

**Hugging the hedges: might agri-environment manipulations affect
landscape permeability for hedgehogs?**

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ABSTRACT

Semi-natural agricultural habitats have declined in northern Europe since the 1950s, to the detriment of habitat connectivity and biodiversity. European agri-environmental schemes to restore them should target the habitats most likely to remedy these impacts. We employed a stochastic individual-based simulation model to predict movements of a model species, the European hedgehog (*Erinaceus europaeus*), across a series of virtual landscapes - digitised from a typical UK lowland agricultural area - in which the abundance of hedgerow, pasture fields and field margin had been manipulated according to a factorial design. The primary landscape determinant of distances that model hedgehogs travelled was the percentage of field boundaries that were hedgerow: doubling this from the status quo resulted in an additional 13% of individuals moving 500 m, 25% 1000m, 35% 1500m and 51% 2000m. Trebling the percentage of hedge yielded no additional benefit over doubling it (mean additional percentage 0.6%). Doubling the landscape percentage of pastures resulted in a 1% increase in model individuals moving 500m and 1000m, but decreases for 1500m and 2000m (-2% and -4%, respectively). Increasing the percentage of hedged fields that also had field margins led to decreases of -1% to -8% in individuals moving any distance. Agri-environmental scheme options to reinstate or repair hedges that double their percentage in lowland farmland would enhance population connectivity for European hedgehogs. Further work should extend these individual-based models to representative sets of species to explore the extent to which management for one species may benefit others.

Keywords *Erinaceus europaeus*; individual-based modelling; Stochastic Movement Simulator; landscape permeability; agri-environment scheme; hedge; pasture; field margin.

1. Introduction

Agriculture is the primary land-use in Europe, accounting for >40% of the area (Eurostat 2012), and agricultural intensification since 1945 has been a major cause of biodiversity loss (Stoate et al. 2001). Farmland typically comprises cropped and grazing areas interspersed with natural or semi-natural vegetation such as semi-natural grasslands, hedgerows, field margins, set asides, waterways, or woodland (Bennett et al. 2006; Diekötter et al. 2008). The loss of these habitats through intensification has resulted in biodiversity declines (Robinson and Sutherland 2002; Stoate et al. 2001). Simultaneously, increase in field sizes has been associated with hedgerow loss (Macdonald and Johnson 2000; Robinson and Sutherland 2002; Stoate et al. 2001). In Britain, in 2010, agriculture covered 18.3 million ha (75% of the land area; Agristats 2013). Between 1977 and 1984 24,600 km of hedgerow was lost (4% of the stock), and a further 121,000 km (22% of stock) by 1990 (Barr et al. 1991).

The loss of semi-natural habitats has direct consequences for the flora and fauna which occupy them – e.g. Cornulier et al. (2011) – but also indirectly through lost connectivity between habitat patches (Macdonald et al. 2000). Therefore the structure of agricultural landscapes, as well as the quantity of semi-natural habitats, affects the abundance of various species (e.g. Marshall et al. 2006), especially mobile ones for which semi-natural habitats facilitate dispersal (Baguette et al. 2013; Janin et al. 2009; Zhang and Usher 1991), thus strengthening metapopulation dynamics (Baguette et al. 2013; Hanski 1999, 2001). For example, the use of small woods by wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*) is influenced by the distance to the next nearest woodland patch and the extent of the surrounding hedgerow (Fitzgibbon 1997), hedgerow being important for the dispersal of both species (Gelling et al. 2007; Zhang and Usher 1991). Similarly the occurrence of common toads (*Bufo bufo*) on farmland is increased by landscape connectivity and decreased by cropland (Janin et al. 2009), and the activity of two bats (*Pipistrellus pipistrellus* and *Eptesicus serotinus*) increases with the number of linear landscape features (Verboom and Huitema 1997).

State funded agri-environmental schemes provide options to restore semi-natural arable habitats (Stoate et al. 2001), raising the question of which habitats, in what quantities and, importantly, spatial juxtaposition, to prioritise (Hodgson et al. 2010).

European hedgehogs (*Erinaceus europaeus*) provide an illuminating model for studying how the connectivity, and therefore permeability, of agricultural landscapes may vary with the availability of semi-natural habitats. The hedgehog is a mobile, generalist species, once common throughout the UK but now declining, resulting in a discontinuous distribution with occupied patches linked by dispersal (Doncaster et al. 2001). Urban settlements often provide suitable habitats (Hof and Bright 2010), but in rural areas are typically separated by an agricultural matrix. Consequently, the dispersion of connective semi-natural habitats on farmland is likely to be critical to hedgehog's survival. In arable landscapes hedgehogs principally select edge habitats (Morris 1986; Huijser 2000), such as hedgerows and field margins (Hof and Bright 2010). Pasture fields are less often selected and arable fields are under-utilised (Hof and Bright 2010). Edge-refuging may result from fear of predation, particularly by badgers (*Meles meles*), and is less marked in their absence (Hof et al. 2012). When dispersing, hedgehogs use linear features (Doncaster et al. 2001), and so hedges, boundaries of woodlands, field margins and road verges represent movement corridors (Doncaster et al. 2001). Movements can be long-range, with daily net displacements up to 2.8km (Reeve 1998), over 4km (Morris et al. 1993) and up to 3.5km (Doncaster et al. 2001) reported.

We analyse the impact on landscape permeability of varying the quantity of hedgerow, field margin and pasture across the landscape for dispersing hedgehogs, using an individual-

based simulation model. We test the hypothesis that increasing the percentage of preferred habitats, in particular edge habitats, will increase landscape permeability and therefore movement distances for individuals of the model species.

2. Materials and methods

2.1 SMS

We used the Stochastic Movement Simulator (SMS) to model individual hedgehogs making dispersal movements across a series of model landscapes. SMS is an individual-based simulation model for predicting the movement of virtual animals between habitat patches across a heterogeneous inter-patch matrix (Palmer et al. 2011). It extends the concept of least cost path (LCP) modelling (Adriaensen et al. 2003), relaxing the implicit assumption of omniscience (that an animal can plan its entire route in advance), by assuming that an animal has a limited perceptual range (PR) within which it can assess the quality of the landscape, and that it does not have a planned destination. The path taken by the animal depends critically on its PR, the (mathematical) method it uses to assess the costs within its PR and its directional persistence (DP), i.e. its tendency to follow a correlated path through the landscape. Here, we use an enhanced version of SMS, in which DP (formerly termed ‘directional bias’; Palmer et al. 2011) is determined over a number of previous steps rather than just the immediately previous step; this number was controlled by an additional memory size parameter (Memsize).

In common with the LCP approach, the landscape is represented as a rectangular grid of equal-sized square cells, each of which has a cost value. Whereas LCP, being deterministic, produces a single, optimum path between any two locations, SMS produces a set of paths, many of which are sub-optimal, but which together represent a probabilistic view of the predicted movement of an animal dispersing from a particular location.

