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Hedgehog *Erinaceus europaeus* mortality on Irish roads

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Hedgehogs are one of the most common mammalian road fatalities in Europe. 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. In addition to the sightings of road kill on the two stretches of road, a further 135 carcasses were collected over the study period from throughout 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. The number of hedgehog road kill per km in the current study was low when compared to countries such as Belgium, Poland and New Zealand. It is suggested that this may be a consequence of hedgehogs having a greater opportunity to encounter larger busier roads in other countries. Over the three years, the majority of the 133 carcasses sighted were located beside pasture, which was the most prominent habitat along both routes. Arable land was the only habitat used in a greater proportion than what was available. K-function analysis detected clustering along the surveyed roads, with fatalities clustering annually at several locations. This would suggest that hedgehogs may use specific crossing points which would be important for the implementation of management strategies and underpass construction. Of the 135 hedgehog carcasses collected from throughout Ireland there was significantly more males than females collected, with peaks in male deaths occurring in May and June. Female deaths only outnumbered males in August, with further peaks in female deaths observed in June and July. It is suggested that these peaks are related to the breeding season (adults) and dispersal/ exploration following independence (juveniles).

Population declines have occurred for a number of wild mammalian species in Europe, sometimes drastically so (Macdonald and Tattersall 2007). One such species where a decline has been reported is the European hedgehog *Erinaceus europaeus*. In the 1950s the hedgehog population in the UK was estimated at about 30 million, by 1995 this had reduced to about 1.5 million(Mac Donald and 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 UK (Mac Donald and Burnham 2011). The expanding network of major roads has been frequently identified as one of the negative factors affecting hedgehog presence and/or abundance in the UK (Hof 2009). 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), partly due to their main line of defence being to roll up in a ball. 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 and Bergers 2000). 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 UK, 35 (47.3%) were road casualties. However, Lodé (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, of a population of 78 hedgehogs, 24% were killed on the road over a year (Orlowski and Nowak 2004).

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. Hedgehog road deaths have been observed to peak during the breeding season (April–July) (Holsbeek et al. 1999, Smiddy 2002) which coincides with an expansion of the male hedgehogs range (Kristiansson 1984). Therefore a strong male bias in road casualties has been recorded (Göransson et al. 1976, Huijser et al. 1998).

Despite hedgehogs being one of Ireland's most distinctive mammals there has been little research on the hedgehog in this country. 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). However, as these previous road kill studies were not concentrated solely on hedgehogs, information was not obtained on the sex of casualties or the habitats from which they were collected. This is data which is important for the successful implementation of management strategies. The hedgehog 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 and Harrington 2001). However, while Hayden and Harrington (2001) reported the hedgehog are widespread throughout Ireland, with no baseline data on this species, it is unclear whether it is as vulnerable as other areas of its range (Dowding 2007, Hof 2009).

In view of the reported decline of the hedgehog in other areas of its range, its protected status and the fact that it is little studied in Ireland, this study aimed to investigate one of the factors felt to be accelerating this decline, road mortality. It aimed to compare road mortality in Ireland with other areas of the species range and examine whether like elsewhere, the greatest numbers of hedgehog road fatalities occur during the breeding season, with a greater number of males killed than females. The location of road kill was also investigated in order to gain an insight into hedgehog habitat selection. Finally this study aimed to examine whether hedgehogs were randomly distributed throughout road networks or whether specific accident hot spots could be identified that would have wider implications in the implementation of mitigation measures.

Material and methods

Focal road survey

To examine for seasonal patterns two stretches of road were selected to be intensively studied. One of these roads was chosen as it was the main arterial road between two Irish cities (Galway and Cork); the second, in Munster, linked Cork City to the county. Between April 2008 and November 2010 (excluding December), these two stretches of road (Fig. 1) were surveyed for road kill. The car, with at least two passengers, travelled at an average speed of 60 km h^{-1}. The survey was conducted in the mornings, and concentrated on the road and hard shoulder but not on the grass verges. Hedgehog carcasses on these road stretches were collected as part of a larger study (Haigh 2011). These roads, representing a total distance of 259.5 km, were surveyed at regular intervals for 11 months of the year, excluding December, when winter break interrupted the regular travel along these routes. GPS co-ordinates were taken of the location of carcasses and the habitat recorded.

