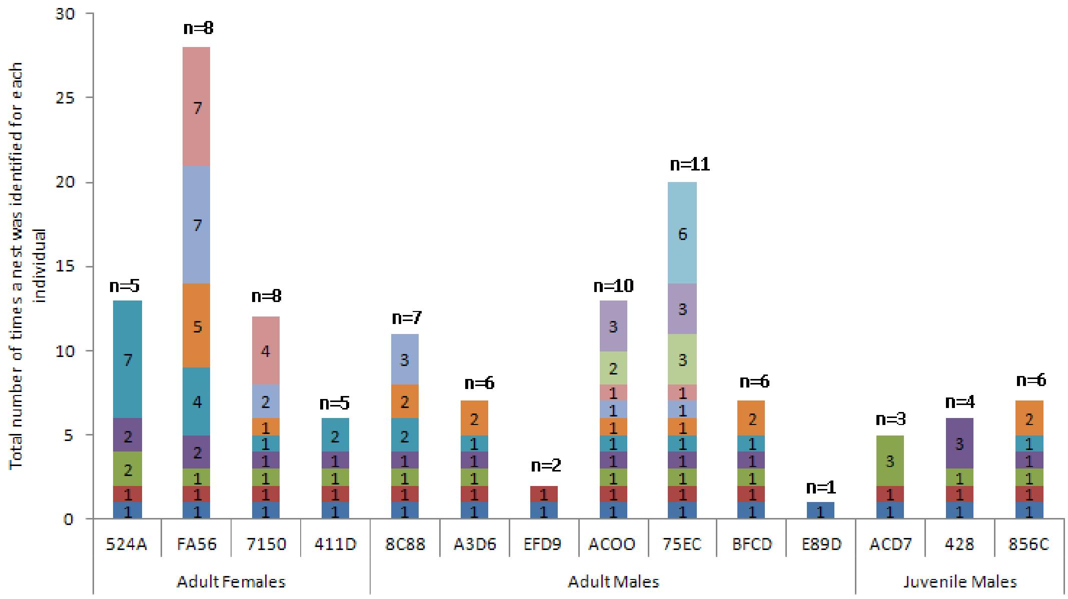


Figure 6.4: The number of times (no. within blocks) that each individual hedgehog returned to a particular nest in 2009 (n=the number of different nests used by each hedgehog). Data are only included for 2009 as they were radio tagged for the whole season in this year.

Males used a greater number of different day nests than females, with two adult males (75EC and ACOO) utilising ten and eleven different nests in 2009 (Fig. 6.4). Females returned to the same nest significantly more often than males (Fig. 6.5). One female (FA56) returned to two nests on seven occasions, while one adult male (75EC) had eight nests that it used just once (Fig. 6.4) (One way anova, following Log(x) transformation: $F=5.511$, $df=1$, $p<0.05$).

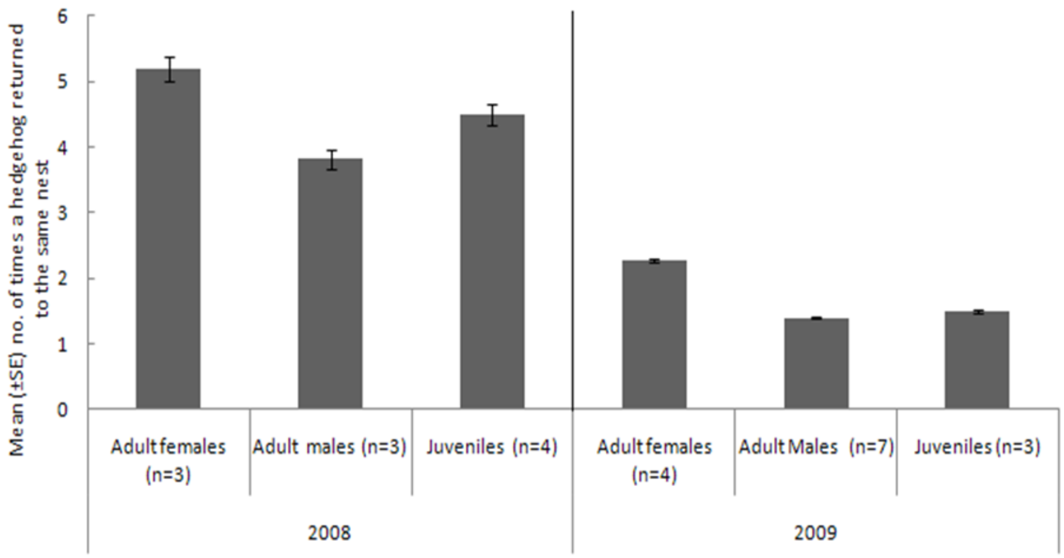


Figure 6.5: Mean number of times (± SE) that an individual hedgehog was observed returning to the same nest in 2008 and 2009 (n=number of individuals). Females returned to the same nest more often than males in both years.

6.4.2 Adult weights

Overall, adult males were significantly heavier than adult females ($Z=2.679$, $n_1=55$, $n_2=27$, $p<0.01$). In all years combined, adult males (n=12) had an overall mean monthly weight of 1065g (± 107.12) (SD) and adult females (n=4) a mean monthly weight (± SD) of 998.9g (± 102.21).

Adult males were heavier than females in every month of the study (Fig. 6.6), their weight ranging from a mean monthly weight of 1026g (± 65.10) in July to 1192g (± 47.61) in October. The Mean monthly weight of females ranged from 877.9g (± 15.70) in August to 1116g (±23.39) in October (Fig. 6.6).

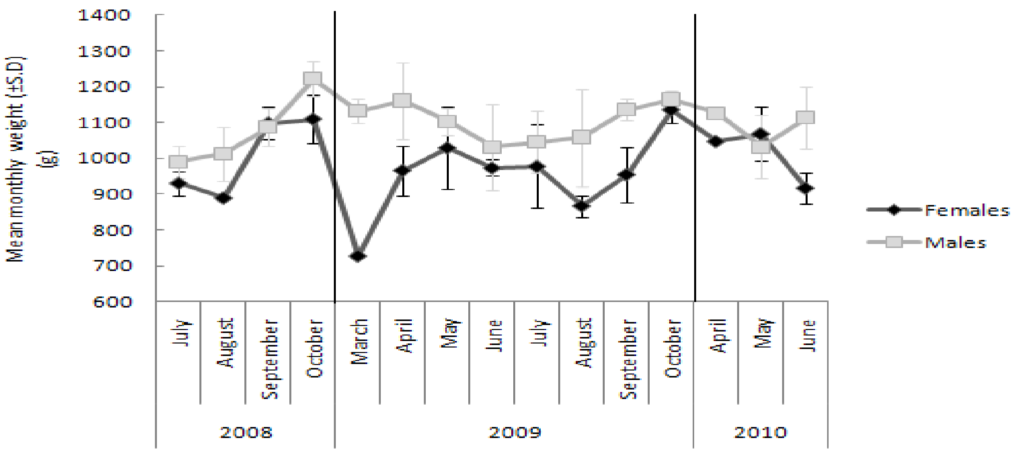


Figure 6.6: Mean (±SD) monthly adult weights of adult males and females.

The eight month study period was divided into four sections (March and April, May and June, July and August) and the months just prior to hibernation (September and October).

Adult females were significantly heavier in the two months just prior to hibernation than they were in July/August or the first two months after emergence (March and April) (One way anova followed by Tukey's post hoc test: F=4.548, df=3 p<0.05).

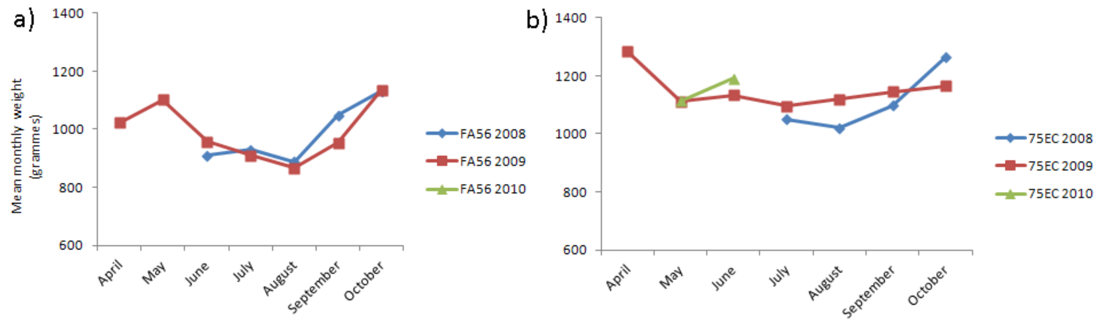
Similar to females, males were significantly heavier in the two months prior to hibernation than the July/August period (one way anova followed by Tukey's post hoc test: F=2.896, df=3, p<0.05). When they entered hibernation there was no significant difference between the weight of males and females (F=0.033, P>0.05).

Individuals tagged for more than one consecutive year were found to be of a similar monthly weight in both years (Table 6.3). Most individuals were only marginally heavier/lighter (<100g) in the following year. The greatest weight difference was between August 2008 and August 2009. Both 75EC and 8C88 were at a lower weight (100g and 151g respectively) in August 2008 than in August 2009 (Table 6.3).

Table 6.3: Mean monthly weights (grammes) of individuals that were tagged for more than one season (four recordings per month)

I.D		Year	April	May	June	July	August	Sept.	Oct.
		2008			909	930	889	1048	1132
		2009	1023	1101	958	910	867	954	1135
FA56	♀	2010							
		2008				1050	1020	1097	1264
		2009	1283	1111	1134	1096	1120	1145	1165
75EC	♂	2010		1114	1191				
		2008						1040	1112
		2009	966	1063					
524A	♀	2010	1047	1068	917				
		2009				1042		1128	1165
856C	♂	2010		1057	1102				
		2008				1041	1112		1149
A3D6	♂	2009	1076	1057	1058	1059			
		2008				1003		1069	1221
ACOO	♂	2009	1163	1136	1158	1128			
		2008				953	902		
8C88	♂	2009	1112	1091	930	1011	1053		

One adult female (FA56), was weighed continually over two years. Her monthly weights were between 3-49 grammes different between the two years (mean 17 ± (1.4) g). An adult male (75EC) was weighed over three years. His monthly weights were between 3-99 grammes different between the three years (mean 26 ± (1.4) g) (Figs. 6.7 a and b and Table 6.3).



Figures 6.7 a-b: The mean monthly weight of an adult female (FA56) and adult male (75EC) weighed monthly for two years or more. * Error bars were not included as they obscured the data.

6.4.3 Juvenile weights

Combining years and sexes, juveniles (n=6) showed a mean weight increase of 7.78g (±2.06) (SD) per day from first capture. They increased weight by a mean of 180.13% (±60.04) (SD) from first capture to hibernation. The maximum weight achieved by a juvenile was 1024g, a weight it reached just prior to hibernation (Table 6.4).

Table 6.4: The weight of juveniles hedgehogs at first capture

I.D		1st weight	Weight prior to hibernation	% increase	Increase per day	Max. weight the following year
9CE2	♀	517g (18/09/08)	856g (25/10/08)	165.6% (37 days)	9.2g	N/A
F620	♀	281g (18/10/08)	445g (12/11/08)	158.4 % (25 days)	6.6g	N/A
56EA	♂	255g (17/10/08)	475g (12/11/08)	186.3% (25 days)	8.8g	922g (April 09)
0C5B	♂	244g (17/10/08)	N/A	N/A	N/A	N/A
E928	♂	258g (18/10/08)	N/A	N/A	N/A	N/A
ACD7	♂	299g (28/7/09)	865g (20/9/09)	289.3% (55 days)	10.3g	N/A
0428	♂	588g (10/9/09)	1024g(10/11/09)	174.2% (61 days)	7.2g	N/A
E89D	♂	855g (30/9/09)	915g (13/10/09)	107.0% (13 days)	4.6g	937g (April 10)

6.4.4 Hibernation

Six hedgehogs were tracked throughout hibernation in 2008/09 and five in 2009/10. Seventeen hibernacula were identified at this time (Figs. 6.8a and 6.8b), with the majority, located in hedgerow (70%) (Fig. 6.9).

Figure 6.8a: Hibernacula 2008/09

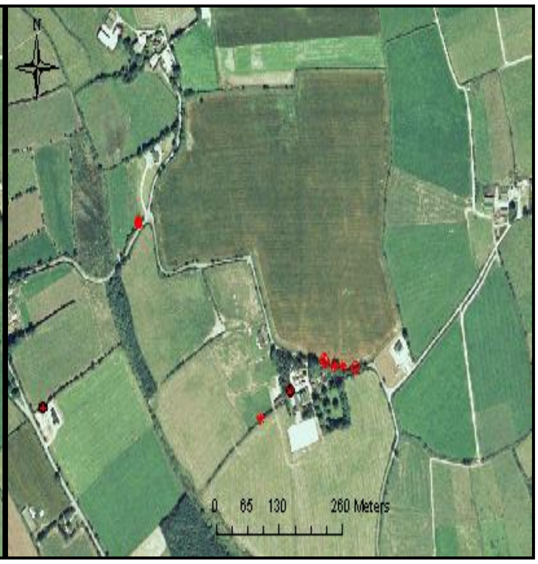


Figure 6.8b: Hibernacula 2009/10

As with the day nests, hibernacula were frequently (35%) located, in the hedgerow of the arable field (Fig. 6.8 a and b). However, more hibernacula (29%) were made in the hedgerow of scrub than day nests (2%) (Table 6.2). Hibernacula were located in pasture hedgerow on only 6% of occasions (Fig. 6.9), despite 54% of day nests being located in this area (Table 6.2).

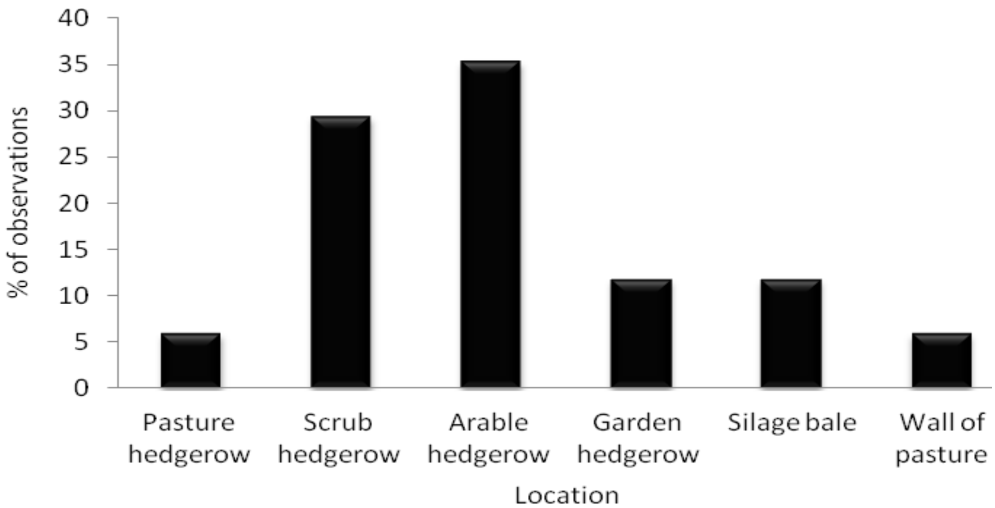


Figure 6.9: The location of hibernacula in 2008/09 and 2009/10.

Hedgehogs used from 1-3 hibernacula and changed hibernation sites up to five times in one winter (Fig. 6.10). Of the six hedgehogs monitored throughout hibernation in 2008/09, only two remained in the same hibernaculum for the entire hibernation period (Fig. 6.10). In 2008/09 and again in 2009/10, adult male (75EC) was the only animal to occupy a single hibernaculum (Fig. 6.10). One adult male (ACOO) moved five times during hibernation between three different hibernacula.

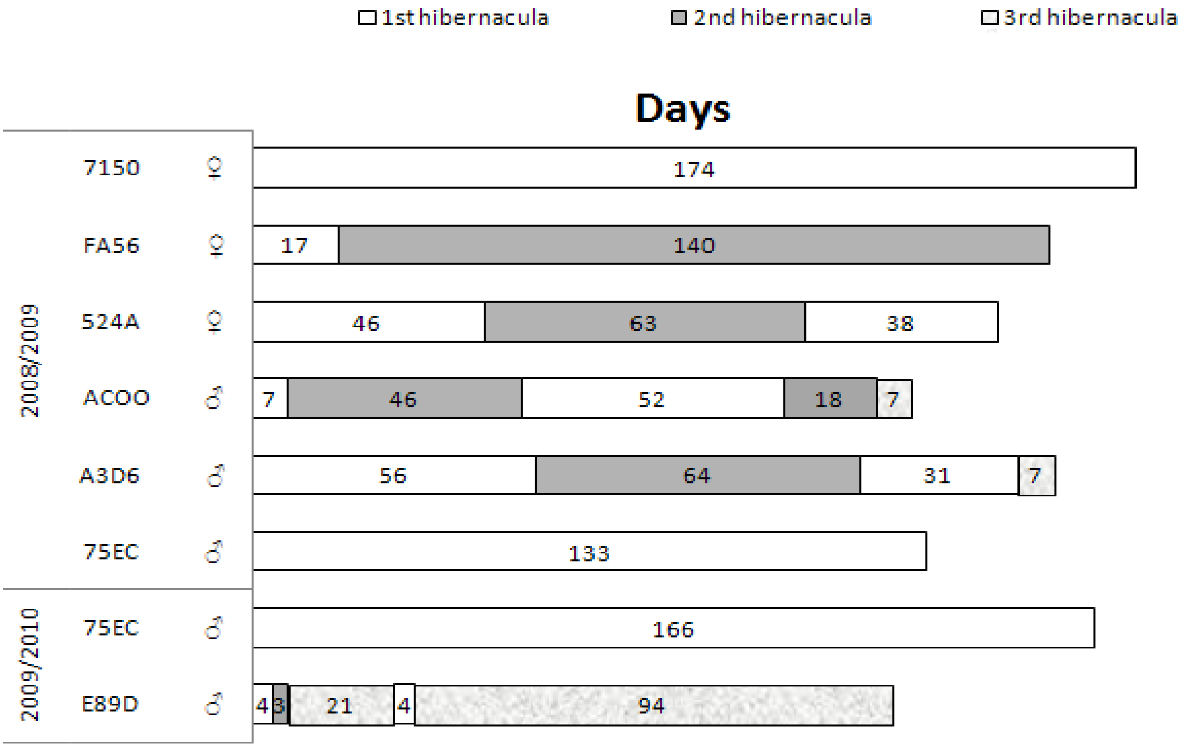


Figure 6.10: The number of days each individual hedgehog remained in an individual hibernaculum from the first day in which they entered hibernation (individuals are only included if they were monitored for the entire hibernation period). Hedgehogs had a maximum of three hibernacula and often returned to a hibernaculum that they had previously occupied. No individual occupied the same hibernaculum in the following year.

In 2008/09 two male hedgehogs (A3D6 and ACOO) swopped hibernacula throughout hibernation and this occurred again three times in 2009/10 with an adult female (FA56) and a juvenile male (E89D). The adult female (FA56) rotated between two hibernacula in the arable field that was also occupied at a different time by the juvenile male (E89D) before moving to a third hibernacula in the pasture. The juvenile male (E89D) moved between the two hibernacula in the arable field five times, occupying the hibernaculum as soon as the female (FA56) had exited it.

Hedgehogs used a nest in an abandoned silage bale as both a day nest and hibernaculum. One male began hibernating in this nest in October 2008 but then moved after seven days. The hibernaculum was then occupied the following night by an adult female. She stayed in the nest for 46 nights before moving to another nest in December for 63 nights. She then returned to the original hibernaculum in the silage bale for the remaining 38 nights of hibernation.

When a hedgehog occupied multiple hibernacula, the first was utilised for a significantly shorter time (19.8 ± 0.6 nights) than the second hibernaculum (81.4 ± 1.2 nights) (Mann Whitney: ($U= 1.5$, $n_1=8$, $n_2=5$, $p<0.05$). When the duration of time spent in hibernacula occupied in mid winter (December and January) was compared to the duration of occupancy at other times, hedgehogs spent significantly (Mann Whitney: $U=1.0$, $p<0.05$) longer in hibernacula occupied in mid winter (December and January) (82.6 ± 1.2 nights) than they did in those occupied at the start (October and November) and end (February and March) (21.8 ± 0.3 nights) of hibernation (Fig. 6.10).

6.4.5 Emergence time

In the 2008/09 season four of the six hedgehogs emerged on the 30th-31st March 2009. One adult female (FA56) emerged two weeks later on the 16th April 2009. Another adult female (7150), who was hibernating in a wall, did not emerge until the 12th May, hibernating for 174 nights. This was the longest hibernation recorded in either year. In 2009/10, the longest duration of hibernation was 166 nights (See Table 6.5); this hedgehog was the first to enter hibernation on the 3rd October 2009 and remained in the same nest until he emerged on the 18th March 2010.

Table 6.5: Hibernation activity in 2008/09 and 2009/10 (± SE).

Year (n=no. of hedgehogs)	Mean stay in one hibernaculum	Min stay in one hibernacula	Max. stay in one hibernacula	Mean duration of hibernation
2008/2009 (n=6)	56 ± 12.6 nights	7 nights	174 nights	150 ± 6.8 nights
2009/2010 (n=5)	46 ± 0.7 nights	3 nights	166 nights	146 ± 2.7 nights (n=2)

6.4.6 Weight loss during hibernation

6.4.6.1 Hibernation 2008/09

In 2008/09, the mean weight of adult hedgehogs on entering hibernation was 1181.3g (±0.9) (SE). In 2008 the heaviest males were the first to enter hibernation followed by the heaviest females. After hibernation females were found to have lost significantly more weight than males ($t=5.100$, $df=4$, $p<0.01$). The maximum weight loss was for an adult female who lost 38% of her weight, while one adult male only lost 3% of his weight (Table 6.6).

Table 6.6: The dates and weights that adult hedgehogs entered and emerged from hibernation.

Year	Animal	Sex	Age	Entered hibernation	Emerged	Initial weight	Emergence weight	% loss
08/09	75EC	♂	A	19/10/2008	30/03/2009	1210g	1171g	3%
	A3D6	♂	A	22/10/2008	31/03/2009	1149g	1092g	5%
	ACOO	♂	A	25/10/2008	30/03/2009	1211g	1137g	6%
	FA56	♀	A	25/10/2008	16/04/2009	1194g	1013g	15%
	524A	♀	A	03/11/2008	30/03/2009	1178g	727g	38%
	7150	♀	A	11/11/2008	12/05/2009	1146g	876g	24%
09/10	75EC	♂	A	02/10/2009	18/03/2010	1165g	N/A	N/A
	856C	♂	A	15/10/2009	N/A	1190g	N/A	N/A
	E89D	♂	A	17/10/2009	23/03/2010	915g	652g	29%
	FA56	♀	A	28/10/2009	N/A	1167g	N/A	N/A
	0428	♂	J	17/11/2009	N/A	1024g	N/A	N/A

6.4.6.2 Hibernation 2009/10

In 2009/10 two adult males were the first to enter hibernation on the 2nd and 15th October, weighing 1165g and 1190g. However, in 2009 although the heaviest males were the first to hibernate, the juvenile male was the third to hibernate on the 17th October, weighing 915g (Table 6.6). Due to tag failure over the winter, only one hedgehog was weighed immediately upon emergence in 2010. This was the juvenile male (E89D) and upon emergence he had lost 29% of his weight over the hibernation period (Table 6.6).

6.4.7 Comparison between years for the same individuals

Two hedgehogs (75EC and FA56) were monitored through both hibernations (08-09 and 09-10). They were of a similar weight (45 and 27 grammes lower in 2009 than 2008) when they entered hibernation in both years (Table 6.6). The adult male (75EC) was the first to enter hibernation in both years (19th October 2008 and 2nd October 2009) and remained in one nest for the entire duration of hibernation. The adult female (FA56) went into hibernation on the 25th October 2008 and 28th October 2009. This hedgehog occupied two nests (entering the second in December) and the one it entered last was the one it occupied for the longest duration in both years. Both hedgehogs used different hibernacula in the following year.

Table 6.7: Hibernation activity of an adult male (75EC) and female (FA56) monitored in 2008/09 and 2009/10.

	Entry 2008	Entry 2009	Wt (g) 2008 /09	Wt (g) 2009/ 10	No. of hibernacula 2008	No. of hibernacula 2009	No. of moves 2008	No. of moves 2009
♂	19th Oct	3rd Oct	1210	1165	1	1	0	0
♀	25th Oct	28th Oct	1194	1167	2	2	1	3

6.5 Discussion

In the present study, 53% of day nests were located in the hedgerows of the pasture and 30% in arable land field. The majority of these were located in patches of brambles. In the U.K., Reeve (1981) found that of 58 day nests recorded, 31 (53.5%) were in prickly vegetation. Of those the majority 24 (77%) were in brambles. Morris (1969) also found that hedgehogs showed a marked preference for building nests in brambles and that these nests lasted longer (Morris, 1973). Although in the present study the use of bramble hedgerow was similar, the location was different, since in other studies arable land has shown to be rarely used by hedgehogs (Dowie 1987, Doncaster 1994, Doncaster *et al.* 2001, Riber 2006, Hof 2009). Although, in the Netherlands Huijser (2000) found over 60% of day nests in hedgerow under bramble, arable land was the least used habitat. The arable field in the present study had a well established hedgerow with a thick bramble understory. However, In the U.K., hedgerows survive least well in districts where arable farming prevails, as they no longer have any function as stock fences and their value for shelter for cereals is too slight to be a valid reason for their retention (Pollard *et al.* 1977).

In the present study hedgehogs utilised up to eleven day nests between which they rotated. In previous studies, males have been found to utilise a greater number of nests than females (Reeve 1981, Boitani & Reggiani 1984), and this was also recorded in the current study. In the present study, during the active season, males occupied a much larger home range than females, occupying an annual mean area of 56 ha (± 0.7) while females had an average home range of 16.5 ha (± 0.5) (Chapter 4). The fact that male hedgehogs had a much larger home range may have made it more difficult for them to return to a particular day nest and therefore necessitated the use of a greater number of nests. This is also supported by the fact that females returned to an individual nest significantly more often than males. However, hedgehogs did not always return to the day nest nearest to where they were foraging, but instead travelled back to specific nests, demonstrating a degree of philopatry. One adult female, in particular, was observed to travel back from the middle of the arable field to a nest located at the bottom of the garden, despite passing two day nests that she used regularly. The nest she returned to was located in an abandoned silage bale and may have offered better protection on colder nights, as on one occasion the temperature had decreased from 8˚C (the previous night) to 6˚C and on another night it was 4˚C. This individual began hibernating in this nest that was also utilised non-simultaneously by another adult female and an adult male. The use of a nest by multiple individuals sequentially has been previously reported by Riber (2006) in Denmark and Reeve (1981) in the U.K. In the present study adults were never observed simultaneously using the same nest and this is in accordance with the findings of other studies.

When in the present study four juveniles were found at the site on the October 17th and 18th 2008, they were all found together at the hedgerow of the arable field. They all returned to the same nest for the first four nights and stayed in the same area. However, they gradually dispersed out further into the centre of the arable field and began to occupy separate nests in the hedgerow of the field. Morris (1969) had noted that litter mates will often disperse incompletely and occupy a single nest.

At monthly mean weights of between 878-1116g for adult females and 1026-1192g for adult males, the hedgehogs in the present study were heavier than in other studies. In the U.K., Reeve (1981) reported weights of between 600-700g in spring increasing to about 900-1000g in autumn and found that it was relatively uncommon for hedgehogs to weigh more than 1000g. Similarly Dowding *et al.* (2010) recorded average weights of 846g ± 119 for males and 792g ± 157 for females also in the U.K. In New Zealand Parkes (1975) recorded a mean weight for males of 706 ± 10.0g and 688 ± 9.9g for females. The heavier weight of hedgehogs in the present study may have been due to optimum feeding conditions at the site, a supposition supported by the high density of individuals occurring there (Chapter 3), and the juveniles ability to increase weight over short time periods. However, this larger weight than hedgehogs elsewhere, was also recorded amongst Irish road kill (see Chapter 10) (mean 918 ± 0.28g, n=42), a maximum weight of 1254g was recorded and twelve individuals weighed above 1kg. Variation has also been found amongst mustelid size in Ireland and England (Erlinge 1987, Dayan & Simberloff 1994). This is thought to be related to variations in prey size (Erlinge 1987) and a reduction in selective pressure in the absence of some potential competitors in Ireland (Dayan and Simberloff 1994). White and Searle (2007) found that body size of common shrews (*Sorex araneus*) on islands was positively related to distance from mainland, suggesting a role for founder events, in determining body size of common shrews on islands. In the current study the lack of genetic variation amongst Irish hedgehogs suggests a small number of founding individuals and there may therefore be a founder effect (Chapter 8) and this combined with the lower number of competitors in Ireland, may result in Irish hedgehogs being larger. It may therefore be any or a combination of all of these effects.

Both sexes showed fluctuations in weight throughout the year, with females being at their minimum weight in August. Morris (1969) suggested that during August the mean weight of females' decreases since few are pregnant at this time. Males on the other hand were at their lowest weight in July in the present study. This was the peak of courtship activity and is probably related to a reduction in foraging at this time, due to a preoccupation with mating (Chapter 7). Individuals that were weighed over the two years showed little fluctuation from one year to the next. However, two of the males (75EC and 8C88) were at a lower weight (100g and 151g respectively) in August 2008 than in August 2009. In August 2008, both males were still engaged in courtship behaviour, but it had ceased by this time in 2009 (Chapter 7). In Sweden, during the mating period, Kristiansson (1984) also observed that the body weight of the adult males decreased by about 10% from May (955g) to June (870g) but increased considerably from June to September (870-1410g). In the present study both sexes were at their maximum weight just prior to hibernation, with males beginning to increase in weight in August and females in September. Morris (1969) and Reeve (1981) both reported a general increase in weight during the active season, similar to the present study, with both sexes reaching a peak in their weight pre-hibernation.

Jackson (2006) found that the weight of adults weighed one year later was on average unchanged. In the present study once individuals had reached adulthood, monthly weights were similar one year later and even two years on. Therefore, despite weight fluctuations due to pregnancy, courtship behaviour or loss through hibernation, adult weights remain stable on an annual basis. This indicates that during the study period food resources must also have been adequate and at least there was no shortage.

Once juveniles reached independence they showed a dramatic increase in weight, demonstrating that even late litters in southern Ireland are capable of reaching the required weight to survive hibernation. Bunnell (2009) reported that in the U.K. late juveniles had a significantly higher growth rate than earlier litters, further emphasising the ability of late litters to survive. Kristiansson (1984) recorded that a juvenile's body weight increased linearly from about 280g in August to about 600g in October, i.e. an increase of about 210% in two months. In the present study juveniles showed a mean increase of 180.1% (±60.4) from their weight when first weighed to hibernation, with one individual increasing by 289.3% in less than two months. As was the case with the adult population, the juveniles in this Irish population were heavier than reports in other studies. In the U.K. Morris (1969) reported that some animals can achieve 800-900g within a year of their birth. However, in the present study, one individual had reached 865g less than two months after independence, with another reaching a pre-hibernation weight of 1024g.

In 2008, the hedgehogs began to enter hibernation on 19th October. On 29th October, the temperature dropped from 9˚C to -2˚C, there was ground frost and no invertebrate activity (Chapters 4 and 5). Slug activity is markedly reduced at temperatures below 10˚C (Young *et al.* 1993), so it maybe energetically cheaper for the hedgehog to enter torpor than to remain active (Webb and Ellison, 1998). All of the hedgehogs in the present study were inactive at this time. At the end of the week as the temperature began to rise (4˚C), some of the lighter hedgehogs (n=4) re-emerged. In New Zealand, Webb and Ellison (1998) also found that under natural winter conditions of temperature and photoperiod wild hedgehogs readily became torpid when access to food is restricted for 48 hours. Therefore the lack of activity during these few days in the present study was probably driven by the lack of prey, brought on by the sudden drop in temperature and thus emphasises the necessity for hedgehogs to hibernate.

Hibernacula were most commonly built in the hedgerow of arable fields and scrub. While day nests were regularly built in the arable field, scrub had been used rarely in the months prior to hibernation. At the onset of hibernation in October and November, hedgehogs began to move into areas of scrub to build hibernacula (Chapter 4). The thick bramble patches in this habitat provided adequate support in which to build secure hibernacula. Morris (1973) found that hedgehogs left the exposed parts of the park that he was studying for a sheltered hibernation site, choosing locations that offered good structural support from surrounding objects. In the present study pasture hedgerow was used regularly as day nests but only two hibernacula were located in this habitat (and both of these hibernacula were situated within walls). Morris (1973) found that grass nests were particularly prone to desertion. Therefore, while hedgerow in the pasture may be sufficient for the often flimsy day nests, they may not have offered sufficient protection for use as hibernacula.

Only one adult male (75EC) and one adult female (7150) remained in the same hibernacula for the whole period of hibernation in 2008. The same adult male was the only animal to remain in the same hibernaculum in 2009. In both years the remaining hedgehogs moved up to five times occupying a maximum of three hibernacula. Morris (1973) reported that 60% of hibernacula were used for less than two months and the longest period of occupation was six months (Morris 1969). In the present study the longest occupation recorded was similar, i.e. six months and nine days. When a hedgehog moved during hibernation, the hibernaculum that the hedgehog utilised half way through the hibernation period (December and January) was occupied for a significantly longer time than hibernaculum occupied at the start (October and November) or end (January and Februray) of hibernation. Jensen (2004) also found that there was a strong tendency for hedgehogs that were using multiple nests to use the one that they had entered during mid winter for the longest time. Hibernating hedgehogs are subject to regular arousals and it has been found that hedgehogs have a less profound winter sleep in the beginning of the hibernation period (Walhovd 1978). Walhovd (1978) suggests they therefore are in a deeper sleep in mid winter and subsequently do not move as frequently. Morris (1973) also noticed a tendency for hedgehogs to move hibernacula following periods of sunshine and this is more likely to occur in early spring than in mid winter. In the present study, the temperature was at its lowest in December and January in both years and only began to rise in February.

Surprisingly, hedgehogs were found to swop hibernacula in both years. This triggers a number of questions, such as what the factors were that prompted this swop, how the hedgehog knew which hibernacula to move to and whether more dominant individuals get access to better hibernacula sites.

At the beginning of this study it was hypothesised that hibernation would be shorter and emergence would be earlier, due to Ireland's milder climate, and this is suggested by the data . The mean (±SE) length of hibernation recorded for the study population was 148.9 (± 0.5) nights, with four of the six hedgehogs emerging on the 30th-31st March 2009 and the following year from 18th March 2010. The majority of reports in the U.K. and Denmark record the average duration of hibernation to be 178.8 ±13.1 days for juveniles and 197.7 ± 2.2 days for adults (Jensen 2004, Morris 1969, Jackson 2006) with hedgehogs leaving their hibernacula during the last two weeks of April, with the remaining hedgehogs resuming activity in the first two weeks of May (Morris 1969, Jensen 2004, Jackson 2006). Similarly, Walhovd (1979) found that in Denmark the hedgehogs stayed in hibernation for six months and never resumed activity before May.

In 2008 the heaviest males were the first to enter hibernation followed by the heaviest females. In contrast Jensen (2004) found that the heaviest females were the first to enter hibernation and were the last ones to resume activity. In 2009, in the present study, the heaviest males were again the first animals to enter hibernation. However, while hedgehogs at the site entered hibernation at different times (19th October-13th November 2008), four of the six hedgehogs resumed activity on the 30th-31st March 2009, but two adult females did not become active until 16th April and the 12th May 2009. In 2009/10, the first hedgehog resumed activity on the 18 March 2010. This was also the first hedgehog that had entered hibernation the previous October. In 2009/2010, Ireland suffered its coldest winter since 1963; with temperatures around 2˚C lower than average (Met Eireann, www.met.ie). An adult female (FA56) and juvenile male (0428) were never seen again after the winter of 2009/10 and therefore they may not have survived.

Winter mortality is high amongst hedgehogs, with Morris (2006) reporting annual mortality among adult hedgehogs in the U.K. at about 30% and Kristiansson (1981) between 26% and 43% in Sweden. However, this harsh winter was unusual for Ireland and it is therefore not suggested that winter mortality would typically be high for hedgehogs here.

However, despite this cold winter, 2010 had the sunniest February in the south for over forty years (Met Eireann, www.met.ie). As stated earlier, Morris (1973) noted a tendency for hedgehogs to emerge following periods of sunshine and the earlier arousal in 2010 may therefore have been a result of high incidence of sunshine in February 2010.

The mean (±SE) weight loss during hibernation was 17.0 ± 0.53%, which was, as expected, low in comparison to other studies, a fact that may be due to milder winters or the availability of more secure nest sites in Ireland. Kristiansson (1984) in Sweden recorded losses of 20-40% and Morris (1969) in the U.K. observed a reduction of 18% in males and 39% in females. However, Jensen (2004) in Denmark observed that although the majority lost between 21.3-37.4% of their weight, one individual only lost 4.5%. In the present study females lost significantly more weight than males during hibernation. This has also been recorded in other studies (Morris, 1969) and may be due to them not building up as much fat reserves, due to late litters. In the present study one litter did not reach independence until October 17/18th 2008 (Chapter 7), and late litters were also recorded amongst road kill (Chapters 7). Walhovd (1979) found that hedgehogs that refused to eat during the hibernation period lost twice as much in body mass as hedgehogs that occasionally fed, but he reported that hedgehogs weighing above 1000g, as in the present study, rarely ate. However, while two of the males in the present study moved between hibernacula the most, the male who lost the least amount of weight did not move for the duration of hibernation. According to Tahti and Soivio (1977), one arousal lasting only 3-4 hrs consumes the energy equivalent of several days in hibernation. While it is not known whether hedgehogs ate when they arose in the present study, it is possible that the two males, who moved five times and yet lost just 5-6% of their weight, ate, and this counteracted the energy lost through waking up. In the present study, an adult female remained in a single nest for over six months but despite this lost only 23% of her weight, while the female who lost the most weight moved twice. This contrasts to Walhovd's (1979) study on captive hedgehogs, where he reported weight losses of between 22-112%, with the greatest losses reported in two males who both remained in the same nest and did not eat for the entire six months of hibernation.