2.2 Study design, study area and rationale

We created 18 model landscapes to examine the outcome of varying the proportions of hedge, pasture and field margin on the permeability of agricultural landscapes for hedgehogs. We used a fully factorial design comprising three levels of hedge, two levels of pasture and three levels of margin (Table 1). The landscapes were modelled on a rectangular area of land of 11.2km by 8.47km located in south Oxfordshire, UK (UK Grid Ref for SW corner SU 37890, 88260, NE corner SU 49040, 96730). Agricultural fields comprise 79% of this area, and urban habitats (gardens, buildings and urban roads) 10%. The remaining 11% comprises a mixture of woodlands (8%), roads (2%) and rivers (1%). These proportions are approximately typical of land-use in the intensively farmed parts of the UK (Countryside Survey, 2009). In the model landscapes the existing land-uses were retained and kept constant between landscapes with the exceptions of the agricultural fields, for which we manipulated the percentages of hedgerow, pasture and margin to create the 18 model landscapes.

We defined the percentage of hedgerow as the percentage of field boundaries that was hedged. Hedgerow percentages were set to 25%, 50% or 75% of the agricultural fields, and the hedges were 2.5m wide to represent the mean width of Oxfordshire hedgerows (unpublished data from preliminary survey). The percentage of agricultural fields that was pasture was set at 13% or 25%. The percentage of margin was defined as the percentage of fields with hedgerows that had additional 6m wide conservation field margins, and was set at 0, 25% or 50%. Margins were added only to fields with hedges in order to separate effects of

increasing the breadth of low-cost features to those of increasing connectivity (increasing connectivity would occur if low-cost margins were added in the absence of hedges; Appendix A in Supporting Information).

Landscape07 in Table 1 approximates reality with the proportions of hedgerow (25%), pasture (25%) and field margin (25%) (Appendix A in Supporting Information). Landscapes with 50% or 75% hedge therefore represent scenarios in which the amount of available hedgerow was doubled and trebled, respectively. Landscapes with 13% pasture represent scenarios in which the availability of pasture was halved. Landscapes with 50% margin represent scenarios in which margin availability was doubled (Table 1).

2.3 Creation of the cost landscapes

The landscapes were created in ArcGIS 10 (Esri Inc., 2010), based on vector GIS layer data from the Ordnance Survey MasterMap (obtained via the EDINA Digimap service under academic licence). Habitat types represented by each polygon in the MasterMap were simplified to one of a range of pre-specified habitats relevant to the study of hedgehog dispersal movements (Table 2, and Appendix B in Supporting Information). We assume, given that dispersing hedgehogs typically follow edge habitats (Doncaster et al. 2001) and that these habitats have the lowest costs in Table 2, that cost in the model is a suitable inverse index of the likelihood of habitat selection by dispersing hedgehogs.

The habitat data in MasterMap were sufficient to populate all habitat types from Table 2 with the exception of the contents of the agricultural fields. To differentiate between fields containing arable crops and those containing pasture, we populated the fields with habitats derived from the Land Cover Map 2007, supplied by CEH (license number: LCM 2012-123vs3), which was sufficient to derive the proportions and spatial distribution of fields containing pasture and those containing arable crops. Hedgerows themselves were not represented in either MasterMap or Land Cover Map, and so were created by selecting a percentage (25%, 50% or 75%; Table 1) of the polygons representing agricultural fields and buffering their borders to produce 2.5m wide hedges. Similarly, field margins were created by choosing a percentage (25% or 50%; Table 1) of fields with hedges and adding an additional 6m buffer inside of the hedge. Agricultural fields were allocated to either pasture or arable by selecting at random the appropriate percentage of polygons containing agricultural habitat.

Each polygon was attributed a cost, based its habitat type (see Appendix B). The landscape was then gridded at a 2m cell size - a compromise between retaining the detail of the landscape polygons, especially of thin, linear features such as hedges, and creating a sufficiently extensive landscape with which individuals could interact (Fig. 1; Fig. 2).

2.4 Model parameterisation and runs

Palmer et al. (2011) demonstrated that the proportion of individuals successfully finding a target varies substantially with DP and PR, nearly all individuals doing so at high values of these parameters. Small values for DP result in model individuals making a series of turns in a conserved area (Palmer et al. 2011; Fig. 2) and not moving far enough to permit testing of differences between landscapes. Conversely, large values of DP result in overly linear paths in which model individuals simply proceed in straight lines, irrespective of the underlying landscape costs, and eventually emigrate from the landscape (Fig. 2). Initial model runs determined that values of DP between 2.5 and 3.5 represented a suitable balance between these extremes (Fig. 2). We ran models with 0.25 increments between these limits.

PR values determine the distance over which model individuals can perceive, and therefore respond to, the landscape. It is unknown how hedgehogs navigate and orient,

although it likely involves a combination of auditory, olfactory and visual cues, (Reeve 1994). We use two values for the perceptual range of hedgehogs: PR = 5 and PR = 10 cells, representing detection distances of 10m and 20m respectively. PR = 5 is likely to be a conservative estimate of the upper limit of a hedgehog's perceptual range. PR = 10 is sufficiently large to avoid potential problems arising from "gapping" in linear features, particularly hedges, by allowing gaps of < 10 cells to be navigated by individuals, while remaining plausibly within a hedgehog's perceptual abilities.

Parameter sets therefore comprised two levels of PR (5, 10) and five levels of DP (2.5, 2.75, 3.0, 3.25, 3.5). Memsize was 8 cells throughout. One thousand independent individuals were simulated for each combination of landscape (Table 1) and set of parameters. To ensure that paths covered as much of each landscape as possible, the start for each was selected randomly from locations along hedgerows within each landscape. Each path comprised 5000 steps, each from the current cell to a directly neighbouring cell (a movement of 2m if in a cardinal direction and 2.83m if diagonal), and ended when either the maximum number was reached, or if the individual reached the edge of the landscape, in which case the end position and the number of steps taken to reach it was recorded.

To test whether the substantial variation in cost estimates for pasture and other grass (Table 2) might affect the relationship between the percentage of hedge, pasture and margin and the proportion of individuals making movements of a given threshold size, we ran additional SMS models for each landscape in Table 1, setting the cost of pasture and other grass habitats respectively to the high and low estimates provided in Table 2. In these model runs PR was maintained at 5 and DP at 3. Similarly, because hedgehogs' use of landscape features may vary with the presence / absence of badgers (Hof 2012; Appendix C) we ran additional models in which landscape costs were adjusted to simulate the absence of badgers (Appendix C).

2.5 Statistical analysis

The measures of landscape permeability provided by the model were the Euclidean distance travelled by an individual from its starting location to its final location, and the total cost of the path. Model paths end before the maximum 5000 steps if a model individual emigrates from the landscape, so with randomised starting locations, Euclidean distances are likely to vary not only with the landscape but with the distribution of path lengths. Use of distance per step to compensate, however, would be complicated by a non-linear relationship between increasing numbers of steps and Euclidean distance travelled, which arises from increasing path tortuosity as steps increase (i.e. short paths are more likely to follow linear features in a straight line and make fewer turns, and therefore have higher distance per step than long paths). To avoid such analytical and interpretive complications, we took as our metric the proportion of individuals for which the Euclidean distance travelled was greater than specified thresholds (500, 1000, 1500 and 2000 m). This metric obviates the need to consider the number of steps in the analysis, assuming that the distribution of runs with differing number of steps remains approximately constant between landscapes, as would be expected given the large simulated population size (1000) for each landscape.