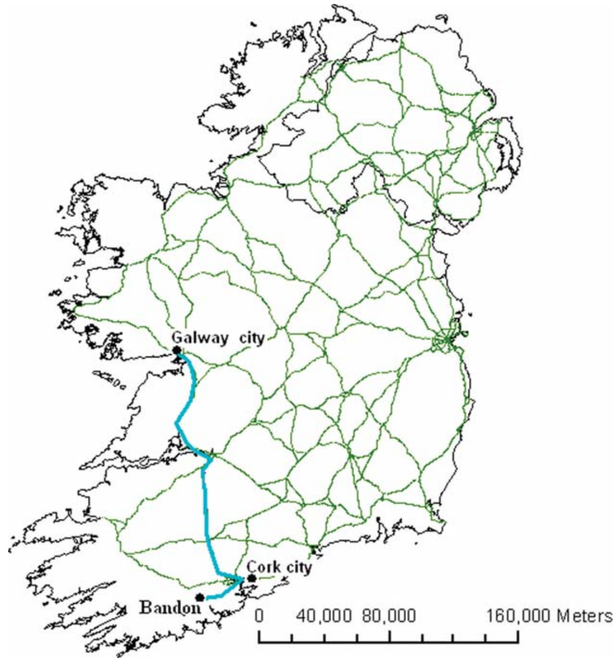

Figure 1. The road from Cork city to Caherlistrane Co Galway (227 km) and Cork to Bandon (32.5 km).

The 227 km from Cork to Caherlistrane, Co. Galway was surveyed 150 times (~5 times $month^{-1}$, spread over the month). This network consisted predominantly of national roads (137.3 km) where there were two lanes of traffic, with stretches of motorway (64.2 km) and single lane regional roads (26.5 km). Towns and villages were situated along the route, and the speed limit was 50 km h^{-1} in these areas. Speed limits on regional roads were 80 km h^{-1}, national roads 100 km h^{-1} and the motorway 120 km h^{-1}. The traffic flow along these routes ranged from an annual average daily traffic flow of 10152 ± 4.7 (SE) to 33517 ± 3.21 vehicles (<www.nra.ie>). Traffic flow was at its highest in August and lowest in January.

The 32.5 km of road linking Cork city to Bandon was surveyed 504 times (~18 times $month^{-1}$). This network consisted of national road in which there were two lanes of traffic (28.5 km) and single lane, regional roads (4 km). The traffic flow along this route consisted of an annual average daily traffic flow of 9696 to 31848 vehicles (<www.nra.ie>).

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 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 at a scale of 50metres (<www.osi.ie>).

Table 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

Clustering

K-function analysis on Arc GIS was used to establish whether road mortalities 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>). 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).

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. All carcasses collected were sexed and aged. The hedgehog was considered to be a juvenile if it satisfied the following criteria: weight less than 600 g; hind foot length of less than 3.6 cm, jaw length of less than 4.5 cm, body length of less than 16 cm; and presence of growing spines (Haigh et al. 2013). In some cases due to the nature of the fact that the individual had been killed on the road, an accurate weight, or some of the measurements, could not be obtained.

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 100 km or 1 casualty per 379 km.

Habitat

There was a significant variation in the habitat along which casualties were observed along the two focal roads ($F_{4,167} = 0.620$, $p < 0.01$). The majority (57%) of hedgehog carcasses were found on road ways that bordered areas of

