

The value of agri-environment schemes for macro-invertebrate feeders: hedgehogs on arable farms in Britain

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Abstract

Agri-environment schemes have been introduced in countries throughout the world in an attempt to reverse the negative impacts of agricultural intensification on biodiversity and the environment. There have been some investigations into the effectiveness of such schemes, which show mixed outcomes but little is known with regard to mammals. The hedgehog is a generalist predator and preys on, among others, an array of macro-invertebrates, prey important for many other taxa. For a non-volant species, it is highly mobile in the environment and should thus be less susceptible to negative effects of habitat fragmentation caused by agricultural intensification. However, it has recently been included in the UK Biodiversity Action Plan, as a result of evidence of a significant decline. We studied the importance of agri-environment schemes for hedgehogs using radio-tracking on arable farms. Both agri-environment field margins and hedgerows appear to be very valuable for hedgehogs. Both habitat types were intensively utilized by hedgehogs; higher food availability/accessibility on agri-environment field margins and higher food or nest site availability along edges and/or lower predation risk by badgers in arable areas may explain these preferences. Badger predation of hedgehogs was high in the study site and the main cause of death. Our study emphasizes the importance of natural habitat in an agricultural landscape and shows that agri-environment schemes can be beneficial to this generalist macro-invertebrate feeder. The implementation of agri-environment schemes that include wide field margins and dense, well-established hedgerows on farmland could significantly contribute to the viability of hedgehog populations in intensive arable-farming landscapes, and by implication benefit other macro-invertebrate feeders.

Introduction

Farm management has been subject to major changes throughout the world since the 1950s; this has resulted in a less diverse landscape and has been the major driver behind the loss of biodiversity (Krebs *et al.*, 1999; Donald, Green, & Heath, 2001; Robinson & Sutherland, 2002; Foley *et al.*, 2005). Agri-environment schemes were introduced into the agricultural policy of a large number of countries throughout the world in the last few decades. They were for instance introduced in the European Union in the late 1980s and provide payments to farmers who commit to measures related to preservation of the environment (European Commission, 2009). In the USA, the Conservation Reserve Program also encourages environmental enhancement on farmland by providing technical and economical assistance to farmers and ranchers, for instance to plant native grasses and trees, and to create wildlife habitat and riparian buffers (United States Department of Agriculture, 2009). In

Australia, the Caring for our Country – Environmental Stewardship initiative has similar aims (Australian Government, 2009). Field margins, hedgerows and set-aside were among the features included in these schemes.

Studies of the effectiveness of agri-environment schemes on biodiversity have reported different outcomes (e.g. Kleijn *et al.*, 2001, 2006; Kleijn & Sutherland, 2003; Bengtsson, Ahnström & Weibull, 2005; Knop *et al.*, 2006). However, well-managed agri-environment field margins and hedgerows can have a beneficial impact on, among others, birds (Vickery, Carter & Fuller, 2002), bumblebees (Pywell *et al.*, 2006) and small mammal populations (Tattersall *et al.*, 2000; Bright & MacPherson, 2002). Hedgerows and agri-environment field margins are frequently mentioned as an important habitat for various small mammals and are known to support a higher abundance of small mammal species than arable fields and pastures (Bright & Morris, 1996; Gelling, Macdonald & Mathews, 2007). They, not

only add to the amount of potentially suitable habitat for mammals, but increased food availability due to a higher abundance of invertebrates and grass seeds may also benefit various mammal species. Several studies confirm, for instance, the positive impact of enhanced invertebrate life in agri-environment field margins and also in set-aside on a variety of farmland birds (e.g. Henderson *et al.*, 2000; Vickery *et al.*, 2002). Macro-invertebrate feeders (defined in this context as species whose diets consists predominantly or partly on macro-invertebrates), like hedgehogs could potentially benefit in a similar way from agri-environment field margins and set-aside land.

In the UK, the hedgehog *Erinaceus europaeus* used to be common and is still considered to be locally so (Harris & Yalden, 2008). However, evidence of significant decline (A. R. Hof & P. W. Bright, unpubl. data) has led to the hedgehog recently being included in the UK Biodiversity Action Plan, created as a response to the Convention on Biological Diversity (UK BAP, 2007). It is of considerable conservation concern that a mobile, generalist species like the hedgehog, thought to be very common and widespread is in decline. It is a generalist predator of macro-invertebrates, which are the staple diet of numerous other taxa; so its decline may signify a continuing loss of environmental quality in the farmed environment.