We performed binomial logistic regression analyses, implemented in R (R Core Team 2012), testing for an effect of variations in levels of hedge, pasture and margin, DP and PR on the proportion of individuals moving further than a threshold Euclidean distance of 500, 1000, 1500 or 2000m from their starting location. Separate tests were used for each threshold distance. We tested only for main effects of all explanatory variables, except for interactions between DP and each landscape variable (hedge, pasture, margin): *a priori* there was no

reason to expect landscape variables to interact, or for PR to interact with either landscape variables or DP. Conversely, because increasing values of DP will increasingly ‘override’ landscape costs, the effect of landscape variables on distances travelled may be expected to be larger at low values of DP, and so these interactions were included. We used Akaike’s Information Criterion, employing the second-order variant (AICc; Anderson 2008) to distinguish the best-fitting combinations of explanatory variables. We therefore conducted four binomial logistic regression analyses of the outputs of SMS runs (analysis of the proportion of movements greater than 500, 1000, 1500 and 2000) and in each analysis tested all 31 combinations of the main effects hedge, pasture, margin, DP and PR, and all 38 additional combinations of these models with DP * hedge, DP * pasture and DP * margin.

We performed a separate binomial logistic regression analysis of the output of the additional (cost uncertainty) models, incorporating variations in the cost of pasture (‘Pcost’: 22, 14, 5) and ‘other grass’ (‘Gcost’: 23, 12, 2) into the explanatory variables. We tested all 31 combinations of the main effects of hedge, pasture, margin, Pcost and Gcost, as well as eight additional combinations of these models with pasture * Pcost to test for interactions between the cost of pasture and the percentage of pasture in the landscape.

3. Results

3.1 *Effect of landscape components on distance travelled*

The proportion of modelled paths in which individuals moved further than a given threshold distance was affected by an interaction between hedge and DP: nine of the ten best fitting models contained this interaction term, and the delta AICc value of the tenth (which contained only main effects of all variables) ranged between 6.9 and 47.7 across the four analyses (Table 3), suggesting this model was a poor relative fit (Anderson 2008). The overall best fitting model contained main effects of all variables and an interaction between hedge and DP. This was the best model in three of the four analyses with a mean model probability of 0.38 (Table 3).

The percentage of hedge had a substantially larger effect on the proportions of individuals making movements of a given size than did the percentage of margin or pasture (Table 4; Table 5). Estimates of the reduction in residual deviance for hedge were at least an order of magnitude larger than those for pasture and margin in all analyses (Table 4). As the threshold movement distance was increased from 500m to 2000m the proportion of individuals moving further than the threshold obviously decreased (as more tortuous paths were excluded) (Table 5), but for each threshold, increasing the percentage of hedge from 25% to 50% increased the proportion of individuals making movements of that size: a mean of 0.083 more individuals made movements of 500m and 1000m and a mean of 0.053 and 0.030, respectively, made movements of 1500m and 2000m (means taken across all values of PR and DP) (Table 5; Fig. 3). By contrast increasing the landscape percentage of margin from zero to 50% resulted in a maximum mean decrease of 0.016 and doubling percentage of pasture resulted in a maximum mean increase of 0.0056 (Table 5; Fig. 3).

In all analyses the addition of DP induced the largest reduction in residual deviance in the proportion of model hedgehogs making movements of a given threshold size (Table 4). This is expected given that this SMS parameter affects the tendency of an individual’s movement to correlate with its previous direction (i.e. of model hedgehogs to move in straight lines; see Fig. 2). The deviance explained by the interaction between DP and hedge, however, was at least an order of magnitude smaller than the main effects of either DP or hedge: the main effect of hedge was modified only to a small extent by variations in DP, across the range of DP used in the SMS models (Fig. 3). Changes to the proportion of

individuals making movements that exceed each threshold distance were substantially smaller for alterations in margin and pasture than for hedge, making it difficult to assess interaction effects of DP with margin and pasture. The absence of such terms in the final statistical models, however, suggests that any such effects were marginal.

The relative effect of increasing the landscape percentage of hedge from 25% to 50% and from 50% to 75% was not the same: there was no evidence for a consistent additional increase in the proportion of individuals moving further than a given threshold when hedge was increased to above 50% (Table 5; Fig. 2). Post-hoc tests confirm this observation: for all four threshold movement distances the hypotheses that the difference between hedge 25% and 75%=0, and that the difference between hedge 25% and 50%=0 were rejected (Tukey test, z values > 3.29 , $P < 0.001$ in every case), whereas in all four tests the hypothesis that the difference between hedge 50% and 75%=0 was upheld (Tukey test, z values < 2.02 , $p > 0.106$ in each case).

3.2 Impact of varying the initial landscape costs

Varying the landscape cost of pasture and other grass (Pcost and Gcost, respectively) did not substantially affect the relationship between the landscape percentages of hedge, pasture and margin and the proportion of hedgehogs that achieved different thresholds (Fig. 4a). The overall best fitting model across all threshold distances was the fully parametrised model (best fitting at 1500m and 2000m, mean delta AICc = 3.6 at 500m and 1000m), containing main effects of hedge, margin, pasture, Pcost and Gcost and the interaction pasture*Pcost. Estimates of the reduction in residual deviance for hedge remained at least an order of magnitude larger (range 308-710 across the threshold distances) than those for pasture (range 0-12), margin (range 5-25) and Gcost (range 8-23; Fig. 4b) throughout. The main effect of Pcost yielded a relatively large reduction in residual deviance (range 40 – 200 across all threshold distances), and varying costs for pasture from 5 to 22 resulted in a maximum difference of 0.07 (range 0.02-0.07) of individuals making a given threshold movement (Fig. 4b). However, evidence that variations in Pcost combined interactively with the landscape percentage of pasture was minimal. The reduction in residual deviance for the term pasture * Pcost was the smallest (range 1-8) across all analyses, and the effect of increasing the landscape percentage of pasture remained substantially smaller than that of hedge for all costs of pasture (Fig. 4a). Similarly, varying the model landscape costs in relation to the presence of badgers also did not substantially affect the relationship between the landscape percentages of hedge, pasture and margin and the proportion of hedgehogs that achieved different thresholds (Appendix C).

4. Discussion

Within a typical lowland agricultural landscape the percentage of field boundaries that are hedgerow appears to be the principal determinant of permeability for hedgehogs. Variation in the proportion of model individuals making movements of a given threshold size was explained principally by the landscape percentage of hedge and by path straightness (the level of DP) (Table 4). Doubling hedge from 25% to 50% resulted in increases of between 0.030 and 0.083 in the proportion of individuals making movements of a given threshold distance (Table 5), representing an additional 13% of model hedgehogs making movements of 500m, 25% of 1000m, 35% of 1500m and 51% of 2000m. Further increasing hedge from 50% to 75% produced no additional increases in these proportions (Table 5). There was little evidence that varying the landscape percentages of margin and pasture had substantial impacts on movement distances.