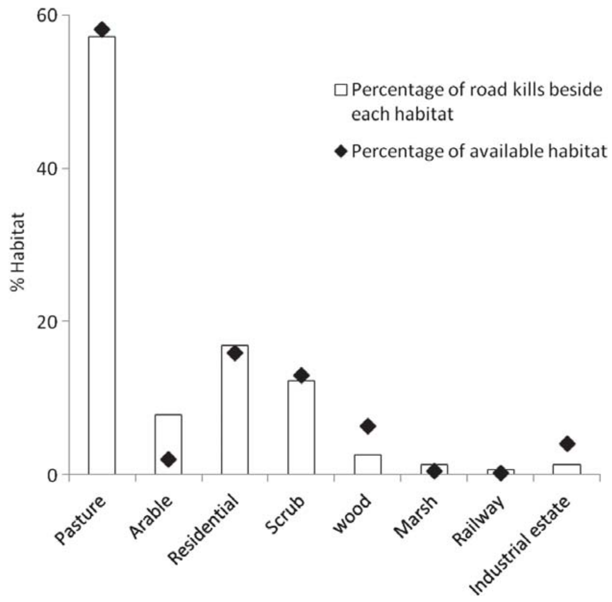

Figure 2. Percentage of available habitats on both stretches of road combined and the % of road kills observed along each habitat category between 2008 and 2010.

pasture (Fig. 2) which was the most prominent habitat on both stretches of road. The number of road kills beside pasture would indicate that it was utilised in accordance with its availability (Fig. 2). By contrast, there was a greater number of road kills near arable lands than expected based on the availability of this habitat (Fig. 2).

Clusters of road kill and yearly patterns

A distance of 259.5 km from Caherlistrane, Co. Galway to Bandon, Co. Cork was analysed in order to detect for signs of clustering (Fig. 3). K analysis indicated that the distribution of hedgehog road mortality was more clustered than what would be expected from chance (Fig. 3). Clusters were observed in thirteen locations along this route, with up to six carcasses located at the same spot over the three year period. Nine (69%) of these clusters were located close to towns and junctions.

Sex ratio of road kill

In addition to the 133 carcasses observed along the two focal roads, 135 hedgehog carcasses were collected from around Ireland, over the study period. It was possible to sex 103 of these carcasses. There was significantly more males collected as road kill (67 ♂ vs 36 ♀ respectively; $\chi^2 = 9.846$, DF = 1, $p < 0.01$) (Fig. 4), with a peak in male fatalities between May and July for all hedgehogs combined (Fig. 4). Female casualties peaked in June, July and August, with female deaths higher than males in August only (Fig. 4).

Discussion

Over the three years 133 hedgehog fatalities were observed over the 50 430 km of the two focal roads, giving a total of

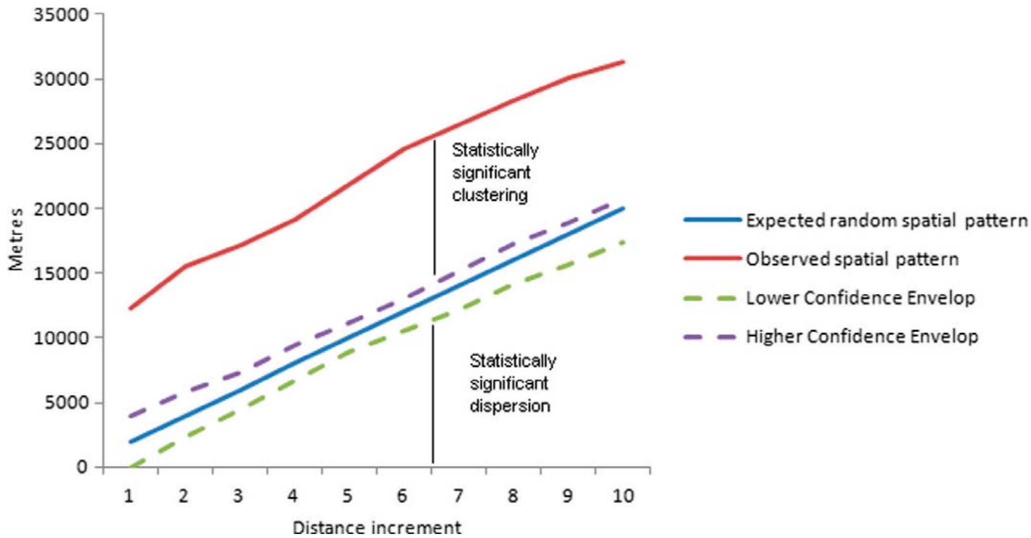

Figure 3. Observed and expected K-function curves for hedgehog road mortality from Caherlistrane Co. Galway to Bandon, Co. Cork.