Arable fields are known to be under-utilized by hedgehogs (Doncaster, 1994; Riber, 2006). Both field margins and hedgerows may enhance the suitability of arable-dominated landscapes for hedgehogs by providing short-grass foraging habitat close to hedgerows and other features which may provide hedgehogs refuge from predators such as the badger *Meles meles*, a known predator (Riber, 2006; Young *et al.*, 2006). Large fields that have a low proportion of edge habitat may be acting as a barrier to movement. The objective of our study was to determine whether agri-environment schemes in an intensively arable-farmed landscape are likely to benefit a common macro-invertebrate feeder, the hedgehog. We used radio tracking to follow their movements and study their habitat selection.

Materials and methods

Study site

The study site was located in the area surrounding the villages of Burnham Deepdale, Brancaster Staithe and Brancaster along the north coast of Norfolk, UK. It covered 609 ha, bounded by the sea to the north and demarcated inland by the outermost sightings of radio-tracked hedgehogs (applying the minimum convex polygon). The study site encompassed two large arable farms. Field sizes varied from 4 to 25 ha, with a mean of 10.4 ha (SE 2.4) for arable fields, 1.6 ha (SE 0.5) for pasture fields, and 4.9 ha (SE 1.0) for set-aside fields. One farm had several fields as set-aside, which were mainly overgrown with thistles, grasses, various weeds and low shrubbery. Nearly all arable fields were surrounded by 6-m-wide field margins which were entered in an agri-environment scheme (Environmental Steward-

ship). In total, about 33 km of hedgerows surrounded the fields. Hedgerows were generally 2–3 m high and 1–3 m wide, with hawthorn *Crataegus monogyna* as the main component, however, they were often sparse, especially at the base. Dense growth of weeds such as nettles *Urtica* spp and alexanders *Smyrnium olusatrum* often bordered the hedgerows. There were a few pasture fields in the area, which were not intensively managed and had a sward height of 10–30 cm. Badgers, predators of hedgehogs which may be a factor causing their decline (Young *et al.*, 2006), are known to be scarce in the study area ($>0.3 \text{ km}^{-2}$) (Harris & Yalden, 2008) and in fact thought to be absent by local farmers and gamekeepers. Nonetheless, badgers were observed twice during fieldwork. We found no badger setts in the study site, but the entire surrounding area could not be searched due to access restrictions.

Radio-tracking

Twelve adult male hedgehogs from wildlife welfare centres were fitted with radio transmitters (10 g, Biotrack Ltd, Dorset, UK) and released in the study area to initiate finding resident hedgehogs. Radio transmitters were equipped with a beta light, as commonly used to allow visual detection at a distance, avoiding disturbance by close approach of the fieldworker. Receivers (Telonics Inc., Mesa, AZ, USA) were used in combination with Yagi antennae (Biotrack Ltd) to track the hedgehogs. Local hedgehogs were found while interacting with the introduced males and by actively searching the area with a spotlight. Newly caught hedgehogs were sexed, weighed and fitted with radio transmitters. Data on released hedgehogs were not used in analyses. Hedgehogs were tracked from dusk until dawn between May and July 2008, for a minimum of 10 nights each. Position fixes were obtained each hour during the night. Habitat type, activity and distance to the nearest neighbouring habitat were recorded. Hedgehogs were not closely approached, to avoid disturbing their behaviour as much as possible.

Analyses

Compositional analysis at the landscape and home-range level was used to determine habitat selection (Aebischer, Robertson, & Kenward, 1993). The habitat in the study site was recorded in the field and digitized into a geographic information system (MAPINFO PROFESSIONAL Version 8, MapInfo Corporation, Troy, NY, USA). The following habitat types were defined: arable field, agri-environment field margin, hedgerow, pasture, set-aside and (mixed deciduous) woodland. Non-farmland habitat types were: village (mostly gardens) and amenity grasslands (such as greens, church yards and playing fields). The behaviour and speed of movement of hedgehogs was used as additional measure of the function and value of different habitats to them. Behaviour was classified as foraging, interacting with other hedgehogs, resting, running and walking. Resting could be determined from a distance by the lack of modulation in the radio-signal. We also examined the proximity of hedgehogs

in arable fields to edge habitats that are likely to provide them with a refuge from predation (hedgerows and woodland). Finally, we recorded causes and sites of mortality during the study.