In our model landscapes, margins were included as an additional width to pre-existing hedges. The intention was to separate the effect of margin in providing wider, low-cost habitats alongside existing movement corridors (hedges) from that of creating corridors in their own right, in the absence of hedges (such margins without hedges would form low-cost corridors in the model, but not in the real world, because they do not offer the protection of a hedge). The (minor) negative effect on the hedgehogs' mean Euclidean distances of adding margins to the landscape (range 0.0066-0.016, or 1-8% of model individuals across all threshold distances; Table 5) suggests that this additional width permitted the model hedgehogs to make lateral movements.

It is unclear why increasing the percentage of pasture in the landscape did not increase landscape permeability (resulting in small increases of 1% in the percentage of model individuals moving 500m and 1000m, but respective decreases of 2% and 4% for 1500m and 2000 m; Table 5), but it is likely – as with the 6m margins – that increasing the area of relatively low cost habitat increased the scope for model individuals to make lateral movements. Indeed, increasing the cost of pasture led to increased movement sizes (Fig. 4b), presumably resulting from model individuals being less likely to select this habitat and then make lateral movements. This observation aside, our results appear robust to our original choice of mid-point values between the estimates of the landscape costs (see Table 2 and Appendix B): varying the costs of pasture and other grass altered little the relative effects of the landscape percentage of hedge, margin and pasture on movement distances (Fig. 4a).

The model individuals did not make directed movements but responded to landscape costs (derived from radio-tracking; Supporting Information, Appendix B). Dispersing hedgehogs are likely actively to remain close to linear features (Doncaster et al. 2001), probably because hedgehogs in unfamiliar locations use linear features, particularly hedges, for navigation (Morris 2006; P. Morris pers. com., cited in Hof et al. 2012), and also to mitigate a perceived risk of predation (for instance the presence of badger scent; Hof et al. 2012). The costs of habitats in our model landscapes were unavoidably derived from resident hedgehogs that were familiar with their habitats (Dowie 1993; Hof and Bright 2010). Possible differences in behaviour between dispersing and resident individuals are likely to support our finding that the proportion of hedgerows, as opposed to field margins or pasture fields, is the principal determinant of landscape permeability: dispersing individuals may be more, not less, likely to follow linear landscape features. Similarly, we represented hedges as 2.5m wide strips of low cost habitat at the field boundaries (see Appendix B), whereas in reality the hedgerow itself is used mainly for day nests and resting during nightly activities (Hof and Bright 2010), as well as for shelter from predation (Hof et al. 2012), rather than movement *per se*. However hedgerows do represent dispersal corridors through croplands (Doncaster et al. 2001; Dowie 1993) and our declared simplifications are unlikely to alter the conclusion that hedgerows offer a primary, low-cost route by which dispersing hedgehogs can traverse unfamiliar farmland.

5. Conclusions

Actions to reinstate or repair hedges in order to double the percentage of hedgerow should enhance connectivity between hedgehog populations, particularly in landscapes where these populations are discontinuously distributed (Doncaster et al. 2001; Hof and Bright 2012), such as rural settings where populations are centred around urban settlements in a wider agricultural matrix (e.g. Hof and Bright 2010). Increasing the availability of field margins or pasture fields may not increase connectivity, but it might improve foraging or mating opportunities. However, given the protection from predators, and access to nests that hedges provide for hedgehogs, recent calls to reinstate hedgerows both to mitigate badger predation

and to increase the connectivity between suitable hedgehog habitats (Hof and Bright 2012), restoration of hedgerows should benefit hedgehogs and many other species, in particular small mammals (Fitzgibbon 1997; Gelling et al. 2007), birds (Cornulier et al. 2011; Green et al. 1994; Macdonald and Johnson 1995), and bats (Verboom and Huitema 1997).

We assessed the relative contribution of agricultural habitats to landscape connectivity for hedgehogs using an individual based model to assess permeability. Least cost path, graph theory and circuit theory approaches (and combinations of them) currently dominate the literature on ecological connectivity, but make some strong implicit assumptions (for critiques see e.g. Cushman et al. 2013; Moilanen 2011; Palmer et al. 2011) that are readily relaxed in an individual-based model (Palmer et al. 2011; Pe'er et al. 2011). In particular, the individual-based approach incorporates limited perceptual ranges (other approaches often implicitly assume full knowledge of the environment) and stochasticity in movement trajectories. Additionally, empirical data on movement trajectories can be used to parameterise individual-based models. Our model hedgehogs illustrate the potential for these models to address conservation in the agricultural landscape (see also (Diekötter et al. 2010) with potential to inform mitigation of the likely unfortunate synergic impacts between climate and land-use change on biodiversity (e.g. Hodgson et al. 2012; Newman and Macdonald 2013). A major outstanding challenge is to apply these models to multiple species on the same landscapes. We suggest that a priority for future work is to develop projects that assembled the necessary ecological understanding to parameterise individual-based models such as SMS for representative sets of species to explore the extent to which management scenarios devised for one species are also likely to benefit others.

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Table 1

Model	Hedge	Pasture	Margin
Landscape01	25	25	0
Landscape02	50	25	0
Landscape03	75	25	0
Landscape04	25	13	0
Landscape05	50	13	0
Landscape06	75	13	0
Landscape07	25	25	25
Landscape08	50	25	25
Landscape09	75	25	25
Landscape10	25	13	25
Landscape11	50	13	25
Landscape12	75	13	25
Landscape13	25	25	50
Landscape14	50	25	50
Landscape15	75	25	50
Landscape16	25	13	50
Landscape17	50	13	50
Landscape18	75	13	50

Table 1. The combinations of levels of hedge, pasture and margin modelled in the study. “Hedge” - the percentage of all agricultural fields that are bordered by hedgerow; “Pasture” - the percentage of all agricultural fields that contain pasture (as opposed to arable); “Margin” - the percentage of those agricultural fields bordered by hedgerow that additionally have 6m field margins. Shaded cells represent the values that reflect the extant real-world proportions of these landscape features.

Table 2

Table 2. Costs of habitat types as revealed by their selection by hedgehogs in radio-tracking studies (see Appendix B, Supporting Information). The cost value of each habitat used to

Habitat type	Costs from Dowie (1993)	Costs from Hoff (2009)	Modelled cost
Hedgerow	1	1	1
Agri-environment field margin	-	1.7	2
Arable field	46.3	46.9	47
Pasture field	22.4	4.6	14
Other grass	22.6	1.9	12
Set aside	-	14.4	-
Deciduous Wood	15.0	10.2	12
Garden	15.3	14.0	15
Water	-	-	200
Road	-	-	100
Building	-	-	1000

populate the cost landscapes is given in the column “modelled cost”. Set aside was not entered as a habitat type, but included as pasture, due to the similarity in the costs between these habitat types.

