# Which landscape features affect species movement? A systematic review in the context of climate change.

**Forest Research & Centre for Evidence-Based Conservation**
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## Contents

# 1. Executive summary

## Introduction

1. There is increasing evidence that climate change is having a direct impact on UK biodiversity. These impacts include: changes in seasonal events such as flowering and species migration; changes in species abundance, habitat preferences and range, and alteration to ecosystem functions such as carbon and nutrient cycling. It is likely that many species, including some UK Biodiversity Action Plan (UKBAP) priority species, will need to alter their range and distribution in response to changes in their “climate space” – the geographical area within which the climate is suitable for population survival – and the distribution of habitat and resources.

2. Habitat fragmentation is thought to be a major factor constraining the ability of species to track geographical shifts in suitable climate space. Functional connectivity is dependant on species dispersal abilities, the size and spatial arrangement of habitat patches and the degree to which land cover and land use in the intervening matrix may facilitate or hinder movement. As such, functional connectivity is species-specific and a landscape may be functionally connected for some species, but not for others.

3. Defra and partners have produced guidance for land-managers on how to reduce the impact of climate change on biodiversity[1]. This includes recommendations for the creation of ecological networks to improve connectivity between habitat patches by: habitat expansion, establishing physical linkages such as corridors and habitat “stepping stones”, and improving the permeability of the matrix to species movement. Although these measures are strongly underpinned by ecological theory, the empirical evidence is in need of review to guide and support actions to improve habitat connectivity (**Main report: Section 2.1)**.

## Aims and Objectives

4. The aim of this project was to assess, through systematic review with expert consultation, the strength of the empirical evidence underpinning the development of functional habitat connectivity as an adaptation to climate change (**Section 2.2**). The main objectives included: assessing the importance of landscape permeability/connectivity for a wide range of species including BAP priority species; categorising the time-scales and distances over which connectivity has been studied; identifying knowledge gaps in the evidence base, and providing recommendations for policy development in relation to landscape “design features” for enhancing species movement.

[1] Hopkins, J.J, Allison, H.M., Walmsley, C.A., Gaywood, M. & Thurgate, G. (2007) Conserving biodiversity in a changing climate. UK Biodiversity Partnership. Published by Defra, London. www.ukbap.org.uk/Library/BRIG/CBCCGuidance.pdf

## Methods

5. A systematic review[2] and synthesis of available evidence was undertaken including database and internet searches, meta-analyses[3] of selected relevant quantitative datasets and exploration of qualitative data. The specific review question was 'Which landscape features affect species movement?' In the qualitative section, specific focus was given to studies of UK species, including UKBAP priority species and non-native species, and to the spatial and temporal scales of those studies. In consultation with the project steering group, priority was given to assessing quantitative evidence that landscape features, specifically corridors and matrix structure, can enhance species movement (**Section 3.1**).

6. A total of 11,270 documents were systematically assessed and 313 studies (all on animals) identified where direct measurement of species movement had been undertaken in relation to the presence/absence of corridors or to matrix structure. Landscape features and experimental designs varied between studies, so the 313 studies were sorted into seven 'evidence pools' according to their characteristics, and the data from two pools were subjected to quantitative synthesis using meta-analysis (**Section 3.3**). A qualitative review was undertaken on the subset of studies concerning UK species (67 studies; 109 species; 18 UK BAP priority species; 9 non-native species).

## Results

7. The meta-analysis was able to provide evidence, for a limited number and taxonomic range of species on which studies have been conducted, that corridors have the potential to facilitate movement between habitat patches. Many of the studies available focused on insects and rodents in experimental spatial populations and should not therefore be used to infer wider application (**Section 4.2.1; Figure 4**). Matrix type was shown to influence the movement of individuals, with matrices that were structurally more similar to the organism's "home" or breeding habitat patch being more permeable to species movement (**Section 4.2.2; Figure 10**). Provision of a corridor (versus no corridor) had a greater effect on inter-movement rates than provision of a permeable matrix (versus non permeable). However, there have been no direct comparisons of the preference of species for using a corridor compared to a permeable matrix (**Section 4.3**).

8. There was uneven coverage of taxonomic groups in the 67 studies retrieved on UK species, and most focused on butterflies and moths, followed by birds and carabid beetles. Among the mammals, rodents were the most widely

[2] A systematic review strives to minimise error and bias through an exhaustive search of unpublished grey literature and research findings, in addition to peer-reviewed journal publications. It can support decision-making by providing an independent and objective assessment of evidence

[3] Meta-analysis is a statistical technique used within a systematic review to integrate and summarise the results from individual studies providing greater statistical power, and allowing comparison of studies yielding contrasting results.

studied. Freshwater invertebrates appear particularly under-investigated and there were no studies retrieved on UK reptiles (**Section 5.2; Table 2**). Plants were not included in the review. Spatial scales of the studies ranged from 0.03 $m^2$ (natterjack toads) to 15,800 $km^2$ (deer) and timescales of the experiment/observations from two minutes to five years (**Section 5.2; Figure 15a**). Positive responses, such as increased movement rate or dispersal distance, to intervening matrix features of a similar structure to the 'home' habitat were recorded across taxonomic groupings, habitat types and scales (**Section 5.4**). Exceptions occurred where the species used less structurally similar features for cover, was highly mobile and did not react to the matrix, or used more permeable features but still dispersed at the same rate (**Section 5.5; Table 6**). Some negative responses (decreased movement or dispersal) to barriers such as roads were recorded (**Section 5.5; Table 6**).

**Conclusions and recommendations**

9. There is quantitative evidence that corridors do facilitate the movement of individual animals in the circumstances tested. However, this evidence comes from a limited range of studies and it is not possible to generalise across taxa and landscapes. Landscape features between habitat patches, such as corridors and intervening matrix structure may have a role in enhancing connectivity for relatively mobile groups like butterflies, birds and large herbivores. For these species, measures to create corridors and an intervening matrix with structural affinity to the "home" habitat may enhance population persistence and could promote longer distance movement (**Section 8.3; 8.5**). This provides some limited support for current policy and guidance on improving functional connectivity by developing ecological networks to enhance species movements in response to climate change.