Results

Habitat selection

In total 44 wild hedgehogs (24 males and 20 females) were caught in the study site, from which a total of 2319 position fixes were obtained (Fig. 1). Habitat preference by male



Figure 1 Fragment of the site used for the radio-tracking study. Hedgerows and agri-environment field margins are not shown but exist around nearly every arable field. The perimeter of the site represents the minimum convex polygon including all position fixes and is limited by the coastline in the north

hedgehogs at the landscape level was ranked as follows: hedgerows \gg agri-environment field margin $>$ pasture-village $>$ woodland $>$ amenity grassland $>$ set-aside $>$ arable, where \gg indicates a significant difference at $P < 0.005$ between two consecutively ranked habitat types and $>$ indicates a ranking which is not significantly different. Females were more frequently seen in non-farmland habitat types than males. The habitat ranking for females was: hedgerows \gg village $>$ amenity grassland $>$ woodland $>$ agri-environment field margin $>$ pasture \gg set-aside $>$ arable. There was significant non-random habitat utilization for both males (Wilk's λ , $\chi^2 = 56.53$, $\lambda = 0.095$, $P < 0.001$) and females (Wilk's λ , $\chi^2 = 78.03$, $\lambda = 0.020$, $P < 0.001$).

Habitat selection at the home-range level was different from the landscape level. Agri-environment field margins were preferred more and amenity grasslands were preferred less than at the landscape level. A distinction between males and females could not be made due to the scarcity of several habitat types within individual home ranges. The habitat type 'set-aside' needed to be ignored due to infrequent availability within home ranges. Hedgehogs that made use of only two or fewer habitat types also had to be ignored due to insufficient data, leaving 29 hedgehogs in the following analysis. There was significant non-random habitat utilization at the home-range level (Wilk's λ , $\chi^2 = 79.55$, $\lambda = 0.064$, $P < 0.001$). Habitat preference by hedgehogs within their home ranges was ranked: hedgerows \gg agri-environment field margins \gg village \gg woodland $>$ pasture $>$ arable $>$ amenity grasslands.

Behaviour and travel speed per habitat type

The frequency of displaying a type of behaviour was dependent on the habitat where hedgehogs were located (Fig. 2). Foraging was the main activity in all habitat types except in hedgerow and woodland, where hedgehogs were observed resting, 61 and 48% of the time, respectively. Hedgehogs spent most of their time in amenity grassland (64%) and in pastures (57%) foraging.

The mean travel speed of hedgehogs, based on two consecutive sightings (pair) of an individual between 30 and 60 min apart was $2.0 \text{ m min}^{-1} \pm \text{SE } 0.06$ ($n = 1079$ radio fixes

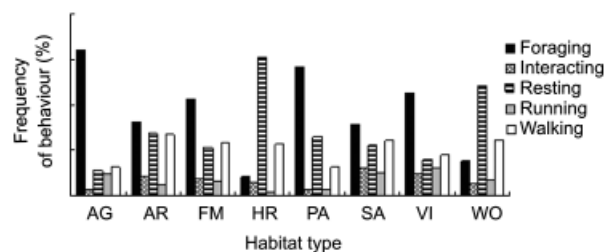


Figure 2 The percentage of sightings of hedgehogs displaying different behaviours per habitat type (AG, amenity grassland $n = 190$ position fixes; AR, arable $n = 146$; FM, agri-environment field margin $n = 346$; HR, hedgerow $n = 118$; PA, pasture $n = 206$; SA, set-aside $n = 41$; VI, village $n = 135$; and WO, woodland $n = 58$)

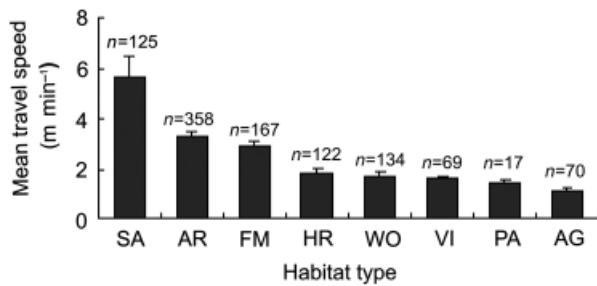


Figure 3 Mean travel speed of hedgehogs in m min⁻¹ per habitat type; n is defined by the number of radio pairs (two consecutive sightings of an individual between 30 and 60 min apart) per habitat type (SA, set-aside; AR, arable; FM, agri-environment field margin; HR, hedgerow; WO, woodland; VI, village; PA, pasture; AG, amenity grassland).