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Table 3

Rank	Model	Mean Delta AICc	Mean model probability (weight)	Model Delta AICc				Model Weight			
				500	1000	1500	2000	500	1000	1500	2000
1	Hedge+Pasture+Margin+PR+DP+Hedge*DP	0.3	0.38	0.0	1.3	0.0	0.0	0.52	0.14	0.54	0.31
2	Hedge+Pasture+Margin+PR+DP+Hedge*DP+Pasture*DP	1.2	0.22	2.0	0.6	0.9	0.9	0.19	0.20	0.28	0.20
3	Hedge+Margin+PR+DP+Hedge*DP	3.3	0.10	4.6	0.0	4.2	4.2	0.05	0.26	0.06	0.04
4	Hedge+Pasture+Margin+PR+DP+Hedge*DP+Margin*DP	2.3	0.14	2.6	2.1	0.4	0.4	0.14	0.09	0.07	0.25
5	Hedge+Pasture+Margin+PR+DP+Hedge*DP+Pasture*DP+Margin*DP	3.1	0.10	4.6	1.4	1.3	1.3	0.05	0.13	0.04	0.16
6	Hedge+Margin+PR+DP+Hedge*DP+Margin*DP	5.3	0.06	7.3	0.8	4.6	4.6	0.01	0.18	0.01	0.03
7	Hedge+Pasture+PR+DP+Hedge*DP	22.2	0.00	12.6	30.7	19.0	19.0	0.00	0.00	0.00	0.00
8	Hedge+Pasture+PR+DP+Hedge*DP+Pasture*DP	23.1	0.00	14.6	30.1	19.9	19.9	0.00	0.00	0.00	0.00
9	Hedge+PR+DP+Hedge*DP	25.3	0.00	17.3	29.5	23.2	23.2	0.00	0.00	0.00	0.00
10	Hedge+Pasture+Margin+PR+DP	39.0	0.00	6.9	36.5	46.6	46.6	0.02	0.00	0.00	0.00

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Table 3. The 10 best fitting models to explain the proportion of individuals moving further than a specified threshold distance (500, 1000, 1500 and 2000m). Overall rank was assessed as lowest mean delta AICc across analyses of all four threshold distances.

Table 4

			Reduction in residual deviance			
Source	D.f.	Residual d.f.	500	1000	1500	2000
Hedge	2	179997	1237.3	1230.0	788.8	470.5
Pasture	1	179996	6.5	0.7	6.3	6.0
Margin	2	179994	16.4	32.2	29.5	22.2
PR	1	179993	19.2	61.6	54.1	36.6
DP	1	179992	2792.7	6565.0	7392.6	5688.9
Hedge:DP	2	179990	10.9	39.2	69.9	50.6

Table 4. The reduction in residual deviance attributed to each term in the overall best fitting model from Table 3 for analyses at each threshold distance (500m, 1000m, 1500m and 2000m).

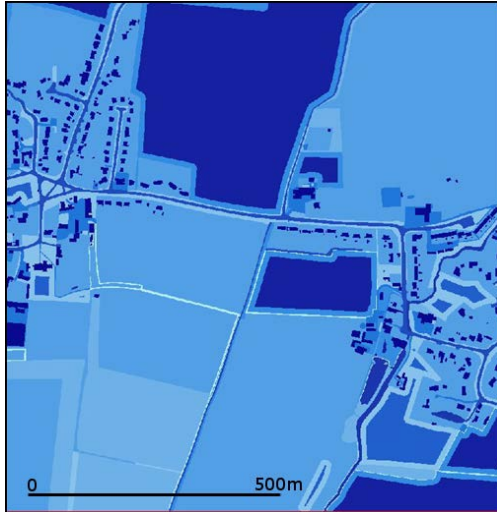
Table 5

Landscape element	Landscape percentage	500	1000	1500	2000
Hedge	25%	0.63	0.33	0.15	0.059
	50%	0.71	0.42	0.20	0.087
	75%	0.71	0.42	0.20	0.089
	Difference (Percentage)	0.083 (13%)	0.083 (25%)	0.053 (35%)	0.030 (51%)
Margin	0%	0.69	0.40	0.19	0.083
	25%	0.68	0.39	0.18	0.077
	50%	0.68	0.38	0.18	0.076
	Difference (Percentage)	-0.010 (-1%)	-0.016 (-4%)	-0.011 (-6%)	-0.0066 (-8%)
Pasture	13%	0.68	0.39	0.19	0.080
	25%	0.69	0.39	0.18	0.0877
	Difference (Percentage)	0.0056 (1%)	0.0020 (1%)	-0.0046 (-2%)	-0.0031 (-4%)

Table 5. The mean proportion of individuals making movements of a given size for each percentage of hedge, margin and pasture in the model landscapes. Proportions are averaged across all values of DP and PR. 'Difference' indicates the total increase or decrease in proportion of individuals making movements of that size across the span of the landscape values (i.e. between 25-75% for hedge, 0-50% for margin and 13-25% for pasture).

Figure 1

a)



b)

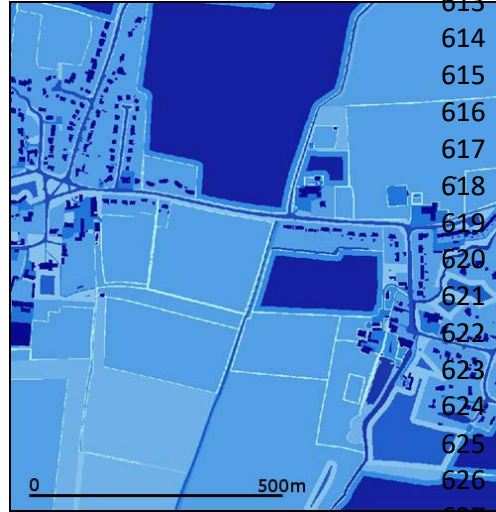


Fig. 1. Details of two representative gridded areas of the model landscape a) with the landscape percentage of hedge set to 25% and b) with hedge set to 50%. Areas shown measure approximately 0.9x1.0km. Shading denotes the cost of each 2 x 2m grid cell, ranging from 1 (lightest shade: hedges) to 1000 (darkest shade: buildings). Boundaries derived from Ordnance Survey MasterMap, ©Crown Copyright/database right 2012. An Ordnance Survey/EDINA supplied service.