At the beginning of this study it was hypothesised that the temperate climate and corresponding milder winters in Ireland might result in certain differences in the hibernation behaviour of hedgehogs in Ireland in comparison to elsewhere. This is suggested by the data, with hedgehogs emerging earlier than reports elsewhere and showing a shorter duration of hibernation. A smaller weight loss in this study in comparison to other countries is not surprising in light of the correspondingly shorter duration of hibernation and the availability of secure hibernacula sites. The location of both day nests and hibernacula in the hedgerow of arable land has shown that these areas will be utilised if hedgerow is maintained. It therefore highlights the importance of maintaining hedgerows in arable areas, particularly with bramble understory which in too many cases is considered unsightly and of little value (Pollard *et al.* 1977).

While this study has successfully answered some of the questions hypothesised at the start of this research, it has also thrown up some further interesting questions. For instance, when hedgehogs swopped hibernacula, what triggered this and how did they know to move to the others hibernaculum? Do hedgehogs feed when they wake up during hibernation and why do females loose more weight? Is this related to the build up of brown fat or is it related to nest construction? While these topics go beyond the scope of the current study, they require further investigation.

6.6 References

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Chapter 7-
Courtship and the first appearance of juveniles in rural Irish hedgehogs (*Erinaceus europaeus*)

Plate 7.1: Hedgehogs engaged in courtship

Plates 7.2: Juvenile hedgehogs

7.1 Abstract

As part of a bigger project on the ecology of the European hedgehog in Ireland, a study began in June 2008, to investigate courtship and the first appearance of juveniles. Between June 2008 and June 2010, 24 hedgehogs (18♂ and 6♀) were caught in a rural habitat and monitored by radio tracking and direct following. Hedgehog road kill was collected and the age and sex of each documented, to investigate whether peaks in road deaths occurred during the breeding season and to compare the appearance of juveniles at the site with their first occurrence as road kill. A preponderance of males was recorded in both adults and juveniles at the study site and deviated significantly from a 1:1 ratio. Courtship behaviour took place between April and July and occurred almost exclusively in a 9 ha pasture. An individual female paired with up to seven males in a breeding season. Individual males were observed trying to mate with the same female up to six times in a single season and sometimes in the same night. Observations of individuals tagged in two consecutive seasons indicated that, the same pairing was encountered. A peak in road deaths was observed between May and July in each year. This coincided with courting behaviour amongst the study group. The majority (n=22) of juvenile road casualties occurred in July but they continued to be recorded up until November (n=1). This, the presence of late juveniles at the study site and a pregnant female being found in September 2009, indicated that late litters can and do occur in Ireland. Juveniles were monitored upon emergence from hibernation, and although they showed exploratory movements into neighbouring habitats in the first few months of independence, they remained in the same core area of the site, where they were first encountered even after hibernation. Data from road kill corroborated the first emergence of juveniles in other areas of Ireland.

7.2 *Introduction*

The breeding season in the European hedgehog has been reported to begin soon after the hedgehog has emerged from hibernation in April until August, with peaks in activity varying between studies depending on latitude (Morris 1961, Morris 1969, Kristiansson 1984, Riber 2006, Jackson 2006). In New Zealand, introduced hedgehogs have a breeding season centred around November-March (equivalent to the April-August breeding season in Europe), but the milder climate in New Zealand permits breeding well outside this core period (Parkes 1975).

Female hedgehogs are polyoestrus and, in the male, spermatogenesis occurs between early April and mid August peaking between mid April and June in the U.K. (Deanesly 1934). Courtship behaviour in hedgehogs is characterised by the male circling around the female with one or both sexes snorting loudly (Reeve & Morris 1986). According to Jackson (2006) this ritual may continue for over an hour, with the majority of displays failing to end in a successful mating.

According to Emlen and Oring (1977), in species where one sex is largely freed from parental care, as is the case with the European male hedgehog, individuals of this sex should remain active for the duration of the period during which members of the other sex become sexually receptive, in order to mate with as many females as possible. For a non-territorial animal, like a hedgehog, which remains receptive for the majority of its active period, the possibility to mate with multiple individuals is high. In previous studies individual males made mating attempts with several females, in some cases during the same night (Reeve 1981, Kristiansson 1984, Jackson 2006, Warwick *et al.* 2006). Males' home ranges increase in order to cover the range of as many females as possible (Kristiansson, 1984, Chapter 4), and multiple paternity has been reported from samples in the U.K. (Moran *et al.* 2009).

In the U.K., following a pregnancy of 31-39 days (Morris, 1961), during which females may accumulate a mass of 50-150g (Jackson, 2006), between 2-7 young are born (Morris 1961, Morris 1966, Jackson 2006) which lead solitary lives after six weeks of age (Reeve 1994). The number of offspring in New Zealand, also falls within this range (Parkes 1975). In Sweden, hedgehogs have a single litter, which is larger, with Kristiansson (1981) reporting a mean litter size of 5.2 with numbers ranging up to 11. Kristiansson (1990) reported an equal sex ratio. However a preponderance of males was found by Morris (1969), Reeve (1981) and Riber (2006) in the U.K. and Denmark.

A late litter (any time after August) (Barrett-Hamilton & Hinton 1911) has been reported in the U.K. (Morris 1966, Jackson 2006) and matings can occur in late August and early September (Morris, 1961). Courtship or pregnancies may therefore be found during most of the active year i.e. March-October (Reeve 1981). However, as the active period is short, it is unlikely that an individual female could successfully rear two litters and gain the required weight to survive hibernation (Reeve 1994). Jackson (2006) found that at least three females, who reared a second litter, died in an emaciated state soon after the young emerged. Therefore, most late litters are thought to be the result of a failed first litter or produced by females born in the preceding August or September, that might not be ready to breed until nearly a year old (Deanesly 1934). Morris (1961, 1966) found that mothers deprived of their earlier litter are highly fertile and will readily breed again during the same season. It Is not known whether a second or late litter occurs amongst Irish hedgehogs.

Juveniles, in the U.K., reach independence at six weeks of age at which time they weigh between 220-235g (Reeve 1994). Hedgehogs have been recorded to reach sexual maturity between nine months (Allanson 1934) and two years of age (Kristiansson 1990). However, Deansley (1934) felt that they reach sexual maturity once they have reached a required weight. There is little known about the dispersal of young hedgehogs (Brockie 2007). Doncaster (1993) suggested that hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage (Doncaster 1993). However, Doncaster *et al.* (2001) observed that although natural dispersals were relatively rare events, hedgehogs were capable of travelling up to 3.8km from a release point and up to 9.9 km in total.

Hedgehogs are one of the most common road casualties (Sleeman *et al.* 1985, Huijser *et al.* 1998, Holsbeek *et al.* 1999, Smiddy 2002, Hell *et al.* 2005), largely due to their main line of defence being to roll up in a ball. Holsbeek *et al.* (1999) reported that of 7706 fatalities in Belgium, 1281

(17%) were hedgehogs. However, Lodè (2000) reported that hedgehogs represented only 2.8% of vertebrates killed on motorways in France and in Seiler *et al.*'s (2004) study in Sweden they represented just 4%. In Belgium, the pattern of hedgehog road kill showed a gradual increase towards a peak in July (>300) gradually decreasing to less than 10 towards December and January (Holsbeek *et al.* 1999). A similar pattern has been shown in Spain (Garnica & Robles 1986), the Netherlands (Huijser *et al.* 1998), and Ireland (Smiddy 2002). During the breeding season males increase their home range (Morris 1969; Kristiansson 1984; Jackson 2006), and so may be found more frequently in road kills in certain months. Huijser *et al.* (1998) estimated that 3-22% of the country's population of hedgehogs were killed on the road in the Netherlands and they were characterised by a preponderance of 3 males: 1 female. Goransson *et al.* (1976) recorded that 80% of traffic victims were male hedgehogs who had survived one winter in Sweden. However, in autumn he observed that high numbers of females were killed which was attributed to a greater need to forage wider, in order to build up fat prior to hibernation after raising young.

With no previous data on the ecology of Irish hedgehogs, the breeding season, courtship behaviour and first appearance of juveniles in Ireland is unknown. Therefore the present study aimed to investigate patterns of courtship behaviour of a study group i.e. the number of mates, duration of courtship and the identity of pairings. The study also aimed to investigate the first appearance of juveniles, the timing of litters, the number of offspring and the possible patterns of dispersal by the juveniles. Finally, by examining road kill data the current study aimed to compare seasonal sex biases and the first appearance of juveniles on a wider geographical area, with the data collected from the focal study group. It also aimed to test the following hypotheses that:

- In view of the male bias at the site and the philopatry observed by both sexes, a high number of repeat pairings occurs among the study group
- A late or second litter occurs amongst Irish hedgehogs and is evident amongst the study group and through the appearance of juvenile road kill

- In view of the site philopatry observed at the site and the results of previous research, little dispersal occurs amongst juveniles.

7.3 Materials and Methods

The study was carried out between June 2008 and June 2010 at Ratharoon, Co. Cork, the site described in Chapters 3 and 4. Individuals were captured by spotlighting and monitored by radio tracking, by the same method described in these chapters. Data analysis was also as explained in these sections.

All hedgehogs caught were classified as adult or juvenile (Table 7.1), sexed and hind foot measurements were taken. Individuals were weighed weekly, using digital scales (Harvard apparatus), to assess weight changes associated with pregnancy and monitor juveniles. The presence of growing and broken spines was recorded. The hedgehog was considered to be a juvenile if it satisfied all of the following criteria: weight less than 600g when first caught; hind foot length of less than 3.6cm (See Chapter 6); and presence of growing spines. There was one exception made to these pre-requisites. One male (E89D) caught on the 30th September had growing spines and a hind foot length below 3.6 cm but weighed 855g. This was a lower weight (200g less) than adults at this time and his weight was instead in accordance with juveniles that had been tracked from earlier in the season.

Table 7.1: Number of hedgehogs caught and monitored at the site over the study period.

Year	Adult males	Adult females	Juvenile males	Juvenile females
2008 (n=14)	6	3	3	2
2009 (n=16)	9	4	3	0
2010 (n=6)	4	1	1	0

7.3.1 Courtship behaviour

Courtship behaviour was identified based on the description by Reeves and Morris (1986), i.e "courtship involves the male circling closely around the female, with one or both sexes snorting loudly". When courtship behaviour was observed, the identification of individuals involved was recorded, in addition to their location, the length of time which they spent engaged in courtship behaviour and whether the behaviour concluded in a successful mating.

7.3.2 Road kill

Carcasses of road kill were collected throughout the study period from around Ireland. These carcasses were collected by both the author and members of the public. These were sexed, weighed and aged using the same criteria as described previously. The time of year and the location of the incident were also recorded. Carcasses of females were inspected for signs of lactation and if pregnant the numbers of foetuses were recorded.

7.4 Results

7.4.1 Sex ratio

Between June 2008 and June 2010, 24 hedgehogs (18♂ and 6♀) were caught at the site. The sex ratio was 3 (male): 1 (female) which deviated significantly from 1:1 (Chi squared test: χ^2= 6.760, df= 1, $p<0.01$)) (χ^2=6.8 following Yates correction). Eight of these hedgehogs were juveniles (6♂ and 2♀) and as was the case with adults their sex ratio was also 3:1.

7.4.2 Courtship behaviour

Courtship behaviour was usually first obvious by the loud hisses of the female. The hedgehogs faced each other (Plate 7.1, Cover page), the male attempting to approach the female who would lunge forward, pushing her head underneath his body, while she used all of her force to push him away. The male would again edge forward and attempt to move behind the female, progressing in wide circles, and moving behind large clumps of grass. The female quickly circled around to avoid the male approaching behind her and again the hissing resumed.

7.4.3 Time of occurrence of courtship

In 2008, when hedgehogs were monitored at the site for 375 hours over 81 nights (Table 7.2) from June to November 2008, there were only two observations of courtship behaviour, both in August (Fig. 7.1).

Table 7.2: The number of nights and hours that hedgehogs were monitored in each year.

Year	Number of hedgehogs	Number of nights	Number of hours
2008	14	81	375
2009	16	104	624
2010	6	38	76

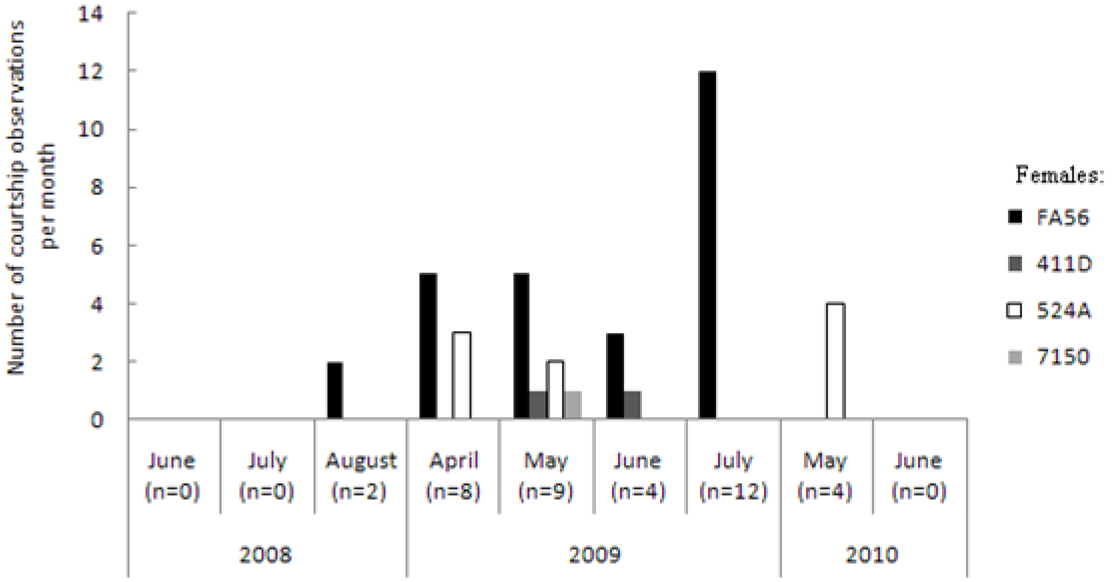

Figure 7.1: The months in which courtship behaviour was observed among four females (n=number of observations of courtship).

In 2009, hedgehogs were observed for a total period of 624 hours over 104 nights (Table 7.2). From emergence in April until July 2009, there were 33 observations of courtship behaviour involving four adult females (Fig. 7. 1), with no further observations of courtship behaviour after July.

In 2010, hedgehogs were monitored for 76 hours over 38 nights (Table 7.2). Courtship behaviour was first observed in May, and there was one female tagged at this time. Four incidents of courtship behaviour were observed between March and June, all taking place in May and involving this female. This female (524A) was killed on the road in June 2010 and no further courtship behaviour was observed (Fig. 7.1). Prior to this all courtship displays had involved this female.

7.4.4 Duration of courtship events

Of the 39 observations of courtship behaviour during the study period, involving 16 individuals (4♀, 12♂) no successful copulations were witnessed. Bouts of courtship behaviour had a mean duration of 60 (± 0.05) minutes. However, on one occasion in 2009 a bout lasted for up to 140 minutes. On this occasion, while one pair were involved in courtship behaviour in the pasture, two males approached from two different directions. One remained stationary behind a clump of grass for the duration of the interaction, while the other approached the female and attempted to mate with her.

Courtship always terminated with the male moving away and immediately starting to forage, while the female remained stationary until the male had moved away from the area.

Of the 1132 fixes from 12 individuals obtained between April and July 2009, during 292 of these, hedgehogs were engaged in courtship behaviour (Fig. 7.2). There was no significant variation in the time females (n=4) and males (n=8) spent engaged in courtship behaviour (χ^2=2.381,df=1, p>0.05).

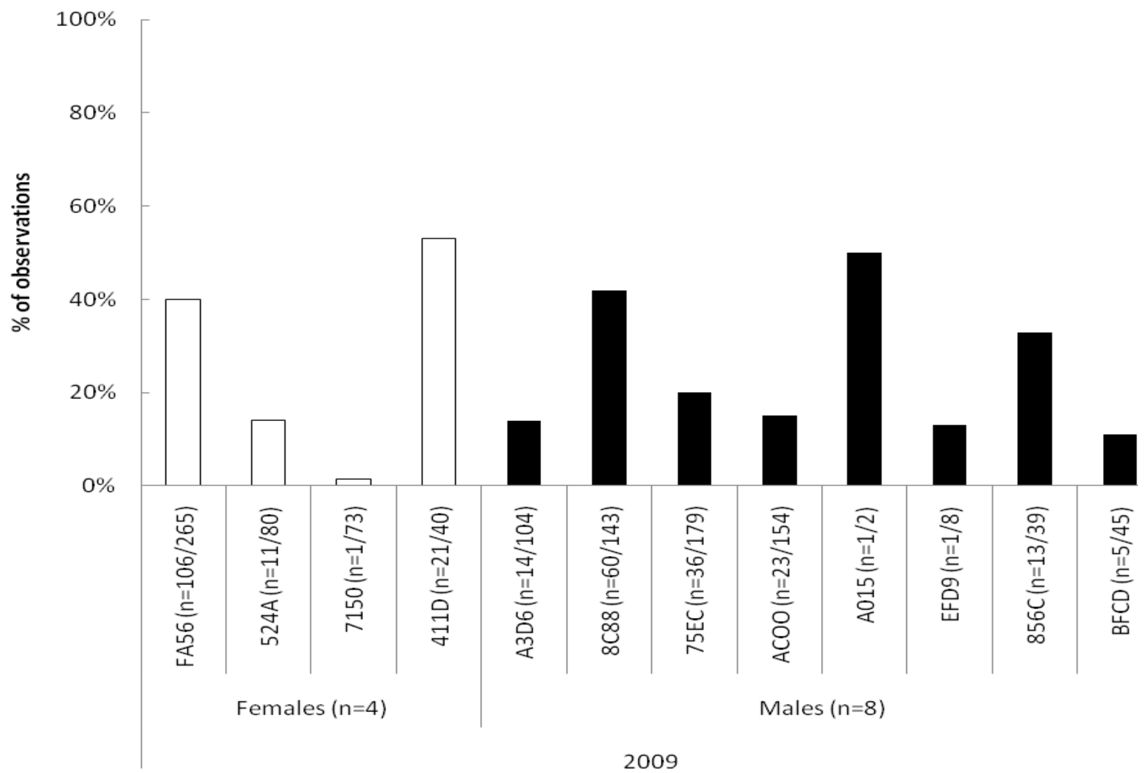

Figure 7.2: The percentage of observations between April and July 2009, where 12 adults where engaged in courtship behaviour (n=the proportion of occurrences of courtship behaviour out of all other fixes for that individual).

7.4.5 Identification of Pairings

In 2008, there were two observations of courtship behaviour and they involved three of the tagged males and one female (FA56). In 2009, a male was observed paired with the same female on up to six different occasions (mean 2.4 ± 0.38 occasions per female). Males were observed in courtship behaviour with up to three different females during the breeding season (mean 1.6 ± 0.31 occasions per male) (Fig. 7.3). For example in 2009, male 8C88 was observed paired with female FA56 on three occasions, female 411D twice and once with female 524A. In 2010, female 524A was the only female observed at the site and all of the tagged males (n=4) were observed attempting to mate with her (Fig. 7.3).

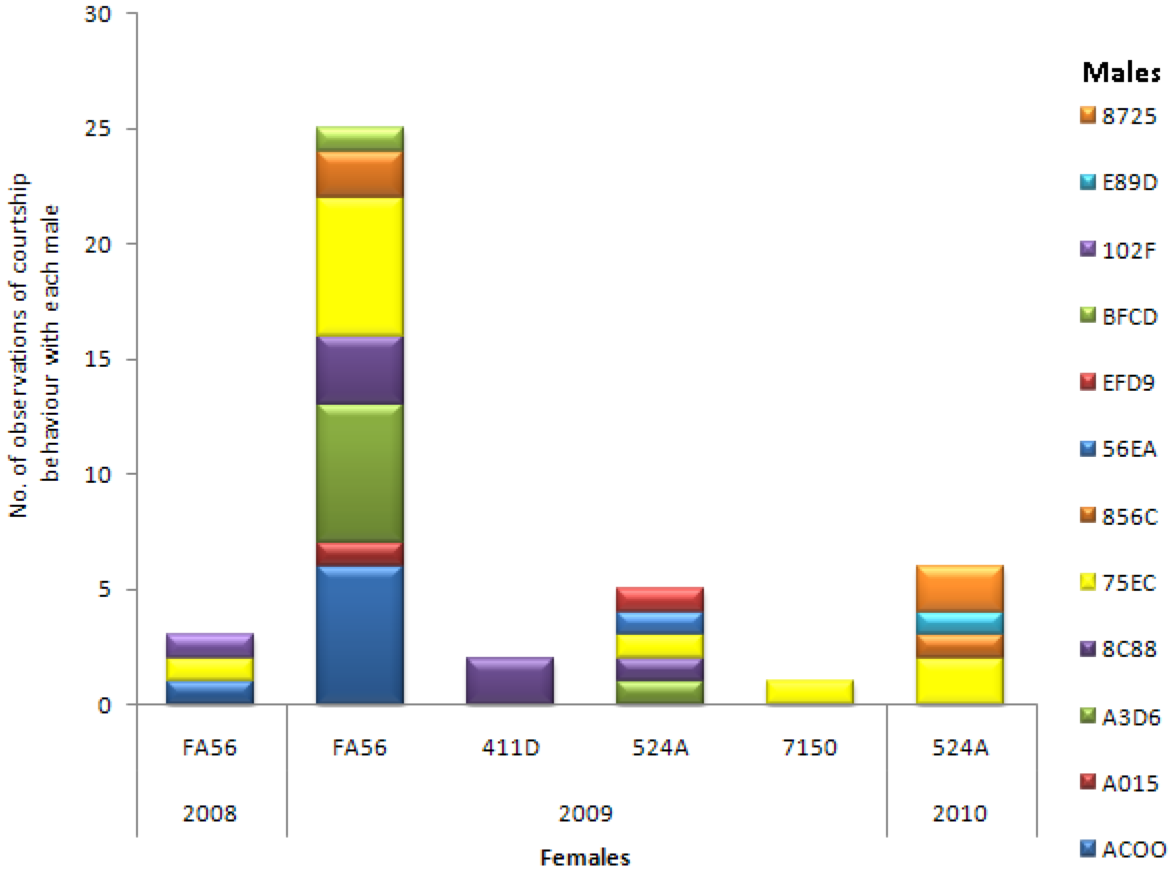

Figure 7.3: The number of observations of females paired with a particular male in 2009.

7.4.6 Location of courtship events

During the breeding season, both sexes concentrated their activity in pasture, and moved out of this area when the breeding season terminated. In total, 92.3% of courtship behaviour took place here, with only one observation in the marsh and two in the garden (Fig. 7.4). Courtship behaviour in the garden occurred in August 2008, when breeding had terminated in the following two years. A female (411D) from the Holland Ivy area (*1, Fig. 7.5) moved down to the pasture (*, Fig. 7.5) where all the courtship was taking place in May 2009. It was as she moved down into this area that a courtship event was observed in the marsh (*2, Fig. 7.5) between her and an adult male (8C88). Females occupied three neighbouring areas of pasture during the breeding season and this area was completely encompassed by the adult males. The pasture represented the core area of the females home range at this time in all years, and while their mean annual home range was 16.5 (± 0.49) ha (n=3 adult females), the males occupied 56.0 (± 0.67) ha (n=4 adult males) (Fig. 7.5).

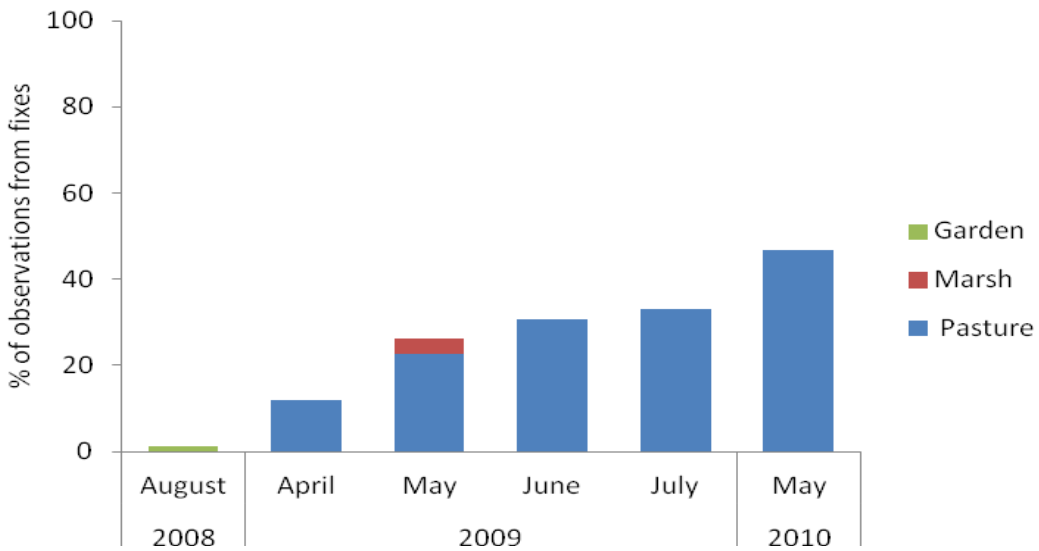

Figure 7.4: The percentage of observations where hedgehogs (male and female) were engaged in courtship behaviour and the habitat in which it took place.

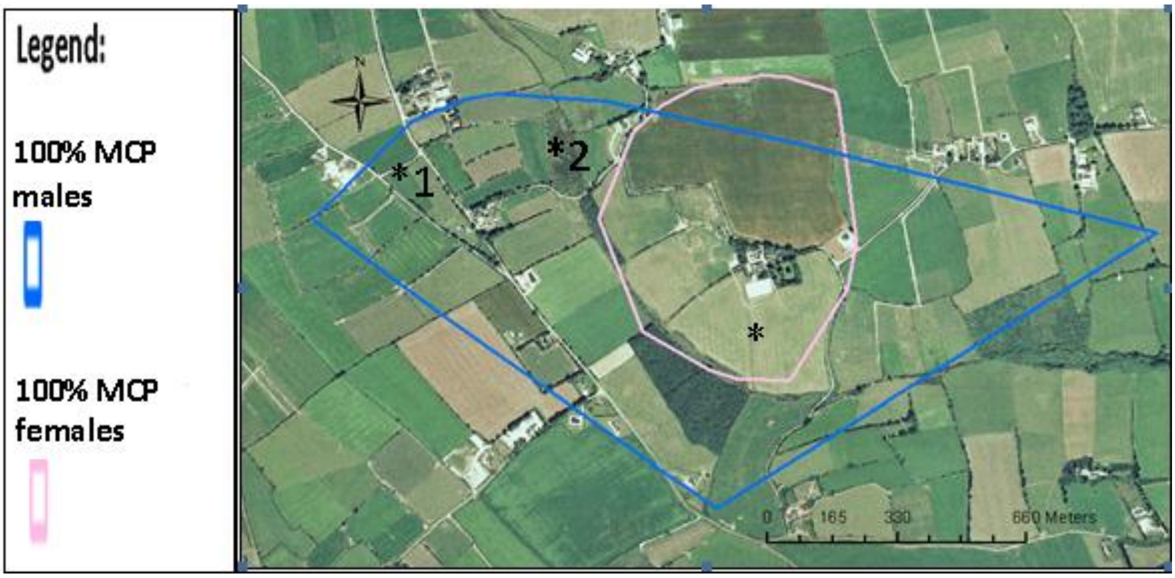

Figure 7.5: The home range of adult males and females (100% mcp).

7.4.7 First occurrence of Juveniles

In 2008, the first juvenile (♀) was caught at the study site on September 19th (Plate 7.2). The remaining (n=4) juveniles were caught on the 17th and 18th October of that year, their weight (244-281g) indicating that they had just reached independence. In 2009, the first juveniles were caught at the site in July.

Hedgehogs were collected as road kill from around Ireland, 31% from Connaught, 67% Munster and 2% Leinster. Four out of 35 road kill females collected in Munster were pregnant when killed. These females were collected as road kill on the 7th, 23rd June, 14th July and 6th September 2009.

In two of these cases the foetuses were well developed (between 4-7 grammes and 14-20 grammes and 2cm long) with one female pregnant with five foetuses and the other with six (Fig. 7.6). Only the litter of six could be accurately sexed and they showed a sex ratio of 1:1. None of the female carcasses showed obvious signs that they were lactating and none of the female carcasses collected in 2008 and 2010 were pregnant when killed.

Figure 7.6: Foetuses collected from two pregnant females that were killed on the road (measurements appear in centimetres).

7.4.8 Seasonal movement patterns of one female

Adult female 524A was first caught in September 2008 in the arable field (1 on Fig. 7.7) and tagged until her death in June 2010. In the two consecutive years she moved away from the core area of her home range(2 on Fig. 7.7), at the end of May, moving to neighbouring pasture (0.53 km) (3 on Fig. 7.7). In September she moved back with the other adults (4 on Fig. 7.7). In May 2009, her weight increased by 112g in six days. When she was next seen active, and weighed, seven days later, she had lost 198g, suggesting that she had given birth.

Figure 7.7: Fixes of an adult female (452A) monitored over three years.

7.4.10 Movement of juveniles from natal nest

7.4.10.1 Juvenile movement in 2008

Juveniles made exploratory movements away from their natal nest, but returned and remained close to the area of their birth. There were 135 fixes obtained from juveniles in October and November 2008. In the first few days after tagging in October 2008, the four late juveniles (3♂ and 1 ♀) confined their activity to a small area of the arable field, and all of them returned to the same nest every morning. This is illustrated by one of these juveniles, a male (56EA) who was radio tagged (Fig. 7.8a). After the first week they all were observed foraging further into the field and occupied separate day nests, however they all remained in the arable field, where the adults were also foraging (Fig. 7.8b). The greatest distance moved was 0.20km in October and 0.24km in November. He remained in the arable field throughout hibernation and did not leave this habitat until the following year. He emerged on the 30th March 2009 and moved 0.06km within the arable field. In April 2009, (Fig. 7.8c), he entered the 9ha area of pasture (0.50km from first capture, 0.33km from hibernacula).

Fig. 7.8: The movement patterns of a juvenile male (56EA) from first capture in October 2008 (a) to November 2008 (b)and March/April 2009.

7.4.10.2 Juvenile movement in 2009

The first juvenile of 2009 was again found in the arable field, but in July (Fig. 7.9a), weighing 299g. This animal, a male ACD7 (blue dots on Figs. 7.9a-c) remained in the southern portion of the arable field for the first two months of independence. He gradually dispersed 0.23 km into the arable field, and was recorded on two occasions making exploratory trips into the neighbouring pasture in September (0.43 km) (Fig. 7.9c) (Fig. 7.10). This individual was killed by a dog in the arable field at the end of September 2009.

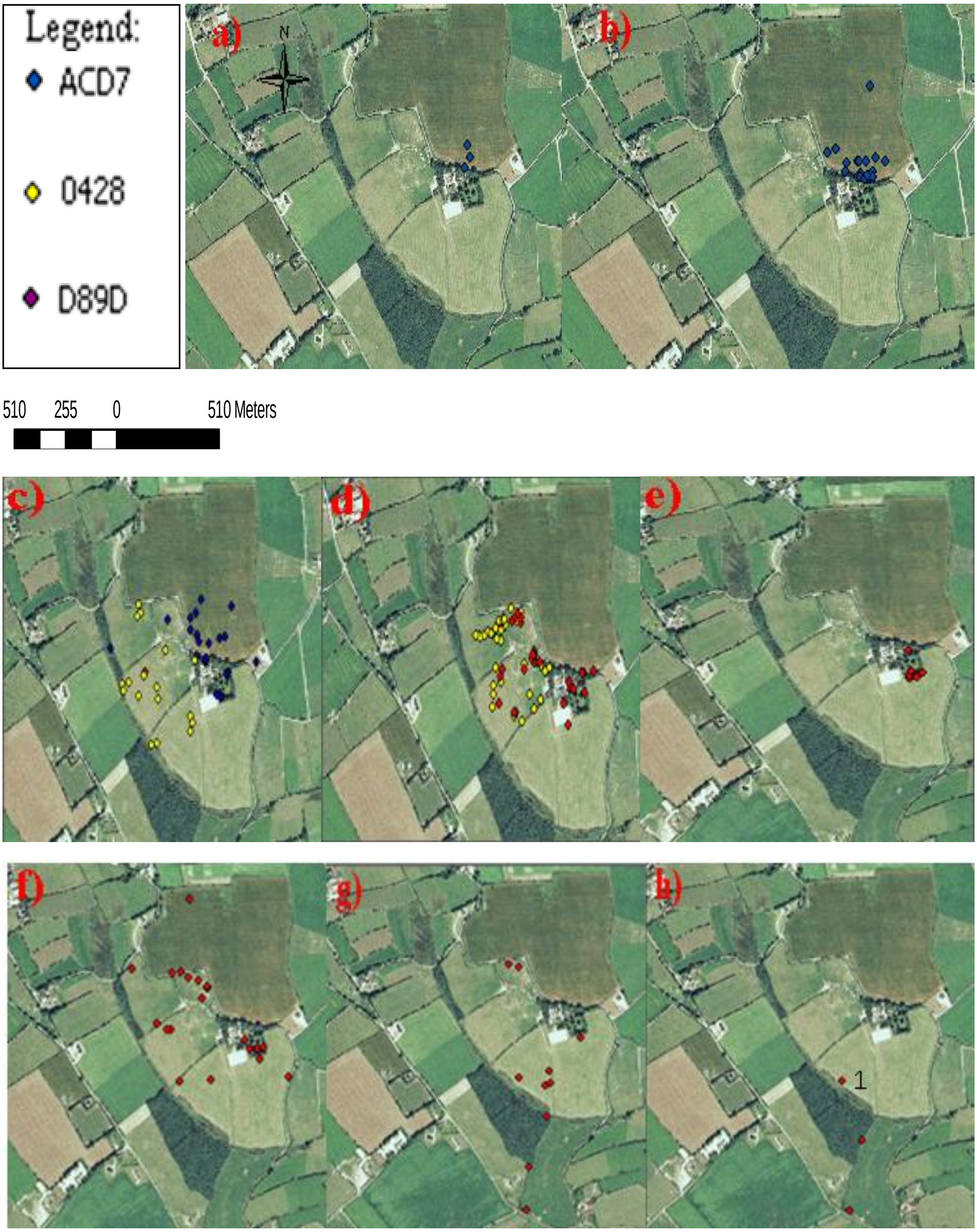

Figure 7.9 a-h: The movement patterns of three juveniles from first capture in July 2009 (a) to August (b), September (c), October (d), March (e), April (f), May (g) until June 2010 (h).

Two more juveniles (♂) were found in 3 ha of pasture, at the site in August and September 2009. They remained in this area throughout the monitoring period (Figs. 7.9c and d). However, in October 2009 one of the juveniles (D89D) entered the arable field and built a hibernaculum there.

Both of these hedgehogs were monitored throughout hibernation. One failed to emerge but the other (D89D) (red dots on Fig. 7.9 c-h) emerged in March 2010. This animal remained in the pasture and despite making exploratory trips of 0.64 km (Fig. 7.9 h) (Fig. 7.10) into the neighbouring pasture (Fig. 7.9g), returned to the core area of the pasture, where he was eventually killed by a mowing machine in June 2010 (1 on Fig. 7.9h).

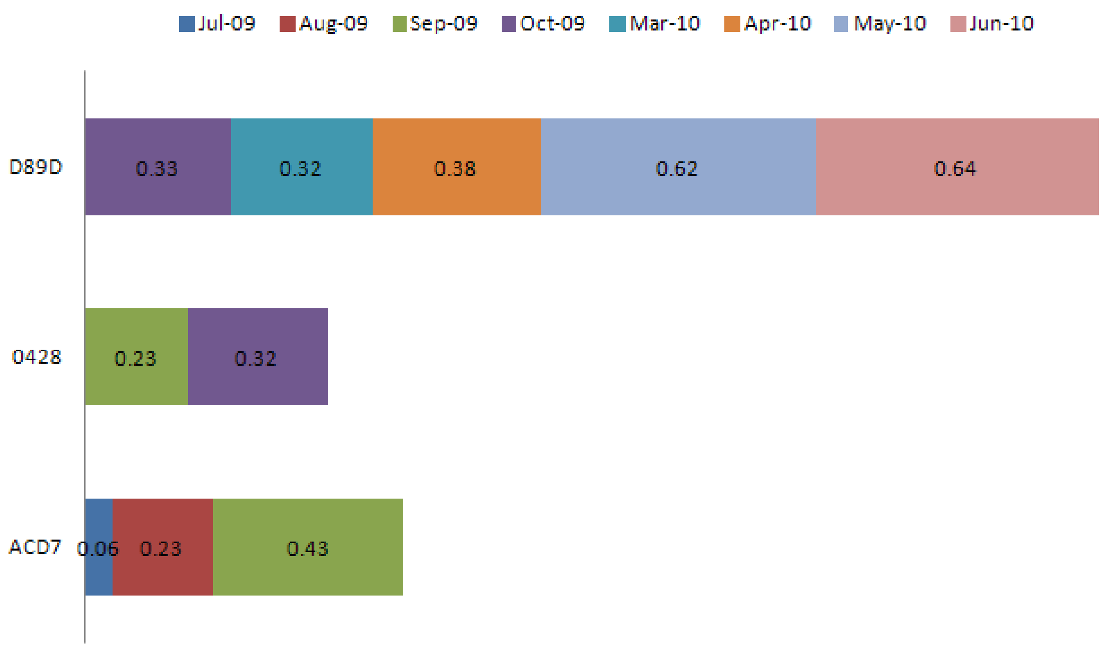

Figure 7.10: The greatest recorded distance (km) that a juvenile moved from the location where it was first captured to the furthest fix each month.