of 44 animals), with a maximum of 4.2 m min⁻¹. The highest mean travel speed was observed when hedgehogs were travelling in set-aside, followed by arable fields and were significantly different from the mean speed in the other habitat types (Kruskal–Wallis, $\chi^2 = 31.72$, d.f. = 7, $P < 0.001$). However, it must be noted that the travel speed in set-aside was male biased, due to the lack of data for females travelling in this habitat. Hedgehogs were most static in woodlands and hedgerows (Fig. 3).

Attraction to edge habitat

Hedgehogs rarely selected arable fields (154 out of 2319 position fixes from 44 hedgehogs), but when situated in the arable field the distance to hedgerow, woodland or agri-environment field margin was 1 m or less for 50% of these fixes. Only in 4% of the cases ($n = 6$) the hedgehog was located > 10 m away from an edge. Hedgehogs were also more frequently situated near an edge in amenity grassland, but not in pasture and set-aside. In woodland the situation was less clear; hedgehogs appeared to avoid the immediate woodland edge, but were found most frequently situated between 1 and 5 m inside the woodland (Fig. 4) [Kruskal–Wallis, $\chi^2 = 20.88$, d.f. = 4, $P < 0.001$ (animal identity is retained in the model)]. Hedgerows and agri-environment field margins were left out of the analyses because these habitat types never exceeded 6 m in width. The distance to the nearest boundary could not be estimated accurately in village habitat because we usually did not have access to domestic premises. In both pasture ($n = 156$) and set-aside ($n = 38$) hedgehogs were located at a mean distance of between 30 and 40 m from the nearest boundary. In amenity grassland ($n = 173$), arable ($n = 142$) and woodland ($n = 38$) hedgehogs were on average located < 10 m away from the nearest boundary.

Mortality

In total, nine hedgehogs out of 44 died during the 75-day long tracking period; a mortality rate of 20%. A failed pregnancy was the likely cause of death for one death. The eight remaining hedgehogs were all predated by badgers, as

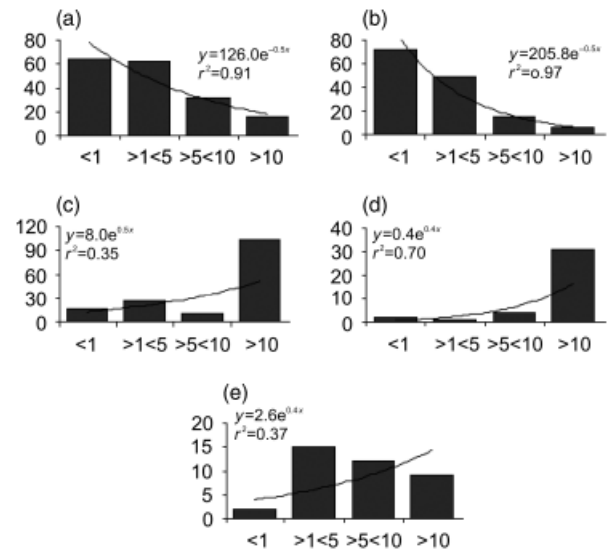


Figure 4 Number of sightings of hedgehogs (y-axis) located at distances from the nearest edge habitat in metres (x-axis) per habitat type. (a) amenity grassland, (b) arable, (c) pasture, (d) set-aside and (e) woodland.

evidenced by the remaining skin and spines (Reeve, 1994). Seven of these predated hedgehogs were male. All these kills took place in farmland, with four remains being found in open, sparse, bare-based, hedgerows, two in an arable field, one in pasture and one in an agri-environment field margin.

Discussion

Habitat selection

Hedgerows and agri-environment field margins were highly selected by hedgehogs at both the landscape and home-range levels. However, there were differences between male and female hedgehogs, at least at the landscape level; females were mostly active in village habitat and this was selected significantly more than agri-environment field margins. This difference mainly reflected the much larger home ranges of male hedgehogs during the mating period ($5.6 \times$ that of females), but also selection by females of relatively small patches of higher quality habitat in villages compared with the adjoining arable landscape. [Note that the sex-disparity in home range size that we found was much greater than the pan-seasonal norm of around $3 \times$ (Harris & Yalden, 2008)]. It is thus clear that hedgerows and agri-environment field margins are very important to hedgehogs in a coarse-scale arable landscape, but that adjoining village habitats are very important for females. We return to the implications of this for population structure and viability below.