10. There was a large number of species for which no information was retrieved; reptiles and species of freshwater habitats were particularly under-represented as were species of low mobility. Plants were not included as no studies on plants fitted the inclusion criteria. In other instances the evidence was equivocal or confounded by other variables and the relative importance of landscape features, compared to other factors which affect species movement, is unclear. Notwithstanding the need for immediate action based on available evidence, further research relating to longer time-scales (over multiple generations) and greater spatial scales (greater than long-distance dispersal events) is required to refine our understanding of the spatial and temporal patterns of use of landscape features by different species and taxa. There is also a need for further evaluation of the effectiveness of landscape interventions in controlled situations (**Section 8.3; 8.5)**.

11. The findings of this study need to be placed in the context of the broader question of the effectiveness of habitat networks. The review covered a relatively narrow slice of the potential full range of evidence that could be brought to bear on this question (**Section 6**). Further reviews (e.g. to capture movement using inferred methods such as landscape genetics) and analysis

of the evidence pools gathered would help build a more complete picture (**Section 7**). In addition, other interventions to increase resilience of species to climate change may be as important as measures to enhance movement. Actions that can promote resilient populations include conserving protected areas and all other high quality habitats, reducing sources of harm not linked to climate, conserving the range and ecological variability of habitat and species, creating buffer zones around high quality habitats, and taking action to control spread of invasive species. In turn, larger populations can produce more individuals capable of dispersal and habitats will be more welcoming to colonisation and establishment, thereby increasing the likelihood and success of chance, long-distance dispersal events which for many species appear to be vital in keeping pace with shift in climate space (**Section 8.5**).

# 2. Introduction

## 2.1 Background

The growing body of evidence regarding the impacts of climate change on biodiversity includes changes in phenology, species distribution, community composition, ecosystem function and a loss of physical space due to sea level rise and increased storminess (Mitchell *et al.,* 2007). Projected shifts in suitable climate space may force species to adjust their ranges if they are to survive (Walmsley *et al*., 2007) and many species groups are already showing range margin movement (Parmesan, 2006).

Many species may not be able to move rapidly enough to track their future climate space and this problem is further compounded by barriers to movement such as habitat fragmentation (Travis, 2003). Habitat isolation, urbanisation and agricultural intensification may all inhibit species movement. Dispersal can become energetically more costly and have higher mortality risks (Pearson & Dawson, 2005; Warren *et al.,* 2001; Thomas *et al*., 2006). Even mobile species such as butterflies have been shown to encounter difficulty moving quickly enough in response to climate change (Gutierrez & Thomas, 2000).

*Policy context*

In the context of commitments to halt the loss of biodiversity and meet other targets in the UK Biodiversity Action Plan, there is a need to consider the impacts of climate change on species, to understand their responses and to provide potential adaptation measures (UK Biodiversity Partnership 2007). This is in addition to commitments in place to reduce the impacts of fragmentation. The EU Habitats Directive (EEC, 1992) obliges the UK to endeavour to improve the ecological coherence of Natura 2000 sites (see Box 1) and maintain or restore favourable conservation status to species of community importance, many of which have been adversely affected by fragmentation.

Defra and country partners have made clear policy objectives to address the impacts of habitat fragmentation and of climate change (Box 1) citing the development of a sound knowledge base as a key aspect. The recent UK Biodiversity Partnership publication '*Conserving Biodiversity in a changing climate: guidance on building capacity to adapt*' advocates provision of ecological networks as one of several measures that can be taken to encourage adaptation (Hopkins *et al*., 2007, p.18).

**Box 1**. Key Policy Statements & Extracts.

Article 10 of the Habitats directive
*'Member States shall endeavour, where they consider it necessary, in their landuse planning and development policies and, in particular, with a view to improving the ecological coherence of the Natura 2000 network, to encourage the management of features of the landscape which are of major importance for wild fauna and flora. Such features are those which, by virtue of their linear and continuous structure (such as rivers with their banks or the traditional systems for marking field boundaries) or their function as stepping stones (such as ponds or small woods), are essential for the migration, dispersal and genetic exchange of wild species*.'

Article 3 of the Birds directive
'…*Member States shall take the requisite measures to preserve, maintain or re-establish a sufficient diversity and area of habitats for all the species of birds referred to in Article 1. 2. The preservation, maintenance and re-establishment of biotopes and habitats shall include […] (b) upkeep and management in accordance with the ecological needs of habitats inside and outside the protected zones*…'

England Biodiversity Strategy
'*Climate change [is] one of the most important factors affecting biodiversity and influencing our policies*.'
'*… ensuring that special sites sit within a wider 'wildlife-friendly' landscape that reduces fragmentation of habitats, helps species populations to disperse…'*

Scottish Biodiversity Strategy
'…*Organisms can move and disperse effectively, and are better able to adapt to… climate chang*e.'

Environment Strategy for Wales
'*We will focus on… finding ways to deliver connectivity and environmental improvement at landscape scale, particularly in relation to biodiversity*.'

*Re-building connectivity as an adaptation measure*

Increasing the permeability of landscapes to species movement between habitat patches and ensuring populations are large enough to provide a viable number of emigrants are key measures identified for facilitating some species' adaptation to changes in climate space. Species movement may be affected by, among other things, the availability and spatial arrangement of habitat, or the intensity of intervening land uses (Hopkins *et al.,* 2007, Mitchell *et al.,* 2007) which can be altered in part by management practices. For these reasons, the development of functional ecological networks has been proposed as one method to manage the effects of habitat fragmentation and so help species adjust to the impacts of climate change (Hopkins *et al.,* 2007, p.18). One such functional ecological network model has already been used in the UK to target and evaluate conservation options at various spatial scales (Catchpole, 2007). The Pan-European Ecological Network (Foppen *et al.,* 2000), is likely to be a more flexible plan including both structural connectedness and functional connectivity elements.

Connectivity is the degree to which a landscape facilitates or impedes the movement of individuals between habitat patches. There are two main ways of looking at connectivity:

1) **structural** connectedness of the landscape is the degree to which habitat patches are physically linked;
2) **functional** connectivity is dependant on species dispersal abilities, the size and spatial arrangement of habitat patches and the nature of land cover and land use in the intervening matrix. The same landscape can be functionally connected for one species but not for another.