7.11 Sex ratios and occurrences in road kill

Only one of the tagged hedgehogs was killed on the local roads during the two and a half year study. The majority of hedgehog road kill elsewhere in Ireland occurred between May and August (Fig. 7.11).

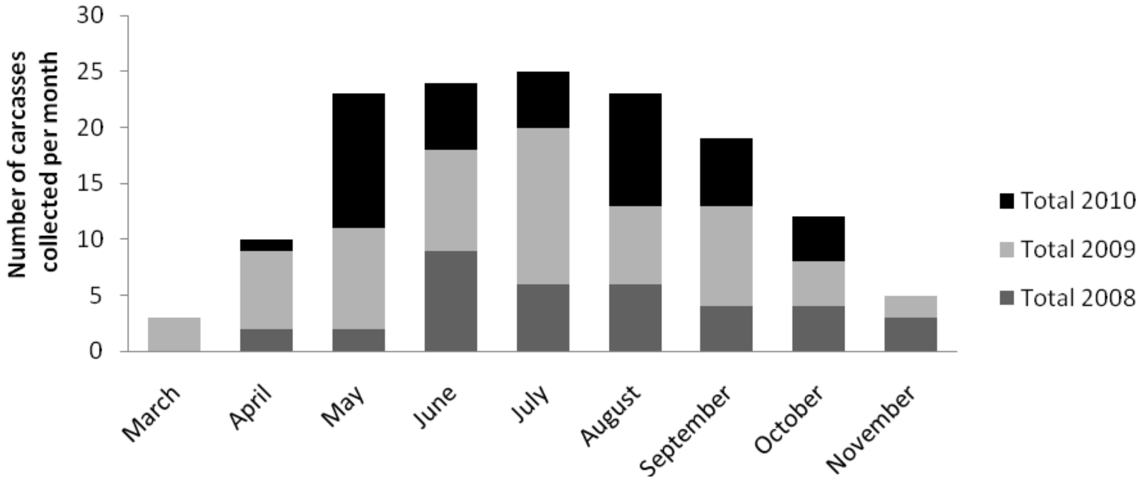

Figure 7.11: The numbers of hedgehogs collected as road kill between March 2008 and November 2010.

Of the 145 carcasses collected between April 2008 and November 2010, 37 were female, 68 were male (Fig. 7.12) and the remaining 36 were too damaged to sex. However, while there was an overall preponderance of male fatalities, a peak in females was observed in July in both 2008 and 2009 and a peak in males in May 2009 and 2010 (Fig.7.12).

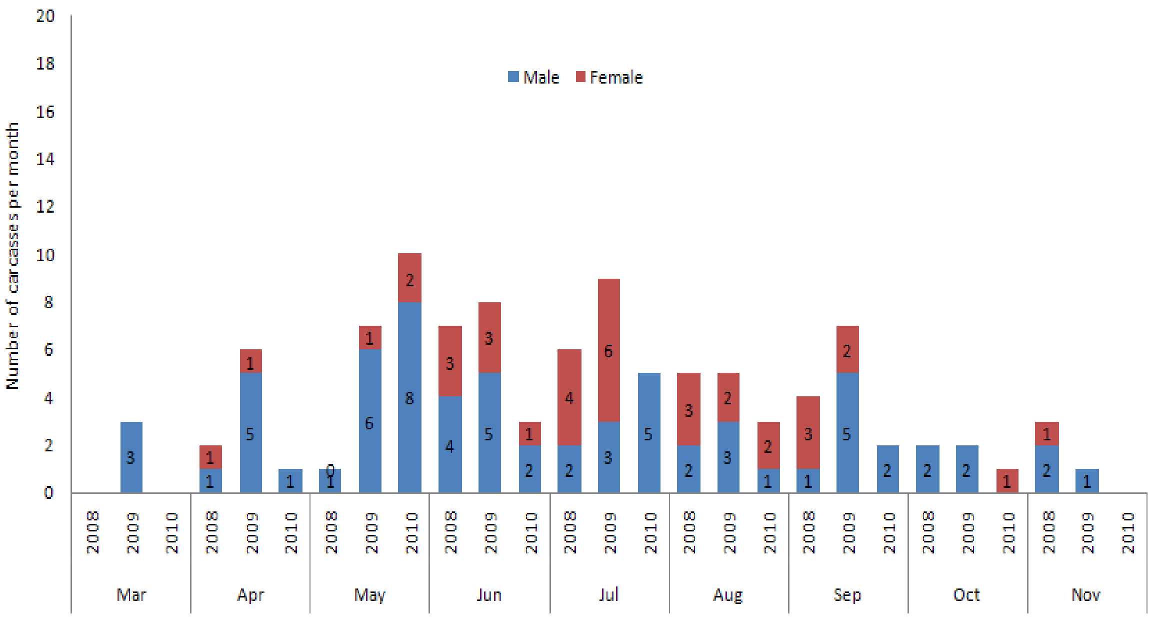

Figure 7.12: The sexes of the carcasses collected as road kill.

Twenty eight of the road casualties were juvenile (Fig. 7.13) and 88 were adult, the remaining 29 were too damaged to accurately identify. The incidences of juveniles being killed on the road peaked in July, but they were found up until November.

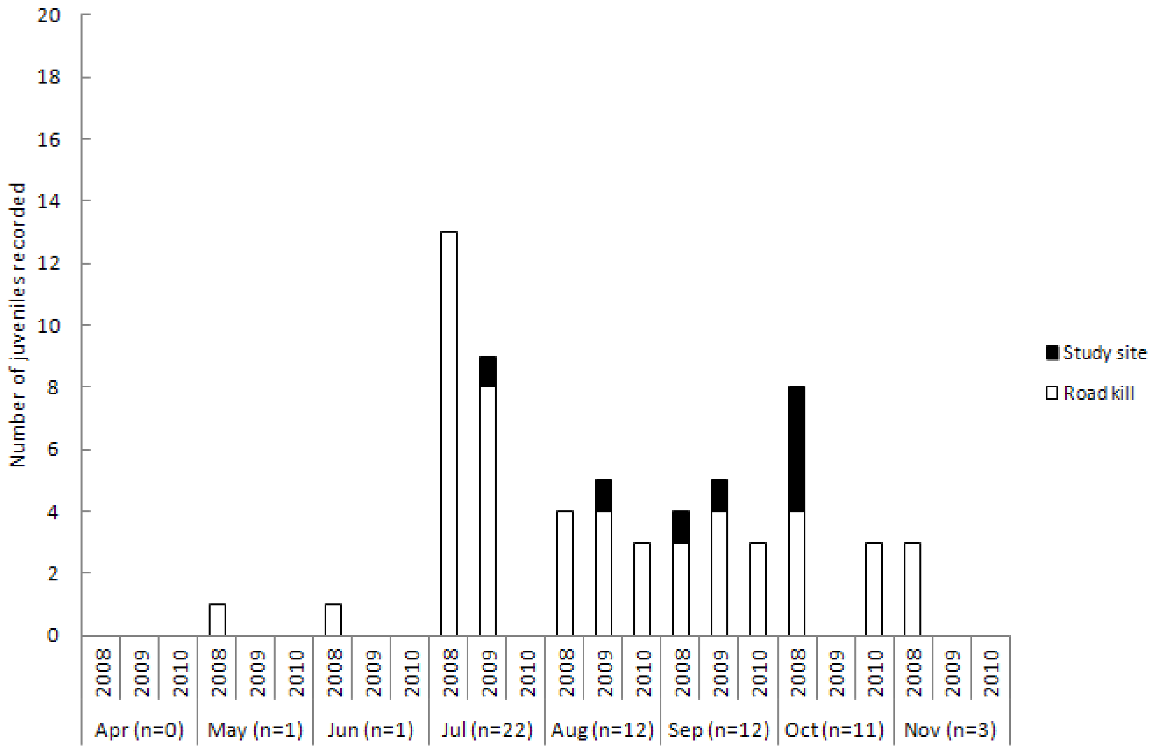

Figure 7.13: First sightings of juveniles at the Ratharoon study site or as road kill from other parts of Ireland.

7.5 Discussion

At the study site there was a sex bias in favour of males, with 16 adult males and four adult females and six juvenile males and two juvenile females caught at the site. Similarly, a strong preponderance of males in both juveniles (7:2) and adults (8:5) was noted by Reeve (1982) and Riber (2006), who caught 24 adult males: 7 females. However, Kristiansson (1990) in Sweden found an equal sex ratio. Reeve (1982) suggested that a male bias may be due to transient males, as he did not notice this bias amongst juveniles. This may partly explain the bias in the current study as four of these males were first caught between April and July 2009, at the height of the breeding season.

Furthermore all of these individuals were first caught while trying to mate with tagged females. Two of the adult males were not seen again and the other two were known to have moved outside the core (56.0 ± 0.7 ha) (Chapter 4) home range after the breeding season ended in August 2009, with one returning again to attempt to mate in May 2010. However, in the present study a bias was also observed amongst juveniles in both years, with a litter of four juveniles in 2008 having just one female. In 2009, all of the three juveniles caught were male. Kristiansson (1990) noting the discrepancy between estimated litter size at birth (6.5) and the recruited number of juveniles per adult (2.79), and suggested a high mortality rate from birth to catchability. Therefore, mortality may be higher amongst female offspring as one of the litter of foetuses recovered from a pregnant female showed a sex ratio of 1:1. Clutton-Brock and Iason (1986) examined mammals increasing their fitness by varying the sex ratio of their progeny, in response to differences in the costs and benefits of producing males and females. They found that in species where males may disperse from their natal area, while females share their mother's home range, the female siblings are likely to compete for resources, so the mothers produce male biased sex ratios. However, as there is little information on whether juvenile hedgehogs disperse, it is unclear whether this could be the case in hedgehogs. This is something that may have been possible to determine by looking at the relatedness of individuals at the site. Tissue samples were taken from the hedgehogs for genetic analysis but due to the lack of genetic variability amongst Irish hedgehogs, relationships could not be established (Chapter 8).

In the present study, a peak in sexual activity was observed in July which was similar to peaks in the U.K. (Reeve, 1981, Jackson, 2006) and Sweden (Kristiansson, 1981). The breeding season of hedgehogs is often characterised by an increased movement of males in order to encompass the range of as many females as possible (Kristiansson 1984). The males who were tagged in the present study increased their range during the breeding season with one male covering an area of up to 30 ha, at its peak movement in July before reducing his range to 11 ha in August when breeding behaviour ceased (Chapter 4). Road kill studies have recorded a peak in road deaths in May and July (Holsbeek *et al.* 1999, Huijser & Bergers 2000, Smiddy 2002) and both Goransson *et al.* (1976) and

Huijser (2000) reported a preponderance of male traffic victims (80 and 71%). This is similar to the present study with a peak in numbers from April to July, when breeding behaviour was also observed at the study site. In the current study 65% of the carcasses were male and Huijser (2000) proposed that the increased activity of males during the summer months is the most probable cause of the high percentage of males among traffic victims.

Jackson (2006) reported that females were promiscuous and were estimated to have sexual encounters, though not necessarily matings, with at least five males. In the present study copulation was never observed but 39 incidents of courtship behaviour were witnessed. Successful matings appear to be rare with Reeve and Morris (1986) reporting only five successful copulations in 76 courtship displays and Jackson (2006) only observing ten. Jackson (2006) felt that this reflected the brevity of mating (minutes) relative to the time spent courting (up to an hour or more). In shrews (*Sorex araneus*), as females cannot always distinguish between close kin and they may copulate with several different males, thereby reducing the risk that all of their offspring will be sired by a close relative (Stockley *et al.* 1993). Multiple paternity which has been reported in shrews and hedgehogs (Moran *et al.* 2009) may be a useful way for a non territorial animal, like the hedgehog, to reduce inbreeding depression and the need for dispersal.

Surprisingly, 92.3% of courtship events occurred in a core area of pasture. Potential prey was consistently poor in this habitat throughout the year (Chapter 4). Prey abundance was also lower here, than in areas of arable, where hedgehogs began to enter once the breeding season terminated (Chapter 4). Therefore, habitat selection appeared to be motivated by courtship behaviour at this time. It is unsurprising therefore that when hedgehogs concentrated their activity in pasture, they spent up to 35% of their time engaged in courtship behaviour and 26% of their time foraging (Chapter 4). Three of the females concentrated their activity in this habitat during the breeding season and the fourth female (411D), moved down here from Holland Ivy, which was at the boundary of the site. While, the selection of this pasture for courtship events is undetermined, it would appear that access to multiple mates is advantageous for both sexes. In other polyandrous species such as the marsupial, *Antechinus agilis*, the female benefits through increased growth rates by mating with multiple males (Fisher *et al.* 2006). In this study, females were found with up to seven different males and males were observed trying to mate with up to three different females. Over the breeding season an individual male attempted to mate with the same female up to six times. On two occasions the male attempted again to mate with the same female later in the same night. However, it was still unsuccessful. With animals that were tagged for more than one season, the same male attempted to mate with the same female the following year. This is in contrast to data from the U.K., where Reeve (1981) and Jackson (2006) both reported that the probability of the male being found with the same partner was low. In Reeve and Morris' (1986) study, ten of the 76 incidents involved partners who had been previously recorded together up to three times, but 12 of the females were courted by at least 10 different partners. The high incidence of repeated pairings of the same individuals in the present study may be due to the high male bias and small number of females at the site, with only four adult females recorded in the two and a half year study. The two juvenile females caught in 2008 were not seen again after hibernation.

In all cases courtship behaviour was characterised by the aggressive behaviour of the female, in the same manner previously described by Reeve and Morris (1986) and Jackson (2006). Cox and Le Boeuf (1977) indicated that this behaviour, of rejecting a suitor, allows the female to test the vigour, tenacity and speed (indicators of fitness) of a potential suitor and select a union which results in optimal genetic consequences. Reeve (1994) too suggested that the courtship ritual allows plenty of time for a female to judge her suitor and less vigorous males may be displaced. In the present study a courting pair of hedgehogs was often approached by up to two other males. The males ran to the pair with their heads raised suggesting that they had been alerted to the pair either by the sound of the aggressive female or through her scent. Reeve (1994) suggested that odour plays an important part in hedgehogs' pre-mating behaviour, with males attracted to females in oestrus and certainly in this study this appeared to be the case with a male seen running towards a lone female from the other side of the 9 ha pasture in June 2010. Aggressive female behaviour during mating has also been described in e.g. elephant seals (*Mirounga angustirostris*) that respond to male advances by loud vocalisations and escape movements, this alerts neighbouring males and competition ensues among males of varying ranks, with the result that the highest ranking male is selected (Cox & Le Boeuf 1977, Christenson & Le Boeuf 1978). As in the present study no observations of courtship behaviour resulted in copulation, it is uncertain whether there was any effect of male dominance in the outcome of a mating attempt. However, in the present study on the two occasions when a male hedgehog, who was known to have been born the previous year, attempted to mate with a female, they were in both cases joined by an older male, who was aggressive towards the younger hedgehog that subsequently retreated.

According to Kristiansson (1990) female hedgehogs do not produce young until their third summer i.e. at about two years old. Jackson (2006) found that only four of 48 sub adults were found paired with a female, and none were definite sub adults. However, earlier estimates of sexual maturity have been reported, with Allanson (1934) suggesting nine months for males and Morris (1969) recording one female reaching an oestrus condition by the end of its first summer at an age of less than 6 months. Deansley (1934) suggested that hedgehogs reached sexual maturity once they have reached a required weight. The two males in the present study would have been seven months and ten months respectively, when found paired with a female, having both reached weights close to that of the adults at this time. However, as mentioned above, in both incidents of courtship behaviour, they were displaced by an older hedgehog.

In 2008, although spotlighting at the site began in June, juveniles were not seen at the site until September and October, 6-8 weeks after the only courtship displays had been observed in August 2008. On October 17^{th} 2008, four juveniles were found with a mean weight of 259.5g (± 0.99). In the U.K. Reeve (1994) reported weights of 200-235g (about 10 times) birth weight, at around 40 days and they are newly independent at about 6 weeks. Their size and the fact that these animals remained in close proximity to one another and returned to the same nest indicated that these animals were newly independent in October 2008. Although late in the year, second or late litters have been reported in a number of studies (Barrett-Hamilton & Hinton 1911, Deanesly 1934, Morris 1961, Morris 1966). Jackson (2006) found that 81% of females bred again in the later part of the season and in his study all nine adult females, that had failed early season breeding attempts, attempted to breed again. It is unlikely that all hedgehogs have two litters a year, since some, including parous animals, do not come into their first oestrus until June or even later (Deanesly 1934). Animals born in the preceding August or September might not be ready to breed until nearly a year old, and these may account for some of the pregnancies in the second half of the breeding season (Deanesly 1934). A late litter was also recorded in the present study in a hedgehog collected as road kill. A hedgehog killed on the 6^{th} September 2009, was in the latter stages of pregnancy with six young. In 2009, courtship was observed from April onwards and similarly juveniles were found at the site earlier than in 2008, with the first observed in July, weighing 299g. This coincided with the month in which there were peaks in newly independent juveniles collected as road kill.

According to Doncaster *et al.* (2001) hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. Becher and Griffiths (1998) examined genetic differentiation among local hedgehog populations in the U.K., and found significant genetic differentiation, and restricted gene flow, among closely spaced hedgehog populations, indicating that dispersal among hedgehog populations occurs rarely. This therefore raises the question of the amount of genetic variation that exists between local populations and the effects of inbreeding (See Chapter 8). As a non territorial animal the hedgehog is largely free from the constraints of moving, to form new territories, and so may remain if there is a sufficient food and nest sites available. In the present study the late juveniles caught in 2008 were at first observed all returning to the same nest, but, as the week progressed they gradually moved further into the 15 ha arable field and began occupying separate nests. One juvenile hedgehog was tagged throughout hibernation and for the first week after emergence in 2009, he remained in the arable field, before moving into the pasture that was occupied by all of the tagged adults. While two transient males were seen at the site in 2009 during the breeding season, all of the tagged hedgehogs remained in the study area for the duration of the study and occupied the same area each year, reaching densities of 3.07/ha in 2008 and 6.06/ha in 2009 when all individuals at the site were included (Chapters 3 and 4). As mentioned previously, while the habitats are not directly comparable, this density is high in comparison to the 2.5/ha in sand dunes in New Zealand and 0.16/ha in rural Switzerland (Egli 2004). In the present study, a juvenile caught in 2009 occupied the same area in the first month after hibernation and then gradually made exploratory trips out of the core area. However, despite this he always returned to the central home range occupied by adults, until he was killed in June 2010. It therefore seems probable that although male hedgehogs may disperse during the breeding season, in order to encompass the range of as many females as possible, they will return to the core area of their home range if sufficient resources are available. The home range of males completely overlapped not only with one another, but also all of the adult females allowing the males to locate more females. In contrast females occupied mutually exclusive areas (Chapter 4). In two consecutive years, the adult female whose range slightly overlapped that of another female, moved away from the core area at the end of May, before moving into the arable field in September with the other adults. In 2009, her weight and condition just prior to this time indicated that she was about to give birth, having put on 112g. When she was next seen active (and weighed) she had lost 198g (Chapter 6). Jackson (2006) found that a female's mass increased by 50-150g during pregnancy and dropped suddenly at birth. With respect to the female who was collected as road kill in the latter stages of pregnancy, the four foetuses were found to weigh 164g in total. In the present study the female's move out of her core home range area to give birth may therefore have been a mechanism for regulating numbers in her central home range, thereby reducing resource competition and the possibility of inbreeding. In rodents of the genus *Peromyscus*, home ranges are maintained by mutual avoidance at low densities and pregnant females will frequently abandon their home range and establish a new home range in a nearby habitat, suggesting that females are more instrumental than males in regulating recruitment (Wolff 1989).

When comparing breeding activity to the number of hedgehogs collected as road kill, a peak in casualties corresponded to the culmination in courtship behaviour observed at the study site (May to July). Male traffic victims were found to peak in May, which coincided with the onset of courtship behaviour at the site. At this time males may make exploratory movements into the home ranges of females and restrict these movements once potential partners are discovered. At the study site adult males had a mean monthly home range (n=4) of 15.1 ha ± 0.42 in April but this doubled to 30 ha ± 1.03 in May (Chapter 4). Their home range remained stable during the breeding season but retracted from 25.3 ha ± 0.6 (July) to 5.13 ± 0.47 (August) thereafter (Chapter 4). In the present study, as previously stated, courtship behaviour occurred almost exclusively in the pasture, which was the core area of the females' home range. When courtship behaviour terminated hedgehogs moved out of this habitat. A preponderance of female road kill was found in July in 2008 and 2009, which as suggested above may be attributed to a move out of their core home range to give birth.

7.5.1 Conclusion

This is the first record of courtship behaviour, sex biases and observations of offspring in Irish hedgehogs. A strong male bias was observed amongst the study group, which could account for the high number of repeat pairings observed in the group, in comparison to studies elsewhere. Similar to research elsewhere in Europe, courtship behaviour was observed between April and July, which corresponded to peaks in hedgehog road kill. The presence of newly independent juveniles in October at the site and as road kill, indicate that, similar to the U.K., late litters occur in Ireland. Little dispersal was observed amongst the study group, outside the breeding season and densities of hedgehogs at the site remained high, indicating that resources must be available to support this high density of hedgehogs (see Chapter 5).

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Chapter 8-
Genetic variation amongst Irish hedgehogs

8.1 Abstract

The first records of hedgehogs in Ireland are from the 13th Century, and there has been some suggestion that they were introduced as a source of food. Hedgehogs are polygynous and, although the home range of males increases during the breeding season, there is no known dispersal period. The aim of this work was to examine genetic variation between local hedgehog populations to investigate whether dispersal occurs. In addition, 11 samples from a small area of North West France were examined as an out group for comparison. Ear clips were obtained from 20 individuals at a site in Co. Cork. An additional 74 tissue samples were collected from Irish road kill. These samples were screened for genetic variability at eleven available microsatellite loci. There was greatly reduced variability among the Irish samples when compared with those from France, and with the data from U.K. samples included in the primer notes of Becher and Griffiths (1997) and Henderson *et al.* 2000. Three of the loci were monomorphic in the Irish samples. The lack of genetic variation and the fact that three of the loci in the current study were monomorphic indicates a historical genetic bottleneck amongst Irish hedgehogs and may even imply a single introduction of this species.

8.2 Introduction

It is suggested that the majority of Ireland's fauna was introduced either accidentally or deliberately, with over 50% of all Ireland's mammals, reptiles, amphibians and freshwater fish coming to Ireland in this way (Hayden & Harrington 2001). For example, the Pygmy Shrews (*Sorex minutus*) was previously thought to have colonised Ireland via a landbridge linking Britain and Ireland, however research by Mascheretti *et al*. (2003) suggested they were introduced by boat from south west continental Europe. Molecular dating with both mitochondrial DNA and microsatellite data by McDevitt *et al.* (2009) was also consistent with a human introduction.

Britain has a fauna similar to the nearby areas of continental Europe. By contrast, Ireland has some species that occur in southwest Europe (Martínková *et al.* 2007) i.e. a Lusitanian distribution.

Between some species that occur in Britain and Ireland a degree of genetic variation is evident. The Scottish and Irish mountain hare (*Lepus timidus hibernicus*) populations have very different genotypic distributions, and are believed to have colonised by different easterly and westerly routes (Hamill *et al.* 2006). Ireland's pine marten (*Martes martes*) population is more differentiated than in other areas of its range, with less genetic differentiation (Kyle *et al.* 2003) and in research by Finnegan *et al.* (2008), the red squirrel (*Sciurus vulgaris*) in Ireland was found to share just one haplotype with the U.K.

In the fossil record of Europe, the hedgehog (*Erinaceus* sp.) appears for the first time during the older Pleistocene (> 25 Kyrs BP), and during the Pleniglacial (>23000 BP) (Sommer, 1997). During the last Glacial Maximum, the western European hedgehog (*Erinaceus europaeus*), was restricted to the Iberian and Italian peninsulas and showed a gradual dispersion out of the glacial refugia (Sommer 2007). The distribution of this species seems to have been fairly constant since the early Holocene (Sommer, 2007) and within *Europaeus*, three monophyletic clades are seen, termed E1, E2 and E3. The E2 clade is found only in Western Europe, from Spain northwards through France, the Netherlands and into the U.K. and Ireland (Seddon *et al.* 2001). In Ireland the hedgehog was first recorded in the 13th Century in Waterford (Yalden 1999). It is unclear, how it arrived in Ireland but there is some suggestion that it was intentionally introduced as a source of food (Savage 1966).

Little attention has been paid to patterns of genetic variation in hedgehogs. To date, just 11 sets of primers for microsatellite loci in the European hedgehog have been published (Becher & Griffiths 1997, Henderson *et al.* 2000). These have previously been used to examine dispersal amongst localised populations (Becher & Griffiths 1998) in the U.K. and to determine whether multiple paternity occurs (Moran *et al.* 2009).

After six weeks of age, juvenile hedgehogs lead solitary lives and although not territorial exhibit mutual avoidance (Reeve 1994). There is little known about the dispersal of hedgehogs (Brockie 2007) and Doncaster (1993) suggested that hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. However, Doncaster *et al*. (2001) found that although natural dispersals were relatively rare events, hedgehogs were capable of travelling up to 3.8km from a release point and up to 9.9 km in total. Becher and Griffiths (1998) examined genetic differentiation among local hedgehog populations in the U.K. and found significant genetic differentiation and restricted gene flow among closely spaced hedgehog populations, indicating that dispersal among hedgehog populations occurs rarely. This together with the recording of tagged individuals at the same site in successive years (Chapter 4) and Reeve's (1982) findings that individual hedgehogs showed a tendency to remain in the same locality from one year to the next, indicate that some hedgehogs at least, may show site philopatry and will remain in an area if sufficient conditions are maintained.

This study aimed to investigate the relationship between the group of twenty individuals (including adults and juveniles) captured and recorded at the 93 ha focal study site over three years. Of particular interest were the question of dispersal and the identity of parents. In addition, clusters of road kill collected at three other Irish sites in the same time period were also examined to determine whether these clusters were more closely related to one another than to other Irish populations. This was to examine the hypothesis that there would be a lack of genetic variation amongst both the field site and these clusters in accordance with reduced dispersal amongst localised populations. Finally, road kill samples collected throughout Ireland were studied to look at genetic variation amongst the national population of hedgehogs, using samples from France as an out group for comparison.

8.3 Materials and methods

8.3.1 Local scale (Ratharoon)

From June 2008-2010, 24 hedgehogs were radio tagged in a 93 ha site at Ratharoon, Co. Cork. Nineteen of these hedgehogs were considered residents and caught regularly over the three years. Ear clippings were taken from 20 of these individuals, consisting of both adults and juveniles (Table 8.1, Fig.8.1).

Table 8. 1: The sexes and ages of 20 hedgehogs from which tissue samples were obtained, at Rathroon Co. Cork.

	Juvenile	Adult
Male	6	8
Female	2	4

8.3.2 Regional scale (clusters of road kill)

At three other sites, road kill were collected at the same spot over a three year period. Two of these sites were in County Cork, with 18 collected from a site in Muskerry and ten in Ballinhassig. At a third site in Caherlistrane Co. Galway, nine were collected (Fig.8.1).

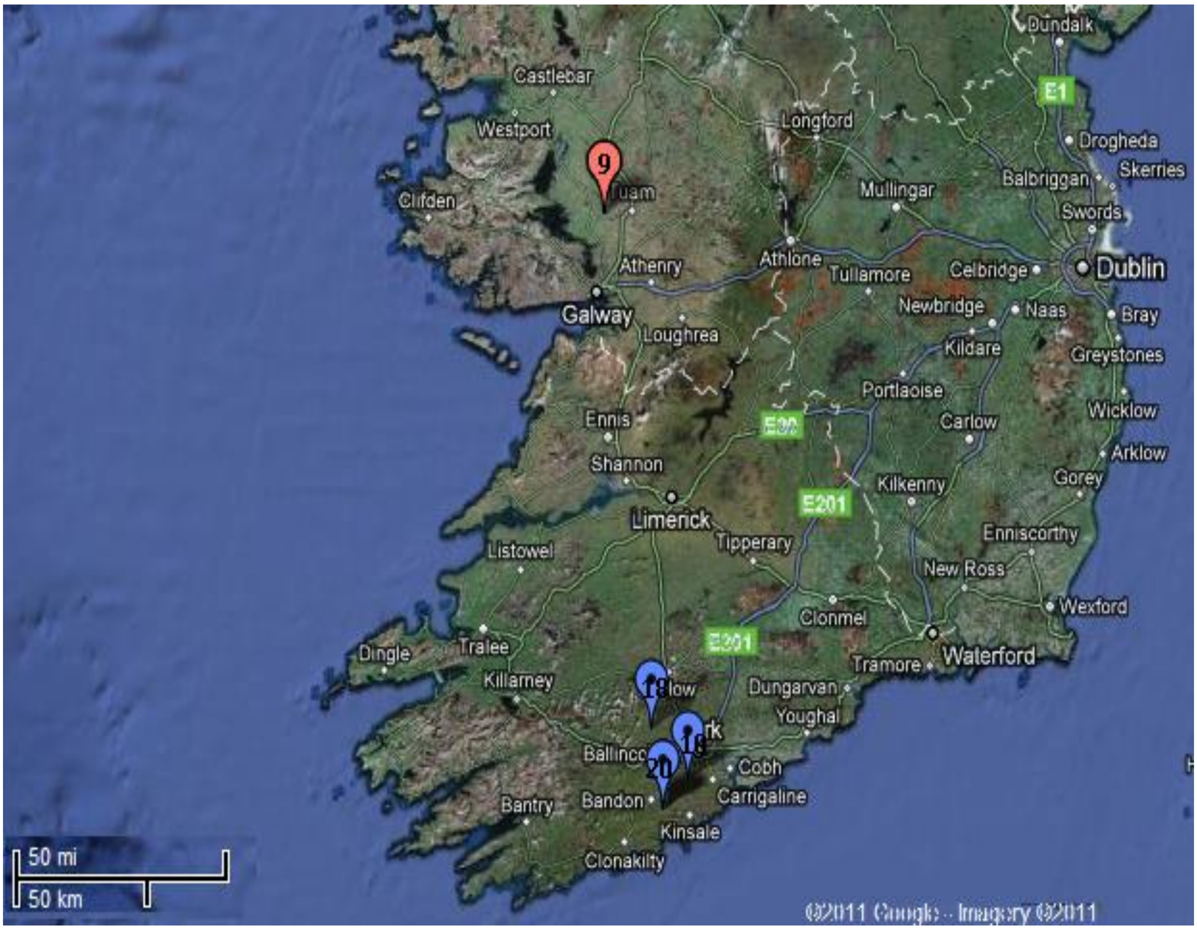

Figure 8.1: The location of the study site and the three areas where hedgehogs were collected regularly over the three year study.

8.3.3 National scale

An additional 37 hedgehogs were collected from random locations from around Ireland (Fig. 8.2), including two pregnant females with their foetuses (n=5 and n=6). These samples were checked for multiple paternity. A further 11 samples were collected opportunistically from road kill in North West France.

Figure 8.2: The location of where 37 hedgehog road kills were collected.

All of the samples (n=105) were screened for genetic variability by Dr Eileen Dillane (School of Biological, Earth and Environmental Sciences (BEES), UCC), at the eleven available microsatellite loci (Table 8.2) (Becher & Griffiths 1997, Henderson *et al.* 2000). Analysis was confined to nuclear DNA, with no analysis of mitochondrial DNA. Microsatellite DNA markers consist of a short sequence of one to 6 nucleotides and have the advantage that they are highly polymorphic which results from a high mutation rate. A microsatellite mutation usually results in a change in the number of repeats (Allendorf & Luikart 2007). Variation in the number of repeats of each allele is detected by amplifying DNA using PCR (Frankham *et al.* 2004). Of the eleven available microsatellite loci, one of these loci (*EEU*6) (Becher & Griffiths, 1997) was dropped because it failed to reliably amplify products in individuals.

8.4 Results

Genetic variability was somewhat less among the Irish samples when compared with the French samples, and with the data from U.K. samples included in the primer notes (Becher & Griffiths 1997, Henderson *et al.* 2000) (Table 8.2). In eight out of the ten loci more alleles were observed in the French samples (n=11) than in the entire Irish sample set (n=94). In fact, there was more genetic variation between French samples that were situated geographically close to one another than there was in the entire Irish sample. Three of the loci were monomorphic in the Irish samples. These levels of variation were so low that it was not possible to determine family relationships within the study group at Ratharoon or amongst the clusters. There was no indication of multiple paternity in the foetuses examined.

Table 8.2: Numbers of alleles (as an indication of inherent genetic variability) observed at each locus.

Microsatellite loci	Original study (Becher and Griffiths, 1997)	All Irish samples	French samples
N	**150**	**94**	**11**
***EEU*1**	8	1	3
***EEU*2**	7	5	7
***EEU*3**	6	6	5
***EEU*4**	9	4	5
***EEU*5**	8	5	7
	Henderson *et al.* 2000		
	132	**94**	**11**
***EEU*12H**	7	1	4
***EEU*36H**	5	1	2
***EEU*37H**	6	3	5
***EEU*43H**	9	4	7
***EEU*54H**	8	7	3

8.5 Discussion

There was greatly reduced variability among the Irish samples when compared with the French, and with previous data from U.K. samples. The variation was so little that it was not possible to ascertain family relationships and dispersal among clusters and the study group. However, the fact that hedgehogs at the study site displayed philopatry following the same pattern of habitat selection annually (Chapter 4), suggests that dispersal events are rare amongst local populations. This is also suggested by research by Becher and Griffiths (1998) who found no significant genetic differentiation and restricted gene flow among closely spaced hedgehog populations, indicating that dispersal among hedgehog populations occurs rarely. Greenwood (1980) stated that "Philopatry will favour the evolution of cooperative traits between members of the sedentary sex. Disruptive acts will be a feature of dispersers". As a non territorial polygynous species, the hedgehog is largely free from the constraints of moving, to form new territories and so may remain if there is sufficient food and nest sites available. As mentioned in Chapter 7, in shrews (*Sorex araneus*), since females cannot always distinguish between close kin they may copulate with several different males, thereby reducing the risk that all of their offspring will be sired by a close relative (Stockley *et al.* 1993). Multiple paternity has been reported in shrews and in the hedgehog (Moran *et al.* 2009) and may be a useful way for a non territorial animal, like the hedgehog, to reduce inbreeding depression and the need for dispersal. Multiple paternity was not apparent in the foetuses of the two pregnant females included here. This may have been because multiple paternity did not occur, or again because the low levels of genetic variability which characterise the Irish samples meant that it could not be determined with these markers.

Based on the research on their behaviour and home ranges (Chapter 4) females in contrast to males occupied mutually exclusive areas (Chapter 4) and in two consecutive years, an adult female whose range slightly overlapped that of another female, moved away from the core area at the end of May, before moving back in September (Chapter 7). As stated in Chapter 7, the female's move out of her core home range area to give birth may have resulted in a reduction of resource competition and the possibility of inbreeding. In rodents of the genus *Peromyscus*, home ranges are maintained by mutual avoidance at low densities and pregnant females will frequently abandon their home range and establish a new home range in a nearby habitat, suggesting that females are more instrumental than males in regulating recruitment (Wolff 1989). While, only based on a small sample over two years, it is suggested that this may also happen amongst hedgehogs.

Frankham (1997) found that a significant majority of island populations have lower levels of genetic variation than corresponding mainland populations and introduced populations typically have lower levels of genetic variation than native ones. The difference between the Irish, French and

U.K. samples, suggests that the Irish hedgehogs were founded from a small number of individuals, resulting in a genetic bottleneck.

The observed monomorphic profiles for nuclear coding loci in the cheetah (*Acinonyx jubatus*) has been attributed to an ancient Pleistocene bottleneck that rendered the cheetah depauperate in genetic variation for nuclear coding loci (Menotti-Raymond & O'Brien 1993). The northern elephant seal *(Mirounga angustirostrus)* was heavily exploited in its recent history and as a result, it displays a low genetic variation which is consistent with an extreme founder event in the recent history of the species (Hoelzel *et al.* 1993). This has also been observed amongst the similarly exploited Guadalupe Fur Seal (*Arctocephalus townsendi*) (Weber *et al.* 2004). A low genetic diversity was also apparent in the pygmy shrew in Ireland; something McDevitt *et al.* (2009) suggested was related to a small number of founders and a rapid expansion thereafter. The hedgehog was first recorded in Ireland in the 13th Century, with no records predating this time (Yalden 1999). In areas where it has been introduced it has expanded rapidly, which is consistent with Doncaster *et al's.* (2001) research that demonstrated that although natural dispersals were relatively rare events, hedgehogs were capable of travelling up to 3.8km from a release point and up to 9.9 km in total. Four individuals were believed to have been introduced to the southern end of South Uist in 1974. By the mid 1990s hedgehogs were abundant throughout the more fertile areas of South Uist, Benbecula and the extreme south of North Uist, reaching densities as high as 30-50 per km^2 (Jackson *et al.* 2004). Similarly in New Zealand, where the hedgehog was introduced in the late 19th Century (Brockie 1990) to the South Island (Bolfikova & Hulva 2011), hedgehogs reached the limits of their range in the South Island in the 1940s and the limits of the North Island in the 1950s (Brockie 1975).