The behaviour and travel speeds of hedgehogs in hedgerow habitat suggest that they were primarily used for resting during short nocturnal inactive periods (hedgerows are, of course, also a major site of diurnal nest sites; Reeve, 1994) and less for movement around the landscape in a concealed

habitat. Agri-environment field margins were most used for foraging (and to a lesser extent for walking and resting). Given the degree to which they were selected, agri-environment field margins were therefore important foraging habitats in the arable-dominated landscape.

Attraction to edge habitat

In arable fields, the least selected habitat, hedgehogs were seldom found >5 m from the field edge. This was not the case in set-aside, formerly arable, fields or pasture, where hedgehogs moved well away from the edge. The hedgehog is well-known to be an edge-refuging species (e.g. Huijser, 2000), which has profound consequences for the conservation of hedgehogs in coarse-grained landscapes (i.e. with large field sizes as in most UK arable-dominated landscapes), especially where hedgehogs suffer significant predation pressure. There are three evidence-based hypotheses that may explain this behaviour. First, that proximity to hedgerows offers a refuge from predation; this is supported by studies showing that badgers (the most significant predator of hedgehogs in the UK [Young *et al.*, 2006]) rarely forage along linear landscape features (White, Brown & Harris, 1993; Neal & Cheeseman, 1996). A higher complexity in landscape structure, as offered by hedgerows, has been shown to decrease intraguild predation (Janssen *et al.*, 2007), such as hedgehogs receive from badgers. Second, that macro-invertebrate food for hedgehogs may be more abundant on the margins rather than in the interior of arable fields (Curry, 1998; Thomas *et al.*, 2001; Meek *et al.*, 2002; Woodcock *et al.*, 2007). Third, that hedgehogs often nest in the base of or adjoining long grass or bramble-dominated vegetation (e.g. Reeve, 1994) and thus may be more likely to be active close to field edges.

Our results suggest that edge refuging in hedgehogs is likely primarily to be a consequence of concealment from predators; where the sward was very short (<10 cm) as in amenity grassland or open as in arable fields, hedgehogs were most active close to edges. Where sward heights were higher and the vegetation was denser, as in pasture and set-aside, hedgehogs ventured into the interior of these habitats. Our results suggest that food availability may also be an important factor. For instance in set-aside, although hedgehogs were observed feeding they also travelled rapidly despite the high sward height of that habitat (note though that our data for this habitat type are biased towards males, which travelled faster). Set-aside fields in our study area tended to be especially dry and stony and were thus not likely to have high abundance of macro-invertebrate prey. Further work is required to clarify these relations, but predation rates dependent on cover and distance from edges are very widespread ecological phenomena (Moller, 1988; Sih, 1997; Hartley & Hunter, 1998).

Mortality

Mortality was largely (eight out of nine deaths) due to predation by badgers. This amounts to an 18% predation

rate and that in a landscape where badgers were scarce. Extrapolated over an entire active season the predation rate we observed would amount to about 52%; clearly unsustainable for a population in solely arable habitat. However all but one of the badger-predated hedgehogs were male and hedgehogs have a promiscuous mating system, with males travelling over relatively large areas during the mating period (Reeve, 1994). Thus these male losses probably had a disproportionately low impact on population viability. Previous studies have also detected high levels of badger predation: 23% among translocated hedgehogs in a landscape with high badger density in southern England (Doncaster, 1992) and 35% of 17 radio-tracked hedgehogs in Norway (Strøm Johansen, 1995). It is possible that food availability for badgers in our study area, especially earthworms *Lumbricus terrestris* which are a staple food (Neal & Cheeseman, 1996), was limited and this may have enhanced predation on hedgehogs.

Hedgehogs were only found predated by badgers well away from the villages, where badgers were presumably more active (e.g. Neal & Cheeseman, 1996). This supports the contention that villages and suburban areas can act as refugia from badger predation and facilitate hedgehog persistence (Doncaster, 1992; Micol, Doncaster & MacKinlay, 1994; Young *et al.*, 2006).

Management implications

The present study has clear implications regarding the value of agri-environment schemes for hedgehogs and the management of arable landscapes to promote their conservation.