A basic principle of functional connectivity is that the land use between habitat patches (matrix) impacts on species movement, (Tischendorf & Fahrig, 2000; Murphy & Lovett-Doust, 2004) and that some land covers or land uses are more permeable to movement than others (Donald & Evans, 2006). Management, expansion, restoration and creation of suitable habitat, provision of buffer zones around habitat, provision of corridors and stepping stones between habitats and improving matrix permeability, are the 'building blocks' for functional ecological networks. From a practical perspective, in the UK there may be limited potential for creation of structural networks based on large core areas and corridors of near-continuous habitat, applied elsewhere in the world (e.g. North and South America and Europe; Jongman & Pungetti, 2004), because of the scale of land tenure, current landscape and our current species composition (Bennett, 2004).

Functional ecological networks are based on first principles derived from ecological theory (e.g. island biogeography, MacArthur & Wilson 1967; metapopulation dynamics, Hanski 1999; dispersal ecology, Bullock *et al.* 2001).

However some authors have noted that there is little supporting empirical evidence to demonstrate the practicality and effectiveness of ecological networks in general (e.g. Jongman & Pungetti, 2004) or to guide design features such as size, shape, spacing, or structure. Dawson (1994) reviewed the evidence for corridors acting as movement 'conduits' and concluded that there was a large amount of data but little of it 'comes near to meeting the formal requirements of hypothesis testing'. In addition, there are a number of complex links and feedback processes in moving from increasing individuals' movement to predicting changes in the ranges of populations as a climate response. The link between increased species movement and (meta) population persistence has strong foundations in ecological theory (Hanski & Gaggiotti, 2004) but the importance of dispersal on population dynamics can vary with the spatial structure of the population (Thomas & Kunin, 1999; Barrett & Anderson, 1999).

The timescales necessary to provide the empirical evidence on the link between dispersal and population dynamics make research difficult; however, some studies within experimental systems have shown the potential importance of dispersal for population abundance and persistence (Gonzalez *et al.*, 1998). In the context of climate change the risk of remaining in a patch may be greater than the risks associated with movement and there may be an increase in selective advantage of dispersal at the range margin (Thomas *et al.,* 2006; Hughes *et al.,* 2007). It is therefore important to test the general principles of landscape connectivity with empirical observations.

## 2.2 Objective

We aimed, through systematic review and meta-analysis, to examine evidence that certain landscape features, particularly those between habitat patches, can affect species movement.

Within this a specific aim was to summarise the evidence available for UK species (particularly BAP priority and non-native species) and describe the spatial and temporal scales of relevant studies.

## 2.3 The systematic review approach

Systematic review is a tool used to collate, summarise, appraise and communicate the results and implications of a large quantity of research and information. It can support decision-making by providing an independent and objective assessment of evidence. It is designed to inform the decision-making process but not to make decisions on behalf of the user-community.

Systematic review is particularly valuable as it can be used to synthesise results of many separate studies examining the same question, which may have conflicting findings. The process can also highlight areas where further original research is required. A systematic review strives to minimise error and bias through a comprehensive search of unpublished grey literature and research findings, in addition to peer-reviewed journal publications. The process of inclusion of studies in the systematic review is transparent and repeatable. Due to its systematic nature, the approach is more robust and powerful than a traditional or narrative literature review (Pullin & Stewart, 2006).

Meta-analysis is a statistical technique that is used to integrate and summarise results from individual studies within the systematic review. It can generate a single summary estimate of the effect of an intervention on a subject, with more statistical power than each study alone. Meta-analytical techniques also allow factors affecting differences in results between studies to be explored.

The study followed the methodology successfully developed for conservation and environmental management from the medical model (NHS CRD, 2001; Pullin & Stewart, 2006). The steering group (listed in the front of this report) comprised a UK-based range of subject experts and representatives from a number of statutory and non-governmental conservation organisations, gathered together by Defra before the project began.

1. The question was formulated by the steering group and a review protocol agreed (Appendix 1)
2. Scoping searches tested the applicability of keywords individually and in complex search strings
3. Searches were carried out using online databases, internet search engines and relevant statutory agency websites, to retrieve both peer reviewed research and grey literature
4. Articles were assessed for relevance using pre-defined criteria (Section 3.2.2 Study inclusion criteria)
5. Articles containing data about directly measured movement of species comparing different elements of the matrix between habitat patches were sorted into pools according to the experimental strategy (Section 3.3)
6. Quantitative meta-analysis was performed on studies comparing directly-measured successful rates of inter-patch movement in controlled experiments that tested movement between patches with and without corridors (Section 4).
7. A second quantitative meta-analysis examined studies where different pairs of patches had different matrix (non-habitat) types between them, e.g. grass compared to bare ground (Section 4)
8. All studies including UK species were described, tabulated and qualitatively synthesised according to taxonomic group, spatial and temporal scale and landscape feature (Section 5).

# 3. Review methods

This section covers how the systematic search was formulated from a review question, a keyword based search carried out and the resulting body of literature filtered for relevance and sorted.

## 3.1 Question and search word formulation

We aimed, through systematic review and meta-analysis, to examine evidence that certain landscape features, particularly those between habitat patches, can affect species movement.

For systematic review following the approach used here, the formulation of a specific research question is the first stage. Questions need a 'subject', an 'intervention' and an 'outcome'. For a review examining the effectiveness of asulam herbicide in the control of bracken, for example, the subject would be '*bracken'*, the intervention '*the application of asulam herbicide*', and the outcome to be assessed would be a '*change in bracken abundance*' (Stewart *et al.,* 2007).

The specific question for this review was developed through iterative discussion between the review team, DEFRA (The UK Department for Environment, Food and Rural Affairs) and the steering group. An initial, broad topic for focus was determined as: "*Which landscape features affect species movement*?" Question elements were agreed as follows:

- **Subject:** all species
- **Intervention:** landscape features - natural *and* man-made (including for example:- corridors, stepping stones, 'green bridges', barriers, matrix permeability, spatial pattern)
- **Outcome:** a change in movement recorded in individuals of study species

A draft protocol was developed to set out the review objectives, proposed search strategy and the criteria for the inclusion and exclusion of studies. The protocol was then circulated to the stakeholder group for comment, and a revised version posted on the Centre for Evidence-Based Conservation website (www.cebc.bangor.ac.uk) for a one-month open consultation period. The protocol also underwent peer review by anonymous invited experts. The version of the protocol published at the time of publication of this report is included as Appendix 1.