0.264 casualties per 100 km (1 per 379 km). This was a very low number and would suggest that road deaths do not cause a significant effect on the population. However, in view of the declines in hedgehog numbers in other areas of its range, if the existing population is low, even these relatively small numbers of casualties could have a significant effect. This also raises the question of whether this low number suggests a moderate vulnerability to road deaths or simply a lower density of hedgehogs in Ireland. At a field site in County Cork, live hedgehogs were found at high densities of 3.07 individuals ha^{-1} and up to 6.06 individuals ha^{-1} in similar habitats to the road kill survey (Haigh 2011). In this area, only one incidence of road mortality was observed in the three year study, so road deaths would not have reflected the high density of hedgehogs there (Haigh et al. 2012a). Instead the low number of road deaths in the current study suggests a lower vulnerability to roads which may be a consequence of Ireland's road density. This is further implied by the fact that the numbers of road kill for all mammal species was conservative (Haigh 2012). 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 km^2 (<www.nra.ie>). This equates to 1.28 km of road per km^2. In New Zealand, where an extensive study on hedgehog road deaths was conducted, Morris and Morris' (1988) found an average of 6.4 hedgehogs per 100 km (1 per 16 km)(range 3.4–58.3 per 100 km). This is considerably higher than the frequency of deaths recorded in the present study. With New Zealand having a greater road density than Ireland at 2.86 km of road per km^2 (calculated from statistics from New Zealand Transport Agency, <www.nzta.govt.nz>), the higher number of deaths may reflect this greater road density. Similarly, in Belgium, where there is a particularly high density of roads at 3.8 km roads per km^2, Holsbeek et al. (1999) found that 2.3 hedgehogs per km were killed. Therefore, the greater number of road casualties in other countries may not be an obvious effect of density but may result from a greater opportunity for hedgehogs to encounter larger busier roads.

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, as it was used in accordance with its availability. These pasture fields were characterised by well developed hedgerow and in many cases were situated amongst a mosaic of different habitats. In all cases

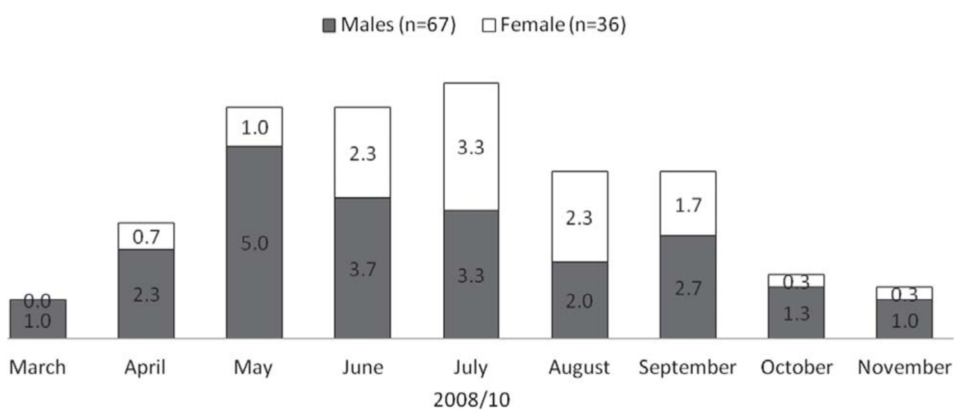

Figure 4. The monthly mean $year^{-1}$ of males and female hedgehogs collected as road kill from 2008 to 2010.

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 (Jensen 2004, Riber 2006, Haigh et al. 2012b). 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 and English 1969). This may represent a higher density of hedgehogs but it may also suggest 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 availability of this habitat along these routes. This suggests that similarly to what was observed from a radio tagged group of hedgehogs in County Cork (Haigh 2011), that arable land was selected along these routes. This habitat has been observed to be avoided by hedgehogs elsewhere (Dowie 1987, Riber 2006, Hof 2009), and its selection in Ireland is thought to be related to Ireland's more heterogenous landscape and the maintenance of hedgerow.