Figure 2

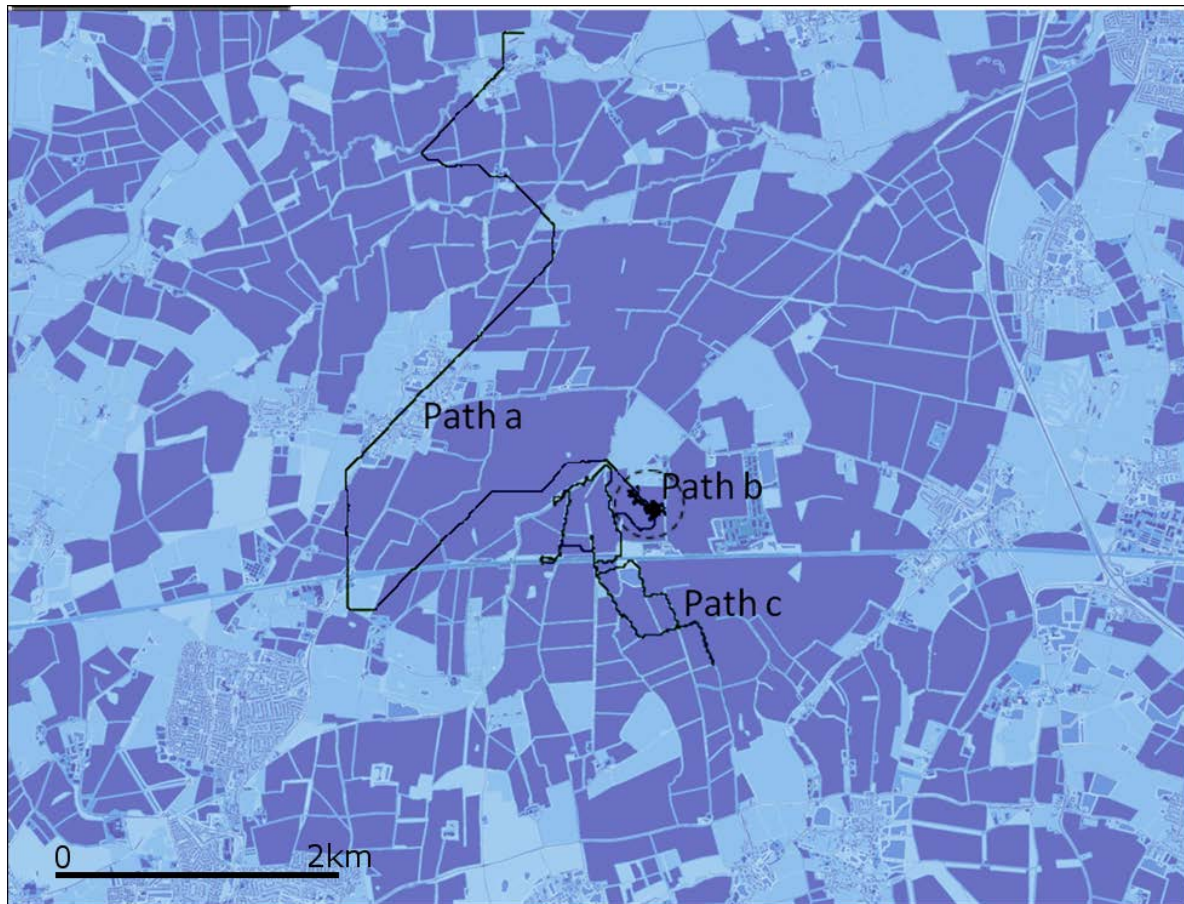
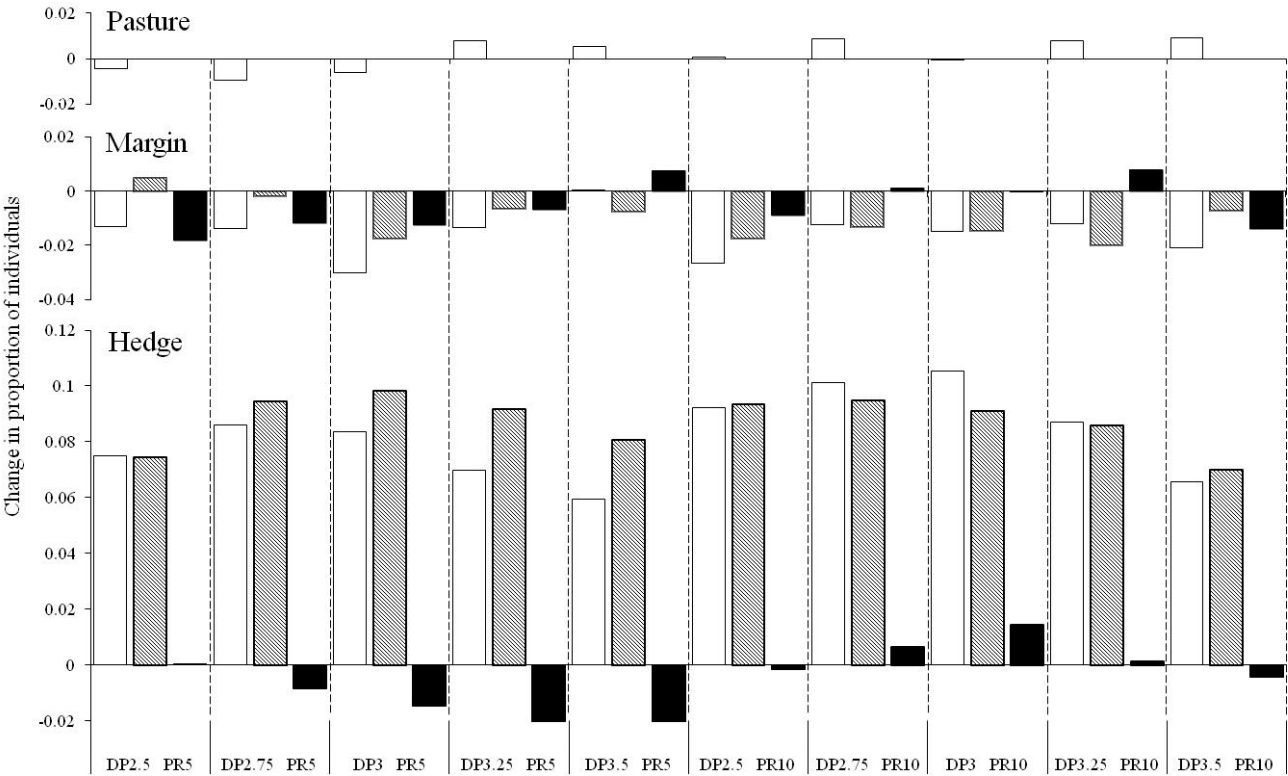


Fig. 2. Landscape01 (11.2x8.47km) showing three demonstration paths for model hedgehogs. Each path comprises 5000 steps from the same starting point (the closest hedge to the centre of the landscape) with varied DP: Path a, DP = 6; Path b, DP = 1; Path c, DP = 3.5. When DP = 6, DP overrides the difference in landscape costs. When DP = 1 the path responds principally to immediate landscape costs, resulting in a tortuous path in a conserved area (delineated by the dashed circle). DP = 3.5 produces a path that follows landscape low-cost features. Boundaries derived from Ordnance Survey MasterMap, ©Crown Copyright/database right 2012. An Ordnance Survey/EDINA supplied service.

663 Figure 3
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 668 Fig. 3. Mean change in the proportion of individuals moving further than a threshold distance
 669 of 1000m in relation to the percentage of hedge, margin and pasture in the model landscapes.
 670 Data are presented for every combination of DP and PR. For hedge, white bars represent the
 671 effect of increasing the landscape percentage from 25% to 75% (i.e. the total increase), grey
 672 bars from 25% to 50% and black bars from 50% to 75%. For Margin, white bars represent the
 673 effect of increasing the proportion from zero to 50%, and gray bars from zero to 25% and
 674 black from 25% to 50%. These relationships remain consistent for thresholds of 500m,
 675 1500m and 2000m.