The lack of genetic variation and the fact that three of the loci in the current study were monomorphic would indicate a historical genetic bottleneck amongst Irish hedgehogs and may even imply a single introduction of this species. However, further genetic investigation into the Irish hedgehog is required using mitochondrial DNA to get a clearer idea of the colonisation routes and origins of the Irish hedgehog.

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Chapter 9-
Road mortality of hedgehogs *(Erinaceus europaeus)* in Ireland.

9.1 Abstract

Hedgehogs are one of the most common mammalian road fatalities. Between April 2008 and November 2010, two stretches of road measuring 227 km (Cork City to Caherlistrane, Co. Galway) and 32.5 km (Cork City to Bandon, Co. Cork) respectively were surveyed for hedgehog road kill. During the same time period carcasses were collected from around Ireland and the sex and age group were recorded. Over the three years, a total of 50,430 km were surveyed and 133 hedgehog fatalities were observed between the two surveyed roads, representing 0.264 per 100km. The greatest number of casualties was detected during the summer months, with monthly peaks occurring in April, May and August. In addition to the sightings of road kill on the two stretches of road, a further one hundred and thirty five carcasses were collected over the study period from throughout Ireland. There were significantly more males than females collected as road kill, with peaks in male deaths occurring in May and June. Female deaths only outnumbered males in August, with a further peaks observed in June and July. Peaks in juvenile casualties were detected from June to September. It is suggested that these peaks are related to the breeding season (adults) and dispersal/ exploration following independence (juveniles). Over the three years, the majority of the 133 carcasses sighted along the scheduled routes were located beside areas of pasture, which was the most prominent habitat along both stretches of road. A greater number of hedgehog road kill were observed beside arable land than what would be expected from the proportion of this habitat that was available along these routes. This would indicate that this habitat is selected by hedgehogs. K function analysis detected clustering along the surveyed roads, with fatalities clustered annually at several locations. While the annual numbers of hedgehogs killed on the road remained stable on the road from Cork to Bandon, there was a decrease on the route from Cork to Caherlistrane between 2008 and 2009/10. The lower densities of hedgehog road kill per km in the current study when compared to elsewhere, may indicate a lower number of hedgehogs in Ireland. However, low incidences of road kill in areas where hedgehogs were observed at high densities would instead

imply a greater opportunity for hedgehogs to encounter larger busier roads in other areas of their range.

9.2 Introduction

The European hedgehog (*Erinaceus europaeus*) is strictly protected in the Republic of Ireland and is listed in Appendix III of the Bern Convention as a species requiring protection and under the Wildlife Act 1976, 2000 (Hayden & Harrington 2001). Hedgehog numbers are thought to be in decline in the U.K. and Hof (2009) estimated that, although hedgehogs still occur throughout the U.K., the relative abundance had fallen by about 16% in the past 30 to 40 years. In the Netherlands it is estimated that between 113,000 and 340,000 hedgehogs are killed each year on roads reducing the population by between 3-22% (Huijser *et al.* 1998). According to Forman and Alexander (1998) sometime in the last three decades, roads probably overtook hunting as the leading direct human cause of vertebrate mortality on land.

Hedgehogs are one of the most common mammalian road casualties (Sleeman *et al.* 1985, Huijser *et al.* 1998, Holsbeek *et al.* 1999, Smiddy 2002, Hell *et al.* 2005), largely due to their main line of defence being to roll up in a ball. Holsbeek *et al.* (1999) reported that of 7706 fatalities in Belgium, found over a period of 24 months, 1281 were hedgehogs, with hedgehogs and rabbits representing over 60% of the road kill. Keymer at al. (1991) observed that of 74 hedgehogs examined for parasites in the U.K., 35 (47.3%) were road casualties. However, Lodè (2000) reported that hedgehogs represented only 2.8% of vertebrates killed on motorways in France and in a study in Sweden they represented just 4% (Seiler *et al.* 2004). In Poland, the annual loss of hedgehogs on the road in the 1990’s, constituted 24% of the population (Orlowski & Nowak 2004).

The expanding network of major roads has been frequently identified as one of the negative factors affecting hedgehog presence and/or abundance in the U.K. (Hof 2009). As well as causing significant mortality in this species, Jaeger *et al.* (2005) found that populations living in habitat surrounded by roads are less likely to receive immigrants from other habitats, and thus may suffer from lack of genetic input and inbreeding. Similarly Huijser and Bergers (2000) also suggested that roads and traffic are likely to reduce hedgehog density by about 30%, which may affect the survival probability of local populations. Rondinini and Doncaster (2002) observed that there was a significant tendency for both sexes to avoid crossing roads, with avoidance increasing in proportion to road width.

In Belgium the pattern of hedgehog road kill shows a gradual increase towards July (>300) gradually decreasing to less than 10 towards December and January (Holsbeek *et al.* 1999). Smiddy (2002) also observed this in Ireland, with a peak in casualties occurring between April and June. The majority of sexual activity occurs from May to mid August (Reeve 1981) and Kristiansson (1984) noted that in Sweden male hedgehogs increased their home range during the breeding season. Huijser (1998) reported a 3 to 1 preponderance of males amongst hedgehog traffic victims in the Netherlands. Similarly, in Sweden, Goransson *et al.* (1976) found that 80% of traffic victims were male hedgehogs who had survived one winter. A preponderance of males in road kill may affect population structure and the resulting reduced competition between males could eventually lead to negative effects on population vitality (Huijser 2000). However, in autumn Goransson (1976) recorded that high numbers of females were killed, which was attributed to a greater need to forage wider, in order to build up fat prior to hibernation after raising young.

This study aimed to test the following questions:

- Do the greatest numbers of hedgehog road fatalities occur during the breeding season?
- Are more males are killed than females?
- Can road kill confirm that a late/second litter occurs in Ireland?
- Are there fewer road casualties in Ireland than elsewhere?

9.3 Materials and Methods

9.3.1 Focal road survey

To examine for seasonal and sex biased patterns two stretches of road in different parts of the country were selected to be intensively studied. One of these roads was chosen as it was the main arterial road between two Irish cities; the second, in Munster, was the main road to the focal study site, and linked Cork City to the county. Between April 2008 and November 2010 (excluding December), these two stretches of road (Fig. 9.1a and b) were surveyed for road kill. These roads, representing a total distance of 259.5 km, were surveyed at regular intervals for 10 months of the year, excluding December and January. The 227 km from Cork to Caherlistrane, Co. Galway was surveyed 150 times (~ 5 times/month) and the 32.5 km from Cork to Bandon 504 times (~18 times/month). This gave a total survey distance of 50,430 km over the three year period. GPS co-ordinates were taken and the habitat recorded.

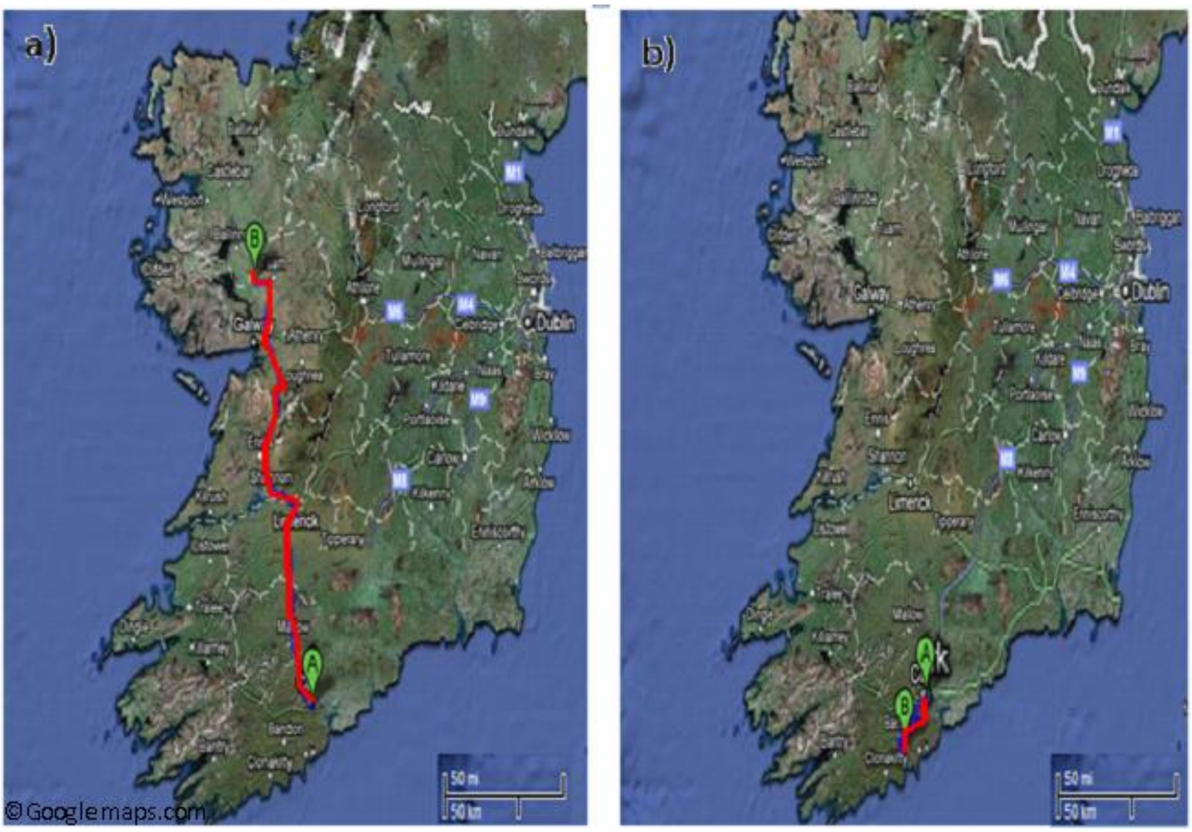

Figure 9.1 a -b: The road from Cork city to Caherlistrane Co Galway (227 km) (a) and Cork to Bandon (32.5 km) (b).

9.3.2 *Unscheduled journeys*

On all other unscheduled journeys around Ireland by the author, all hedgehog road kill were recorded and converted to numbers per km. These roads representing a total distance of 7,036.66 km and were driven from 2008 to 2010 (Fig. 9.2). Hedgehogs were only recorded if they could be positively identified and in the majority of cases the carcass was collected for further analysis.

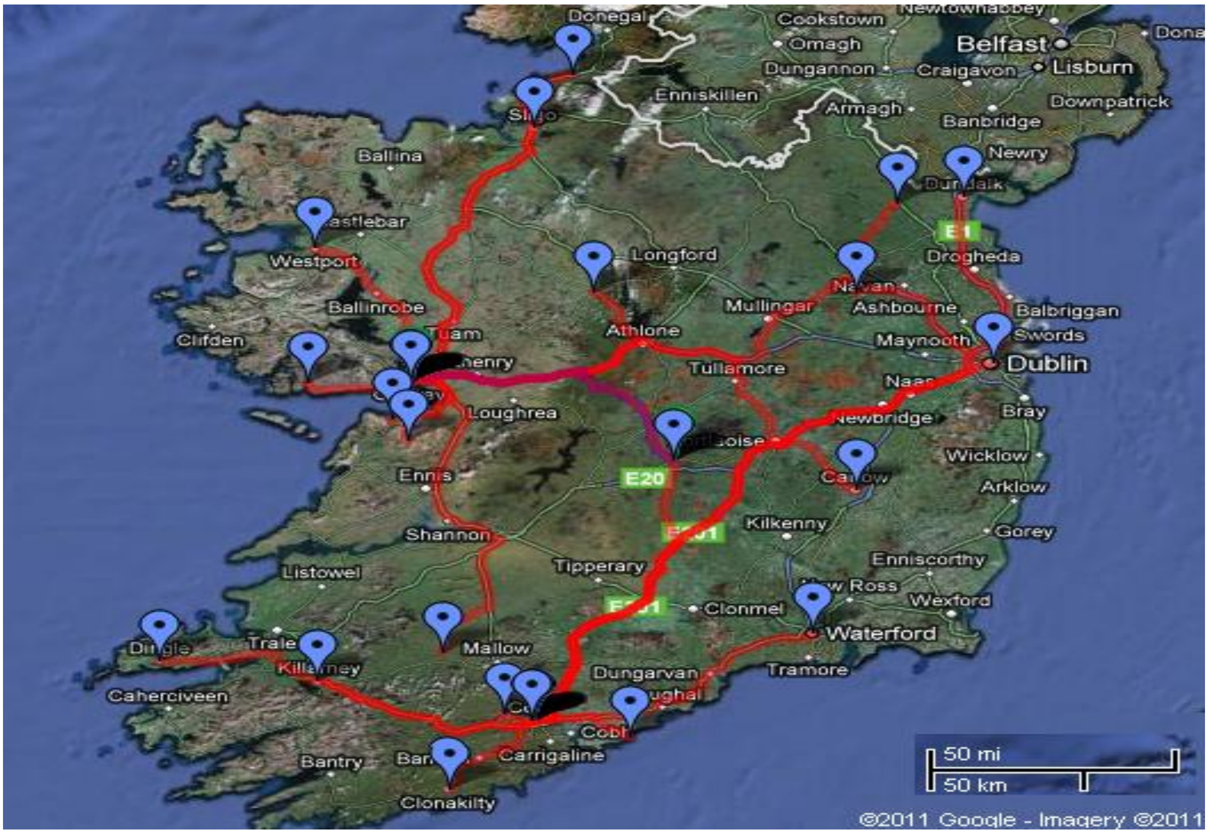

Figure 9.2 : The 7,036.66 km of unscheduled journeys taken throughout Ireland over three years.

9.3.3 Age and Sex ratio of road kill

In the same time period, hedgehog carcasses were collected by the author and members of the public from all over Ireland (Appendix 6). All carcasses collected were sexed and aged. The hedgehog was considered to be a juvenile if it satisfied two or all of the following criteria: weight less than 600g; hind foot length of less than 3.6cm (See Chapter 6); and presence of growing spines. In some cases due to the nature of the fact that the individual had been killed on the road, an accurate weight could not be obtained.

7.3.4 Habitat

Habitat along the two scheduled routes were scored in accordance with that of Morris and Morris (1988), i.e. the habitat type on either side of the road of the casualty location recorded. When the habitat type occurred on both sides it was given a rating of 1 and if only on one side a score of 0.5. The habitat categories are listed in Table 9.1. The proportion of each habitat along both routes was quantified through examining aerial photographs of the route on Google Earth and the Ordnance Survey Ireland website (www.osi.ie).

Table 9.1: Habitats encountered along the routes and their definition.

Habitat	**Definition**
Pasture	Grassland (grazed or silage)
Arable	Barley or wheat
Residential	This includes single houses and gardens or housing estates.
Woodland	Deciduous woodland
Scrub	Areas that were predominantly made up of bramble and gorse bushes.
Marsh	Wetland areas consisting predominantly of reeds.
Railway	Areas predominantly bordered by an active railway line.
Industrial estates	Business parks, office blocks and shopping complexes.

7.3.5 Clustering

K function analysis on Arc GIS was used to establish whether road mortalitys occurred randomly along the road network or were clustered. The calculation of K functions allows the determination of the level of clustering exhibited by one set of spatial events relative to another(Jones *et al.* 1996). This consists of two classifications of points, one representing what would be expected if road kill occurred randomly and the other where the road kills have been observed. Deviation of the observed line above the expected line indicates that the dataset is exhibiting clustering at that distance (http://resources.esri.com). Conversely any values which lie above the confidence envelops are considered a significant deviation from what would be expected from complete spatial randomness (Spooner *et al.* 2004). As K functions cannot detect where clusters are located geographically, clusters were defined as areas where two or more carcasses had been observed less than 500 metres distance from one another.

7.4 Results

Over the three years 133 hedgehog fatalities were observed over 50,430 km (i.e. the sum of the two focus roads, for all survey dates combined) giving a total of 0.264 casualties per 100km. Hedgehogs constituted 24% of all recorded mammalian road kill over all, with only rabbits occurring more often (Table 9.2, Appendix 5).

Table 9.2: Total number and relative proportions of mammalian road kill on the road between Cork and Galway from April 2008-November 2010 and the road from Cork to Bandon between February 2009 and November 2010.

Species	Total	%
Rabbit (*Oryctolagus cuniculus*)	140	26
Hedgehog (*Erinaceus europaeus*)	130	24
Badger (*Meles meles*)	75	14
Fox (*Vulpes vulpes*)	83	15
Rodent	72	13
Mink (*Mustela vison*)	15	3
Hare (*Lepus timidus hibernicus*)	10	2
Otter (*Lutra lutra*)	10	2
Pine Marten (*Martes martes*)	7	1
Stoat (*Mustela erminea hibernicus*)	6	1
Total	548	100

7.4.1 Months in which hedgehogs were killed on the focal roads.

When the data for the two roads were combined these casualties peaked in April, May and August (Fig. 9.3). Summer (May-July) represented the period where the greatest numbers of fatalities were observed, followed by autumn (August-October) and the lowest number occurred in Spring (February-April), however, this variation was not significant (F=0.722, P>0.05).

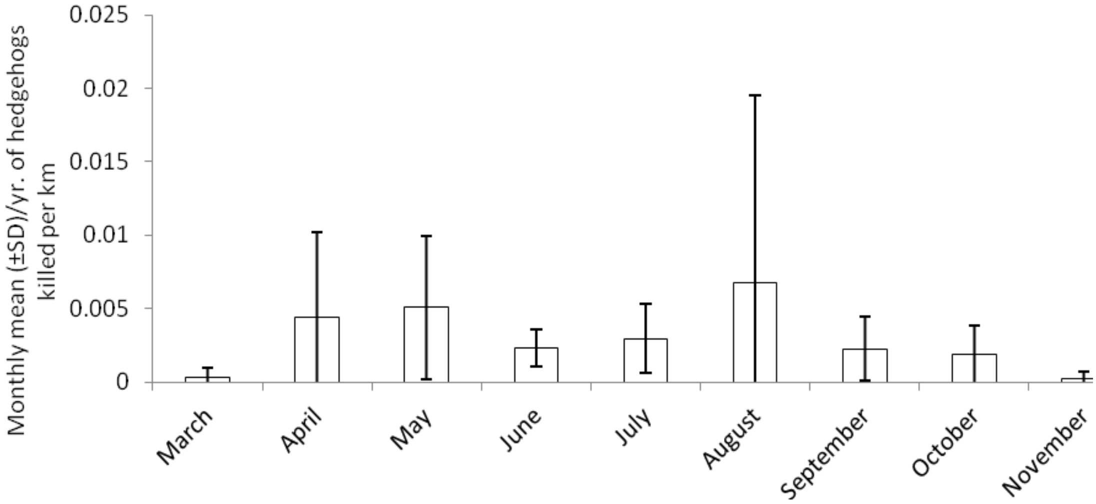

Figure 9.3: The monthly mean (± SD) of hedgehogs per year killed from 2008-2010 on both focal roads.

The route from Cork to Caherlistrane, Co. Galway constituted 34,050 km over the three years. Over that time 112 hedgehog casualties were observed (0.329 per 100km). Cork to Bandon made up a further 16,380 km and over the study period, 21 hedgehogs were observed, representing 0.128 per 100km.

Peaks in fatalities occurred on the road from Cork to Caherlistrane in May and August, whereas on the road from Cork to Bandon peaks were observed in June and September (Fig. 9.4).

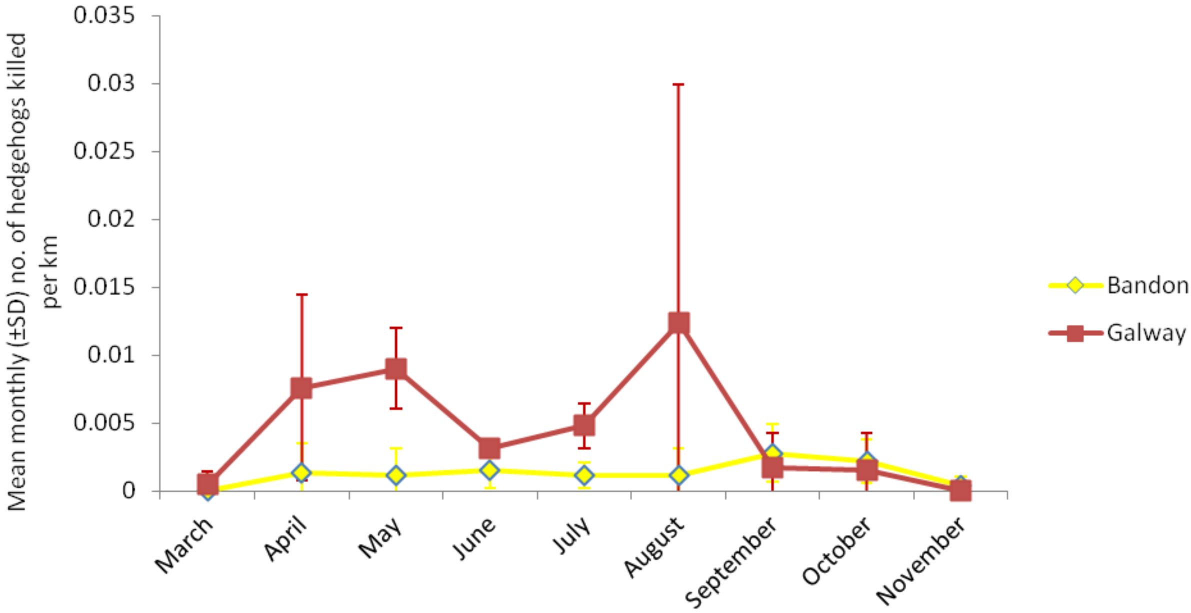

Figure 9.4: The monthly mean (± SD) number of hedgehogs per km/yr recorded as road kill on the road from Cork to Caherlistrane, Co. Galway and Cork to Bandon from 2008 to 2010. Hedgehogs were not seen as road kill from January to March in any year.

7.4.2 Unscheduled journeys

A further 7,036.66 km was undertaken by the author in random/unscheduled journeys in Ireland, over the three years. In this time, 88 further fatalities were observed, representing. 1.3 per 100km. On these other routes, peaks were detected in July and August (2008 and 2009) and April and July (2010) (Fig. 9.5). However, journeys were not undertaken every month over the three years.

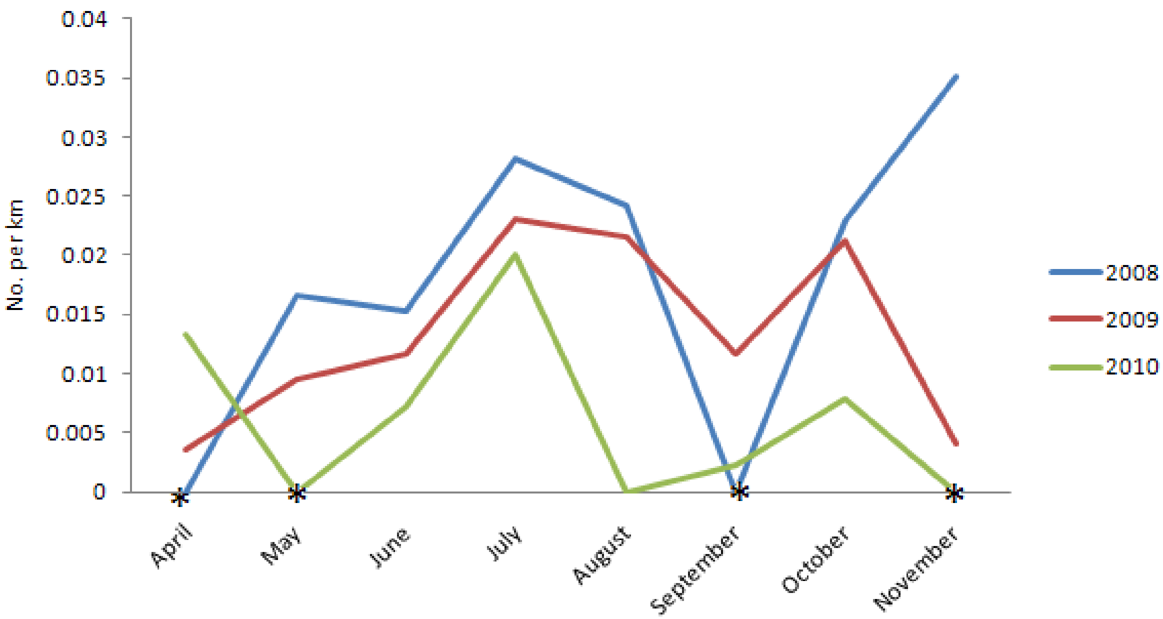

Figure 9.5: The number of hedgehogs observed per km on all other journeys around Ireland from March 2008 to November 2010. * Indicates a month and year when no journeys were undertaken

9.4.3 Age/sex ratio of road kill

One hundred and thirty five hedgehog carcasses were collected over the study period from all roads combined (Chapter 5). It was possible to sex 103 of these carcasses. There was significantly more males collected as road kill (χ^2=9.846, df=1, $p<0.01$) (Fig. 9.6), with a peak in male fatalities between May and July for juveniles and adults combined (Fig. 9.6). Female casualties peaked in May, June and August, with female deaths higher than males in August only (Fig. 9.6).

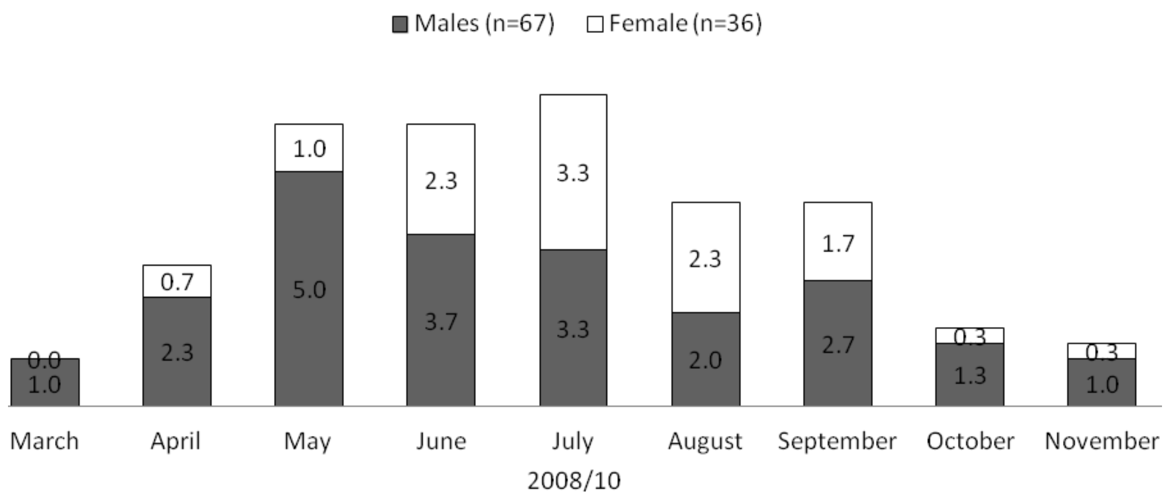

Figure 9.6: The monthly mean /yr of males and female hedgehogs collected as road kill from2008 to 2010.

Of the 113 carcasses that could be categorised as adult/juvenile, 37 (39%) were juveniles and 95 (61%) adults (Fig. 9.7). Juvenile fatalities peaked from July-September and adults from May to July (Fig. 9.7).

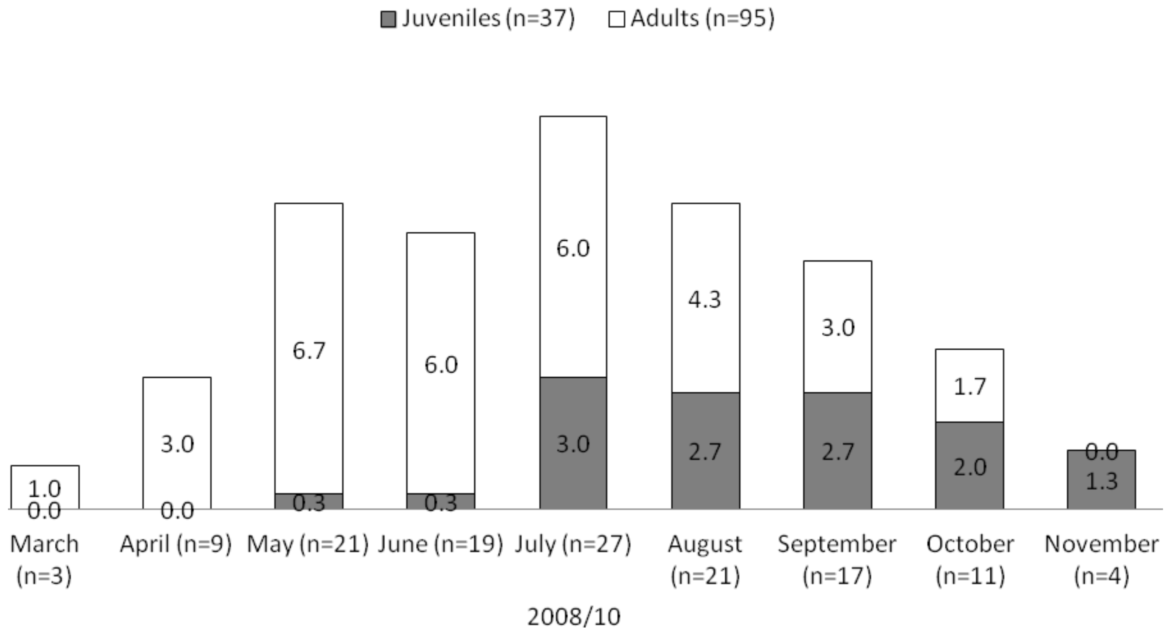

Figure 9.7: The monthly mean/yr of adults and juveniles collected as road kill per month between 2008 and 2010 (n=number collected per month).

7.4.4 Habitat

There was a significant variation in the habitat along which casualties were observed along the two focal roads (F=0.620, df=4, p<0.01). The majority (57%) of hedgehog carcasses were found on road ways that bordered areas of pasture (Fig. 9.8), which was significantly more than those found beside residential areas (p<0.01,Tukeys post hoc). Pasture was the most prominent habitat on both stretches of road, and the number of road kills beside these habitats would indicate that it was utilised in accordance with its availability (Fig. 9.8). These fields generally had good well developed hedgerow but on the few occasions where this was not the case; the pasture was bordered by areas of scrub. In most cases (n=30) when a carcass was found beside a residential area it was outside a solitary house bordered on the other side by pasture (n=23), arable (n=2), scrub (n=2), marsh (n=2) and railway (n=1). Only on one occasion was the site bordered by houses on both sides and this was in the centre of a town. All woodland was deciduous and hedgehogs were found on 13 occasions beside these areas. Woodland was situated on both sides of the road three times, on four occasions scrub was on the opposite side of the road and six pasture. Based on the number of road kills observed beside woodland, this habitat did not appear to be selected (Fig. 9.8). Arable land however, did appear to be selected with a greater number of road kills along this habitat than what would be expected based on the proportion of this habitat that was available (Fig. 9.8).This was the only habitat where habitat selection was observed (Fig. 9.8).

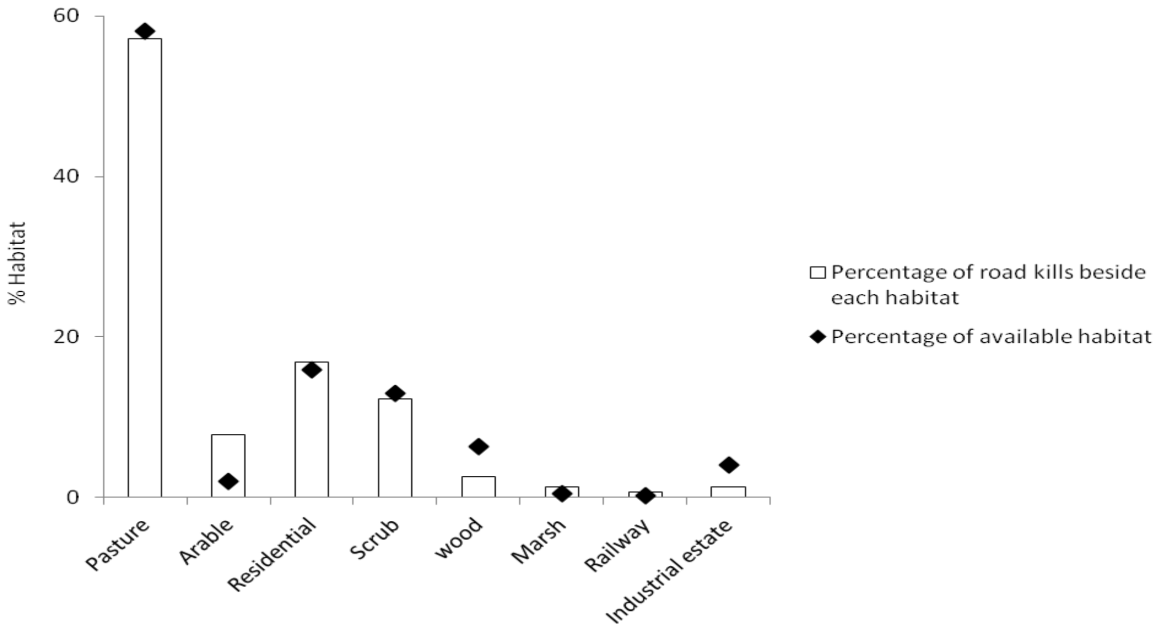

Figure 9.8: Percentage of available habitats on both stretches of road combined and the % of road kills observed along each habitat category between 2008 and 2010.

7.4.5 Clusters of road kill and yearly patterns

K analysis indicated that the distribution of hedgehog road mortality was more clustered than what would be expected from chance (Fig. 9.9).

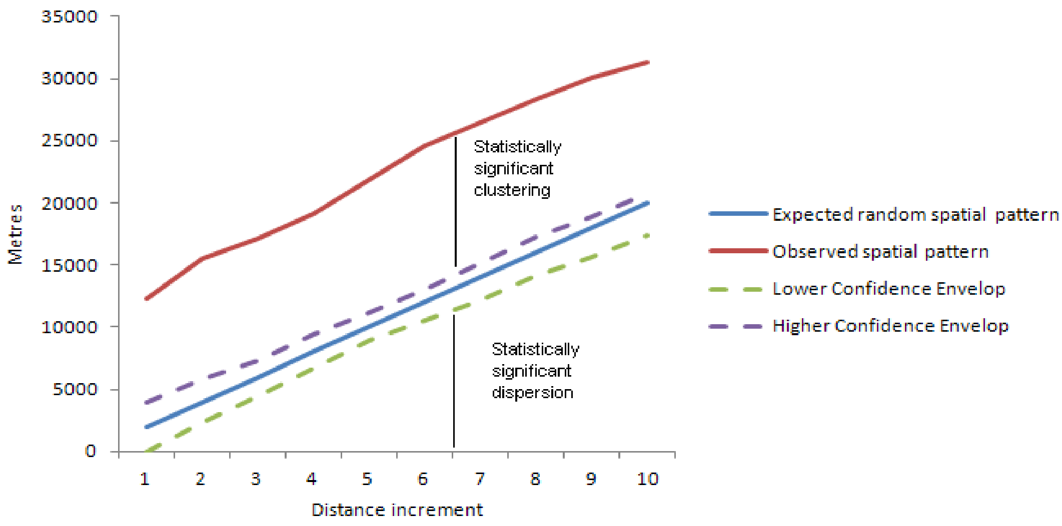

Figure 9.9: Observed and expected K-function curves for hedgehog road mortality from Caherlistrane Co. Galway to Bandon, Co. Cork.

Clusters were identified as areas where hedgehogs were killed at the same spot (<500 metres distance) on two or more occasions. In some cases this was in the same year or casualties may have been located at the same spot over the three year period. Clusters were observed in thirteen locations along the route from Cork to Caherlistrane, Co. Galway with up to six located at the same spot over the three year period (Fig. 9.10a-d). Nine of these clusters were located either at the entrance to a town or immediately before a junction.

Figure 9.10a: Section 1 (Caherlistrane to Gort)

Figure 9.9b: Section 2 (Gort to Limerick)

Figure 9.10c: Section 3 (Limerick to Buttevant)

Figure 9.9d: Section 4 (Buttevant to Cork)

Figure 9.10a-d: Hedgehog fatalities on the route from Cork to Caherlistrane Co. Galway over three years, with each blue symbol representing a hedgehog carcass.

On the road from Cork City to Bandon, Co. Cork six hedgehog carcasses were located in the same spot over a three year period, immediately before the junction at Five Mile Bridge (See “x6” on Fig. 9.11). A further six were located less than 1.8km away from this spot, with fatalities observed in all three years (Fig. 9.11).