It is clear that agri-environment field margins were heavily utilized by foraging hedgehogs and provided places to forage in an otherwise inhospitable arable landscape. The addition of such margins to arable fields, especially in the vicinity of villages or other parts of the landscape where badgers are less active, will thus be beneficial to hedgehog conservation. Existing agri-environment schemes in countries like for instance the UK, the Netherlands and Switzerland already have provision for grassy field margins beneficial to hedgehogs.

Our findings are also a reminder of the importance of hedgerows to hedgehogs, for foraging, building nests and probably avoiding predators (see Reeve, 1994; Huijser, 2000). The great loss of hedgerows in previous decades and the creation of much larger fields (Robinson & Sutherland, 2002) is likely to have significantly reduced the hedgehog carrying capacity of arable-dominated landscapes especially. Again, existing agri-environment schemes in Europe have provision for the (re)creation of hedgerows. Appropriate management of hedgerows and adjoining vegetation is probably also important if they are to be suitable for nesting. This requires further research; we simply make the point that many of the hedgerows in our study area were too open at the base to provide sufficient cover for nests.

Set-aside fields were not selected by hedgehogs. We speculate that this may at least partly be due to lower food availability and this is the subject of ongoing research.

Meanwhile, our evidence suggests that grassy field margins will be much more beneficial to hedgehogs than set-aside, although it has been suggested that both habitat types are able to provide a higher abundance of invertebrates than arable fields (Moreby & Aebischer, 1992; Vickery *et al.*, 2002), general invertebrate availability is said to be larger on grassy field margins (Gates *et al.*, 1997).

Implementation of agri-environment schemes that include field margins and hedgerows is likely to benefit macro-invertebrate feeders and their prey in agricultural landscapes worldwide. The hedgehog is a general macro-invertebrate feeder and highly mobile mammal. The edge-refuging habit hedgehogs displayed in our study may be stronger in less mobile species, which increases the necessity of such measures.

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References

- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.
- Australian Government. (2009) Caring for our Country – Environmental Stewardship. Available at <http://www.nrm.gov.au/stewardship/index.html> (accessed 11 December 2009).
- Bengtsson, J., Ahnström, J. & Weibull, A. (2005). The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.* **42**, 261–269.
- Bright, P.W. & MacPherson, D. (2002) *Hedgerow management, dormice and biodiversity*. Report, English Nature No. 454, Peterborough.
- Bright, P.W. & Morris, P.A. (1996). Why are dormouse rare? *Mamm. Rev.* **26**, 157–187.
- Curry, J.P. (1998). Factors affecting earthworm abundance in soils. In *Earthworm ecology*: 37–64. Edwards, C.A. (Ed.). Boca Raton: CRC Press LLC.
- Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. Roy. Soc. Lond. Ser. B: Biol. Sci.* **268**, 25–29.
- Doncaster, C.P. (1992). Testing the role of intraguild predation in regulating hedgehog populations. *Proc. Roy. Soc. Lond., Ser. B: Biol. Sci.* **249**, 113–117.
- Doncaster, C.P. (1994). Factors regulating local variations in abundance: field tests on hedgehogs, *Erinaceus europaeus*. *Oikos* **69**, 182–192.
- European Commission. (2009) Agriculture and the Environment. Available at http://ec.europa.eu/agriculture/envir/measure/index_en.htm (accessed 21 September 2009).
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Navin Ramankutty, N. & Snyder, P.K. (2005). Global consequences of land use. *Science* **309**, 570–574.
- Gates, S., Feber, R.E., Hart, B.J., Tattersall, F.H., Manley, W.J. & Macdonald, D.W. (1997). Invertebrate populations of field boundaries and set-aside land. *Aspect. Appl. Biol.* **50**, 313–322.
- Gelling, M., Macdonald, D.W. & Mathews, F. (2007). Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landsc. Ecol.* **22**, 1019–1032.
- Harris, S. & Yalden, D.W. (2008). *Mammals of the British Isles: handbook*. 4th edn. Southampton: The Mammal Society.
- Hartley, M.J. & Hunter, M.L. (1998). A meta-analysis of forest cover, edge effects and artificial nest predation rates. *Conserv. Biol.* **12**, 465–469.
- Henderson, I.G., Cooper, J., Fuller, R.J. & Vickery, J. (2000). The relative abundance of birds on set-aside and neighbouring fields in summer. *J. Appl. Ecol.* **37**, 335–347.
- Huijser, M.P. (2000) *Life on the edge. Hedgehog traffic victims and mitigation strategies in an anthropogenic landscape*. PhD thesis, Wageningen University, Wageningen.
- Janssen, A., Sabelis, M.W., Magalhães, S., Montserrat, M. & Van der Hammen, T. (2007). Habitat structure affects intraguild predation. *Ecology* **88**, 2713–2719.
- Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A. & Johl, R. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* **9**, 243–254.
- Kleijn, D., Berendse, F., Smit, R. & Gilissen, N. (2001). Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* **413**, 723–725.
- Kleijn, D. & Sutherland, W.J. (2003). How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* **40**, 947–969.
- Knop, E., Kleijn, D., Herzog, F. & Schmid, B. (2006). Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *J. Appl. Ecol.* **43**, 120–127.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999). The second silent spring? *Nature* **400**, 611–612.
- Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. (2002). The effect of arable field margin composition on invertebrate biodiversity. *Biol. Conserv.* **106**, 259–271.