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 County Cork (Haigh 2011), it was observed that individual hedgehogs entered fields and crossed roads at specific spots and this was observed amongst both adults and juveniles (Haigh et al. pers. obs. 2008–2010). This could have important implications for the successful implication of mitigation measures. It would be particularly important to identify these hedgehog crossing points in areas of high road density. Equally it should be considered when identifying areas where underpasses should be constructed in new road developments.

In the present study, with the exception of August, hedgehog fatalities were predominantly male-biased with peaks of hedgehog mortality in May, June and July. A peak in the hedgehog breeding season occurs in these months with an associated expansion of male hedgehog's home range (Morris 1969, Kristiansson 1984, Jackson 2006). It is therefore not surprising that significantly more male hedgehogs were killed at this time. 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 and Robles 1986), the Netherlands (Huijser et al. 1998), and Ireland (Smiddy 2002). In Sweden, Göransson et al. (1976) found that 80% of hedgehog traffic victims were males who had survived one winter. However, in autumn they found that, like the present study, 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. The appearance of juveniles as road fatalities peaked in May, June and July (Haigh et al. 2012a), which may account for female movement once their offspring had reached independence. 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) (Haigh 2012). This therefore suggests that these peaks represent activities that occur on a yearly basis such as breeding (adults) and dispersal/exploration (juveniles).

Conclusion

This study has shown that although the hedgehog is one of the most commonly occurring mammal road casualties in Ireland, the number of hedgehogs killed on Ireland's roads is relatively low, in comparison to other countries. As the numbers of all species of mammals killed on Irish roads is also low, it is suggested that the lower density of roads in Ireland may result in Irish hedgehogs encountering larger busier roads less often than in other areas of their range. Interestingly, arable land, which is usually avoided by hedgehogs (Dowie 1987, Riber 2006, Hof 2009), was the only habitat beside which carcasses were located in a greater proportion then what was available. The use of this habitat is thought to be a consequence of Ireland's higher density of hedgerows, smaller field sizes and more heterogeneous habitat structure of agricultural lands, including arable land. Hedgehogs were not distributed randomly but on all routes clustering was observed where hedgehogs were killed regularly. This implies that hedgehogs have specific crossing points and annual cycles of activity which is suggested to be related to movement in relation to breeding. This would have implications for the development of mitigation measures aimed at reducing road mortality and providing safe crossing opportunities.

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References

Doncaster, C. et al. 2001. Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. – J. Anim. Ecol. 70: 33–46.

Dowding, C. V. 2007. An investigation of factors relating to the perceived decline of European hedgehogs (*Erinaceus europaeus*) in Britain. – PhD thesis, Univ. of Bristol.

Dowie, M. 1987. Rural hedgehogs many questions. – Game Conserv. Annu. Rev. 18: 126–129.

Forman, R. T. T. and Alexander, L. E. 1998. Roads and their major ecological effects. – Annu. Rev. Ecol. Syst. 29: 207–231.

Garnica, R. and Robles, L. 1986. Seguimiento de la mortalidad de erizos, *Erinaceus europaeus*, producida por vehiculos en una carretera de poca circulacion. – Misc. Zool. 10: 406–408.

Göransson, G. et al. 1976. Road mortality of the hedgehog *Erinaceus europaeus* in southern Sweden. – Fauna Flora, Stockholm 71: 1–6.

Haigh, A. 2011. The ecology of the European hedgehog (*Erinaceus europaeus*) in rural Ireland. – PhD thesis, Univ. College Cork

Haigh, A. 2012. Annual patterns of mammalian mortality on Irish roads. – Hystrix doi:10.4404/hystrix-23.2-4747

Haigh, A. et al. 2012a. Courtship behaviour of western hedgehogs (*Erinaceus europaeus*) in a rural landscape in Ireland and the first appearance of offspring. – Lutra 55: 41–54.

Haigh, A. et al. 2012b. Nesting behaviour and seasonal body mass changes in a rural Irish population of the western hedgehog (*Erinaceus europaeus*). – Acta Theriol. doi:10.1007/s13364-012-0080-2

Haigh, A. et al. 2013. Non-invasive methods of separating hedgehog (*Erinaceus europaeus*) age classes and an investigation into the age structure of road kill. – Acta Theriol. doi:10.1007/s13364-013-0142-0

Hayden, T. and Harrington, R. (eds) 2001. Exploring Irish mammals. – Town House Dublin.