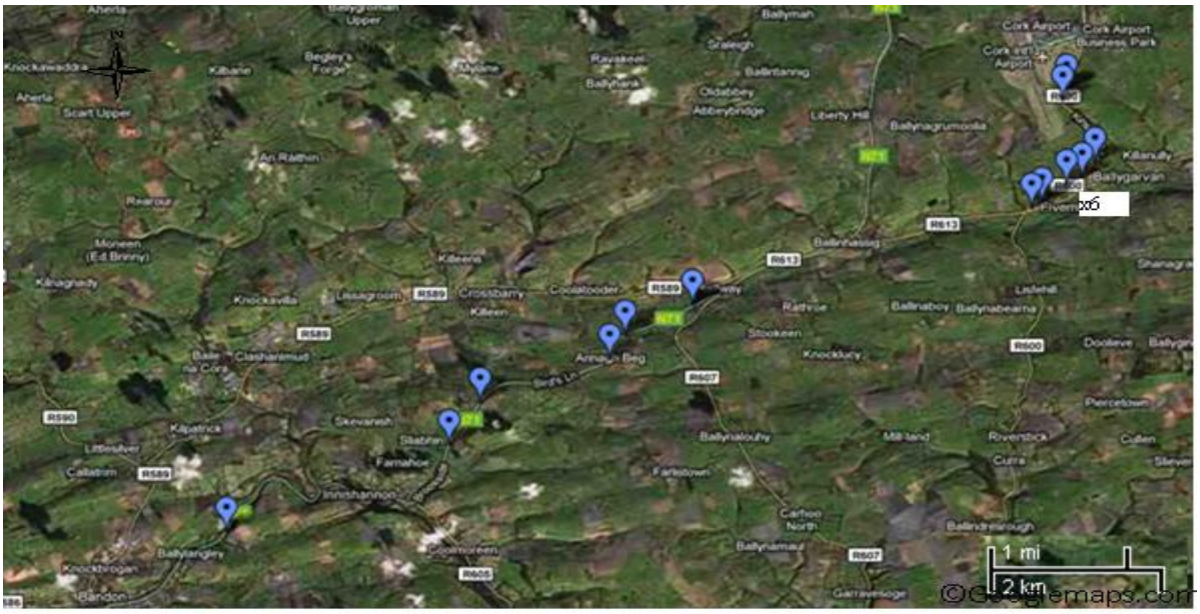

Figure 9.11: Hedgehog fatalities on the route from Cork city to Bandon over three years.

The number of fatalities observed each year remained stable on the route from Cork to Bandon but decreased each year on the road from Cork to Caherlistrane going from 58 in 2008, to 38 in 2009 and 16 in 2010 (Fig. 9.12).

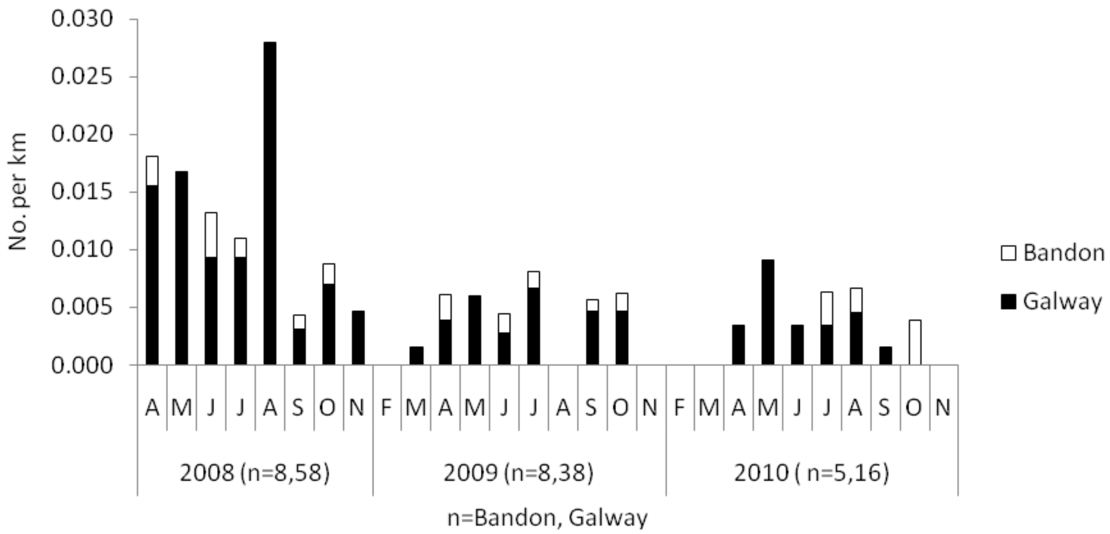

Figure 9.12: The number of hedgehog road kill observed per km each month from 2008 to 2010 on the road from Cork to Bandon and Cork to Galway (Caherlistrane) (n=the numbers observed along each road).

7.5 Discussion

Hedgehogs represented 24% of mammalian road kill, with only rabbits occurring more often. While the high incidence of rabbits may be accounted for by their high population densities ranging from 15 per ha in winter to up to 40 per hectare in summer(Hayden & Harrington 2001), this may or may not be the case with hedgehogs. Hedgehogs can run fast, reaching average speeds of 30-40 metres per minute (Morris 2006) but they will often not run when approached and will, instead, roll up, relying on their spines for protection. This therefore makes them particularly vulnerable to being killed on the road and perhaps more so than larger more conspicuous species like foxes and badgers, which were the next most commonly occurring mammals on Ireland's roads.

Over the three years 133 hedgehog fatalities were observed over the 50,430 km of the two focal roads, giving a total of 0.264 casualties per 100km. This was very low in comparison to Morris and Morris' (1988) study in New Zealand, where they found an average of 6.4 per 100km (range-3.4-58.3 per 100km). Including both national and local road networks, the Republic of Ireland has an extensive road network of 78,972 km over an area of 70, 273 km² (www.nra.ie). This equates to 1.28 km of road per km², which is lower than the 2.86 km of road per km² in New Zealand (calculated from statistics from New Zealand Transport Agency, www.nzta.govt.nz). This may partly explain the reduction in road kills in comparison to New Zealand, as this low number of fatalities was evident amongst all mammals recorded as road kill (See Appendix 5). In Belgium, where there is a particularly high density of roads at 3.8 km roads per km², Holsbeek *et al.* (1999) found that 2.3 hedgehogs per km were killed. Live hedgehogs were found at high densities of 3.07/ha and up to 6.06/ha in a mosaic habitat in Ireland (Chapter 3), with only one incidence of road mortality in the three year study (Chapter 4) and no reports from residents prior to this time(Chapter 2). Therefore, the greater number of road casualties in other countries may not be an obvious effect of density but more a greater opportunity for hedgehogs to encounter larger busier roads in other countries.

In the present study, hedgehog fatalities were observed on the two focal roads most commonly in the summer season followed by autumn, with monthly peaks in April, May and August.

On unscheduled roads these peaks were observed in July and August in 2008 and 2009 and April and July in 2010. In Belgium, the pattern of hedgehog road kill showed a gradual increase towards July (>300) gradually decreasing to less than 10 towards December and January (Holsbeek *et al.* 1999). A similar pattern has been shown in Spain (Garnica & Robles 1986), the Netherlands (Huijser *et al.* 1998), and Ireland (Smiddy, 2002). Approximately 20% of mammal species show dispersal of both sexes, however, it is the male who most commonly disperses, with most dispersing just prior to breeding (Greenwood 1980). While, hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage (Doncaster 1993), the breeding season from April-August in the U.K., Sweden and Denmark (Morris 1961, Morris 1969, Kristiansson 1984, Riber 2006, Jackson 2006) represents a period of range expansion in male hedgehogs (Morris, 1969, Kristiansson, 1984, Jackson, 2006). As a result, males may become more vulnerable to being killed on the road and in the current study significantly more males were collected as road kill with peaks in May and July. Of the 3-22% of hedgehogs killed on the roads in the Netherlands there was a preponderance of 3 males : 1 female (Huijser *et al.* 1998). In Sweden, Goransson *et al.* (1976) found that 80% of hedgehog traffic victims were males who had survived one winter. However, in autumn they found that high numbers of females were killed, which was attributed to a greater need to forage more widely in order to build up fat prior to hibernation after raising young. This may account for the second peak in the current study, as the only time in which there were a greater number of females killed was in August. However, the appearance of juveniles as road fatalities peaked in May, June and July, which may account for female movement once their offspring had reached independence. The fact that juveniles were still observed up to October and November, indicates that, Ireland is similar to the U.K., where courtship or pregnancies may be found during most of the active year (Reeve 1981). These peaks continued to be observed in the same months in subsequent years. Consecutive peaks in the same months over subsequent years was also observed in foxes (July and September) and badgers (March and May) (Appendix 5). This therefore suggests that these peaks represent activities that occur on a yearly basis such as breeding (adults) and dispersal/exploration (juveniles).

Pasture was the most dominant habitat along both focal routes, so it is not surprising that the majority of casualties were located beside these habitats. These pasture fields were typified by well developed hedgerow and in many cases were situated amongst a mosaic of different habitats. In all cases where the immediate pasture did not have well developed hedgerow, areas of scrub were located nearby. Hedgerow is particularly important for a hibernating species like the hedgehog (See Chapter 6). In Denmark, Jensen (2004) found that 55% of hibernacula occurred in forested areas, with a similar result found by Riber (2006) for day nests in Denmark. In Ireland only 9.6% of the land area is covered by forest (Rudel *et al.* 2005) , much of which is conifer plantation. However, while Ireland has the lowest proportion of forest cover by percentage of land area of all European Countries (EPA 2008), 1.5% of the landscape consists of hedgerow, giving a total length of 416,000km (Smal 1995). Hedgerows may therefore provide suitable habitat for nest sites that would be provided by forests elsewhere. A further 17% of carcasses were located beside residential areas. Doncaster *et al.* (2001) observed that the habitat preference of hedgehogs shifted significantly towards urban sites and urban hedgehogs live at higher densities than those in rural areas (Morris & English 1969). This may represent a higher density of hedgehogs but it may also signify a greater traffic volume in these areas and therefore a greater vulnerability to road mortality. A greater number of hedgehog road kill were observed beside arable land than what would be expected from the proportion of this habitat that was available along these routes. This suggests that like the study group at Ratharoon (Chapter 4), arable land was selected along these routes. This raises the question of whether as was apparent amongst the study group (Chapter 4), other Irish populations move into arable land at certain times of the year, and become vulnerable to road mortality along busier routes, as a result.

During the present study clusters of hedgehog road kill were observed and sites were identified where hedgehogs were killed annually. Nine (69%) of these clusters on the Cork to

Caherlistrane road, were located close to towns and junctions, and they may therefore represent specific crossing points. When radio tracking hedgehogs in Ratharoon (Chapter 4), it was observed that individual hedgehogs entered fields and crossed roads at specific spots and this was observed amongst both adults and juveniles (pers. obs. 2008-2010). The fact that hedgehogs were observed at the same spot over, in some cases, three consecutive years suggests that under favourable conditions hedgehog populations can persist at a site. This is supported by the present study where radio tagged individuals were found to remain in the same area (Chapter 4) and Reeve (1982) who noted a tendency for individual hedgehogs to remain in the same area year after year. However, while Campbell (1973) observed that of 100 hedgehogs caught in 2 and half years, at least 20 were considered resident a further 80 may have left the area. Therefore these clusters, although they indicate that hedgehogs are resident, may also represent periods of dispersal amongst a proportion of the population. This could have been determined through genetic analysis. However, the lack of genetic variation amongst Irish hedgehogs meant that this was not possible.

On the road from Cork to Galway a peak in hedgehog road deaths was observed in August. On two stretches of this road in Gort (Fig. 9.9a) and Charleville (Fig. 9.9c), devices were in place to measure traffic flow (www.nra.ie). In all years traffic flow was highest on both of these stretches in August (www.nra.ie) and this month represented a peak in hedgehog road casualties on this road. The fact that high numbers of other mammals such as rabbits, foxes and badgers were also killed on this road in August indicate that higher traffic volumes may result in a greater incidence of road kill. However, Morris and Morris (1988) felt that traffic volume had little effect as the U.K. has at least 10 times more vehicles than New Zealand, yet a lower hedgehog road casualty density.

While the annual number of hedgehog road kill remained stable on the route from Cork to Bandon, the number between Cork to Caherlistrane showed a steady decrease over the three years. While the road from Cork to Caherlistrane has undergone major development in the last few years and is a major arterial road linking two of Ireland's largest cities, the traffic flow from Cork to Bandon has remained relatively stable and has undergone none of the same extent of development. While the reduction in road deaths may indicate a decline in hedgehog numbers, this may not necessarily be the case. This drop in numbers may also be a result of road avoidance by hedgehogs, as Rondinini and Doncaster (2002) found that there was an overall significant tendency for both sexes alike to avoid crossing roads, with avoidance increasing in proportion to road width. Similarly, Mulder (1999) suggested that hedgehogs avoided the synthetic surface of the road. When radio tracking hedgehogs (Chapter 4), individuals would always run when crossing roads despite the fact that there was no traffic and hedgehogs were observed moving around as normal in other areas where there was no cover (pers. obs. 2008-2010). Much of the route from Cork to Caherlistrane, consists of dual carriageway and motorway. The Ennis bypass which was opened in 2007, just prior to this survey constitutes 20km of the route, 14 km of which is dual carriageway (www.nra.ie). While mitigation measures (underpasses and fencing) have been put in place on these new roads, these are mainly targeted at otters and badgers (Dolan 2006). This fencing in particular may act as a barrier preventing them accessing the road and it is interesting that over the three year study no hedgehog carcasses were observed on this stretch of road (See red circle on Fig. 9.9b). Clevenger *et al.* (2001) observed that, following fencing, there was 80% fewer accidents involving wildlife, in Canada. However, Jaegar and Lahrig (2004) found that although fencing reduced mortality it also increased the barrier effect. Could it be that hedgehogs instead of crossing the roads are utilising the underpasses? In other countries hedgehogs have been found to use underpasses (Mata 2004), however, this has not been investigated in Ireland. Also, while the underpasses along the Ennis bypass, are being successfully utilised by bats (Abbott, pers. comm. 2011), in other countries there is some suggestion that these structures may act as prey traps (Little *et al.* 2002). In particular, there is a suggestion that these structures may be avoided by prey species who detect the scent of potential predators. Hedgehogs use olfactory cues to detect badgers and according to Ward *et al.* (1997) avoid sites tainted with badger odour. However, Ward *et al.* (1997) did find that although hedgehogs initially avoided areas tainted with badger odour this did not persist, particularly if the gain outweighed the risk of predation. In addition, Ford and Clevenger (2010) found no evidence that predator behaviour was effected by prey movement, with proximity of ungulate kills being similar before and after crossing structures were in place. It is therefore important for further investigation into the effectiveness of these structures for hedgehogs.

While the hedgehog is thought to be widespread across Ireland (Hayden and Harrington, 2001), the lack of baseline data on this species makes it difficult to estimate the density of hedgehogs in Ireland. They have been found to occur at high densities (6.06/ ha) in a mosaic habitat in County Cork (Chapter 4), while the habitats are not directly comparable, this was higher than the 2.5/ha (Parkes 1975) in sand dunes in New Zealand and the 0.16/ha (Egli 2004) in a rural area of Switzerland. With only one detailed study so far on a single population it is difficult to determine whether there is a decline in Irish hedgehogs. It is therefore important that more research is undertaken on the abundance of this species in Ireland. In particular, as one of the mammals most vulnerable to being killed in the road (Sleeman *et al.* 1985, Smiddy 2002) and in light of the reduction in their numbers in the U.K. (Hof, 2009) and elsewhere (Holsbeek *et al.* 1999), it is important that the relationship between hedgehogs and roads is further investigated as well as the effectiveness of mitigation measures such as underpasses.

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Chapter 10-

An investigation into ageing techniques and the parasite load of Irish hedgehogs *(Erinaceus europaeus)*

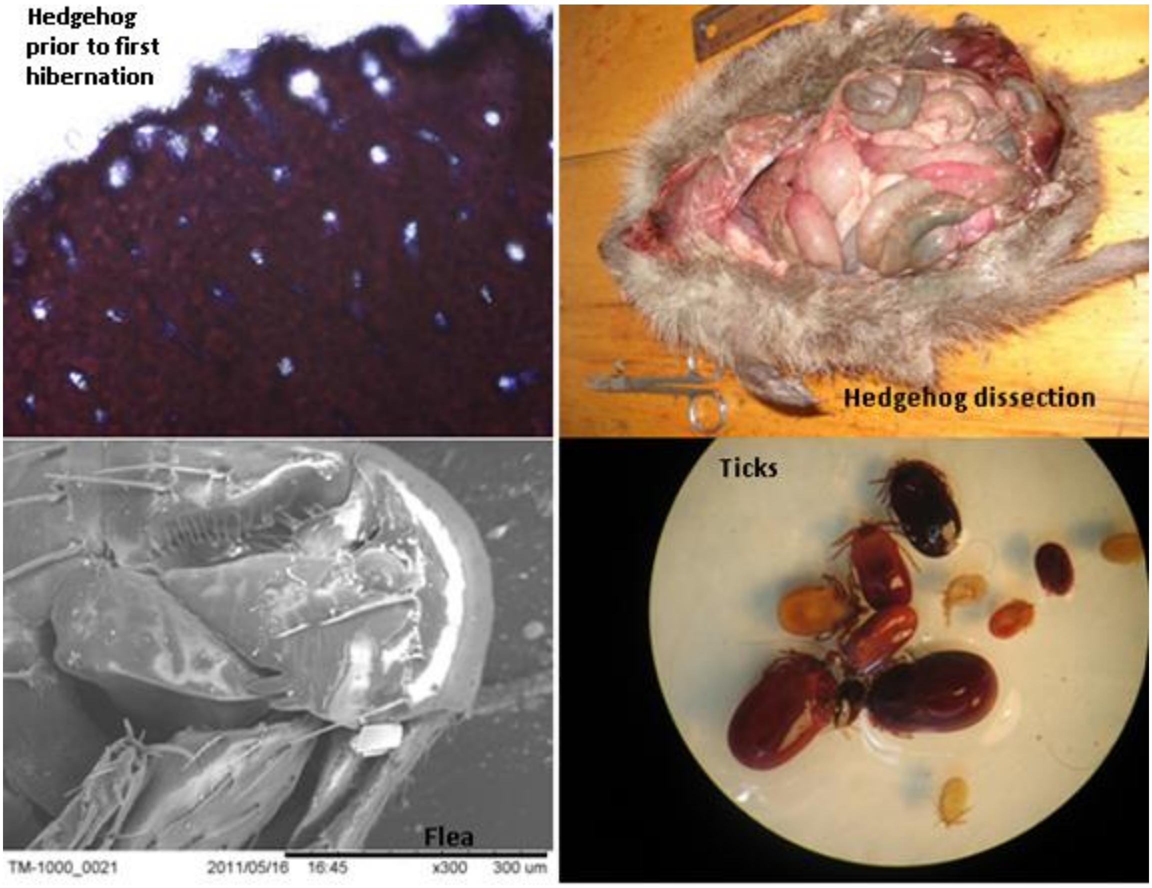

Plate 10: Clockwise from top left-Section of dentary bone from a juvenile hedgehog, a hedgehog dissection, a flea and ticks obtained from hedgehog carcasses. All pictures ©Amy Haigh.

10.1 Abstract

The European hedgehog is strictly protected in the Republic of Ireland; therefore carcasses such as road kill casualties can provide valuable information on population demographics, parasite load and general body condition. In total, 146 carcasses, collected from around Ireland between 2008 and 2010 were examined. Of these 135 were killed on the road and a further eleven were the result of predation or anthropogenic related accidents. These carcasses were investigated for the development of ageing techniques and to investigate parasite load of individuals. There was no significant difference in the body length of adult males and females, nor was there a difference in the jaw length of juveniles and adults. There was a significant correlation between the weight of the hedgehog and its hind foot length and between the weight and body length. It is suggested that these parameters combined with the presence of growing spines could provide a way of separating age classes in the field. Road kill were also aged using the dentary bone. The majority (17%) of hedgehogs killed on the road were males who had survived one hibernation; however 54% of all hedgehogs were one year old or less. The majority of hedgehogs (87%) were between 0-3 years old, the oldest females (n=2) were nine and the oldest males (n=2) were eight years old respectively. Hedgehogs had an average longevity of 1.94 years, and the average lifespan of females was higher (2.10) than males (1.87). Few ectoparasites were detected on hedgehog carcasses with the ticks, *Ixodes hexagonus* and *Ixodes canisuga* found on just four of the 146 individuals. The endoparasites, *Crenosoma striatum* and *Capillaria erinacei* were both positively identified. *Crenosoma striatium* was confined to the lungs, while *C. erinacei* was the most prevalent (87%) endoparasite occurring in the stomach and intestines. In only two cases were no parasites found. A mean of 30.4 (± 0.64) (SE) parasites were found in adult males, which was significantly higher than the 9.9 (± 0.41) found in adult females. This is thought to be related to the male's larger home range and the effects of oestrogen levels on immunity.

10.2 Introduction

The Western European hedgehog (*Erinaceus europaeus*) is one of four species within the genus *Erinaceus* that contribute to the five genera of hedgehogs found throughout Europe, Africa and Asia (Pfäffle 2010). It is a medium sized insectivore, with a body length of between 20-30cm (Reeve, 1994) a hind foot length of between 4 and 4.5cm (Hayden & Harrington 2001) and a skull length of between 5.50-6cm (Corbet 1988). Other studies (Reeve 1994) have found the dimensions to be within this range, with Hrabe (1975) observing a mean body length of between 18-26 cm and a hind foot length of between 3.4-4.4 cm, when investigating various age classes in the Czech republic. Hedgehogs replace their spines about every 18 months (Morris 2006) and Jackson (2006) found that at certain times of the year there were marked differences between the number of growing spines in known juveniles and adults, with juveniles having a greater number. This suggests that this would be useful way of separating age classes.

Various methods have been successfully used to age a variety of mammals. Teeth have been used to age deer (Gilbert 1966, Mitchell 1967), squirrel (Fogl & Mosby 1978), otters (Bodkin *et al.* 1997) and bison (Moffitt 1998). However, this has been found to be less accurate for determining the age of hedgehogs (Morris, pers. comm. 2010) and instead other methods have been utilised such as x-ray radiographs of hedgehog forelimbs to examine epiphyseal fusion (Reeve 1981). Periosteal growth lines have previously been used to age hedgehogs (Morris 1970, Hrabe 1975), as well as rabbits (Henderson & Bowen 1979) and paddle fish (Adams 1942). During the hibernation period bone deposition in the periosteum slows and such seasonal changes produce growth lines, visible in stained sections of the lower jaw (Reeve 1994). This is considered the only direct method of absolutely aging hedgehogs as the use of eye lenses is considered unsuitable in most field studies (Morris 1970).

There has been little research carried out on the European hedgehog in Ireland. Mulcahy (1988) investigated the occurrence of the hedgehog flea *Archaeopsylla erinacei,* and found a total of 1063 fleas from 19 hedgehogs. All hedgehogs examined carried A*rchaeopsylla erinacei* and the mean intensity of fleas per hedgehog was 55.9. This was low in comparison to the 129 fleas per hedgehog from a study in Sweden (Brinck and Lofqvist 1973). Hedgehogs may also harbour ticks, mites and fungal infections of the skin (Reeve 1994). Gaglio *et al.* (2010) found that tick prevalence(proportion of infected hosts among all the hosts examined) was positively related to body condition and these ectoparasites, especially ticks may induce anaemia (Pfäffle *et al.* 2009). Habitat type and vegetation is thought to affect the abundance of ticks (Gaglio *et al.* 2010). Pfäffle (2010) found that almost half of the ectoparasite species found in hedgehogs from Europe, such as ticks (*Ixodes ricinus*, *I. hexagonus*), fleas (*A. erinacei*) and trematodes (*Brachylaemus erinacei*) could not be detected in hedgehogs from New Zealand. Additionally, prevalences, abundances and intensities of the detected parasites were significantly lower in the new range compared to the native one. Reeve (1994) suggested that hedgehogs had gained their reputation of being "flea ridden" due to the fact that heavily infected hedgehogs will often appear lethargic and may be seen active in day light.

Numerous helminths have been described from hedgehogs of several species (Reeve, 1994). In the U.K. Gaglio *et al.* (2010) observed that parasite prevalence was 91% in 74 European hedgehogs obtained from wildlife hospitals, and a total of six helminths species were isolated. The most common parasite was *Crenosoma striatum* in the lungs, and the most abundant was *Capillaria* spp. in the stomach and small intestine (Gaglio *et al.* 2010). Similarly, Mayeed *et al.* (1989) found that of thirty five animals, 66% showed lungworm infection, of these 40% had *Crenosoma* only, 14% *Capillaria* only and 46% had both. Boag and Fowler (1988) detected a prevalence of 77% for *C. striatum*, 85% for *C. erinacei*, while Bunnell (2002) observed that 11% of hedgehogs were infected by *C. striatum*. Pfäffle (2010) revealed that intestinal *Capillaria* spp. infections have a negative effect on the body condition both in the European and the New Zealand populations causing a major effect on morbidity and also, potentially, on the survival of their hedgehog hosts, especially in times of increased stress or energy demand, like the breeding season or hibernation.

Ova and larvae of *Capillaria* may be ingested directly or via consumption of earthworms (Mayeed *et al.* 1989). Infection by *Crenosoma striatum* is believed to be transmitted via a molluscan intermediate host (Gregory 1985). Therefore, well fed hedgehogs may accumulate higher parasite burdens and older individuals are generally not only in better condition but also more heavily infected with parasites (Gaglio *et al.* 2010). This may be related to changes in prey selection with age, as Dickman (1988) observed that young hedgehogs sample prey from the entire spectrum of prey types, while older hedgehogs specialise in the same narrow range of prey, eating more large prey such as molluscs. The consumption of these intermediate hosts of parasites would therefore make juveniles more susceptible to infection.

This study aimed to investigate the use of non-invasive measures for separating age classes, such as the measurement of body and hind foot length that could be used in the field. By using the dentary bone to more accurately age individuals, the study aimed to investigate whether patterns emerged relating to the age in which hedgehogs were killed on the road. This method of ageing was also used to investigate the age distribution of hedgehogs in Ireland. The parasite load of road kill, was examined in order to test the following hypotheses that:

- Older hedgehogs have a higher parasite load
- Males have a greater parasite load than females

10.3 Materials and methods

In total 146 hedgehogs were collected from around Ireland from March 2008 to February 2011. Of these 135 were collected as road kill and a further eleven were found dead in peoples' gardens, were predated or did not survive hibernation (See Appendix 6).

10.3.1 *Ageing*

10.3.1.1 Ageing using morphometrics

Carcasses were initially frozen before dissection and defrosted 24 hours prior to processing. Before dissection, the hedgehog was sexed, weighed using digital scales (Harvard apparatus, Kent, U.K.) and checked for the presence of ectoparasites and growing and broken spines. Only specimens in good condition were used to obtain measurements. The body (tip of nose to anus), skull (length of lower jaw) (Fig. 10.1a) and hind foot length (heal to the base of the nail) (Fig. 10.1b) were measured using vernier callipers.

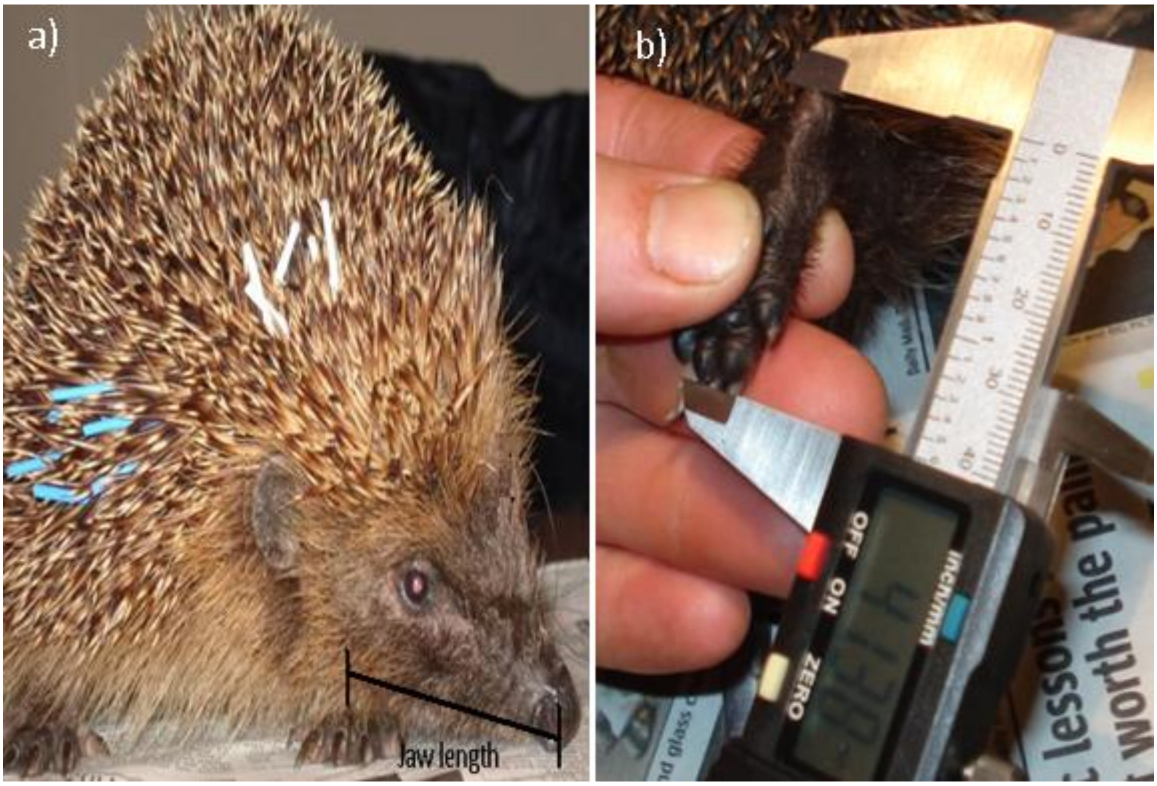

Figure 10.1a-b: The ways in which measurements were obtained, showing a) the area of the jaw that was measured and b) a hind foot being measured.

Individuals were considered to be juveniles if they satisfied at least two of the following criteria: weight less than 600g; hind foot length of less than 3.6cm (See Chapter 6); and presence of growing spines. However, as many of the specimens were damaged, it was not always possible to obtain an accurate measure of weight. For 83 individuals, the age was also verified by examination of the jaw bone (See 10.3.1.2). The lower jaw was removed and refrozen until they were processed.

10.3.1.2 Ageing using the dentary bone

The method for processing the dentary bone was developed by a combination of the techniques used by Morris (1970), Henderson and Bowen (1979) and Murphy (2004)and are as follows:

- After removing the jaws from the freezer the lower jaws were placed in individually labelled containers and fixed in formalin for 24 hours.
- Each lower jaw was placed in individually labelled bags made from nylon tights; they were then placed in a beaker and placed under running water for 24 hours.
- The jaws were then returned to labelled containers and decalcified using RDO (Rapid decalcifier), for a period of 6 hours.
- They were then returned to the bags and placed under running water for 24 hours.
- 5mm sections were cut at the location of the last molar.
- Jaws were sectioned on a cryostat microtome (Leica CM1850 UV).
- Sections were cut at a temperature of -20˚C, and a thickness of 30 µm, with four replicates of each jaw produced.
- Each section was stained by first placing it into a bath of Harris' haemotoxylin for 5 minutes until it turned dark pink. The removal of sections between the baths was achieved with the use of a soft bristle paint brush.
- Sections were then placed in a small sieve and rinsed gently with distilled water until the water ran clear.
- The sections were placed in alkaline water (ten drops of water to 3 drops of ammonia) until they turned blue.
- Sections were transferred to a bath of acidic tap water.
- Sections were washed with distilled water again before mounting the sections on gelatine coated slides.
- Slides were coated with DPX and covered with a coverslip and left for 5 days to dry.
- Once dry the slides were examined under a microscope.
- Four sections from each jaw were examined.
- This work was carried out in conjunction with a BSc. Student (Martina Kelly).

10.3.2 Ectoparasites

Ectoparasites were removed at the time of dissection and preserved in 70% alcohol. Ticks were identified by Drs Tom Kelly and Paddy Sleeman (School of BEES, U.C.C), with the aid of Arthur (1963). Fleas were photographed using a scanning electron microscope and identified with the aid of slide records and the descriptions of Pfäffle (2010).

10.3.3 Endoparasites

At the time of dissection the intestines and stomach were removed and refrozen until they were processed. Lungs were either frozen or preserved in 70% alcohol. Endoparasites were sampled using histology and direct examination of gut and lung contents. In some cases the whole lung was not intact, so sections could not be obtained from all four regions.

10.3.3.1 Investigation of endoparasites using histology

- Histological work was carried out on 59 individual hedgehogs.
- Four sections (Top section of cranial lobe, outer section of cranial lobe, longitudinal section of middle lobe and horizontal section of inner middle lobe) (See Fig. 10.2) were cut from each lung and placed in histocassettes.

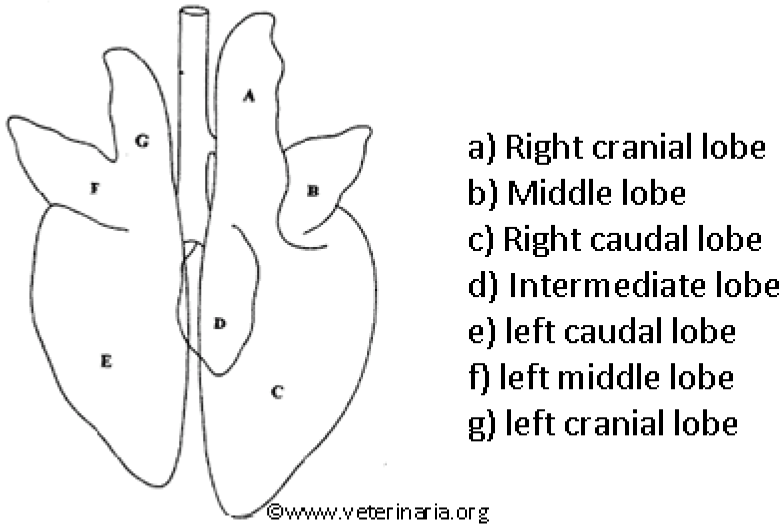

Figure 10.2: The sections of the lung.

- Samples were fixed in formaldehyde for 24 hours.
- They were placed in a citadel tissue processor 1000 for 20 hours.
- After processing, samples were embedded in paraffin wax using the tissue-Tek machine. They were each placed into a container that was filled with liquid wax, heated to 67˚C, cooled on a cooling plate at -7˚C and stored in a cool room at 4˚C for 24 hours.
- They were sectioned to 6 µm
- Samples were stained with haemotoxylin and eosine, using a Leica autostainer XL.
- After 50 minutes, samples were removed from the machine and placed on a flat surface. DPX mountants was placed on each slide, a coverslip was placed on the mountant and it was left to dry for 5 days.
- A total of 212 histological slides were made.
- This work was carried out in conjunction with a BSc. Student (Joanne O'Keeffe).

10.3.3.2 Investigating parasite load using direct examination

- The digestive tracts were defrosted and cut open and divided into stomach (n=17) and intestines (n=22).
- The stomach, lung and intestine was washed through a 250 µm and 150 µm sieve. The contents of each sieve were separated and washed using 70% alcohol and placed into sterile labelled containers.
- The samples were examined Using a Nikon SMZ645 stereoscopic microscope and identified following the descriptions of (Lapage 1956, Davis & Anderson 1971, Barutzki *et al.* 1987).

10.4 Results

10.4.1 Ageing

10.4.1.1 Ageing using morphometrics

10.4.1.1.1 Body length

Adult hedgehogs were a mean length of 20.7 (± 1.84) cm (SD). Juveniles had a mean length of 16.4 (± 3.39) cm. There was a significant difference in the length of adults and juveniles ($Z=5.022$, $n_1=118$, $n_2=31$, $p<0.01$). There was no significant difference between the length of adult males and females ($Z=0.516$, $n_1=49$, $n_2=25$, $p>0.05$). The body length of hedgehog carcasses were significantly correlated with the weight of the individual ($R_S=0.475$, $n=55$, $p<0.01$) (Spearman rank). Due to damage, leading to an inaccurate estimate of weight, only four juveniles could be included in the analysis (Fig.10.3).

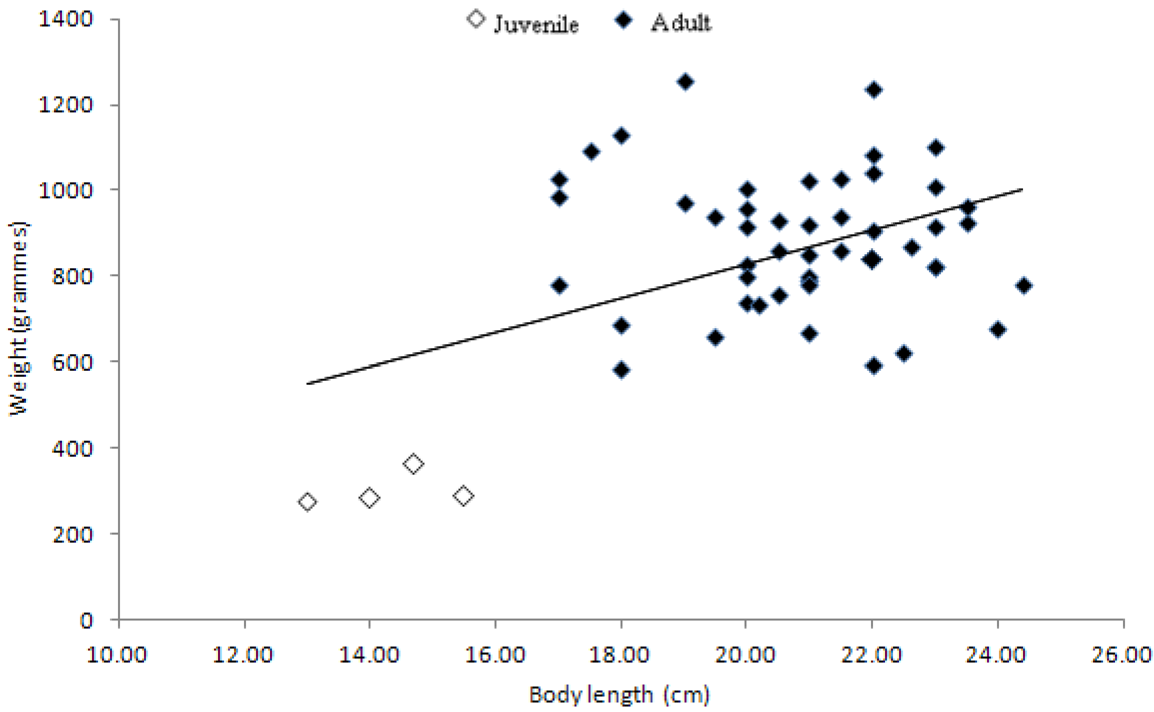

Figure 10.3: A correlation of the body length of hedgehogs collected as road kill vs their weight.