The development of an appropriate set of key words to be used in the searching phase of the review was driven by the stakeholder group and further guided by 'scoping' searches to allow the identification of the most useful sets of words. These were grouped into sub-sets, based on the intervention and outcome elements of the question. The formulation of a set of spatial and subject context words helped to ensure that only the most relevant studies were identified. Thus the search terms were as follows:

- **Intervention:** corridor*, barrier*, bridge*, “stepping stone*”, highway*, link*, network*, “buffer zone*”, patch*, edge*, connect*, mosaic*, “spatial pattern*”, heterogen*, permeab*
- **Outcome:** movement, dispersal, isolation, migration, coloni*, invasion, immigration, emigration
- **Spatial context:** habitat, landscape, matrix, fragment*
- **Subject context:** biodiversity, conservation, species, population*, metapopulation*.

Note: * indicates a ‘wildcard’, which allows the database or search engine to look for multiple word endings, e.g. connect / connected / connection / connectivity / connectedness.

## 3.2 Systematic data search and retrieval

*3.2.1 Search strategy*

The search strategy was designed to capture as many relevant references as possible, both published and unpublished (‘grey literature’). Relevant studies were identified through searches of the following electronic databases:

- ISI Web of Science
- CAB Abstracts
- Directory of Open Access Journals
- Index to Theses Online
- Conservation Evidence.com

For these searches, the individual key words were combined into complex ‘Boolean’ strings (where searches are limited or expanded using ‘AND’, ‘OR’ and ‘NOT’ indicators) to maximise the efficiency of searching. All terms from the ‘outcome’, ‘spatial’ and ‘subject’ context word lists were combined with a single ‘intervention’ word per search, for example:

> “((movement OR dispersal OR isolation OR migration OR coloni* OR invasion OR immigration OR emigration) AND (habitat OR landscape OR matrix OR fragment*) AND (biodiversity OR conservation OR species OR population* OR metapopulation*) AND corridor*)”

In addition to the online databases, general internet searches were conducted to identify further studies and unpublished literature. Three search engines were used in the web searching phase: www.alltheweb.com, www.scirus.com, and www.google.com. The first 50 hits (restricted to .doc .txt .xls and .pdf documents, where this could be separated) for each search were examined for studies meeting the inclusion criteria. No further links from the captured documents were followed. To allow for the variation in search engine capability, a standardised search was used for each engine, utilising their advanced search options, as follows:

- Using the “find any of the words” feature (or “at least one of the words”), the following terms were entered: “species, metapopulation, habitat, landscape, fragmentation, dispersal”.
  AND
- Using the “find all the words” feature, the following terms were used individually: ‘connectivity’, ‘barrier’, ‘bridge’, ‘corridor’, ‘stepping stone’, ‘network’, ‘link’, ‘spatial pattern’, ‘highway’, ‘mosaic’, ‘permeability’, ‘buffer zone’, ‘heterogeneity’, ‘patch’, ‘edge’.

The total number of search term combinations (or ‘search strings’) to be searched in each engine was fifteen. The number of words per search string was necessarily different from that used in the electronic database to reflect the increased ambiguity of particular words in a search of the World Wide Web compared to scientific publication databases.

The websites of the following organisations were inspected for further relevant material including useful grey literature or unpublished datasets: Natural England, Scottish Natural Heritage, Countryside Council for Wales, Department of Agriculture and Development Northern Ireland, Joint Nature and Conservation Committee, US Forest Service, Environment Canada (including Canadian Wildlife Service) and The Commonwealth Scientific and Industrial Research Organisation (CSIRO).

### *3.2.2 Study inclusion criteria*

References listed in the search results were first checked for duplicates, then underwent a three-stage iterative filtering process to assess their relevance for inclusion into the analyses. First the titles of all articles were assessed for relevance by a single reviewer (AE), using a pre-defined set of inclusion and exclusion criteria (Box 2) developed from a hierarchical list in the protocol. References were accepted into the next stage when there was any uncertainty, as article title often did not accurately reflect content.

A more stringent set of inclusion and exclusion criteria was formulated for the second, abstract level assessment. Two reviewers (LBA & AE) examined a subset of 500 articles derived from the electronic database search to check the repeatability of the relevance assessment. Kappa analysis was performed to ascertain the level of agreement between the two reviewers (see Edwards *et al.*, 2002): a ‘moderate’ rating (Cohen’s Kappa test: K = 0.47) was initially achieved.

Inclusion/exclusion rules were refined (Box 2) and a further 100 references were then assessed, incorporating these rules, by both reviewers. Agreement on these was 'almost perfect' at K = 0.89, indicating that the inclusion of studies was repeatable. The remaining abstract level assessment was completed by AE & LBA each examining half of the remaining studies independently.

At the abstract inclusion stage it became apparent that there was a larger than expected body of evidence looking at matrix features. As it was not possible to review both patch size/distance and matrix feature data in the time available, the latter group was chosen to reflect the increased interest in the effects of matrix features in both scientific and policy contexts (e.g. Kupfer *et al.,* 2006 and the England Biodiversity Strategy respectively). Studies concerning patch size or distance were saved in a separate list for potential further investigation in the future.

The third, full text assessment stage was conducted by a single reviewer (AE). The same inclusion and exclusion criteria as for the abstract assessment were used, with input and agreement from other review authors in cases of uncertainty.

### *3.2.3 Study quality assessment*

Although part of many systematic reviews, an assessment of study quality was not used to exclude articles from this review. Instead, it was deemed more appropriate to tabulate the methodological characteristics of the studies accepted, to enable the differences in approach to be described and to ensure that potentially interesting information was not excluded from the analyses.

### *3.2.4 Retrieval summary statistics*

Searching was completed in February 2008. A total of 20,264 articles were retrieved in the search. After the removal of duplicates, 11,270 were found to be unique (see Figure 1). After the first stage of relevance assessment based on an examination of article titles, 7,153 documents remained for the next stage of the review. Study abstracts were then assessed for relevance. At the end of the second stage 525 articles remained and after the third (full text) level of selection 313 studies were finally included in the review.

**Box 2**. Inclusion and exclusion criteria.

**Relevance assessment at study title level:**
**Include:**
Anything in the field of whole-organism biology

**Exclude:**
The range of subjects outside of this field (e.g. molecular biology, palaeontology)

**Relevance assessment at abstract and full text level:**

**Include:**
All studies presenting primary data concerning *directly-measured* movement (i.e. *not* inferred movement) in relation to:

- landscape features outside of habitat patches
- the shape of habitat patches.

Only studies with appropriate spatial or temporal controls or comparators were included in the review.