Figure 4

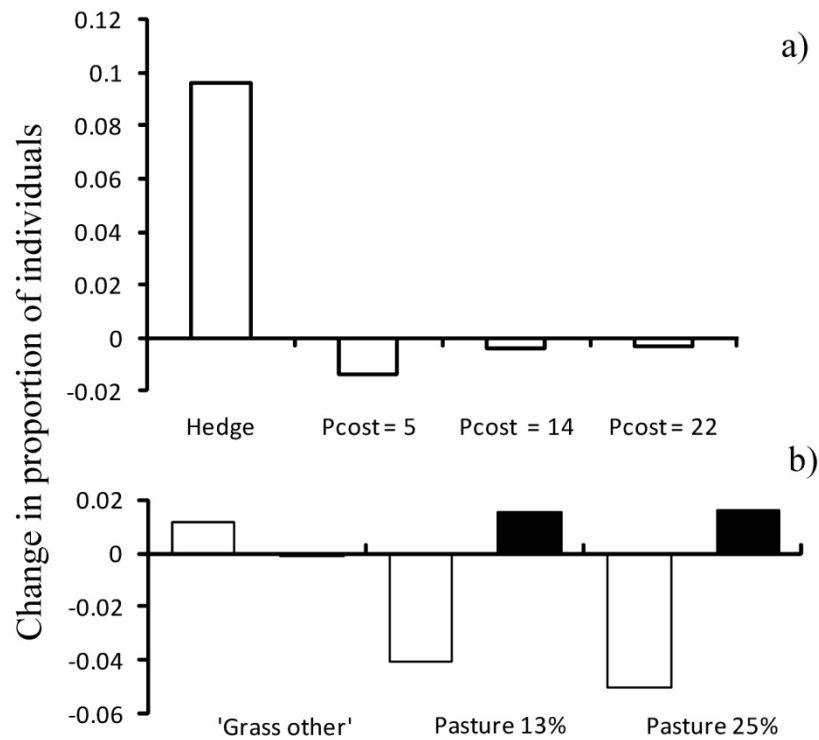


Fig. 4. The effect of varying the costs of pasture and other grass habitats on the proportion of individuals moving further than 1000 m. Panel a presents the effect of increasing the landscape percentage of pasture from 13% to 25% for each cost of pasture (Pcost). The effect of increasing the percentage of hedge from 25% to 50% is presented for comparison. Panel b presents the main effects of varying the cost of other grass and pasture relative to the default (mean) costs used in the main model, where white bars show lowered costs and black bars raised cost. Costs for other grass are: low=2, default=12, high=23; for pasture these are 5, 14 and 22, respectively. The relationships remain consistent for thresholds of 500m, 1500m and 2000m.

Supporting information

Appendix A: Calculating the extant percentages of hedge, pasture and margin in the real-world landscape.

The actual percentage of agricultural fields with hedgerow borders in the study area is approximately 25%. This figure is derived from the Countryside Survey Hedgerow Data from 2007, hosted by the Centre of Ecology and Hydrology (CEH), to provide the total length of hedgerow (401.1 km) in the area and the total length of field perimeter available (1559.3 km; data from the Ordnance Survey MasterMap) to give an approximate 26% of field margins with hedgerow. This figure was ground-truthed from aerial photographs by randomly selecting 50 fields and estimating the percentage of margins that were hedgerow, providing an estimate of 30%. While neither measure can be expected to be exact, the figures suggest that the initial modelled percentage of hedgerow of 25% would be representative of the actual proportion in the study area. Similarly, the Land Cover Map 2007 (provided by CEH and used under licence LCM2012-123v2), categorises 74% of the agricultural land in the study area as arable, while 26% was grassland (pasture). Finally Environmental Stewardship data provided by Natural England (downloaded from http://www.gis.naturalengland.org.uk/pubs/gis/gis_register.asp) indicates that 104 of the 1656 polygons containing agricultural land had ESS field margin options employed. This gives an approximate percentage of 6% of *all* agricultural fields having field margins, which is the approximate equivalent of 25% of only those fields that also have hedges. Assessing what proportion of field margins in the real-world landscape is represented by a given value for margin in the model landscapes is complicated by the consideration of whether those margins were added to all fields, or only to those fields that also have hedgerow. The distinction is important because adding field margins to existing hedges would simply increase the breadth of existing low-cost habitat, whereas adding margins to fields without hedges would also increase connectivity of low-cost habitats across the landscape. It was desirable to add margins only to fields with existing hedgerows for two reasons: first, the low-cost of margins derives in part from their proximity to the shelter of hedgerows, and so it would be incorrect to model them as entirely separate features; and second we wished to separate the effects of habitat breadth and connectivity (connectivity being provided by the hedges, and breadth added by the margins) For these reasons in the model margins were added only to fields with existing hedgerows. Because the value for margin reflects the percentage of fields with existing hedgerow that additionally have margins (see main text) a value of 25% for margins in Table 1 represents $[25 / 4 \sim] 6\%$ of all fields having margins.

Appendix B: Derivation of relevant habitats and attribution of costs

Hedgehog-relevant habitats and their costs were drawn from categories from two previous radio-tracking studies of hedgehogs' ranging behaviour by Dowie (1993), Hof (2009) and Hof and Bright (2010), and are presented in Table 2 of the main document. Dowie (1993) divides radiofixes for hedgehogs in his study between the following habitats: hedgerow, arable, pasture, deciduous wood, garden, 'other grass' and 'other habitats'. The classifications from Hof (2009) and Hof and Bright (2010) are hedgerow, arable, pastures, woodland, village, amenity grassland, field margin and set-aside, and so differ in the latter four categories. The 'village' habitat, however, was described by Hof (2009) as "mainly gardens", and so is here treated as the direct equivalent of Dowie's (1993) 'Garden' category. Similarly,

‘other grass’ (Dowie) and ‘amenity grass’ (Hof and Bright 2010) refer to similar habitat types, and so were combined into “Other Grass” in the present study. Of the two remaining habitat types - field margin and set aside - field margin was relevant to the experimental design and therefore retained (Table 2); ‘set aside’ and ‘pasture’ had similar costs (Table 2) and so were combined into a single category of ‘pasture’ to limit the agricultural habitats to two: arable and pasture.