10.4.1.1.2 Jaw length

There was no significant difference between the jaw length of adults and juveniles (Z=1.679, n_1=41, n_2=12, p>0.05). Adults had a mean jaw length of 5.6 (± 0.46) (SD) cm and a head width of 3.1 (± 0.52) cm. Juveniles had a mean jaw length of 5.03 (± 0.84) cm and a head width of 2.7 (± 0.59) cm.

10.4.1.1.3 Hind foot length

The hind foot lengths of hedgehog carcasses were significantly correlated with the weight of the individual (R_S =0.43, n=57, p<0.01) (Spearman rank). Adults had a mean hind foot length of 4.2 (± 0.01) cm (SE) and a mean weight of 883.4 (± 0.26) g (SE) (Fig. 10.4). Juveniles had a mean hind foot length of 3.6 (± 0.67) cm and a mean weight of 418.6 (± 1.79) g. In order that errors would not be made due to variations in carcass weight after death, the dry weight (without the gut) was also correlated with hind foot length (R_S=0.35, n=55, p<0.01) (Fig. 10.5).

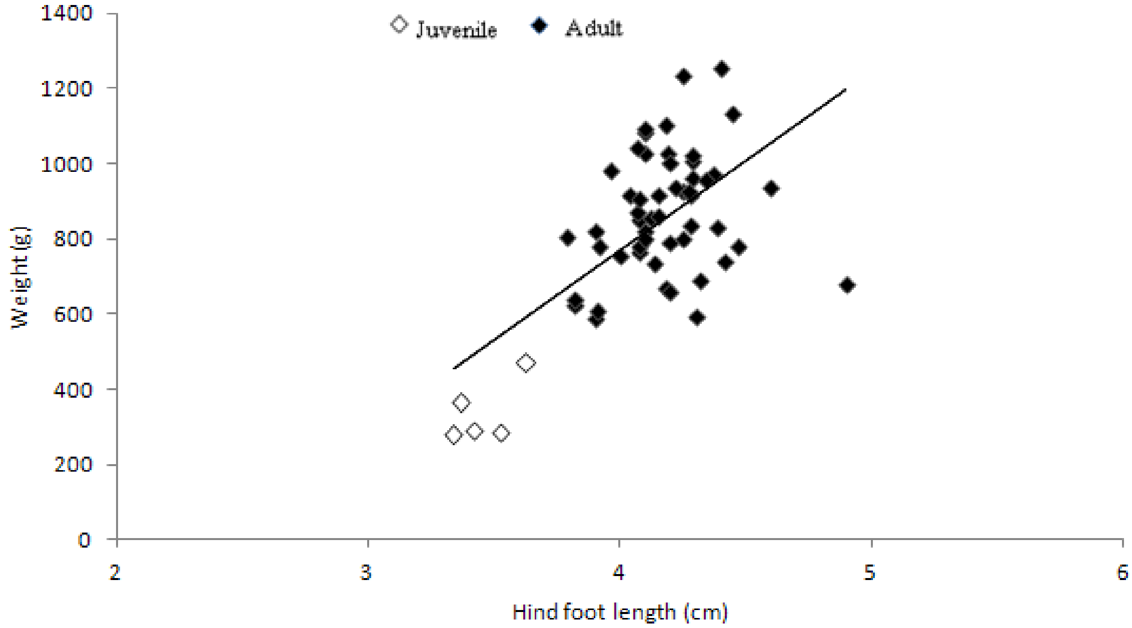

Figure 10.4: A correlation of the hind foot length (cm) and total weight (g) of adult and juvenile hedgehogs collected as road kill.

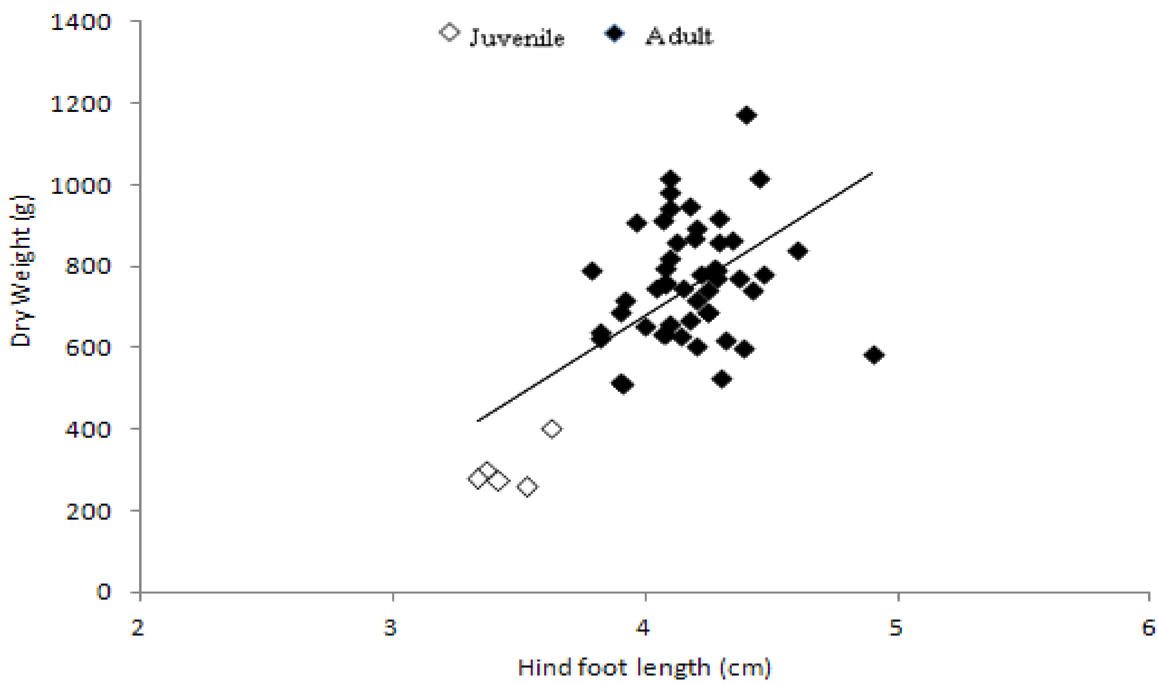

Figure 10.5: A correlation of the hind foot length (cm) and dry weight (g) of adult and juvenile hedgehogs collected as road kill.

10.4.1.1.4 Spines

Forty seven of the hedgehogs had growing spines, 24 of these were juvenile. 69.1% of the carcasses had broken spines. In juveniles growing spines were found all over the pelage, whereas in adults they were confined to small patches and generally associated with areas of broken spines. In the majority of cases these broken spines were in small patches of <5 and confined to the head region.

10.4.1.2 Aging using the dentary bone

One jaw from 83 individuals was successfully sectioned and it was possible to sex 77 of these. Hedgehogs were a mean age of 1.94 (males-1.87 and females-2.10) when they died. There was a significant variation in the age in which hedgehogs were killed on the road (χ^2=62.105, df=7, $p<0.01$), and the majority (54%) were killed, at the age of 1 year or less (Figs. 10.6 and 10.7).

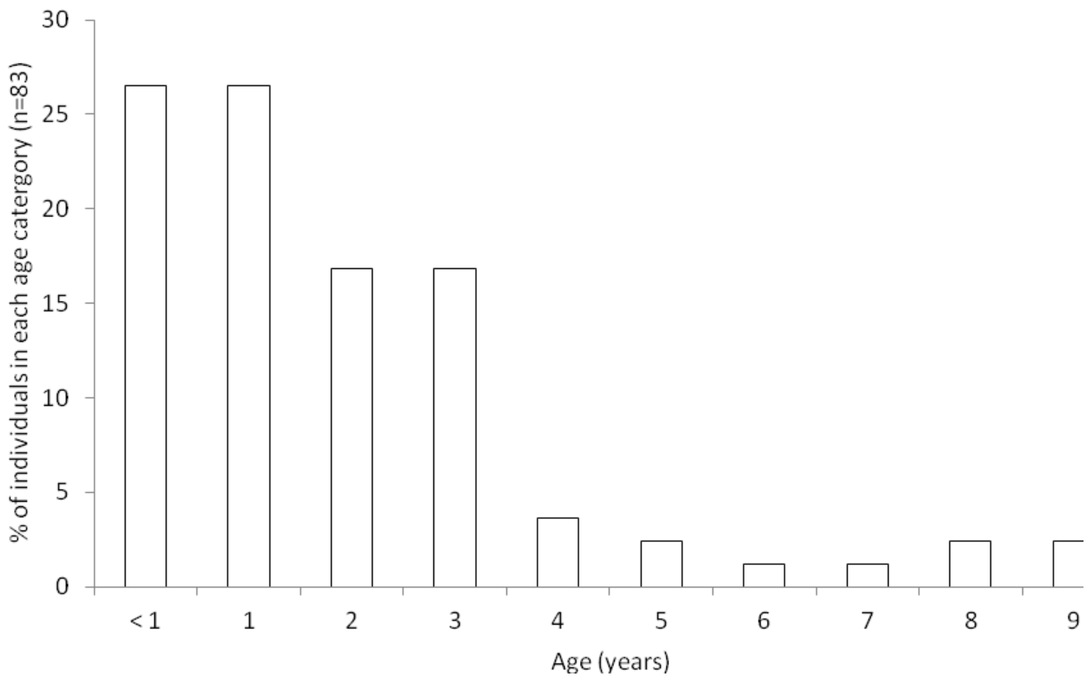

Figure 10.6: The proportion of hedgehogs (n=83) in each age class.

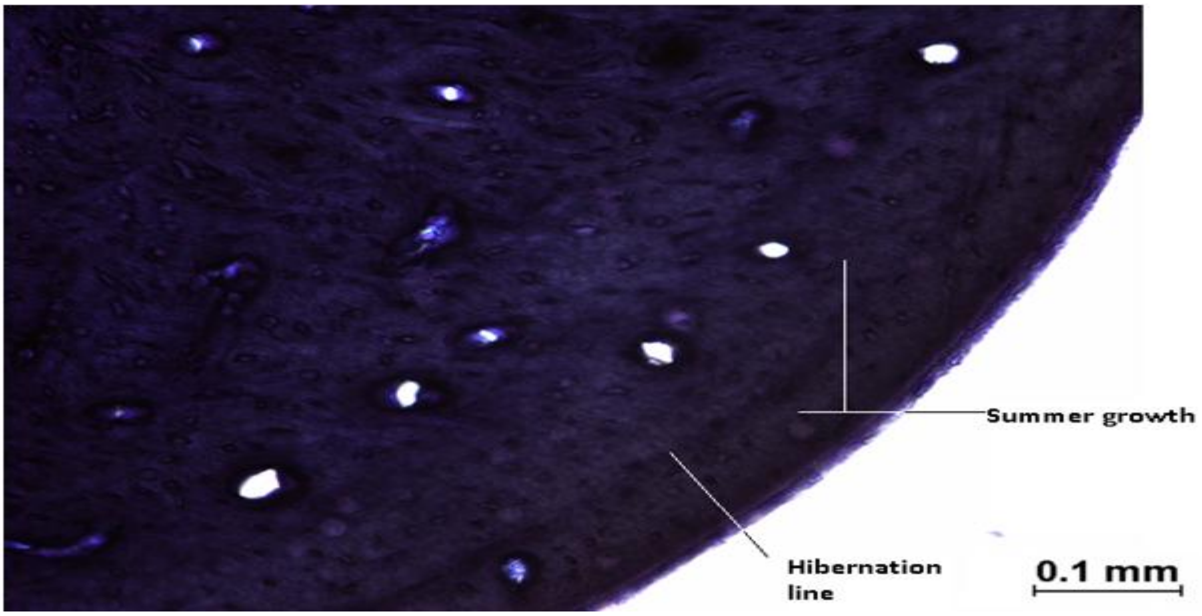

Figure 10.7: Jaw section displaying summer growth and a hibernation line.

There was no significant variation in the age at which sexes were killed on the road (χ^2= 3.368, df=1, p>0.05), but the majority (n=13) were males who had survived one hibernation (17%) (Figs. 10.7 and 10.8).

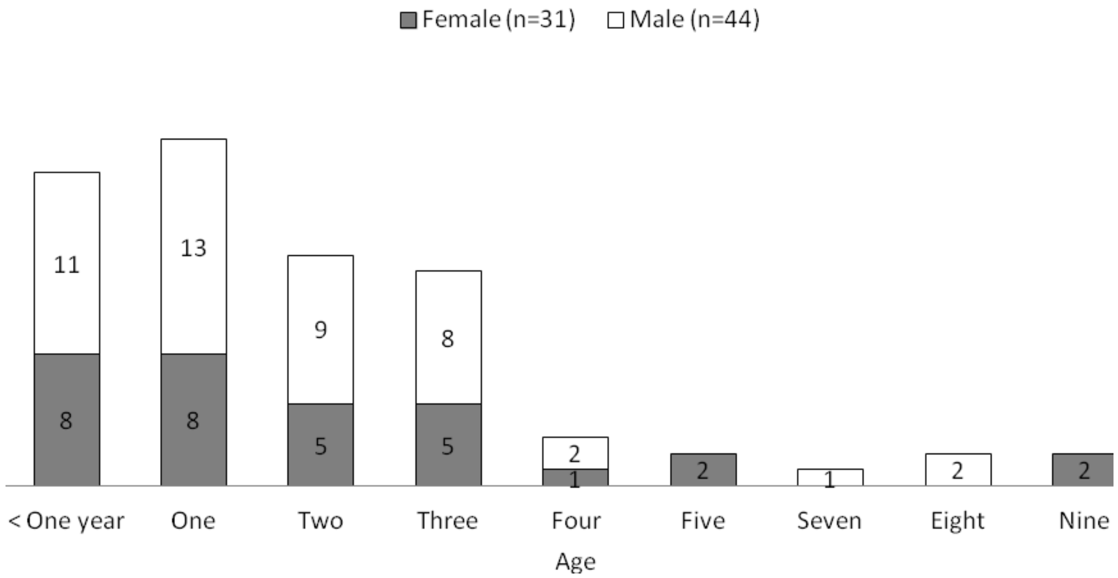

Figure 10.8: The age distribution of seventy seven of the hedgehogs aged by examining sections of the lower jaw (six hedgehogs could not be sexed).

The oldest hedgehogs had survived nine (n=2 ♀) (Fig.10.8) and eight (n=2 ♂) (Fig. 10.9) hibernations.

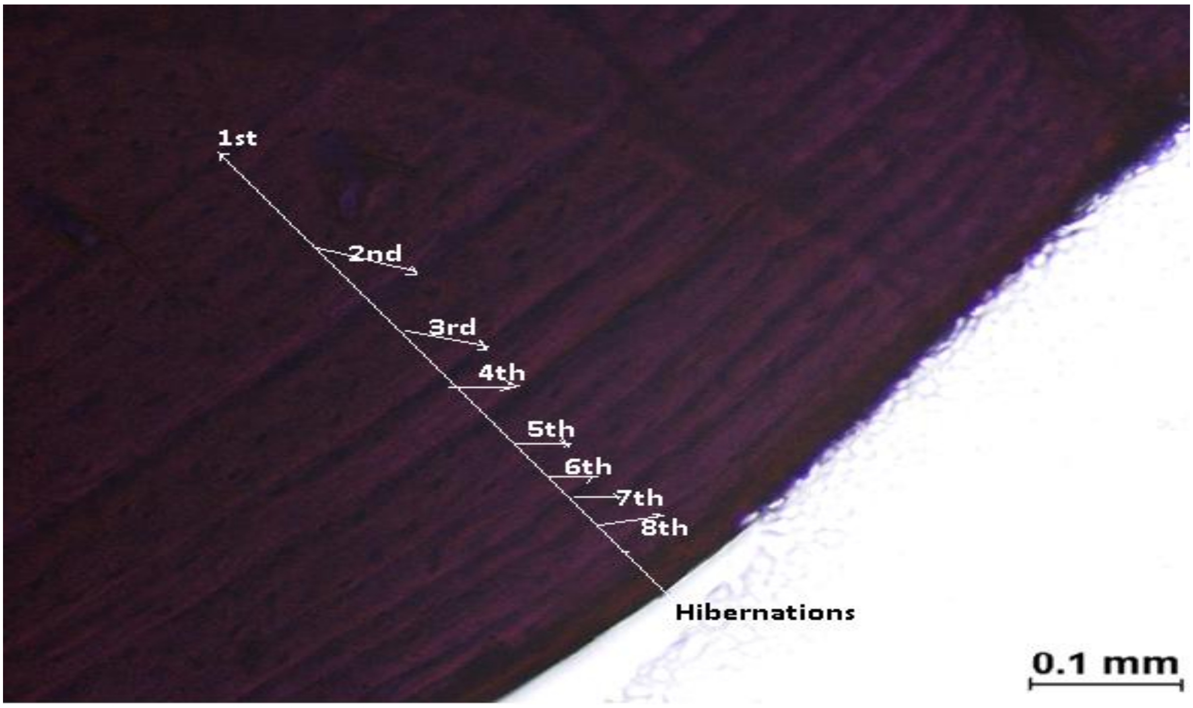

Figure 10.9: Jaw section of an individual who had survived eight hibernations.

10.4.2 Parasites

10.4.2.1 Ectoparasites

Only five of the 146 hedgehog carcasses examined had ectoparasites remaining. On two of these hedgehogs, fleas (n=2) were collected (Fig.10.10). At the focal study site (Ratharoon) (Chapter 3), fleas were observed on six (2♀, 4♂) of the 24 individuals over the three year study. However, <5 fleas per individual were observed and these hedgehogs were not continuously infested with fleas. One adult female was observed immediately post hibernation to harbour fleas all over her body. However, when she was captured one week later, no fleas were observed.

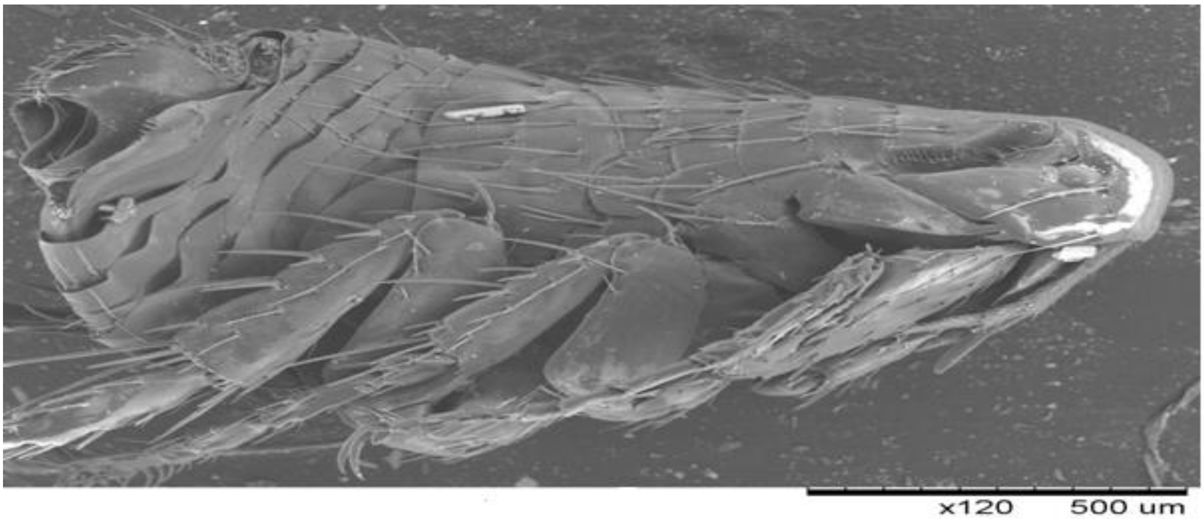

Figure 10.10: Scanning electron microscope image of the hedgehog flea (*Archaeopylla erinacei*) collected from a road casualty.

Ticks were found on four individuals with one hedgehog having seven on the ears and six amongst its under fur (Table 10.1) (Figs. 10.11 and 10.12 a and b). This was a female who died during her first hibernation, after being found active in a garden in December (Table 10.1). *Ixodes hexagonus* were found on all five of these individuals, with *Ixodes canisuga* confined to the hibernating female. The majority of the ticks were adult females (n=14), however nymphs (n=8) were found on two of the individuals (Fig. 10.11).

Figure 10.11: Adult *Ixodes hexagonus* and I. *canisuga* and nymph *Ixodes canisuga* found on the ears and under fur of an adult female who died during hibernation.

Table 10.1: The details of ticks collected from four hedgehogs.

Hedgehog					Tick (all ♀)	
	Age	Wt	Cause of death	Month of death	Species x n	Life stage
♀	Juv.	792g	Road	September	*I.hexagonus* x6	Adult
♀	Adult	735g	Hibernation	January	*I.hexagonus* x2, *I. canisuga* x 11	Adult 5 Adult, 6 Nymphs
♂	Adult	1254	Road	May	*I. hexagonus* x1	Adult
♂	Adult	937g	Road	April	*I. hexagonus* x2	Nymphs

The largest of these ticks was 0.3 x 0.8 cm (Figure. 10.12 a-b) and the smallest 0.1 x 0.3 cm. The infested hedgehogs ranged in age from juvenile (< 1 year) to nine years old.

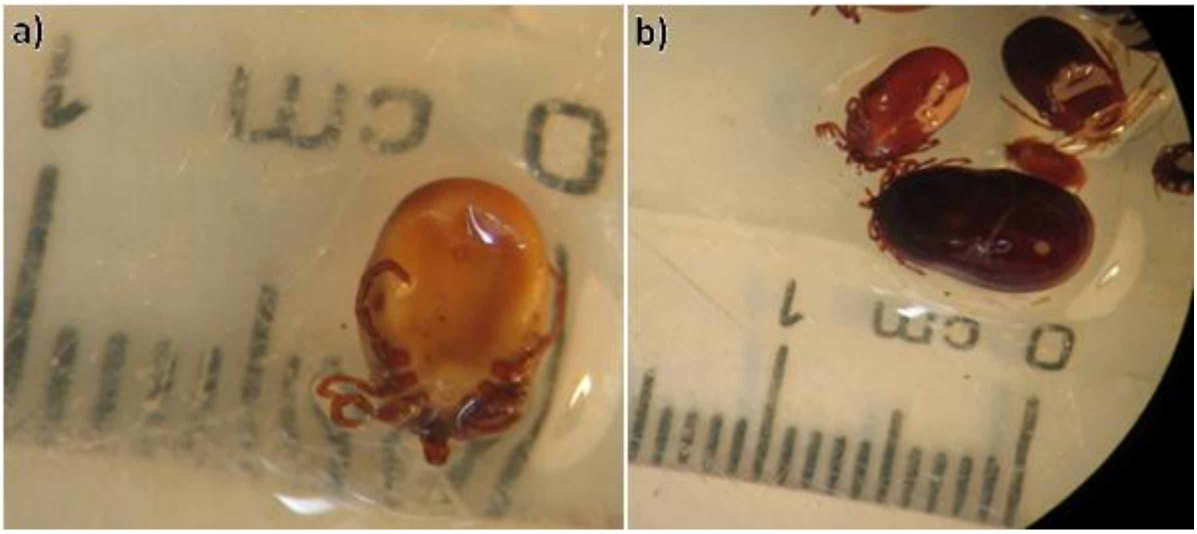

Figure 10.12 a-b: Partially engorged (a) and engorged (b) adult female *Ixodes hexagonus.*

10.4.2.2 Endoparasites

10.4.2.2.1 Endoparasite identification using histology

Histological examination indicated the presence of endoparasites, as lung damage was observed (Fig. 10.13). However, species of helminth could not be identified or quantified in lungs stored in 70% alcohol. Therefore the results of the endoparasite aspect of the study are given for those obtained through direct examination.

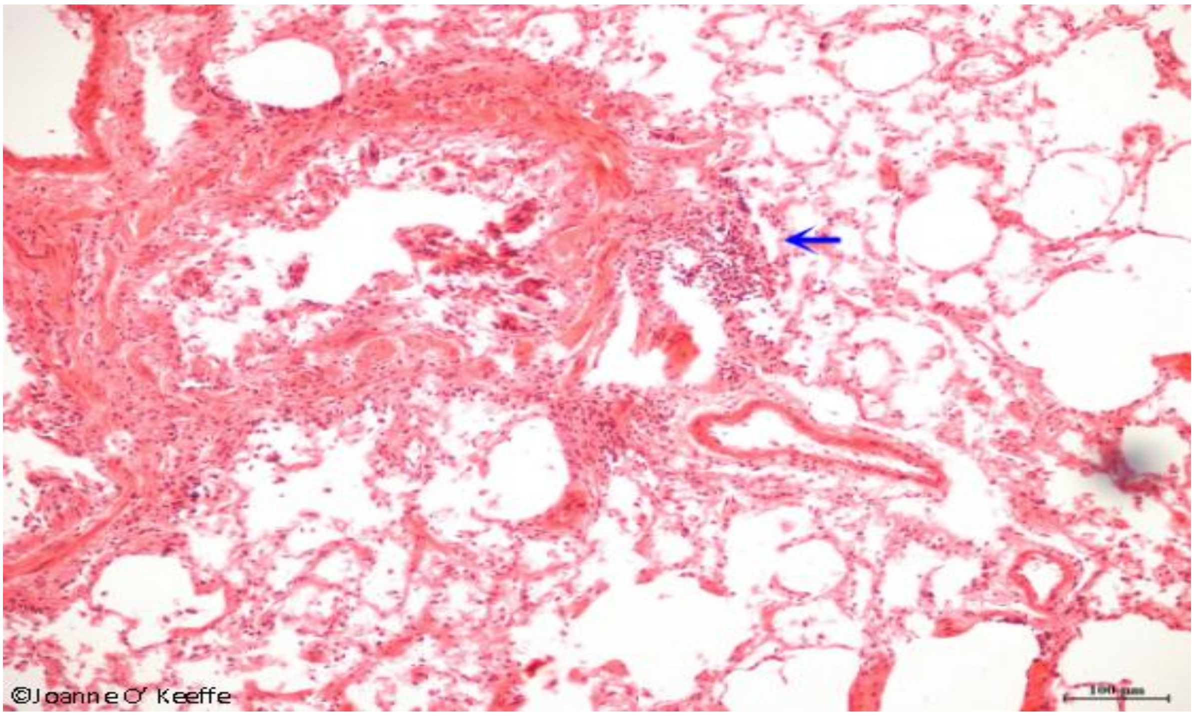

Figure 10.13: Lung section displaying damage (blue arrow) possibly from endoparasite infestation.

10.4.2.2.2 Endoparasite identification using direct examination

The lungs, stomach and intestines were examined in twenty-three individuals (10♀, 13♂). *Crenosoma striatum* and *Capillaria erinacei* (Fig. 10.14) were both positively identified. Male hedgehogs had significantly more endoparasites than females. This significance was observed with and without the inclusion of juveniles (Table 10.2).

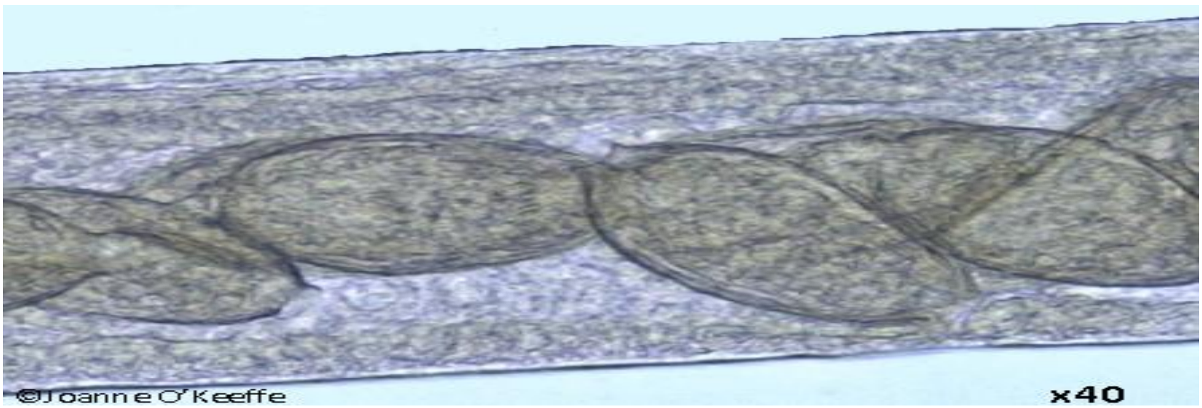

Figure 10.14: *Capillaria erinacei*, showing the distinct bipolar egg shape.

Table 10.2: The Mean number of endoparasites per adult male and female hedgehog.

	Mean (± SE) number of Endoparasites per individual	t	df	p
Adult Male (n=11)	30.4 (± 0.64)	1.15	17	P<0.05
Adult female (n=8)	9.9 (± 0.41)			
Including Juveniles(2♀, 2♂)		1.24	21	P<0.05

While *Crenosoma striatium* was confined to the lungs, *Capillaria erinacei* was the most prominent endoparasite with 65.2% prevalence in the stomach and 87% in the intestines (Table 10.3). In only two cases were no parasites found (2 adult ♂), while 158 *C. erinacei* were found in the stomach and intestines of one adult male.

Table 10.3: The occurrence of endoparasites in hedgehogs collected as road kill.

	Crenosoma striatum	*Capillaria erinacei*	*Capillaria erinacei*
Tissue	Lungs	Stomach	Intestines
No. tissues parasites were observed in	7/7	15/17	19/22
Prevalence (%)	30.4	65.2	87
Total	90	249	115
Mean (± SE)	14.7(±0.32)	16.6(±26.98)	6.1(±0.17)
Range	0-59	0-109	0-40

Of the 17 stomachs examined, *C. erinacei* was found in all but two individuals with a mean occurrence of 14.7 (± 0.32) (SE) per individual (Table 10.3). In 22 intestines examined, endoparasites were found in all but three. Seven lungs were examined and *C. striatum* was found in all of them at numbers of up to 59 in one adult male (Table 10.3).

There was no significance variation between the parasite load and the age of the individual hedgehog (χ^2 =7.190, df=15, p<0.05), but the greatest number of parasites was found in hedgehogs who had survived three hibernations (2♂, 1♀) (Fig. 10.15).

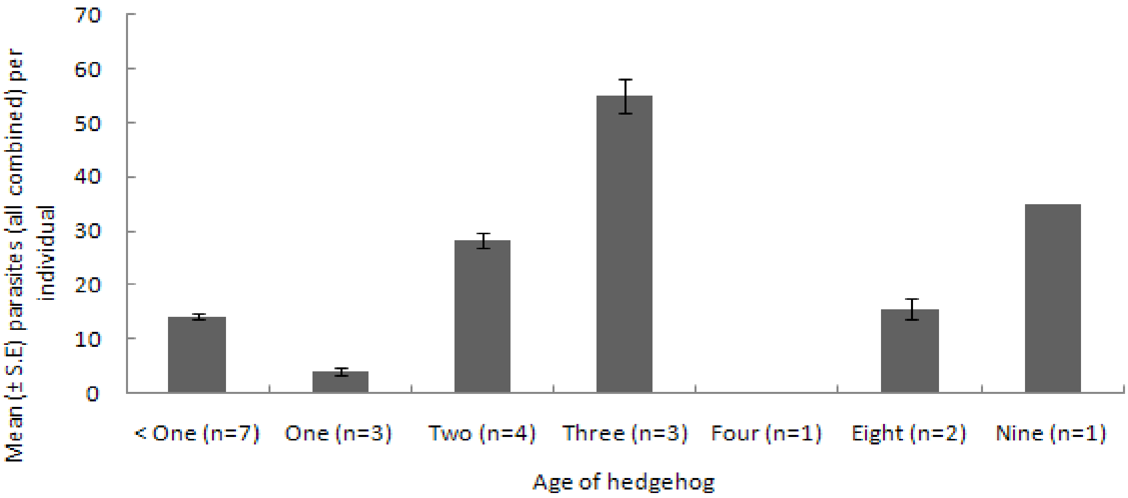

Figure 10.15: The mean (± SE) number of total endoparasites per individual, in the hedgehogs that were aged using the dentary bone (n=21).

10.5 Discussion

Male and female hedgehogs cannot be distinguished on body length but adults (> 1year) are significantly longer than juveniles. Hrabe (1975) noticed the greatest difference to be between individuals in their first year who were 70% of the size of those aged three or more. Those in their second year had increased in length by 22% (Hrabe, 1975). Dickman (1988) observed that hedgehogs attained a maximum body size at 2 years old. There was a significant correlation between the weight and body length of hedgehogs in the present study. However, as shown by the low number of juveniles that could be used for analysis, this method of ageing may have limitations when used on the often damaged road kill. However, this parameter when used in conjunction with hind foot length and the presence of growing spines would be a useful method for separating juveniles and adults, and either technique could be successfully used as a sole method on live animals.

The mean length of adult hedgehogs was smaller in the present study than the estimates by Hrabe (1975) in the Czech Republic. Schmidt and Jensen (2003) examined records of hedgehog body lengths over the last 175 years in Denmark and they established that over this time period they had increased from 20.9-29cm. They considered that this was related to increasing habitat fragmentation and other selective forces such as the effect of traffic mortality. Habitat fragmentation they felt lead to a pattern consistent with the island effect, where larger mammals get smaller and smaller mammals increase in size (Schmidt & Jensen 2003).

Morris (1969) noted that the jaw measurements of hedgehogs increased in size from 2.95 cm (2-3 weeks old) to over 4.5 cm in “old” adults. However, he did notice variation even amongst individuals of the same litter. Due to the nature of the present study there were no measurements of individuals as young as the 2-3 weeks, described by Morris (1969). However, amongst juveniles (<1 year) and adults, there was no significant variation in the length of the jaw. This therefore cannot be used to separate age classes.

In the present study there was a significant correlation between the hind foot length and both the dry weight and complete weight of individual hedgehogs. Jackson (2006) observed that juveniles were on average nearly a third heavier one year later, whereas adults who were weighed one year later were on average unchanged, indicating that there is a rapid increase in the body size of hedgehogs in the first year. This is consistent with the rapid weight increase of juveniles observed in the present study (Chapter 6). In the focal study population, the hind foot length of radio tagged juveniles had increased when it was re-measured in the summer, following their birth while that of adults remained unchanged (Chapter 6). Hrabe (1975) found a highly significant difference in the hind foot length of hedgehogs in different age classes with the hind foot length of hedgehogs who were three years old or more being 78% larger than hedgehogs in their first year. In the present study, the size difference was more conservative with the largest hind foot length of an adult killed on the road being 30% larger than the hind foot of the smallest juvenile. While there was a significant correlation between the weight (full and dry) and hind foot length of the road kill and the live individuals at the main study site (Chapter 6), the R_S value was higher amongst the live hedgehogs than the collected carcasses. As 92% of the carcasses were road kill, many were in a poor state when recovered which may have given a less accurate measurement of weight. However, this lower significance was also observed when the dry weight was correlated with the hind foot length.

In the present study 51% of the hedgehogs who had growing spines were juveniles. While growing spines of adults were generally in small patches and associated with areas of broken spines, those of juveniles were located all over the body. Jackson (2006) reported a marked difference between the number of actively growing spines between known age juveniles and adults. Therefore, the body length, hind foot length and the presence of growing spines may provide useful indicators of the estimated age of hedgehogs in the field. In road kill studies where the carcass may not always be in adequate condition for other aging methods, the hind foot length may prove particularly useful.

The hedgehogs in the present study were a mean age of 1.94 years when they died. This was similar to findings in both the U.K. (Morris 1969) and New Zealand (Parkes 1975) where an average longevity of 1.86 and 1.97 years was reported. In the present study females were found to have a longer lifespan than males with females having an average lifespan of 2.10 and males 1.87 years. Kristiansson (1984) recorded that males in their first year had an average life expectancy of 1.6 years and juvenile females 1.8 years, with males and females having a further life expectancy of 1-2 years (males) and 1-3 years (females). Males have a larger annual home range than females (Chapter 4) (Reeve 1982, Riber 2006) and travel a greater distance on a nightly basis (Morris 1986, Dowding *et al.* 2010). Male hedgehogs were killed on the road more often than females, particularly during the breeding season (Chapter 9). As previously stated, although hedgehogs are not known to have a clearly defined dispersal period (Doncaster 1993), hedgehogs are capable of travelling up to 3.8km (Doncaster *et al.* 2001)and 5.2 km (Morris 1997) from a release point. This movement is particularly evident in the breeding season (April-July) when males increase their range to encompass that of females (Kristiansson 1981, Jackson 2006). Huijser *et al.* (1998) reported that 3-22% of hedgehogs were killed on the road in the Netherlands and they represented a preponderance of 3 males: 1 female. Clutton-Brock and Isvaren (2007) suggested that in polygynous species, intense intrasexual competition between males restricts the number of seasons for which individual males are able to breed successfully. This weakens selection pressures favouring adult longevity in males relative to females and they observed that in 16 out of the 19 polygynous species, adult males showed lower annual survival than adult females (Clutton-Brock & Isvaran 2007).