**Exclude:**

- Studies of colonisation/invasion where the source (i.e. distance moved) is not known
- Studies that inferred dispersal from measures of species abundance/density (as opposed to direct measurement)
- Articles in which movements measured were within a single habitat patch
- Modelling studies which did not present field data used for model validation/parameterisation
- Genetic studies (except where precise identification of parents was possible) on the basis that these infer, rather than directly measure, movement
- Studies examining pollen dispersal (this is a means of genetic dispersal but not population dispersal)
- Studies of seed movement by animals or disease/parasite movement – any form of 'lift-hitching' (though dispersal of seeds by animals is very important, the effect of landscape features on the seeds vs. the 'carriers' is difficult to separate)
- Studies of the effect of inter-patch distance or patch size.

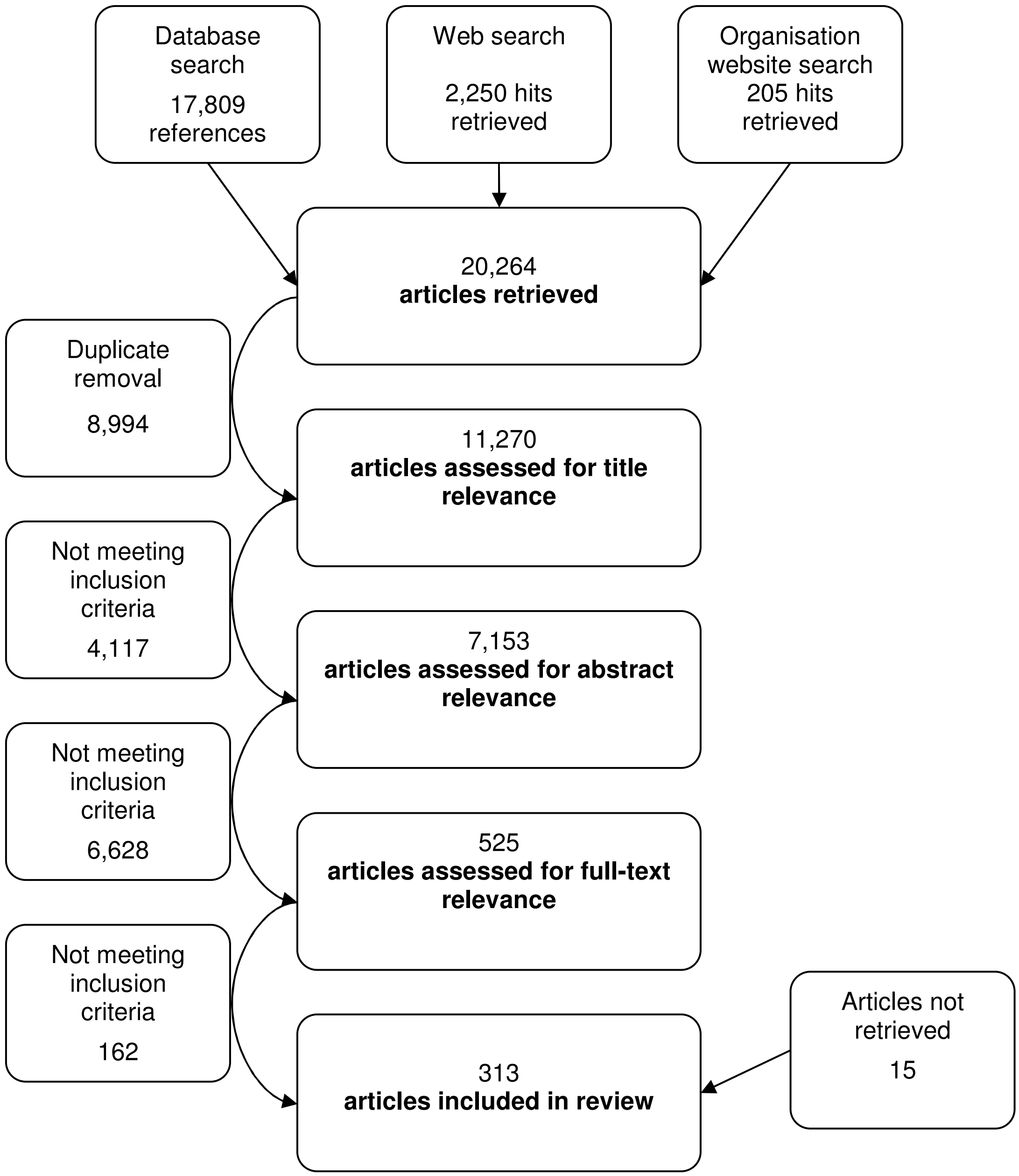


**Figure 1**. The number of studies remaining at each stage of the selection process.

### 3.3 Study characterisation & organisation into pools

The 313 articles remaining after full-text assessment varied greatly, both in terms of the landscape feature tested and the way the outcome was measured. To assist synthesis they were further organised by division into pools (Figure 2). Studies in each pool addressed similar questions and had similar experimental design.