Hell, P. et al. 2005. Losses of mammals (Mammalia) and birds (Aves) on roads in the Slovak part of the Danube Basin. – Eur. J. Wildlife Res. 51: 35–40.

Hof, A. 2009. A study of the current status of the hedgehog (*Erinaceus europaeus*), and its decline in Great Britain since 1960. – PhD thesis, Royal Holloway, London.

Holsbeek, L. et al. 1999. Hedgehog and other animal traffic victims in Belgium: results of a countryside survey. – Lutra 42: 111–119.

Huijser, M. and Bergers, P. 2000. The effect of roads and traffic on hedgehog (*Erinaceus europaeus*) populations. – Biol. Conserv. 95: 111–116.

Huijser, M. et al. 1998. Hedgehog traffic victims: how to quantify effects on the population level and the prospects for mitigation. – Proc. Int. Conf. Wildlife Ecol. Transportation, pp. 171–180.

Jackson, D. B. 2006. The breeding biology of introduced hedgehogs (*Erinaceus europaeus*) on a Scottish island: lessons for population control and bird conservation. – J. Zool. 268: 303–314.

Jaeger, J. et al. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. – Ecol. Modell. 185: 329–348.

Jensen, A. 2004. Overwintering of European hedgehogs *Erinaceus europaeus* in a Danish rural area. – Acta Theriol. 49: 145–155.

Jones, A. P. et al. 1996. The application of K-function analysis to the geographical distribution of road traffic accident outcomes in Norfolk, England. – Soc. Sci. Medi. 42: 879–885.

Keymer, I. et al. 1991. Zoonoses and other findings in hedgehogs (*Erinaceus europaeus*): a survey of mortality and review of the literature. – Vet. Record 128: 245.

Kristiansson, H. 1984. Ecology of a hedgehog *Erinaceus europaeus* population in southern Sweden. – PhD thesis, Univ. of Lund.

Lodé, T. 2000. Effect of a motorway on mortality and isolation of wildlife populations. – Ambio 29: 163–166.

Mac Donald, D. and Burnham, D. 2011. The state of Britains mammals. – WildCru, Peoples Trust for Endangered Species Report.

Macdonald, D. and Tattersall, F. 2007. Mammals, agri–environment schemes and set-aside-what are the putative benefits? – Mamm. Rev. 37: 259–277.

Morris, P. and English, M. 1969. *Trichophyton mentagrophytes* var. *erinacei* in British hedgehogs. – Med. Mycol. 7: 122–128.

Morris, P. and Morris, M. 1988. Distribution and abundance of hedgehogs (*Erinaceus europaeus*) on New Zealand roads. – N. Z. J. Zool. 15: 491–498.

Mulcahy, R. 1988. Studies on the life cycle of the hedgehog flea (*Archaeopsylla erinacei*). – MS thesis, Trinity College, Dublin.

Orlowski, G. and Nowak, L. 2004. Road mortality of hedgehogs *Erinaceus* spp. in farmland in Lower Silesia (southwestern Poland). – Pol. J. Ecol. 52: 377–382.

Riber, A. B. 2006. Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. – Acta Theriol. 51: 363–371.

Rondinini, C. and Doncaster, C. 2002. Roads as barriers to movement for hedgehogs. – Funct. Ecol. 16: 504–509.

Seiler, A. et al. 2004. Road mortality in Swedish mammals: results of a drivers' questionnaire. – Wildlife Biol. 10: 225–233.

Sleeman, D. P. et al. 1985. Irish Mammal road casualties. – Irish Nat. J. 21 (12).

Smiddy, P. 2002. Bird and mammal mortality on roads in counties Cork and Waterford, Ireland. – Bull. Irish Biogeogr. Soc. 26: 29–38.

Spooner, P. G. et al. 2004. Spatial analysis of roadside *Acacia* populations on a road network using the network K-function. – Landscape Ecol. 19: 491–499.