Morris (1969) observed that mortality rates were higher in the hedgehogs first and second summer and that after two years the chances of survival were quite high. There is a pattern of severe juvenile mortality, with relatively good annual survival rates for adults aged between 1-4 years, after which the annual rate of survival falls rapidly (Reeve 1994). In the present study, 31% of males and 21% of females overall were killed before or during the summer following their first hibernation. Goransson *et al.* (1976) found that 80% of traffic victims were male hedgehogs who had survived one winter in Sweden. Allanson (1934) suggested that male hedgehogs reach sexual maturity at nine months and Morris (1969) recorded one female reaching an oestrus condition by the end of its first summer at an age of less than 6 months. While they are not known to disperse, the first summer is a time when males are sexually active for the first time and therefore developing their ranges. In Parkes (1975) study in New Zealand, only 11 female and 5 males out of 150 captured hedgehogs were considered resident because they were captured greater than five times. However, in the present study, 19 of the 24 hedgehogs captured over the three years were considered resident and displayed site philopatry (Chapter 4). Similarly, Reeve (1981) noted a high tendency for individual hedgehogs to maintain the same range from one year to the next. This suggests that hedgehogs of both sexes may remain in an area presumably if the site meets basic requirements, such as sufficient nest sites and food or if the males do not succumb to increased intrasexual competition and are expelled by other males. This first season may therefore mark a period of transience in some individuals and therefore greater vulnerability for young hedgehogs as they find a suitable site to inhabit.

In the present study although significantly more hedgehogs (54%) died just prior to or after their first hibernation, 10 (13%) (1:1 sex ratio) hedgehogs were found between four and nine years old. Morris (1969) reported that 52% of hedgehogs died either before or after their first hibernation, with a further 23% dying between the ages of four and seven. Morris (1969) found that in a sample of 244 hedgehogs only one adult female had survived to her seventh summer. It is therefore interesting that five hedgehogs (3♂, 2♀) in the present study were between seven and nine years old. In Sweden, Kristiansson (1981) reported that no hedgehogs were greater than five years old. In his study 33% of hedgehogs died during the harsh Swedish winters which may not be as significant a problem in light of the milder Irish winters. Morris (1969) suggested that the relatively few hedgehogs in their 5th summer or more suggested that the effects of old age appear after about 4 years, although he did note that one hedgehog had visited a garden for many years and was estimated to be in its eighth year. In the present study of the hedgehogs who survived to be greater than five years old (4♀ 3♂, 1N/A), six had been killed on the road, one of which was a radio tagged hedgehog who was known to be resident at the main study site for at least three summers. Of the other two hedgehogs, a male was also radio tagged and had been resident at the site (Ratharoon) for at least the same duration as the female and was killed by an electric fence. The other individual had been found at a garden in distress and died the following day.

Fleas (n=2) were found on only one of the hedgehogs, and this individual was still warm when it was collected. The lack of fleas is not surprising as the majority of hedgehogs were collected as road kill and fleas would be expected to leave very soon after death. However, it was observed that the hedgehogs caught and tagged in County Cork, harboured very few fleas (<5) and in most cases none were observed. On one occasion a female that had just emerged from hibernation had fleas all over her body. The eggs and larvae of the hedgehog flea develop in nest lining and from there infest the hedgehog host (Morris 1973). When this hedgehog was recaptured one week later, the fleas were no longer evident (pers. obs, 2010). Does this therefore mean that the fleas only need to feed once and then remain in the hedgehog's day nests and hibernacula? As nest sharing (though not simultaneously) was observed (Chapter 6), this may explain how hedgehogs would contract flea infestations. In Mulcahy (1988) investigation of the hedgehog flea in Ireland, she found that the average number of fleas per hedgehog was 55.9. This was low in comparison to the 129 fleas per hedgehog from a study in Sweden (Brinck & Lofqvist 1973). Pfäffle (2010) recorded a higher abundance of fleas in German hedgehogs (Range-7.1-34.8 for adults, 2.5-50 for juveniles) than those from the U.K or New Zealand, but, as these were collected from dead hedgehogs, she did not feel that this represented numbers in the wild. Morris (1969) found 1,557 fleas on 244 hedgehogs (6.38 per individual), all of which were *Archaeopsylla erinacei*, which he felt indicated a high degree of host specificity.

The two species of ticks recovered were the highly specific (Pfäffle, 2010) hedgehog tick *Ixodes hexagonus* and the fox tick *Ixodes canisuga*. These two species were also found to be the only ones infecting suburban foxes (*Vulpes vulpes*), with their occurrence suggested to be related to nest use (Harris & Thompson 1978). *Ixodes canisuga* attachment has previously been positively associated with exposure to catteries and boarding kennels (Ogden *et al.* 2000). The only individual found infected with this species died during hibernation in a garden shed. This individual may therefore have been in contact with a cat or dog.

In a study of the infection of cats and dogs by ticks in Britain and Ireland, *Ixodes ricinus* was the most common (52% of animals), followed by Ixodes *hexagonus* (39%) and *Ixodes canisuga* (11%) (Ogden *et al.* 2000). This was also the case in Pfäffle *et al*.'s (2009) study on the hedgehog; however, *I. canisuga* was not detected. The absence of *Ixodes ricinus* from the Irish hedgehogs was surprising as this species is widespread in Ireland and large numbers occur in pasture and along road verges, particularly in association with cattle, sheep and deer (Gray *et al.* 1994). However, as many of the carcasses were road casualties, many of the ticks may have dropped off the carcasses by the time that they were recovered. The infestation by this species may also vary according to the time of year in which the hedgehogs were killed as Pfäffle (2010) observed seasonal peaks in the occurrence of *I. ricinus*.

Ticks were found in 5 of the 146 hedgehogs in the present study. Ticks mate in the nests of hedgehogs (Pfäffle 2010), so it is unsurprising that the highest number of ticks per individual (n=13) were found on a female who had died during hibernation. This female had emerged in December, eaten and re-entered hibernation in a garden shed, where it eventually died in January. This female harboured a combination of *Ixodes canisuga* (n=7), consisting of adult females and nymphs and adults of *Ixodes hexagonus*. The adult ticks were in an engorged state and Pfäffle *et al.* (2009) reported that female ticks predominate in the ticks infesting a hedgehog and that they can induce anaemia. Gaglio *et al.* (2010) observed that tick presence was positively related to body condition and Reeve (1994) stated that heavily infected hedgehogs will often appear lethargic and may be active in day light. This female was 735g when she died and the combination of her arousal in December, and the fact that she was found foraging during the day, may indicate that she had not reached the required weight to survive hibernation and was unwell.

While there was no significant sex difference in infestation rates in the research of Mayeed *et al.* (1989), in the present study, there were significantly more endoparasites in males than females. Male hedgehogs have a much larger home range than females (Reeve 1981, Kristiansson 1984, Riber 2006) and could therefore be expected to have a greater opportunity to become infested, as they forage over a wider area than females (Chapter 4). However, Wilson *et al.* (2003) found that there was no relationship between the mean home range size and parasite prevalence amongst mammals. Schalk *et al.* (1997) observed that a male bias in parasite load was only evident in adults, something that was thought to be due to the fact that oestrogens stimulate immunity, whereas androgens depress immunity. Hedgehogs are polygynous and individual males make mating attempts with several females, in some cases during the same night (Kristiansson, 1984) (Chapter 7). Zuk and McKean (1996) reported that the sex differences in parasite load was greater in polygynous species, as they are subject to greater sexual selection than monogamous species and the development of secondary sexual characteristics, often characteristic of males with a polygynous mating strategy, are testosterone-dependent.

The majority of hedgehogs (91%) harboured helminth parasites, with their presence confirmed in all but two individuals. This is consistent with the findings of other studies, as in

Mayeed *et al.*'s (1989) study 90% of adults were infected with both *C. erinacei* and *C. striatum and* Gaglio *et al.* (2010) detected parasites in 67 of 74 hedgehogs inspected. While in the Gaglio *et al.* (2010) study, 5 species of nematode were discovered the presence of only two were recorded in the present study. *Crenosoma striatum* was confined to the lungs, while Capillaria *erinacei* was the most prevalent endoparasite in the stomach (65.2%) and intestines (87%). Boag and Fowler (1988) also found a high prevalence of *Capillaria erinacei* (85%) and *Crenosoma striatum,* as did Gaglio *et al.* (2010).

Ova and larvae of *Capillaria* may be ingested directly or via consumption of earthworms (Mayeed *et al.* 1989). It is therefore not surprising that nematode infections in the badger (*Meles meles*), including that of *Capillaria erinacei* are also common (Jones *et al.* 1980), as earthworms are a common dietary component of both species (Wroot 1984, Neal & Cheeseman 1996). *Crenosoma striatum* is believed to be transmitted via a molluscan intermediate host (Gregory 1985). Amongst the focal study group, hedgehogs were observed to respond to fluctuations in mollusc numbers, with corresponding shifts in habitat use (Chapter 4). Both Obrtel and Holisova (1981) and Wroot (1984) found a clear tendency for hedgehogs to concentrate on a single type of prey at a time and to switch from one prey group to another according to season, therefore the risk of infection may change seasonally. Dickman (1988) observed that hedgehogs tended to eat more large prey such as molluscs, larvae and carabid beetles as they aged, but less small prey. However, this is unconfirmed by the present study. However, if this age related dietary change occurred it would be expected that older hedgehogs may be more susceptible to infection. There was no significant variation between the age and parasite load of hedgehogs observed in the present study. However, this may be related to the small sample size.

Hauer (2002) commented on how in most parts of Europe road kill was the only way of obtaining data on reproduction, age and sex distribution in protected species such as the otter (*Lutra lutra*). As a protected species under appendix III of the Berne convention and under the Wildlife Act 1976, this would be the only method of obtaining information on the hedgehog such as absolute age and parasite load. However, the current study has also demonstrated how road kill can be used to develop ageing techniques that can be used on live animals. Body length, hind foot length and the presence of growing spines all provided successful methods for separating age classes. Hedgehogs of both sexes were found to be most vulnerable to road mortality prior to and during their first summer following hibernation. However, individuals were found up to eight and nine years of age. Females had a longer lifespan than males which may be a reflection of the males' polygynous mating strategy and larger home range. It is suggested that this may also account for the higher endoparasite load observed in male hedgehogs.

10.6 References

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Chapter 11-

Conclusions

At the start of this study, there was no information on the ecology of the European hedgehog in Ireland and this research has started to fill in some of the gaps we have on this species in rural Ireland. While some of the findings have been similar to that found in neighbouring areas of the hedgehogs range such as the U.K. the Netherlands and Denmark, there has also been some interesting differences. It is these variations and the possible explanations for these that I will discuss further in the following paragraphs.

11.1 Agricultural intensification

As mentioned in Chapters 3-6, there is increasing evidence that wildlife inhabiting farmland, especially arable ecosystems, are in widespread and severe decline throughout much of northern, western and central Europe (Sotherton 1998). With agriculture becoming more and more intensive, Ireland offers a unique opportunity to study rural habitat use of hedgehogs in a landscape which is still less intensive than other areas of the species range. This is important as it provides baseline data in a less intensive system. Variations in the hedgehog behaviour can be used not only for the implementation of future management strategies to benefit the species in Ireland, but also to suggest changes that will be advantageous to hedgehogs in other areas of its range, particularly where it has been found to be on the decline.

In the U.K. regular and intensive post-harvest flailing of hedgerows in arable land has resulted in some hedges becoming very reduced, and sometimes shorter than the crops that they surround (Croxton *et al.* 2004). Heterogeneity in field margin structure has been deemed necessary for the retention of high levels of invertebrate abundance (Sheridan *et al.* 2008) and winter stubble has been found to benefit slug numbers (Glen *et al.* 1989). The arable field in the present study had a well developed hedgerow, with bramble understory and winter stubble. This clearly benefited invertebrates, which were abundant throughout this habitat and much higher than in areas of pasture where hedgerow had been removed. The latter was consequently more comparable to the hedgerow on intensely managed farmland. Invertebrate abundance was correspondingly poor in these pastures, where hedgerow had been removed, particularly as you moved away from the edge of these fields. This had a knock on effect in the habitat selection and spatial habitat use of hedgehogs. Unlike in previous studies, where hedgerow was maintained hedgehogs were found to forage in the very centre of fields. Since badgers were regularly seen at the site, this appeared to be a clear consequence of the availability of potential prey. Hedgehogs reacted to the distribution of potential prey by foraging in the centre of the arable field and at a time when building up fat reserves became a priority, arable land was the most favoured habitat (Chapter 4). The value of hedgerows was further emphasised by the hedgehogs' use of this habitat for both day nests and hibernacula (Chapter 6).

As already stated (Chapter 4), in Ireland, areas which are predominantly arable still have pockets of grassland mixed in the habitat mosaic, as was the case in the focal study site, while in the U.K. vast areas are devoted almost totally to tillage (Bracken & Bolger 2006). The fact that the study group displayed philopatry and responded to the spatial location of prey, following the same pattern of habitat selection annually (Chapter 4), emphasises the threat of habitat degradation at the local level and the need to maintain structures such as hedgerows. Patterns of range expansion during the breeding season were observed amongst both the radio tagged group and through male road kill. This was also apparent in previous research by Kristiansson (1984). The greatest mortality due to roads was observed amongst males in their first year. However, lack of dispersal amongst juveniles at the site and the fact that only five of the 24 hedgehogs caught were considered transients indicated that dispersal events were not a big feature of this population. As with Reeve (1982), the home range of males completely overlapped with one another and encompassed that of all of the adult females. However, in contrast, females were found to occupy small mutually exclusive areas. This suggests that the mutual avoidance exhibited by females in this study may be instrumental in regulating numbers in an area. As the home ranges of all the females were encompassed by all of the males, females may determine whether a habitat is colonised. The sex bias in both adults and juveniles was significantly skewed towards males and this was also apparent in Ribers' (2006) study.

Males had a larger home range than females and the highest incidence of road mortality was observed amongst males in their first year. The first summer may therefore represent a time when males make exploratory trips away from their natal area and establish territories. While the home ranges of males shifted and overlapped the ranges of both sexes, females occupied small mutually exclusive areas which shifted little. This may emphasise the benefits of producing a male biased litter as females may be more likely to compete for resources.

It is therefore suggested that hedgehogs in the rural Irish landscape exist at the metapopulation level, characterised by subpopulations dependent on small numbers of females. When the last known female at the site was killed, males appeared to move out of the site (Chapter 4). The lack of genetic variation amongst the Irish samples meant that it was not possible to confirm this through genetic analysis (Chapter 8). However, this was consistent with the clusters of road kill observed on the focal roads surveyed (Chapter 9).

Food, shelter and the ability to reproduce are basic needs that must be met by all animals. Hedgehogs selected different habitats seasonally in response to these needs, accentuating the importance of maintaining habitat heterogeneity. This study stresses how rapidly a high density of hedgehogs can be reduced in response to a few anthropogenic events emphasising the importance of maintaining heterogeneity on a broader level, in order to prevent the isolation of suitable sites for hedgehog colonisation.

11.2 Weight variations of Irish hedgehogs

At mean weights of between 878-1116g for adult females and 1026-1192g for adult males, the group in the present study were heavier than in other studies where hedgehogs were rarely observed weighing more than a kilogram (Reeve 1981, Parkes 1975, Dowding *et al.* 2010). This may have been related to a greater length of time to build up weight due, to prey being available for longer, as a consequence of Ireland's milder climate and the optimum feeding conditions at the site. This was further emphasised by the rapid increase in juvenile weight. They increased weight by a mean of 180.13 % (±60.04) (S.D) from first capture to hibernation. The maximum weight achieved by a juvenile was 1024g, a weight it reached just prior to hibernation. While late litters are thought to have a great ability to put on weight (Bunnell 2009), and Kristiannson (1984) recorded an increase of 210% in two months, amongst juveniles, Morris (1969) reported that it took a year for juveniles to reach a weight of 800-900g. Deanesly (1934) felt that hedgehogs reach sexual maturity once they have reached a required weight. This would further explain why, unlike Jackson (2006) who found that only four of 48 sub adults were observed paired with a female, and none were definite sub adults, all subadults in the present study attempted to mate with females (Chapters 7), all having reached a similar weight to adults at this time.

However, as already mentioned, significant differences in size have been reported between some of the British and Irish populations of the same morphospecies, suggesting the possibility of ecological release in Ireland (Dayan & Simberloff 1994). There are a smaller number of mammals in Ireland and Dayan and Simberloff (1994) suggested that the greater variability may result from reduced selective pressures in the absence of some potential competitors. White and Searle (2007) found that body size of common shrews on islands was positively related to distance from the mainland, suggesting a role for founder events (smaller mammals being larger) in determining body size of common shrews on islands. In the current study the lack of genetic variation amongst Irish hedgehogs suggested a small founder effect (Chapter 8) and this combined with the lower number of competitors in Ireland, may result in Irish hedgehogs being larger.

11.3 Irelands' milder climate

It was expected that due to Ireland's milder winters and the fact that much of Ireland's hedgerow has remained intact since the 18th Century (Cabot 1999), that there would be consequent variations in hibernation behaviour in Ireland. This proved to be the case. Similar to elsewhere, females lost significantly more weight than males (Morris 1969, Kristiansson 1984). However, weight loss of between 3-38% was conservative in contrast to studies in the U.K and the rest of Europe

(Morris 1969, Kristiansson 1984, Jensen 2004). Hedgehogs also hibernated for a shorter duration at a mean of 148.9 (± 0.5) nights, with four of the six hedgehogs emerging on the 30th-31st March 2009 and the following year from 18th March 2010. The majority of reports in the U.K. and Denmark record the average duration of hibernation to be 178.8 ± 13.1 days for juveniles and 197.7 ± 2.2 days for adults (Jensen 2004, Morris 1969, Jackson 2006) with hedgehogs leaving their hibernacula during the last two weeks of April, with the remaining hedgehogs resuming activity in the first two weeks of May (Jensen 2004, Morris 1969, Jackson 2006).

This milder climate than countries like Sweden also appears to have had an effect on the breeding season. The majority of juveniles were observed in July both at the site and through road kill surveys. However, like the U.K. and unlike Sweden, late litters were found to occur in Ireland and were detected as road kill and through the appearance of newly independent young at the site on October 17th 2008. The shorter duration of hibernation in Ireland and the ability of juveniles to both put on weight quickly and survive hibernation at a weight of 475g, would suggest that, unlike in Sweden, it is viable for an Irish hedgehog to produce late/ second litters.

11.4 Further study

This study on the ecology of the rural Irish hedgehog has shown interesting differences to research conducted in other areas of this species range. While data on activity patterns of the focal group were successfully supplemented through information obtained by road kill, there now is a clear need to expand in order to investigate other Irish populations. It would be interesting to explore populations in other parts of the country and in habitats with different levels of habitat intensification and land use practises, in order to determine whether the variations in habitat selection are uniform throughout Ireland. With the difficulties in successfully locating hedgehogs in an area, it would be advantageous to investigate techniques for the initial detection of hedgehog populations.

With the reported decline in hedgehog numbers in the U.K. (Dowding 2007, Hof 2009, Macdonald & Burnham 2011), it is imperative that estimates are obtained on hedgehog numbers and distribution maps are attained for the whole of Ireland, for rural and urban populations. It is only through these baseline data that changes can be successfully monitored. With the human population rising all the time, roads are likely to become busier and larger. It is therefore important that the effect of these structures on hedgehog populations is established, so that future design and mitigation measures are in place at the time of their construction.

With technology becoming more sophisticated and advanced, the opportunity has become available to gather even more concise information on the movement patterns of hedgehogs. GPS tags are being successfully used on hedgehogs, by researchers in the University of Otago, New Zealand. This is in order to gain a greater understanding of movement patterns and the effects of this introduced species on native fauna (www.news.bbc.co.uk). This technology would greatly facilitate the expansion of some of the knowledge first explored in the current research. For instance, it would provide valuable information on finer scale intrahabitat movement patterns, activity budgets and the activity of hedgehogs who wake up and move nests during hibernation.

The genetic aspect of this research has shown that there is little genetic variation amongst Irish hedgehogs and implies a small founder effect. However, there is now scope for a more detailed genetic investigation using mitochondrial DNA, in order to investigate the origins and colonisation route of the Irish hedgehog.

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Appendix 1-

Questionnaire

Appendix 1: Hedgehog Survey 2008

 

Name:	Address:
Email:	Telephone:

1. Are you aware of hedgehogs in the vicinity of your home/farm?

Yes ☐ No ☐

2. How are you aware?
Live sightings ☐ road kill ☐ Other (please specify) ____________

3. Is the area you live?
Urban ☐ Suburban ☐ Rural ☐

4. When was the last time you saw them dead or alive (approximately)?
This year ☐ 1-2 years ago ☐ > 2 years ago ☐

5. Have you seen them?
Once ☐ Regularly ☐ 1-5 Occasions ☐> 5 times ☐Never ☐

6. At what time did you approximately see the hedgehog?
________am __________pm

7. At what time of year did you see them?
January ☐February ☐March ☐ April ☐ May ☐ June ☐ July☐ August ☐ September ☐ October ☐ November ☐December ☐

8. How would you describe the habitat in which you saw the hedgehog?
Garden ☐Hedgerow ☐Scrub☐ Deciduous/broadleaf woodland Coniferous woodland i.e.Fir/pine ☐ Playing Field ☐ Open pasture ☐ Arable/Tillage ☐ Road verge ☐Wet grassland ☐Other (please specify) _________________

9. Would you be willing to contribute further to the study?
Yes ☐ No ☐

Appendix 2-

Ethogram

Appendix 2: Ethogram

Behaviour	**Description**
Foraging Behaviour	Eating, actively searching for food, walking with its nose to the ground
Walking	Moving with head lifted from the ground
Running	Legs extended, moving quickly
Stationary	Stood still either resting or within a nest
Shakes/Scratches	Scratching head with hind leg.
Cleaning	Hind foot raised licking belly.
Sexual Interactions	Courtship and mating
Male interactions	Aggressive interactions amongst males.
Climbing	Vertical locomotion
Vigilant	Hedgehog frozen to the spot, head raised or tucked body under while in the open.

Appendix 3-

Poster Presentations

Appendix 3a: Poster presentations

Mammal Society Easter Conference York 2008

The Ecology Of The European Hedgehog, With Particular Reference To Habitat Use And Mortality Factors

Amy Haigh, Dr Ruth Ramsay and Dr Fidelma Butler

Funded by Crawford Hayes

Introduction

The European hedgehog (*Erinaceus europaeus*) is widespread throughout Ireland; and is protected under appendix 3 of the Berne Convention. However, while research has taken place else where little work has been done on hedgehogs from an Irish perspective.

The hedgehog is one of the most frequently killed animals on Irelands roads (Smiddy, 2002) (Sleeman et al., 1985). The National Road authority is putting measures in place to include underpasses in new road constructions to mitigate this. These are often placed along known badger routes. In previous studies (Ward *et al.*, 1996), found that hedgehogs will avoid areas where they detect badger odour. This therefore may restrict hedgehogs movements through these underpasses.

There has been a gradual growth in intensive farming and a renewed drive to encourage more extensive organic farming. However, the benefits of such measures to mammals such as the hedgehog is largely unknown.

Fig. 1: Picture showing a hedgehog fitted with both a radio tag and yellow heat shrink resistant tubes. (Picture courtesy of Dr. Digger Jackson).

Aims and Objectives:

- Identify the main mortality factors with particular emphasis on their interaction with roads.
- Investigate habitat use and identify whether differences occur among farms with different intensities of use and who adopt different farming methods.
- Compare population density and home range amongst different habitat types.
- Identify whether they occupy the same home range post hibernation and whether overlap occurs.
- Determine the nightly distances travelled and variation amongst the population.
- Investigate nesting habits during the summer and the hibernation period.

Year One (2008)

- A mark recapture study will take place in four rural sites representing different farming practices and within access of a wildlife underpass. P.I.T receivers will be placed at these underpasses, in order to record movement of marked individuals.
- Animals will be caught using a spotlight, biometric measurements will be taken and the animals will be marked using P.I.T tags. The animal will also be marked on a temporary basis using heat shrink resistant tubes.
- Footprint tubes will be placed around the site in order to compare relative hedgehog density with individuals caught (Huijser and Bergers, 2000).
- Carcasses from road casualties found around the sites, will be collected throughout the year, in order to identify whether there is a bias according to sex, season and age. Animals will be aged by periosteal growth line counts from stained sections of the dentary bone (Reeve, 1994).

Year Two/ Three (2009/2010)

- One of the sites will be looked at more closely, to identify nightly movements and home range.
- Around 6-8 individuals will be tagged with both a spool and line device and a radio tag, in order to compare the two methods.
- Fieldwork will follow the same pattern in 2010, in order to identify whether they maintain the same home range and winter losses.
- Nest boxes will be placed around the sites. They will be fitted with microchip receivers in order to identify the number of individuals utilising the box.
- Individuals will be continually weighed to investigate weight fluctuations throughout the year and the optimal weight prior to hibernation.

References

- Huijser, M.P., Bergers, P.J.M. (2000) The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. *Biological conservation*, Vol. 95, issue 1, pp. 111-116
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Appendix 3b: Mammal Society Easter Conference Winchester 2009

European Hedgehog (*Erinaceus europaeus*) Habitat Use in the Irish Rural Landscape

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Introduction

The European hedgehog, is widespread throughout Ireland and is protected under appendix 3 of the Berne convention. However, with the exception of Mulcahy's (1988) work on the lifecycle of the hedgehog flea there has been little research carried out on the hedgehog in Ireland.

There has been a growth in intensive farming and a renewed drive to encourage more extensive organic farming. However, the benefits of such measures to mammals such as the hedgehog are largely unknown, hence this study to investigate rural habitat use by hedgehogs.

Aims and Objectives

To investigate habitat use by hedgehogs in the Irish rural landscape and observe whether differences occur seasonally and in areas with different intensities of land use and farming practices.

Materials and Methods

- Animals were caught using a spotlight; biometric measurements were taken and they were marked using P.I.T. tags and heat shrink tubes.
- Hedgehogs were fitted with holohil radio tags and beta lights.
- Hedgehogs were observed by a combination of direct following and radio tracking.
- Day nests were identified and hibernacula were monitored to observe the duration of use by each animal.
- Transects were traversed throughout the site

Fig 1: Adult female fitted with Holohil radio tag

Results

- Five juveniles and nine adults were caught, comprising five females and nine males.
- Hedgehogs used a variety of habitats during the study period (Fig 2).
- Their pattern of habitat use changed from predominantly garden in July and August to a harvested barley field in September-October. At this time hedgehogs were rarely observed to move outside this field (fig 3).

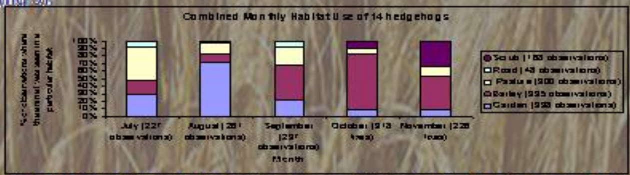

Fig 2: Hedgehog were found to spend greater amounts of their time in the garden earlier in the year but often entered the barley field later in the night.
In September they started spending the majority of their time in the barley field.

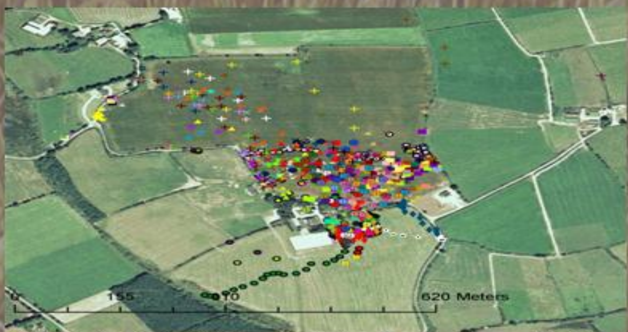

Fig 3: Map showing the habitat use of hedgehogs throughout the year. The different symbols refer to different individuals and the colours to different nights. The area where the animals centred their activity was a 12 ha arable field. Hedgehog activity corresponded to a greater abundance of surface invertebrates at the lower portion of the field.

Conclusions and Future Work

- Hedgehogs used open habitats (barley stubble) and in a food rich situation as this, the home range was extremely small. This will be investigated by looking at other populations in a similar landscape.
- Tissue samples have been taken from the animals and will be analysed in order to investigate the relationship between them.
- Differences in farming practices and land use will be examined, in order to investigate variation in abundance of hedgehogs.

Acknowledgements: This project has been funded by The Department Of Zoology, Ecology and Plant Science through The Crawford Hayes studentship.

Appendix 4-
Oral Presentations

Appendix 4a: Oral presentations

AIMS –All Ireland Mammal Symposium

Waterford 2009

Home range and habitat use of hedgehogs (Erinaceus europaeus) in a rural Irish landscape

Amy Haigh, Fidelma Butler and Ruth M. O'Riordan

Although the European hedgehog is a characteristic member of the Irish fauna, there has been little data on this species in Ireland. In order to investigate home range and seasonal habitat use, 24 hedgehogs were caught and radio tracked in a mixed agricultural landscape in Co. Cork, between June 2008 and June 2010. There was a home range overlap between sexes and throughout the year, which was more pronounced in males. Males had a mean home range of 56.0± 0.67 ha (100% MCP), which was significantly larger than females (16.5 ± 0.49ha). The male home range was at its maximum during the breeding season (April to July). Hedgehogs showed the same temporal pattern of habitat use annually. Activity was concentrated in pasture during the breeding season and in a 15 ha arable field after this time. In previous studies, in the UK and Denmark, arable land had ranked as the lowest habitat preference, which was not the case in this study. This entry into the arable field coincided with a rise in mollusc density in this area and suggests that hedgehogs responded to this increase. The suggestion that hedgehogs learn the spatial location of potential prey is further emphasised by the fact that within the arable field hedgehogs concentrated their activity in the lower portion of the field which corresponded to a greater density of potential prey. This is the first record of habitat use by Irish hedgehogs and presents some interesting differences to findings elsewhere in Europe, which may be related to Ireland's less intensive agricultural landscape.

Appendix4b: European Mammal Conference

Paris 19th-23rd July 2011

Where to eat? Prey availability and habitat choice by hedgehogs (Erinaceus europaeus) in a rural Irish landscape.

Amy Haigh, Fidelma Butler and Ruth O' Riordan

The European hedgehog is a characteristic member of the Irish fauna yet there has been little previous research on this species in Ireland. In order to investigate home range and seasonal habitat use, 24 hedgehogs were caught and radio tracked in a mixed agricultural landscape in Co. Cork, Ireland, from June 2008-2010. The density of surface invertebrates was monitored in arable and pasture land throughout this period. Males had a mean home range of 56 ± 0.67 ha (100% minimum convex polygon), which was significantly larger than females (16.5 ± 0.49 ha). Male home range encompassed that of a number of females and was at its maximum during the breeding season (April to July). In both years activity was concentrated in pasture during the breeding season and in a 15 ha arable field after this time. Previous studies, in the UK and Denmark ranked preference of arable land as the lowest, but such was clearly not the case in this study. Use by hedgehogs of arable land in the present study coincided with a rise in mollusc density. Hedgehogs concentrated their activity in areas with greatest prey density. Furthermore, contrary to previous studies, hedgehogs consistently foraged in the centre of both arable and pasture fields. This is the first analysis of habitat use by hedgehogs in Ireland and presents some novel differences to studies elsewhere in Europe. It is suggested that these differences are related to prey distribution. Reasons for the observed pattern of prey remain unclear and warrant further study.

Appendix 4c: German Mammal Society Conference

Luxembourg, 13th-17th September 2011

Nesting and hibernation behaviour in a rural hedgehog (Erinaceus europaeus) population

Amy Haigh, Fidelma Butler and Ruth O'Riordan

As the agricultural industry continues to grow, an increase in efficiency has led to an amplified use of pesticides, removal of hedgerows and a subsequent loss of potential nesting sites for animals like the hedgehog. U.K. hedgerows have been reduced by 50% (Robinson & Sutherland 2002) and it has been suggested that field margins and hedgerows may enhance the suitability of fields for hedgehogs (Hof, 2009). In most of Europe hedgerows have become special features, while in Ireland the majority have remained intact since the 18th Century (Cabot, 1999). The day nests and hibernacula of 15 (four ♀ and 11 ♂) radio tagged hedgehogs from a rural Irish site were recorded from June 2008 until November 2009. In total 117 different day nests were detected. Individual hedgehogs occupied up to 11 nests during the summer, returning to a particular nest up to seven times. Over the two years individuals were found to occupy a mean of 1.8 (±0.9) (SD) hibernacula per year (maximum of 3) and they moved hibernacula up to five times during the winter (mean of 2.5 ±1.6). Hedgehogs built both day nests and hibernacula in hedgerows of arable land, a habitat that is poorly utilised by hedgehogs elsewhere. This research suggests that these areas will be exploited if hedgerow is maintained and highlights the importance of hedgerows in arable areas.

Appendix 5-

Annual patterns of mammalian mortality on Irish roads

[redacted]

Appendix 5: Annual patterns of mammalian mortality on Irish roads.

Abstract

Roads are fast becoming one of the leading causes of mortality in a number of mammalian species. Between April 2008 and November 2010, 227 km of road between Cork and Galway were monitored for mammalian road kill. A further 32.5 km, between Cork city and Bandon Co. Cork, was screened from January 2009 and November 2010. In total 45,815 km were surveyed over the three year period. In this time 548 mammal fatalities were observed, representing 1.20 per 100km. Rabbits, hedgehogs, badgers and foxes were the four most common fatalities on both stretches of road, constituting 78% of the mammals killed. Autumn was the season of greatest mortality however, and May and August were the two months in which the greatest numbers of casualties were observed. Peaks in fatalities varied on a species basis and coincided with breeding and dispersal patterns.

Introduction

Ireland is currently undergoing the largest extension to the national road network in recent years (Dolan 2006). Roads are a major cause of mortality in a number of species, and sometime in the last three decades, they probably overtook hunting as the leading direct human cause of vertebrate mortality on land (Forman & Alexander 1998). The number of wildlife casualties on roads and railways have constantly grown worldwide as traffic and vehicle speeds have increased and infrastructure networks expanded (Seiler *et al.* 2004). Road traffic represents the most important cause of death of otters in most European Countries (Hauer *et al.* 2002). Philcox *et al.* (1999) noted that with regard to otters, an increase in the number of road traffic accidents (RTAs) recorded nationally began in 1983 and has been more rapid than the increases in any other known cause of otter mortality in Great Britain. In a survey of 32km of roads in Slovakia between September 2000 and December 2002, a total of 3,009 carcasses were found of which 45.5% were mammals (Hell *et al.* 2005). Similarly, the results of a study on a motorway section in France emphasized that traffic considerably affected vertebrate populations (14.5 animals per day/100km), of which 43.2% were mammals (Lodé 2000). Seiler *et al.* (2004)reported that in several of the commonly occurring mammal species in Sweden, road traffic causes an average loss of 1-12% of the estimated population sizes, approximately 10-100% of the annual game bags (Seiler *et al.* 2004). In the Netherlands it is estimated that between 113,000 and 340,000 hedgehogs are killed each year on roads (Huijser *et al.* 1998), which may reduce hedgehog density by around 30% (Huijser & Bergers 2000).

Roads affect animal populations in three adverse ways. They act as barriers to movement, increase mortality due to collisions with vehicles, and reduce the amount and quality of habitat (Jaeger & Fahrig 2004). With the increase in new roads further mortality may occur when new roads cross traditional tracks, unless under-passes and fencing are provided (Smiddy 2002). Furthermore, very high traffic levels may even inhibit road crossings (Morris & Morris 1988). Rondinini and Doncaster (2002) found that there was an overall significant tendency for hedgehogs to avoid crossing roads, with avoidance increasing in proportion to road width. Similarly Clark *et al.* (2001) found that roads were partial barriers to the movements of rodents. Forman and Alexander (1998) suggested that road kills are a premier mortality source, yet except for local spots, rates rarely limit population size. However, road avoidance has a greater ecological influence. Populations living in habitat surrounded by roads are less likely to receive immigrants from other habitats, and thus may suffer from lack of genetic input and inbreeding (Jaeger *et al.* 2005). Philcox *et al.* (1999) found that 56% of fatalities were male otters. Reasons suggested for this were: home range expansion, greater dispersal distances, higher energetic requirements and less cautious behaviour than females. This is something that has also been suggested as responsible for the 3:1 predominance of male hedgehogs killed on roads in the Netherlands (Huijser *et al.* 1998). This preponderance of males may affect population structure and reduced competition, between males, could eventually lead to negative effects on population vitality (Huijser 2000).

Despite the negative effect of roads, road kill can provide valuable sources of data particularly for protected species where there are restrictions on their capture. Hauer *et al.* (2002)

commented how in most parts of Europe road kill was the only way of obtaining data on reproduction, age and sex distribution in otters. Counts of road kill may also prove useful in monitoring changes in abundance of mammalian species (Baker *et al.* 2004). If a particular road is monitored for several years, the dynamics of populations of certain species can be accessed from the findings, and seasonal patterns of mortality identified (Hell *et al.* 2005). Generally the frequencies of mammalian road kills are highest in summer and lowest in winter (Hell *et al.* 2005). However, this varies depending on the species' breeding season and dispersal patterns. Holsbeek *et al.* (1999) observed that the pattern of hedgehog road kill shows a gradual increase towards July (>300) gradually decreasing to less than 10 towards December and January. In Ireland, Smiddy (2002) recorded that for road kills hares peaked in December and January, red squirrels in November, foxes from May to July, badgers in March to June, stoats in April, mink in July and otters from January to March. By identifying accident hot spots and the times of year when a species was most vulnerable to RTAs, affective mitigation measures may also be effectively put into place.

The aim of the current study was to identify the most frequently killed mammals on a subset of Ireland's roads and examine seasonal fluctuations in RTAs for a number of mammalian species.

Materials and Methods

Between April 2008 and November 2010 (excluding December), the road from Cork city to Caherlistrane Co. Galway (Fig. 1a) was monitored for mammalian road kill. In January 2009, a further stretch of road from Cork city to Bandon, Co. Cork was also monitored and this continued until November 2010 (Fig. 1b). These roads, representing a total distance of 259.5 km, were surveyed at regular intervals for 11 months of the year, excluding December. The road between Cork and Bandon was surveyed 362 times (~11,765km) over two years and that between Cork and Galway 150 times (~34,050km) over three years.