To attribute costs to each habitat type, for each of the above studies we created an index of habitat selectivity of hedgehogs from the raw numbers of fixes in each landscape element and the proportion of the total habitat represented by each element. For example in (Hof 2009) study 58% of the available landscape was arable land and 1% was hedgerow. From 1240 fixes (see Hof 2009), Fig 4.6; Fig2 in Hof and Bright (2010), we would therefore expect 719 and 12 fixes respectively in these landscape elements, assuming habitats were used in proportion to their prevalence. The observed fixes, however, were 146 and 118 fixes, respectively, giving a selectivity index (calculated as observed / expected fixes for a given element) of 0.2 for arable and 9.8 for hedges. These indices were then converted to a “cost” relative to the most highly selected landscape element by taking the inverse of each index and dividing them by the lowest value (i.e. the most selected: in each case this was hedgerow). The mean of the costs for each habitat from Dowie (1993) and Hof (2009) (see Table 2) were used to populate the polygons for each habitat in the landscapes. One complication, however, is that Hof and Bright (2010) demonstrate that when using amenity grassland (n=173), arable (n=142) and woodland (n=38) habitats hedgehogs were on average located < 10m away from the nearest boundary, i.e. the hedgehogs in these habitats remained close to the habitat edges and avoided areas in the middle of the area. To capture this behaviour in the model it was necessary to increase the cost of each of these habitats for locations > 10m from the nearest boundary. Polygons containing these habitats were therefore buffered to 10m and the costs for the resulting internal polygons were multiplied by five to reflect the greatly reduced probability of a hedgehog being found at distances of < 10m from a field margin (Hof and Bright 2010; Fig 4 of that study).

The list of habitat categories in Table 2 was sufficient to populate all of the GIS polygons from the original Ordnance Survey Mastermap with the exception of roads, buildings and water. Suitable costs needed to be estimated for these habitats. Buildings were given a cost of 1000 to prevent model hedgehogs from entering them. Roads were given a cost of 100 and water a cost of 200.

Appendix C: Would reduced perception of predation risk alter the effect of landscape elements on the proportion of hedgehogs making movements of a given size?

Hof et al. (2012) demonstrate that hedgehogs’ use of edge habitats and field interiors is mediated by the presence of badgers, such that hedgehogs were found a greater distance (approximately 27m) from hedgerows when badgers were absent, than when badgers were present (approx. 7m). Notwithstanding that the hedgehogs in Hof et al’s (2012) study were most likely to be moving within known home ranges, and dispersing hedgehogs may be more likely than residents to remain close to linear landscape features (Doncaster et al, 2001; Discussion), the possibility exists that any relationship between the landscape percentage of hedge, pasture and margin and dispersal distances may be altered if landscape costs varied with the presence of a predator. It is unclear whether the radio-tracking observations from Dowie (1993), upon which our costs were based (Table 2), were made in the presence of badgers, but those from Hof (2009) were, albeit at low density (Hof and Bright 2010).

We created two alternative sets of cost landscapes in which hedgehogs' selection of hedgerow was reduced by 10% and 50% (in two separate analyses) and their selection of pasture and arable habitats proportionately increased. The 10% reduction scenario represents a low, but non-zero reduction in perceived predation risk, and the 50% scenario a substantial reduction in perceived predation risk (Table C.1). These percentages were selected in the absence of data from the literature that would allow us to quantify the precise expected shift in the behaviour of hedgehogs in response to a reduction in perceived predation risk. We did not create cost landscapes in which the perceived predation risks were increased because this would increase the cost of all non-edge habitats, meaning that the importance of hedgerows as movement corridors would become higher, not lower. Each model landscape was run with 5000 steps for 1000 individuals, with PR maintained at 5 and DP at 3.

The 10% and 50% reduction scenarios did not substantially affect the relationship between the landscape percentages of hedge, pasture and margin and the proportion of hedgehogs that achieved different thresholds, compared with the original cost landscapes (Table C.2). The overall best fitting model across all threshold distances contained only hedge and margin in the 10% scenario and only hedge in the 50% scenario. For both scenarios estimates of the reduction in residual deviance for hedge remained at least an order of magnitude larger (range 71-127 and 26-110 across the threshold distances for the 10% and 50% scenarios, respectively) than those for pasture (ranges 0.1-1.0 and 0.6-1.0) or margin (range 0.4-4.7 and 1.3-1.4) throughout.

The increase in the proportion of model individuals making movements of a given threshold size, in response to increasing the landscape percentage of hedge, pasture and margin in the 10% and 50% scenarios were similar to those in the original model runs. Table C.2 (cf. Table 5) presents the results only for the 50% scenario (the more substantial reduction in costs of non-edge habitats) but shows that increasing the landscape proportion of hedge from 25% to 50% resulted in a 0.069 and 0.070 more individuals making movements of 500m and 1000m and 0.037 and 0.019, respectively, making movements of 1500m and 2000m. By contrast increasing the landscape percentage of margin from zero to 50% resulted in a maximum difference of 0.0045 and doubling percentage of pasture resulted in a maximum difference of 0.0049 (Table C.2). These results closely approximate those from the original cost landscapes.

For both the 10% and 50% scenarios, as with the original model runs, the relative effect of increasing the landscape percentage of hedge from 25% to 50% and from 50% to 75% was not the same: for all four threshold movement distances the hypotheses that the difference between hedge 25% and 75%=0, and that the difference between hedge 25% and 50%=0 were rejected (Tukey test, z values > 4.301 $P < 0.001$ in every case), whereas in all four tests the hypothesis that the difference between hedge 50% and 75%=0 was upheld (Tukey test, z values < 0.67 , $p > 0.27$ in each case).

The above evidence indicates that decreases in the hedgehogs' perceived predation risk, and even relatively large concordant reduction in edge-refuging, would not be expected substantially to alter the conclusions from our study.

Habitat type	Original cost	10% scenario	50% scenario
Hedgerow	1	1	1
Agri-environment	2	2	1
Arable field	47	40	19
Pasture field	14	13	7
Other grass	12	12	7
Deciduous Wood	13	12	7
Garden	14	13	8
Water	200	200	200
Road	100	100	100
Building	1000	1000	1000

Table C.1. Adjusted costs of habitat types in the model landscapes for two scenarios which model reductions in hedgehogs' perceived predation risk by badgers. The 10% scenario represents a low reduction in perceived predation risk, in which 10% of hedgerow fixes from the studies of Hof (2009) and Dowie (1993) were reapportioned to arable and pasture habitats to create a new set of costs, and likewise the 50% scenario.

Landscape element	Landscape percentage	500	1000	1500	2000
Hedge	25%	0.66	0.37	0.16	0.055
	50%	0.74	0.44	0.19	0.075
	75%	0.73	0.44	0.20	0.074
	Difference	0.069	0.070	0.037	0.019
	(Percentage)	11	19	23	35
Margin	0%	0.71	0.42	0.18	0.069
	25%	0.70	0.41	0.18	0.070
	50%	0.71	0.42	0.18	0.065
	Difference	-0.0010	0.0007	0.0023	-0.0045
	(Percentage)	0	0	1	-6
Pasture	13%	0.71	0.42	0.18	0.069
	25%	0.70	0.41	0.18	0.067
	Difference	-0.0069	-0.0049	-0.0033	-0.0029
	(Percentage)	-1.0	-1.2	-1.8	-4.2

Table C.2. The mean proportion of individuals making movements of a given size for each percentage of hedge, margin and pasture from model runs on landscapes in which 50% of fixes have been reapportioned from hedgerow to arable and pasture. 'Difference' indicates the total increase or decrease in proportion of individuals making movements of that size across the span of the landscape values (i.e. between 25-75% for hedge, 0-50% for margin and 13-25% for pasture).

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