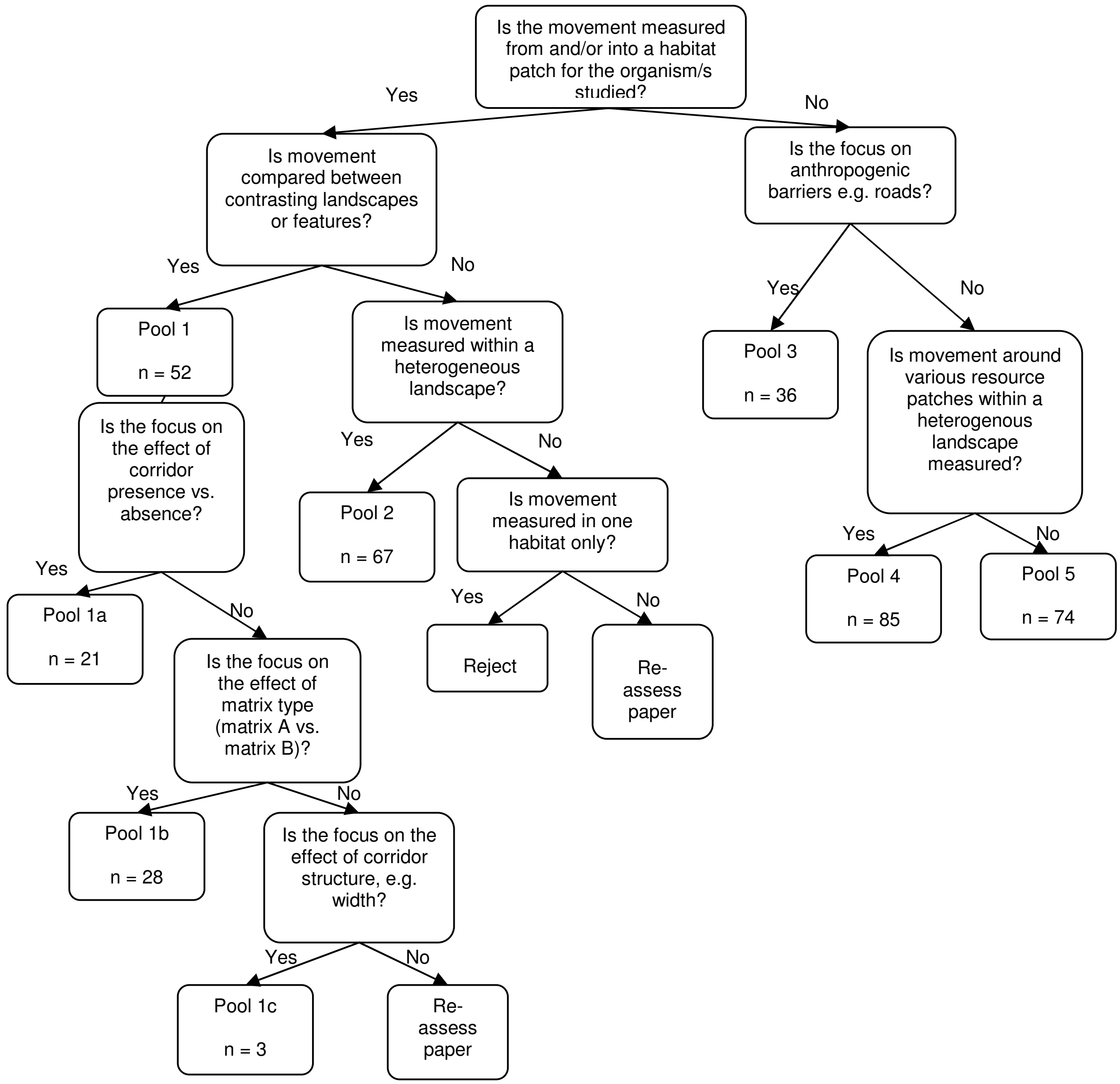


**Figure 2**. Criteria for the division of studies accepted at the full text stage into pools.

Pool 1 *Direct comparisons*: Comprised studies providing explicit, direct comparisons of movement to or from patches (i.e. emigration or immigration) including two (or more) different matrix elements. This pool is one of the most amenable to meta-analysis due to the control of confounding factors. To reflect the heterogeneity in study focus within this relatively broad category, pool 1 was further divided into:

- **1a**: Corridor presence/absence (note: a corridor in this project was defined as a linear element of the same vegetation type as the habitat patch (see glossary) and *not capable of supporting a breeding population according to the study text*)

- **1b**: Two kinds of matrix
- **1c**: Two kinds of corridor, e.g. narrow/wide or continuous / discontinuous.

Pool 2 *Interpatch movement*: Consisted of studies of movement to or from patches in heterogeneous landscapes. These included, for example, mark-recapture studies relating the number of individuals moving between patches to matrix composition in agricultural-forest mosaics.

Pool 3 *Anthropogenic barrier features*: Comprised studies of movement rates across anthropogenic barriers (predominantly roads) where at least two types of barrier or two types of crossing are compared. These were separated out into an individual pool because they have a potentially valuable practical application to the UK where the road density is high.

Pool 4 *Movement around complex landscapes*: Comprised studies of movement (especially home-range movement) without a specific 'home' habitat patch being defined, and where species utilise a range of patches in a landscape.

Pool 5 *The remainder*: Comprised those remaining studies that passed the inclusion criteria but did not fit into any of the above pools, e.g. studies of patch-edge shape, speed of movement, and movement compared between habitat patches and one matrix type.

Note: where single articles reported two different datasets, each dataset was included in the most appropriate pool.

### 3.4 Analyses

The pools of data were examined to assess which would be most suitable for meta-analysis. Two subsets of Pool 1 were selected (direct comparisons of corridors and of matrix types) as they contained many papers measuring similar outcomes in a relatively controlled manner. The results of the meta-analyses are in Section 4.

As only a small subset of data testing two kinds of landscape features were meta-analysed, qualitative tabulation and descriptive analyses were also used (Section 5) to explore the data in all pools for UK species.

# 4. Quantitative meta-analysis

Meta-analysis is a statistical technique used to integrate and summarise the results from individual studies within a systematic review providing greater statistical power, and to examine why different studies produce different results.

Of the seven pools of studies accepted at full-text assessment, pools 1a (corridors) and 1b (matrix comparisons, see Figure 2 for details of pooling) contained a large number of studies with relatively consistent experimental strategies (21 and 28 studies respectively) and were used to address the following questions:

Pool 1a: What is the impact of the presence of a corridor on movement?

Pool 1b: What is the impact of different matrix types on movement?

These studies estimated dispersal using different measures such as dispersal distance, number of individuals leaving the patch, and time taken to leave the patch. However, the number of individuals making a successful movement between patches was a larger subset and considered meaningful to the objectives of the review. Meta-analyses comparing successful inter-patch movement rates were performed separately for data on the impact of corridor presence/absence (Pool 1a) and direct comparisons of two matrix types (Pool 1b).

## 4.1 Meta-analytical methods

### *4.1.1 Data extraction*

Data from those studies in Pools 1a and 1b which contained successful inter-patch movement rates were extracted into a spreadsheet. In some cases, data were extracted by multiplication of proportions shown in graphs with numbers of individuals in the experiment (see Appendix 4 for details). Where it was not possible to extract data, authors were contacted with a request to provide missing information.