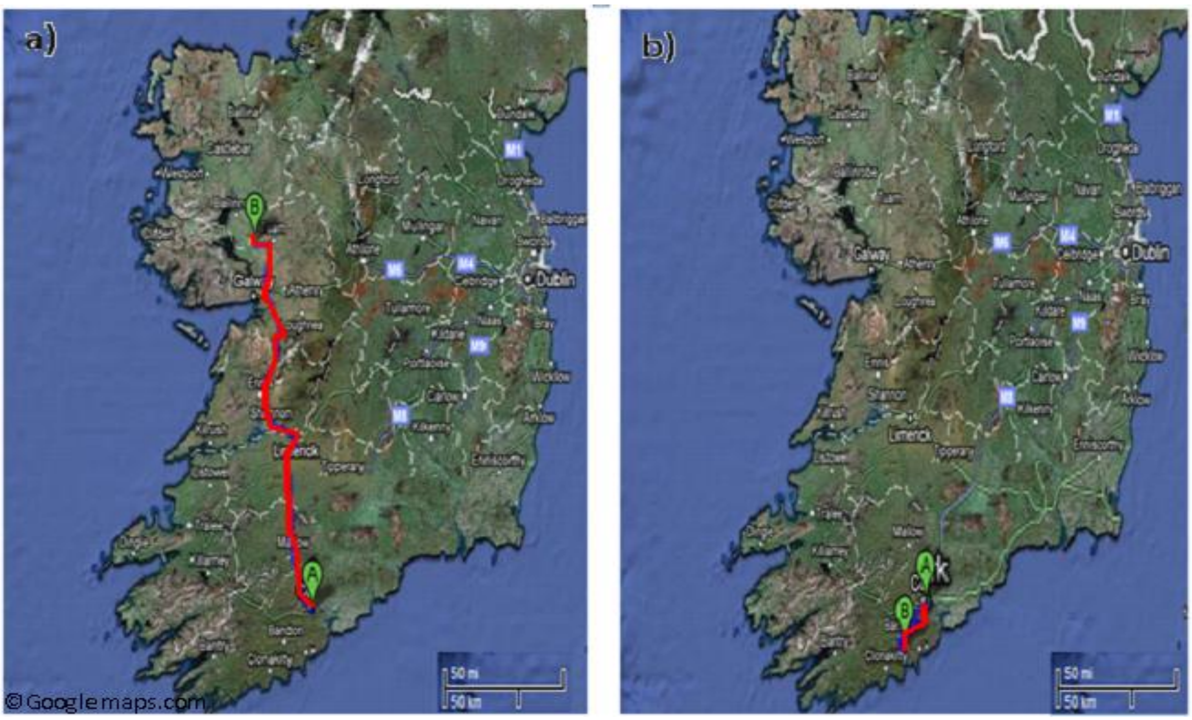

Figure 1a-b: The road from a) Cork city to Caherlistrane Co Galway (227 km) and b) Cork city to Bandon Co. Cork 32.5km).

Bird casualties and domestic animals were not included in the survey and rodents were not separated into species. Sightings were converted to numbers per km, to allow for differences in the number of times the roads had been surveyed per month.

Results

Most commonly killed mammals on both stretches of road

In total 45,815 km were monitored and 548 mammal casualties were observed representing 1.20 per 100km (Bandon-1.29 per 100km and Galway-1.17 per km). The most commonly killed mammals were rabbits, hedgehogs, badgers and foxes, and both stretches of roads exhibited a similar pattern of peaks in road casualties over the two years that both were surveyed (Fig 2a-d).

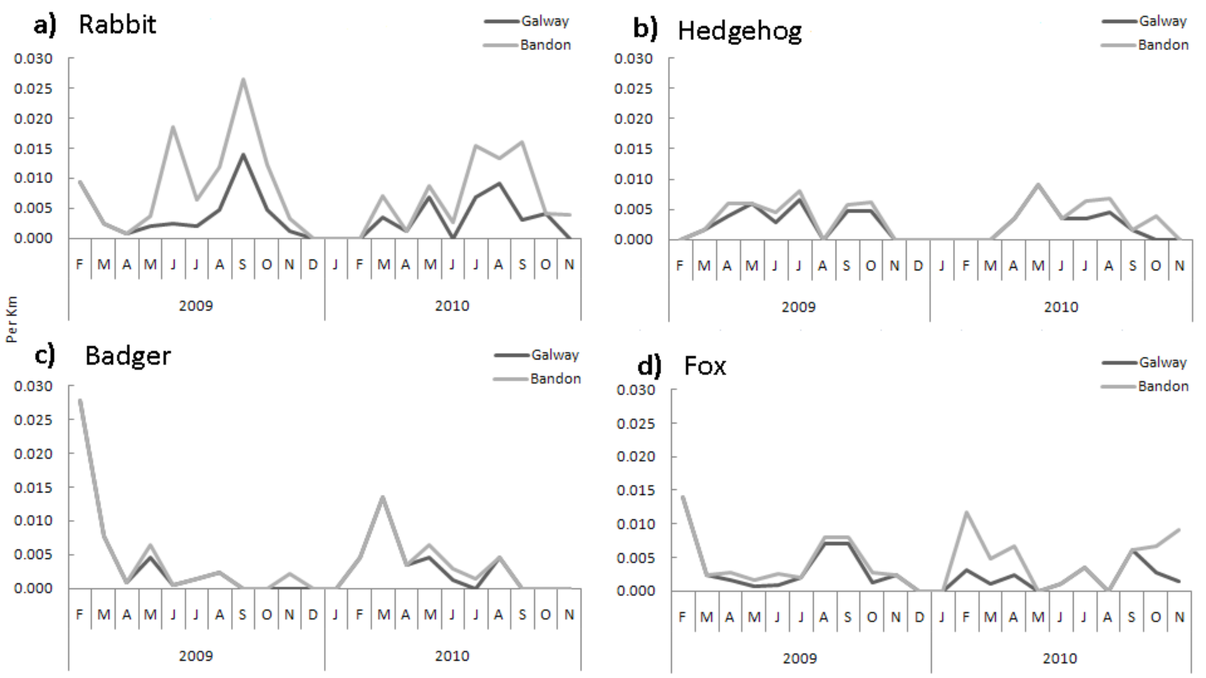

Figure 2a-d: The months in which the four most commonly killed mammals were found over the two years on both stretches of road.

Months when there was the greatest number of road kill

May and August represented the months in which the greatest number of road casualties were observed. There was a significant difference in the number of fatalities each season (F= 7.959, df=3,p<0.01). There was significantly more fatalities in summer and autumn than winter (p<0.05, Tukeys post-hoc), but no significant difference between these months and spring (p>0.05). Overall, autumn was the season in which mammals were most vulnerable to being killed on the road (Fig. 3).

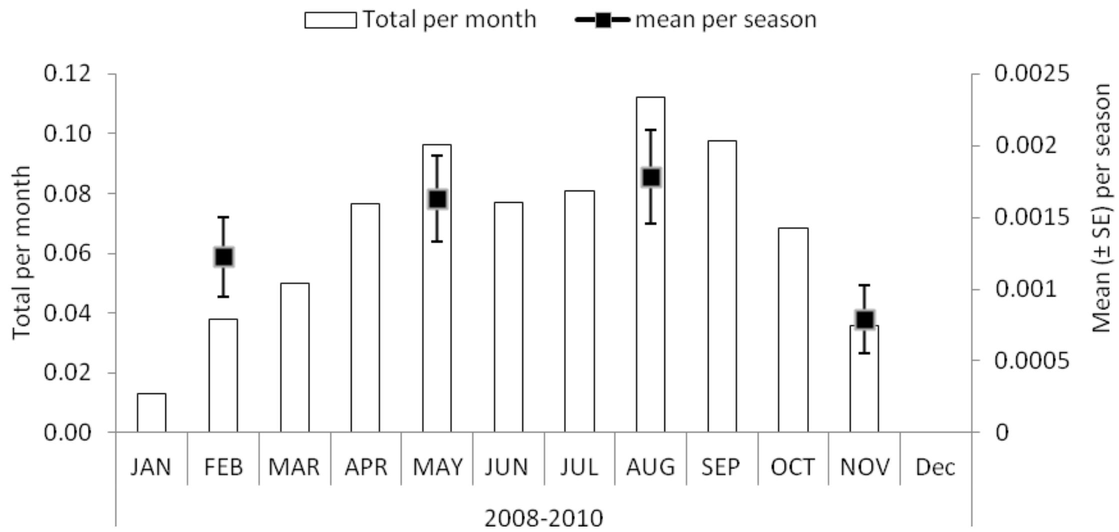

Figure 3: The months in which there was the greatest number of fatalities on both stretches of road and the mean (±SE) of casualties per season.

Months in which each species was most vulnerable

The months in which an animal was most vulnerable to being killed on the road varied amongst species. However, the majority displayed a bimodal pattern with peaks during the summer and autumn period (Table 1).

Table 1: Total number of mammalian road kill on the road between Cork and Galway from April 2008-November 2010 and the road from Cork to Bandon between February 2009 and November 2010, and the months in which there was a peak in each species when comparing the means.

Species	Total	%	Highest Occurrence
Rabbit	140	26	August and September
Hedgehog	130	24	May and August
Badger	75	14	March and May
Fox	83	15	July and September
Rodent	72	13	September- November
Mink	15	3	August and November
Hare	10	2	April and November
Otter	10	2	August and September
Pine Marten	7	1	February and July
Stoat	6	1	March and November
Total	548	100	

Cork to Galway over three year

The four most commonly killed mammals showed a similar pattern of fatalities over the three years that the road from Cork to Galway was monitored(Fig 4 a-d, Table 2).

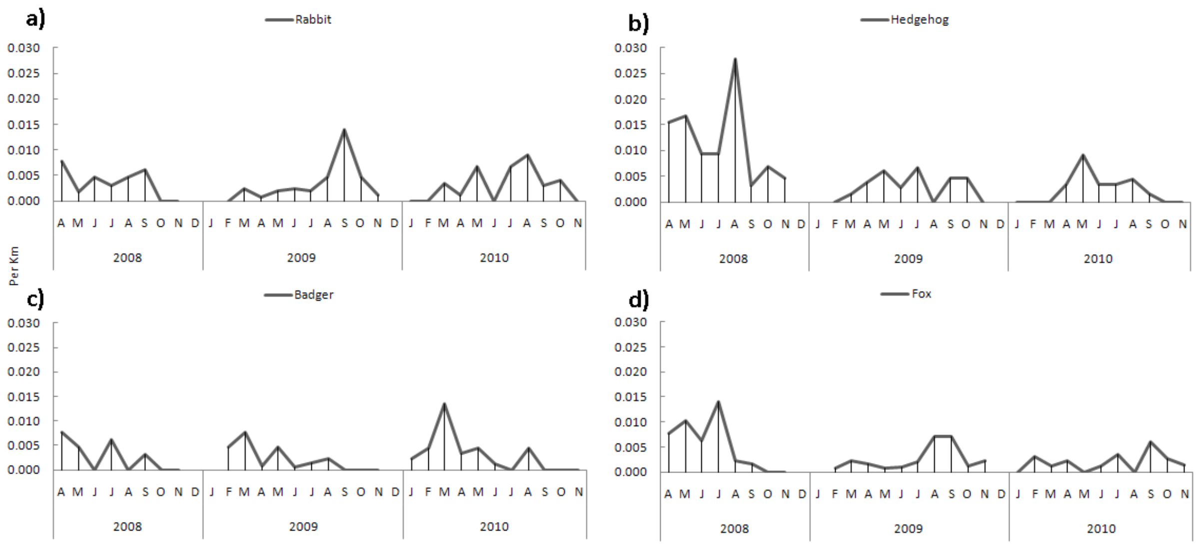

Fig 4 a-d: The months in which the four most commonly killed mammals were killed over the three years that the road from Cork to Galway was monitored.

If the peak was not observed in the same month in the following years, it was found to occur either the month before or after (Table 2). Hedgehogs for instance, peaked in May in all three years and while they peaked again in August 2008 and 2010, in 2009 they peaked one month earlier in July (Table 2).

Table 2: The months in which there was a peak in fatalities each year on the road from Cork to Galway for the four most commonly killed species.

Species	Year	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Rabbit	2008	N/A	N/A	*					*		
	2009				*	*			*		
	2010				*			*			
Hedgehog	2008	N/A	N/A		*			*			
	2009				*		*				
	2010				*			*			
Badger	2008	N/A	N/A	*			*		*		
	2009		*		*			*			
	2010		*		*			*			
Fox	2008	N/A	N/A		*		*				
	2009		*					*	*		
	2010						*		*		

Discussion

Including both national and local road networks, the Republic of Ireland has an extensive road network of 78, 972 km over an area of 70, 273 km² (www.nra.ie). This equals 1.28 km of road per km², which is lower than the 3.8 km roads per km² in Belgium (Holsbeek *et al.* 1999) and the 1.73 km roads per km² in Great Britain (calculated from statistics from the Ministry of Transport, transport statistics, Great Britain, 2007 addition, *www.transport.govt.nz/research*).It is therefore not surprising that fatalities are also lower on Irelands roads than in the U.K. In Slovakia, Hell *et al.* (2005) found 6.3 mammals per 100km, which was higher than the 1.20 fatalities per 100km found in the current study. When comparing the results of this study with previous work in Ireland Smiddy (2002) recorded 1.54 casualties per 100 km (domestic cats were removed from calculations in order to compare with the present study). With increased road construction, the National Roads Authority in Ireland has also increased the number of crossing structures for wildlife. In Ireland these are mainly targeted at protected species whose habitat is directly disturbed by road such as otter and badger, however, it is also hoped that they will be utilised by non target species (Dolan 2006). Various wildlife passages (tunnels, pipes, underpasses, overpasses) operating for animal movement have been installed in order to minimise detrimental ecological impacts in other countries (Forman and Alexander, 1998). A number of studies (Clevenger *et al.* 2001, Mata 2004, Dolan 2006, Ascensão & Mira 2007), have reported the successful use of these mitigation schemes by mammals including rodents, badgers and deer. Included in the roads monitored in the present study was the Ennis bypass. This opened in 2007 and consists of 14km of standard dual carriageway and 6km of single carriageway (www.nra.ie). Included in the construction were wildlife underpasses and fencing for badgers, otters and pine martens and the provision of alternative bat roost sites (Clare County Council). However, while these underpasses have been found to be successfully utilised by bats (Abbott, pers. comm. 2011), their use by other species is currently unclear. While the lower number of fatalities in the present study is encouraging, the avoidance of these large roads with high traffic volumes by mammals must also be taken into account. Forman and Alexander (1998) reported that road avoidance, has a greater ecological impact on population size than the mortality caused by roads and that road width and traffic density were major determinants of the barrier effect. Similarly, Clark *et al.*(2001) observed that 9.4% of individual rodents captured more than once spontaneously crossed roads.

In the present study autumn was the season in which mammals were seen to be most vulnerable to road mortality. This is a period of dispersal for a number of species (Gerell 1970, Erlinge & Sandell 1986, White & Harris 1994, Macdonald *et al.* 2008). Natal dispersal is defined as the definitive movement of an individual from its birth site to the place of its first breeding attempt (Howard 1960). It is possible that dispersing individuals benefit from both increased access to unrelated mates and increased intrasexual competition (Dobson & Jones 1985). While in birds, females are known to disperse more, in mammals it is more common in males (Greenwood 1980). While no difference in road kill numbers was found between the sexes in badgers (Macdonald *et al.* 2008) and a female bias in dispersal amongst hares (Avril *et al.* 2011) Rushton *et al.* (2006) observed that male foxes dispersed further than females and this has also shown to be the case in mink (Gerell, 1970), rabbits (Kunkele & Von Holst 1996) and stoat (McDonald & Harris 2002). This period of greater movement would be expected to make males more vulnerable to road mortality and Philcox *et al.* (1999) recorded that fifty-six per cent of otter fatalities were males, representing a statistically significant bias. Sleeman (1988) found that stoat fatalities were predominantly male, with peaks in March, April and May. This corresponds with the results of this study and the further peak in November may be attributed to the establishment of territories by stoats in autumn/ winter (Erlinge & Sandell 1986). Doncaster (1993) suggested that hedgehogs do not have a fixed natal territory from which to disperse, nor a clearly defined dispersal stage. However, during the breeding season males increase their home range (Morris, 1969, Kristiansson, 1984, Jackson, 2006) and Huijser *et al.* (1998) reported that 3-22% of hedgehogs were killed on the road in the Netherlands and they represented a preponderance of 3 to 1 male. This male bias in road kill was also recorded amongst Irish hedgehogs (Chapters 7 and 9). Hedgehogs were the second most commonly killed mammal in the present study, with peaks observed in May and August. Road kill studies have reported a peak in road deaths in May and July in Belgium, The Netherlands and Ireland (Holsbeek *et al.* 1999, Huijser & Bergers 2000, Smiddy 2002). The breeding season in the European hedgehog has been reported to occur between April and August, with peaks in activity varying between studies (Morris 1961, Morris 1969, Kristiansson 1984, Riber 2006, Jackson 2006). As already stated, the breeding season is associated with male hedgehogs increasing their home range in order to encompass the ranges of as many receptive females as possible. This may therefore explain a peak in road kill in the present study. While Goransson *et al.* (1976) found that 80% of traffic victims were male hedgehogs in Sweden, in autumn he found that high numbers of females were killed which was attributed to a greater need to forage wider, in order to build up fat prior to hibernation after raising young.

Rabbits were the most commonly killed mammal on the roads surveyed. This may be accounted for by their high numbers and widespread distribution, with population densities ranging from 15 per ha in winter to up to 40 per hectare in summer (Hayden & Harrington 2001). In Germany, Kunkele and von Holst, (1995) recorded that rabbits breed between March/April and September/October every year and that at 5 months of age 72% of the litter had dispersed, by the following spring this number had increased to 88%. This peak in rabbit road deaths in the August/September period may therefore be represented by juvenile dispersers born earlier in the year.

In Britain, road traffic is the largest cause of recorded deaths of badgers, with an estimated 50,000 badgers being killed on the roads each year (Davies *et al.* 1987) which equates to 48.8% of all adult and post-emergence cub fatalities (Clarke *et al.* 1998). Permanent dispersal is not common in badgers, however, in the U.K. movements between social groups were most common in autumn (17.1%, n = 626 trapping events) and least common in winter (10.9%, n = 339) (Macdonald *et al.* 2008). Badger road fatalities have been found to be bi-modal with peaks in late spring and summer (Clarke *et al.* 1998) no difference has been observed between the seasonal distribution of deaths between the two sexes and it has been suggested that peaks in mortality reflect increased activity in conjunction with mating (Davies *et al.* 1987). February and March is a period of increased boundary marking behaviour just prior to breeding (Delahay *et al.* 2000) and the results of this study corresponds to the peaks in badger road deaths observed elsewhere (Davies *et al.* 1987, Clarke *et al.* 1998, Smiddy 2002).

Foxes showed a bimodal pattern in road deaths with peaks in July and September in the present study. Fox cubs begin to forage with their parents in July and are usually self sufficient by this time (Fairley 1975) and this period of exploration may lead to an increase in road deaths. During September and October, competitive behaviour in both the dog fox and male offspring stresses their relationship until the young male’s disperse (Henry 1986). Dispersal occurs once a year in foxes from autumn to winter and all subadults that did not find space in their natal social groups dispersed (Rushton *et al.* 2006). Harris and Trewhella (1988) found that by the end of march 67% of males and 31.8% of females had dispersed and dispersal distances for foxes marked as cubs and retrieved as adults was 1.6 ± 0.2 km for females and 2.8 ± km for males. These dispersing individuals would be at a greater risk of being killed on the road and would explain the peak observed in September in the present study.

Of those least frequently observed casualties, hares were observed mostly in April and November. Under ideal weather conditions hares may breed all year and males may increase their home range in order to search for females (Hayden and Harrington, 2001). Peaks in mink casualties occurred in August and November in the present study. Mink have reached subadult size in November (Enders 1952) but the largest-scale movements in a mink population are the dispersal of the juveniles which starts in the beginning of July but families have been found to keep together until the middle of August (Gerell 1970). This may account for the peak in the present study. Winter is a difficult time for many mammals and corresponds to a period of dormancy or decreased activity for species such as the hedgehog and badger. It is a time of reduced prey and food supply for many animals and as a result individuals may have to travel further in search of food leading to a greater susceptibility to road deaths which may account for the peak observed in hare and mink in November.

Roads are particularly damaging to vulnerable and endangered species. In Northern Ireland one of the greatest threats to pine marten currently appears to be the rise in the number of road kill incidents and since the 1960s the number of pine marten killed on the roads has increased from 5 per cent of total records to 22 per cent of total records in the late 20th century (Tosh *et al.* 2007). In Otters, Kubasch (1992) has suggested that 10% of the total population of Saxony has been lost to road accidents. The number of these species observed as road kill in the present study was small with only seven pine marten and ten otter observed over the three years. However for species like the pine marten, who in O'Sullivan's (1983) study were found confined to localised areas of woodland and scrub in mid western Ireland and who may have a population density ranging between one per km² to 1 per 10km² (Hayden and Harrington, 2001), the loss of even small numbers may signification effect the survival of local populations. Although the small numbers make it difficult to incur a pattern in road deaths, peaks were observed in February and July. The breeding season begins in July, and transient pine marten were caught from January to March in Sweden (Helldin & Lindström 1995). Similarly, in Ireland, Tosh *et al.* (2007) observed that records of pine martens are greater during the summer, which is attributed to greater activity associated with breeding.

Hauer *et al.* (2002) found that 69.9% of mortality in otters was due to road fatalities but there was no significant difference in relation to different time periods. Philcox et al (1999) found a seasonal correlation between otter road traffic accidents and rainfall and that floodings are likely to create the critical conditions leading to otter road traffic accidents. In the present study a preponderance of fatalities occurred in August 2010 and September 2008. In both of these months there was a dry period following widespread flooding and exceptionally wet weather the month before. In Munster and Leinster rainfall was 50% lower in August 2010 while in July 2010 rainfall totals were above normal everywhere and were more than twice the average at some stations (www.met.ie). Similarly, August 2008 was a month of exceptionally heavy rain over most of the country, bringing flooding in many areas, while rainfall levels were normal in September 2008 rainfall (www.met.ie).

Of the four most commonly killed species on both stretches of road, a similar pattern was observed over the three years. Peaks were observed in the same months over at least two years, with May proving a vulnerable time for the hedgehog throughout the study. However, in months were a peak was observed differently in a proceeding year, in all cases the peak occurred either the month before or after. It is suggested that this is related to variations in the onset of the breeding season and correspondingly that of dispersal which may be related to annual changes in food supply or weather conditions. Hares for instance are known to breed for a shorter duration of time when food is scarce or almost continuously when conditions are favourable (Hayden and Harrington, 2001).

While this study has successfully identified peaks in mammal fatalities for a number of species and identified those most vulnerable to road mortality, it has also highlighted the need for further investigation into the effect of roads on mammals. In particular, while the number of roads continues to grow, more long term monitoring is warranted to identify accident black spots and the effectiveness of underpasses, so that effectual measures can be implemented to minimise road fatalities.

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Appendix 6-

Carcass records

Appendix 6: The dates, locations, sex age, cause of death and the collectors of 146 hedgehogs. C/T refers to Individuals where the sex or age could not be determine.RTA=road traffic accident.

Date	Location	Collector	Cause of death	Sex	Age
17/04/2008	Clonakilty/Bandon	Ruth Ramsay	RTA	Male	Adult
29/04/2008	Muskerry(51.55'04.26N, 8.36'45.05W)	Padraig Whelan	RTA	Female	Adult
12/05/2008	Ring road, Cork	Mick Mackey	RTA	Male	Adult
15/05/2008	Kerry	Meabh Boylan	RTA	C/T	C/T
05/06/2008	Fota, Cork	Amy Haigh	RTA	Male	Juvenile
05/06/2008	N8, Fermoy	Amy Haigh	RTA	Female	Adult
06/06/2008	51.96263356414209,-8.385186195373535	Isobel Abbott	RTA	C/T	C/T
09/06/2008	Kinsale	T.Kelly	RTA	Male	Adult
17/06/2008	Riverstick	Fidelma Butler	RTA	Male	Adult
20/06/2008	Partry	Conall Hawkins	RTA	Female	Adult
21/06/2008	Riverstick	Fidelma Butler	RTA	Male	Adult
23/06/2008	51.9063399773712,-8.2807087898254	Isobel Abbott	RTA	Female	Adult
26/06/2008	Bandon	Ruth Ramsay	RTA	C/T	C/T
07/08/2008	Woburn ave, Bishopstown	Eoghan Walsh	RTA	Female	Adult
07/07/2008	51.59'02.76"N, 8.42'07.68"W, Fornaght, 15km Muskerry	Padraig Whelan	RTA	Male	Adult
11/07/2008	Dundarrow	Daphne Roycroft	Found ill in garden	Female	Adult
12/07/2008	Rathcormack	J. Twomey	RTA	Female	Adult
23/07/2008	59.54.3.97N, 8.30.55.24W Clogheen, 2km Fitzgerald park	Padraig Whelan	RTA	Female	Adult
25/07/2008	Croom	Padraig Whelan	RTA	Female	Adult
01/08/2008	51.42,14.2N,008.42,15.4 W Mooneen, Ennis	Padraig Whelan	RTA	C/T	C/T
02/07/2008	Cork	Ger Staunton	RTA	Male	Adult
07/08/2008	Balineen	Dave Mc Cormack	RTA	Male	Juvenile
18/08/2008	Castlehackett, Co. Galway	Amy Haigh	RTA	Female	Adult
18/08/2008	Cork Airport	Alan Myers	RTA	Female	Adult
10/09/2008	Fountainstown	Alan Myers	RTA	Female	Juvenile
21/09/2008	51.57,49.95N,8.44,35.20W Knockanare, 6km Berrings	Padraig Whelan	RTA	Female	Adult
25/09/2008	Carewswood	P.Smiddy	RTA	Female	Adult
25/09/2008	Gotre	P.Smiddy	RTA	Male	Juvenile
22/10/2008	Athlone	P. Jackson	RTA	Male	Juvenile
23/10/2008	Ratharoon, Bandon	Amy Haigh	Predation	Male	Adult
27/10/2008	Caherlistrane, Co.Galway	Amy Haigh	RTA	C/T	C/T
27/10/2008	Caherlistrane, Co.Galway	Amy Haigh	RTA	C/T	C/T
08/11/2008	Castlehackett, Co. Galway	Amy Haigh	RTA	Female	Juvenile

	Ballincollig	T.Cross	Drowned	Male	Juvenile
28/11/2008	Ballinhassig	Amy Haigh	RTA	Male	C/T
23/03/2009	Ratharoon, Bandon	D.Roycroft	RTA	Male	Adult
29/03/2009	52.06'11.79''N, 8.53'08.15W, Coolroemore, 4km from Lyre	Fionnuala Walsh	RTA	Male	Adult
31/03/2009	52.05'06.48''N,8.52'49.93''W, Lyre	Padraig Whelan	RTA	Male	Adult
08/04/2009	Dennehys cross, Cork	(021)4541733	Found ill in garden	Male	Adult
09/04/2009	Just before turn to Ballinhassig	Amy Haigh	RTA	Male	Adult
15/04/2009	Justbefore farm in Ballinhassig	Amy Haigh	RTA	Female	Adult
17/04/2009	W39140-93016 Irish grid	Padraig Whelan	RTA	Male	Adult
19/04/2009	N22 O Sullivan garage and petfarm, Kerry	Ruth Ramsay	RTA	C/T	C/T
25/04/2009	Just before Mallow, sign to Mourne abbey	Amy Haigh	RTA	Male	Adult
29/04/2009	NUIG campus	Niamh Quinn	RTA	Male	Adult
02/05/2009	Just after Croom,51224 47357	Amy Haigh	RTA	Male	Adult
05/05/2009	Enniskeane, Bandon	Padraig Whelan	RTA	Male	Adult
07/05/2009	Droumcarra, W29168,68439	Daniel Buckley	RTA	C/T	C/T
09/05/2009	63957,75431, Blarney	Amy Haigh	RTA	Male	Adult
11/05/2009	Mallow to Mitchelstown rd	Amy Haigh	RTA	Male	Adult
10/05/2009	Junction 5, N8, Urlingford	Padraig Whelan	RTA	Male	Adult
10/05/2009	Joyces garden centre, mallow	Padraig Whelan	RTA	C/T	C/T
30/05/2009	Glynns, Caherlistrane, Co. Galway	Amy Haigh	RTA	Female	Adult
31/05/2009	Srelane, Macroom	Mark Wilson	RTA	Male	Adult
01/06/2009	Just before Bandon	Ruth Ramsay	RTA	Male	Adult
07/06/2009	Holland Ivy barn, Bandon	Ruth Ramsay	RTA	Female	Adult
08/06/2009	North of Creans Cross,51.59'03.56N,8.46'57.40W	Padraig Whelan	RTA	Female	Adult
08/06/2009	South of Creans Cross,51.57'55.89N,8.44'50.83''w	Padraig Whelan	RTA	Male	Adult
09/06/2009	Croagh Patrick	Amy Haigh	RTA	Male	Adult
16/06/2009	Gort	Amy Haigh	RTA	C/T	C/T
16/06/2009	Gort	Amy Haigh	RTA	Male	Adult
21/06/2009	Just before Mallow, sign to Mourne Abbey	Amy Haigh	RTA	Female	Adult
23/06/2009	Just before airport roundabout, Cork. Outside Bundunhig house	Amy Haigh	RTA	Male	Adult
06/07/2009	R579, wayside inn	Padraig Whelan	RTA	Male	Adult
07/07/2009	Kerry	Richard O'Callaghan	RTA	C/T	C/T
08/07/2009	Innishannon	Ruth Ramsay	RTA	C/T	C/T
13/07/2009	Ballincollig, Ovens graveyard	Tom Cross	RTA	Female	C/T

	Cork airport/Ballinhassig	Amy Haigh	RTA	Male	Juvenile
14/07/2009	Cork airport/Ballinhassig	Amy Haigh	RTA	Female	Adult
16/07/2009	N8, Butlerstown river crossing	Isobel Abbott	RTA	C/T	Adult
21/07/2009	R579 O'Reagans area	Padraig Whelan	RTA	Female	Adult
23/07/2009	R579, Wayside inn	Padraig Whelan	RTA	Male	Juvenile
27/07/2009	R579, just before O'Regans	Padraig Whelan	RTA	C/T	C/T
27/07/2009	R579, just before O'Regans	Padraig Whelan	RTA	Male	Juvenile
30/07/2009	R579, just before O'Regans	Padraig Whelan	RTA	Female	Adult
31/07/2009	just after the railway, Gort	Amy Haigh	RTA	Female	Juvenile
31/07/2009	Balinasloe	Helen Carty	RTA	C/T	C/T
01/08/2009	Kilmaine	Amy Haigh	RTA	Male	Adult
01/08/2009	Kilmaine	Amy Haigh	RTA	Female	Juvenile
05/08/2009	Balinspittle	Ruth Ramsay	RTA	Male	Juvenile
06/08/2009	Fermoy	Isobel Abbott	RTA	Female	Adult
10/08/2009	Ratharoon, Bandon	Amy Haigh	Euthanised after dog attack	Male	Adult
16/08/2009	Kilmaine, Co. Mayo	Amy Haigh	RTA	C/T	C/T
17/08/2009	Shrule, Co.Mayo	Amy Haigh	RTA	C/T	C/T
05/09/2009	Caherlistrane, Co. Galway	Amy Haigh	RTA	C/T	Adult
06/09/2009	Caherlistrane, Co. Galway	Amy Haigh	RTA	Male	C/T
06/09/2009	Between Dripsey and Eniscarra	Stefanie Brozeit	RTA	Female	Adult
11/09/2009	Ratharoon, Bandon	Amy Haigh	Stuck in net	Male	Adult
24/09/2009	Macroom, Cork	Gema Hermandez	RTA	Female	Adult
26/09/2009	Caherlistrane, Co. Galway	Amy Haigh	RTA	Male	Juvenile
30/09/2009	Ratharoon, Bandon	Amy Haigh	Predation	Male	Juvenile
04/10/2009	Cork	Padraig Whelan	RTA	Male	Juvenile
08/10/2009	Ballinhassig	Amy Haigh	RTA	C/T	Adult
08/10/2009	Ballinhassig	Amy Haigh	RTA	C/T	Adult
28/10/2009	Corrundulla	Amy Haigh	RTA	Male	Adult
09/11/2009	Mullagh, Killrekill-173041,219433	Helen Carty	RTA	Male	Juvenile
01/11/2009	Mahon bridge	Denise O'Meara	RTA	C/T	Juvenile
27/08/2008	Kilgarvan Co Kerry	Daniel Buckley	RTA	Male	Juvenile
22/09/2009	Carriganimme, Cork	Daniel Buckley	RTA	Male	Adult
Jul-09	Wicklow	Daniel Buckley	RTA	Female	Adult
21/01/2010	Cork	Ted Hickey	Hibernation	Female	Adult
25/04/2010	Ballinrobe	Amy Haigh	RTA	Male	Adult
07/05/2010	R579 O'Reagans area	Padraig Whelan	RTA	Male	Adult
07/05/2010	R579 O'Reagans area	Padraig Whelan	RTA	Male	Adult
08/05/2010	R579 O'Reagans area	Padraig Whelan	RTA	Male	Adult
08/05/2010	Farrane	Padraig Whelan	RTA	C/T	Adult
10/05/2010	Berrings	Padraig Whelan	RTA	Male	Adult

10/05/2010	Before turn to Ballinhassig	Amy Haigh	RTA	Female	Adult
12/05/2010	UCC campus	Emer Rogan	RTA	Female	C/T
16/05/2010	Cork airport	Amy Haigh	RTA	Male	Adult
18/05/2010	Kilbrittan	Neil Ramsay	RTA	Male	Adult
20/05/2010	Riverstick	Fidelma Butler	RTA	Male	C/T
25/05/2010	Riverstick	Amy Haigh	RTA	C/T	C/T
25/05/2010	Cobh	Emer Rogan	ill in garden	Male	C/T
12/06/2010	Junction past Starck	Padraig Whelan	RTA	C/T	C/T
11/06/2010	Loughrea to Craughwell156627,217912	Helen Carty	RTA	C/T	C/T
11/06/2010	Loughrea to Craughwell 154569 218241	Helen Carty	RTA	Male	Adult
14/06/2010	Ratharoon, Bandon	Amy Haigh	RTA	Female	Adult
15/06/2010	Berrings	Padraig Whelan	RTA	Male	Adult
26/06/2010	Between Bandon and Clonakilty	Ruth Ramsay	RTA	C/T	Adult
01/07/2010	Ratharoon, Bandon	Amy Haigh	mowing machine	Male	C/T
04/07/2010	Dysart, Co. Galway	Amy Haigh	RTA	Male	Adult
11/07/2010	Ratharoon, Bandon	Amy Haigh	Electrocuted	Male	Adult
17/07/2010	Cork airport, 565567, 567094	Fidelma Butler	RTA	Male	Adult
25/07/2010	Between Balinrobe and Kilmaine	Amy Haigh	RTA	Male	Adult
09/08/2010	R579 O'Reagans area	Amy Haigh	RTA	C/T	Juvenile
10/08/2010	Ballincollig	Nathan Slattery	RTA	Male	C/T
11/08/2010	Ballinspittle	Ruth Ramsay	RTA	C/T	C/T
19/08/2010	Barryroe/ Lislevane	Ruth Ramsay	RTA	C/T	C/T
20/08/2010	Headford, Co. Galway	Amy Haigh	RTA	C/T	Juvenile
17/08/2010	Sligo	Mairead	RTA	Female	Adult
22/08/2010	Caherlistrane, Co. Galway	Tom Haigh	RTA	Female	Juvenile
23/08/2010	Caherlistrane, Co. Galway	Amy Haigh	RTA	C/T	Adult
30/08/2010	O'Donovans, R579	Padraig Whelan	RTA	Female	Adult
30/08/2010	Wayside Inn R579	Padraig Whelan	RTA	C/T	Adult
06/09/2010	Caherlistrane, Co. Galway	Amy Haigh	RTA	C/T	Adult
13/09/2010	Knockanare (51.58.05.3,008.44.56.5)	Amy Haigh	RTA	C/T	C/T
19/09/2010	Kanturk	Padraig Whelan	RTA	Male	Juvenile
19/09/2010	Ballinhassig, just after village	Neil Ramsay	RTA	Male	Juvenile
24/09/2010	Caherlistrane at stables	Amy Haigh	RTA	C/T	Adult
24/09/2010	Kilbrittan	Neil Ramsay	RTA	C/T	Juvenile
04/10/2010	Ballincollig	Tom Cross	RTA	Female	Juvenile
06/10/2010	Kilbrittan	Neil Ramsay	RTA	C/T	Adult
17/10/2010	Kilbrittan	Neil Ramsay	RTA	C/T	Juvenile
30/10/2010	Before turn to Ballinhassig	Amy Haigh	RTA	C/T	Juvenile
07/02/2011	Millstreet	Padraig Whelan	RTA	C/T	Adult

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[redacted]

Thomas Paine once expressed how “what we obtain too cheap, we esteem too lightly” and “it is hardness only that gives everything its value”. I would be lying if I said that doing a PhD was easy but it was also extremely satisfying and with every hurdle I faced I was extremely lucky to always have people around who were willing to give a helping hand. As Alfred North Whitehead stated “no one who achieves success does so without acknowledging the help of others” and I would like to acknowledge some of those people who helped me and made my PhD experience such an enjoyable one, whether it was offering practical advice, acting as an often much needed amateur psychiatrist or the other, not always last resort of sharing a pint with me.

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