- Micol, T., Doncaster, C.P. & MacKinlay, L.A. (1994). Correlates of local variation in the abundance of hedgehogs *Erinaceus europaeus*. *J. Anim. Ecol.* **63**, 851–860.
- Moller, A.P. (1988). Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. *Oikos* **53**, 215–221.
- Moreby, S.J. & Aebischer, N.J. (1992). Invertebrate abundance on cereals and set-aside land implications for wild game-bird chicks. In *Set-aside. British Crop Protection Council Monograph no 50*: 181–186. Clarke, J. (Ed.). Farnham: British Crop Protection Council.
- Neal, E.G. & Cheeseman, C.L. (1996). *Badgers*. London: T & A D Poyser Ltd.
- Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R. & Sherwood, A. (2006). Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biol. Conserv.* **129**, 192–206.
- Reeve, N.J. (1994). *Hedgehogs*. London: T & A D Poyser Ltd.
- Riber, A.B. (2006). Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. *Acta Theriol.* **51**, 363–371.
- Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *J. Appl. Ecol.* **39**, 157–176.
- Sih, A. (1997). To hide or not to hide? Refuge use in a fluctuating environment. *Trends Ecol. Evol.* **12**, 375–376.
- Strøm Johansen, B. (1995) Hedgehog decrease in Norway – effect of badger increase? *Abstract Book 2nd European Congress of Mammalogy*, 1, Southampton, p. 141.
- Tattersall, F.H., Avundo, A.E., Manley, W.J., Hart, B.J. & Macdonald, D.W. (2000). Managing set-aside for field voles (*Microtus agrestis*). *Biol. Conserv.* **96**, 123–128.
- Thomas, C.F.G., Parkinson, L., Griffiths, G.J.K., Garcia, A.F. & Marshall, E.J.P. (2001). Aggregation and temporal stability of carabid beetle distributions in field and hedge-row habitats. *J. Appl. Ecol.* **38**, 100–116.
- UK BAP. (2007) UK biodiversity action plan Available at <http://www.ukbap.org.uk/> (accessed 15 December 2007).
- United States Department of Agriculture. (2009) Conservation reserve Program. Available at <http://www.nrcs.usda.gov/programs/crp/> (accessed 11 December 2009).
- Vickery, J., Carter, N. & Fuller, R.J. (2002). The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agri. Ecosyst. Environ.* **89**, 41–52.
- White, P.C.L., Brown, J.A. & Harris, S. (1993). Badgers (*Meles meles*), cattle and bovine tuberculosis (*Mycobacterium bovis*): a hypothesis to explain the influence of habitat on the risk of disease transmission in southwest England. *Proc. Roy. Soc. Lond. Ser. B: Biol.* **253**, 277–284.
- Woodcock, B.A., Potts, S.G., Pilgrim, E., Ramsay, A.J., Tscheulin, T., Parkinson, A., Smith, R.E.N., Gundry, A.L., Brown, V.K. & Tallowin, J.R. (2007). The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *J. Appl. Ecol.* **44**, 60–69.
- Young, R.P., Davison, J., Trewby, I.D., Wilson, G.J., Delahay, R.J. & Doncaster, C.P. (2006). Abundance of hedgehogs (*Erinaceus europaeus*) in relation to the density and distribution of badgers (*Meles meles*). *J. Zool. (Lond.)* **269**, 349–356.