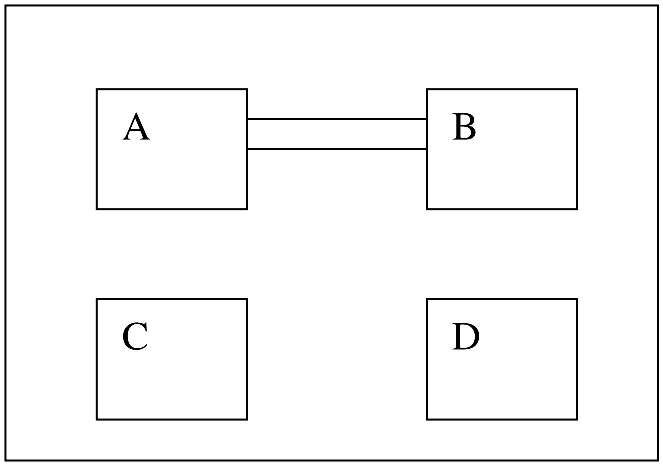


**Figure 3**. Conceptual diagram of experimental design of studies in pool 1a

Corridor data were extracted from 10 studies in pool 1a. Multiple non-independent data points were extracted from the same study where:

- more than one species or subspecies was examined (Haddad, 1999; Andreassen & Ims, 2001; Haddad & Tewkesbury, 2005).
- sexes were separated (Davis-Born & Wolff, 2000; Andreassen & Ims, 2001).
- different matrix habitats or inter-patch distances were used (Haddad 1999, Haddad *et al.*, 2003; Baum *et al.*, 2004).

Zero values for movement rates were substituted with one in two instances for one study (Haddad 1999) to permit calculation of the risk ratio (Lipsey & Wilson, 2001). A further data point was excluded as the movement rate was zero in both treatment and control (Haddad 1999). The data extraction and study characteristics are described in detail in Appendix 4.

Matrix-matrix comparison data were extracted from 7 studies in pool 1b. Multiple non-independent data points were extracted from the same study where:

- more than one species was examined (Desrochers & Hannon, 1997)
- more than two types of matrix habitat were compared (Desrochers & Hannon, 1997; Haynes & Cronin, 2003; Russell *et al.*, 2007).

Twelve movement rates were manipulated by adjusting the treatment event rates to one in one study (Desrochers *et al.,* 1997) to allow calculation of the risk ratio. The data extraction and study characteristics are described in detail in Appendix 4.

In the matrix comparison analysis, matrix types were classified as 'more favourable' or 'less favourable'. This was decided using the classification by the author of each study. In all but one case the assumed more favourable type was the most structurally similar matrix type to the habitat, the exception (Goodwin & Fahrig, 2000) being more ambiguous.[4]

[4] Habitat was tall herbaceous goldenrod vegetation, the 'favourable' matrix was mown goldenrod stems and the 'unfavourable' matrix was camouflage netting over the mown stems intended to impede the movement of goldenrod beetles in a similar manner to dense vegetation

**Table 1**. Studies included in the meta-analysis with experimental designs.

| **Pool 1a – Corridor** | | | | | | |
|---|---|---|---|---|---|---|
| Study | Subject | Patch habitat | Corridor / favourable matrix | No corridor / unfavourable matrix | Inter-patch distance | Location & landscape (* denotes experimentally created) |
| Aars & Ims (1999) | *Microtus oeconomus* | long grass | long grass | bare ground | 50m | Evenstad, Norway * |
| Andreassen & Ims (2001) | *Microtus oeconomus*:<br>males Southern<br>males Northern<br>Females Southern<br>Females Northern | long grass | long grass | short grass | 15m | Evenstad, Norway * |
| Baum *et al.* (2004) | *Prokelisia crocea* | cord grass | cord grass | brome grass | 2m | North Dakota, USA* |
| | | cord grass | cord grass | mud | 2m | |
| Bowne *et al.* (1999) | *Sigmodon hispidus* | clear-cuts | clear-cuts | pine forest | 64 - 256m | Savannah River, USA * |
| Coffman *et al.* (2001) | *Microtus pennsylvanicus* | old field | old field | bare ground | 7.6m | PWRC, USA * |
| Danielson & Hubbard (2000) | *Peromyscus polionotus* | | | | | Savannah River, USA * |
| Davis-Born & Wolff (2000) | *Microtus canicaudus*, males | alfalfa | alfalfa | bare ground | 1m | Hislop, USA * |
| | Females | alfalfa | alfalfa | bare ground | 1m | " |
| Haddad (1999) | *Junonia coenia,* A2 | clear-cuts | clear-cuts | pine forest | 256m | Savannah River, USA * |
| | A4 | clear-cuts | clear-cuts | pine forest | 128m | " |
| | *Euptoienia claudia* A2 | clear-cuts | clear-cuts | pine forest | 256m | " |
| | A4 | clear-cuts | clear-cuts | pine forest | 128m | " |
| Haddad *et al.* (2003) | *Xylocopa virginica* | clear-cuts | clear-cuts | pine forest | 64m | " |
| | | clear-cuts | clear-cuts | pine forest | 384m | " |
| Haddad & Tewksbury (2005) | *Junonia coenia* 2000<br>2001 | | | | | |
| | *Euptoienia claudia* 2000 | clear-cuts | clear-cuts | pine forest | 150m | " |
| | 2001 | clear-cuts | clear-cuts | pine forest | 150m | " |

| Pool 1b – Direct comparison of two matrix types | | | | | | |
|---|---|---|---|---|---|---|
| Study | Subject | Patch habitat | Corridor / favourable matrix | No corridor / unfavourable matrix | Inter-patch distance | Location & landscape (* denotes experimentally created) |
| Baum *et al.* (2004) | *Prokelisia crocea* | cord grass | brome grass | mud | 2m | North Dakota, USA* |
| Bhattacharya *et al.* (2003) | Bumblebees, *Bombus* spp. | sweet pepper bush plants | forest | forest plus road | 40-70m | Webster, USA |
| Desrochers & Hannon (1997) | *Dendroica coronata* | Woodland | clear-cut | field | 45m | Quebec region, Canada |
| | *Dendroica coronata* | Woodland | clear-cut | road | 12m | |
| | *Dendroica stricta* | Woodland | clear-cut | road | 20m | |
| | *Parus atricapillus* | Woodland | clear-cut | road | 10-16m mean 12.4 | |
| | *Parus atricapillus* | Woodland | clear-cut | field | 10-22m mean 14.4 | |
| | *Parus hudsonicus* | Woodland | clear-cut | road | 17.5m | |
| | *Regulus calendula* | Woodland | clear-cut | road | 7 - 15 m mean 11.9 | |
| | *Sitta canadensis* | Woodland | clear-cut | field | 10 - 48 m mean 23.9 | |
| Goodwin & Fahrig (2002) | *Trirhabda borealis* | Goldenrod | cut vegetation | camouflage netting | 5m | Oldfield, Ottawa, Canada * |
| Haynes & Cronin (2003) | *Prokelisia crocea* | | | | 3m | North Dakota, USA* |
| | | | | | 3m | |
| | | | | | 3m | |
| Russell *et al.* (2007) | *Microtus pennsylvanicus* | uncut grass | 35-75cm grass | 5cm grass or bare ground | 4m | Purdue Wildlife Area, USA* |
| | | uncut grass | 30cm cut grass | 5cm cut grass | 4m | |
| Schaefer *et al.* (2003) | *Percina pantherina* | Pool | riffle | road culvert | | Glover River, USA |

*4.1.2 Meta-analytical calculations*

Comparative movement rates for each species from each study were converted to risk ratios (’risk’ defined as successful inter-patch movement of an individual). Risk ratios were calculated by comparing numbers of individuals in patch A which migrated to patch B with the number of individuals in patch C which migrated to patch D (Figure 3). The same procedures were used to derive risk ratios regarding movement through more and less favourable matrix types. **If there is no difference between connected and unconnected patches the risk ratio will be one. If the chance of movement is reduced by corridors or less favourable matrix, the risk ratio will be less than one; if it increases the chance of individual movement, the risk ratio will be bigger than one.**

Risk ratios describe the multiplication of the risk that occurs in the experimental group relative to the control group. For example, a risk ratio of 3 for a treatment implies that events with treatment are three times more likely than events without treatment. Risk ratios are not intuitively straightforward to interpret for ecologists but ‘number needed to treat’ (NNT) can be used to illustrate both clinical and ecological significance. NNT is defined as the expected number of individuals who need to receive the experimental rather than the comparator intervention for one additional individual to either incur (or avoid) an event in a given time frame.

Calculated risk ratios were pooled across studies to generate an overall weighted average risk ratio in a random effects model (DerSimonian & Laird, 1986) with the estimate of heterogeneity (variation in risk among studies) being taken from the Mantel-Haenszel model. Weighting was by inverse variance, the standard weighting in meta-analysis, so studies with more information (lower variance) are given higher weights in the analysis than studies with less information (higher variance).

*Exploration of heterogeneity*

A primary reason for undertaking meta-analyses was to quantify variation in the magnitude of the effect of the landscape feature and to explore possible reasons for outcome heterogeneity. Subgroup analysis was undertaken, which separates and repeats analyses for subsets of the data, to compare the results for rodents from insects (corridor analysis only). Meta-regression was used to investigate the relationship between impact of inter patch distance (both analyses) and experiment duration (Sharp, 1998; Thompson & Sharp, 1999) on the size of the effect of the landscape feature on movement. These analyses were performed univariately (i.e. one variable at a time) as data was only available for different subsets of data and missing data accounted for <10% of the dataset (Schafer, 1997). Further co-variates of interest (e.g. age and sex of individuals) were not examined due to missing data and small sample sizes.

*Robustness of analyses*

Meta-analysis can be very sensitive to apparently innocuous assumptions such as choice of effect size metric (in this case, risk ratio), aggregation and quasi-replication (the use of non-independent data points from the same study; Higgins & Spiegelhalter, 2002). Sensitivity analyses were carried out by comparing the risk ratios to odds ratios, to investigate whether choice of effect size metric was critical to the conclusions of the meta-analysis. Sensitivity analysis was also used to examine ecological bias arising from aggregation of multiple points within a study and quasi-replication arising from disaggregation of multiple species from one study. Multiple points were disaggregated to explore reasons for variation between them, but were also aggregated because separate data points from the same study are not independent of each other. The presence of publication bias was investigated by means of a funnel plot (Sterne, 2001). Cochran's Q tests were used to examine heterogeneity among effect sizes. Statistical analyses were performed using Stata 8.2 (StataCorp, College Station, Texas).

## 4.2 Results

### *4.2.1 Corridor meta-analysis results*

The pooled risk ratio for disaggregated data is 1.598 (95% CI 1.066 to 1.125) indicating that individuals are more likely to move between patches connected by a corridor than between patches without a corridor (Figure 4). (*If there is no difference between connected and unconnected patches the risk ratio will be one. If the chance of movement is reduced by corridors or less favourable matrix, the risk ratio will be less than one; if it increases the chance of individual movement, the risk ratio will be bigger than one*). The pooled confidence interval does not cross the line of "no effect" indicating that the overall pooled effect is statistically significant ($p < 0.006$). Number needed to treat (NNT) indicates that overall one additional individual will successfully move between patches for every 15 animals in habitat patches connected by a corridor compared to unconnected habitat.

There is significant variation between the individual data points (Cochran's Q = 276.92, d.f. = 20, $p < 0.001$) indicating that populations do not have a uniform response to corridors.

There is a weak positive correlation between risk ratio and corridor length (meta-regression coefficient 0.0069, z = 2.56, n = 18, $p < 0.012$; Figure 5) although experiment duration is not related to risk ratio (meta-regression coefficient 0.0019, z = 0.55, n = 12, $p < 0.58$). Variation in the effect of corridors is related to taxon with insects more likely to increase movement in corridors than rodents (pooled RR rodents 1.068 (95% CI 0.923 to 1.237) $p < 0.371$, Figure 6; pooled RR insects 2.37 (95% CI 2.097 to 2.680) $p < 0.001$, Figure 7). Taxon and corridor length were confounded (rodents range 1 m – 256 m, median 15, insects range 2 m – 384 m, median 139) and there are too few data points to separate the effects. There is also variation between sexes and races (although confidence intervals overlap) but small samples sizes prevented further investigation of these factors (Figure 4).

The pooled odds ratio (odds ratios compare how likely an event is between two groups) and risk difference (risk difference compares the risk in terms of an absolute difference, rather than in relative terms) were similarly positive, statistically significant with variation between individual data points suggesting that choice of effect size metric is not critical. Controlling for quasi-replication by aggregating data within studies increased the magnitude of the pooled effect and decreased the statistical significance, although it remained above the 0.05 threshold (pooled RR 1.646, 95%CI 1.037 to 2.612) $p < 0.034$, Figure 8).

The relationship between risk ratio and precision was examined using disaggregated data, to assess the potential for publication bias. Small sample size hinders the interpretation of the funnel plot but there is no compelling evidence of funnel plot asymmetry and therefore of publication bias (Figure 9).

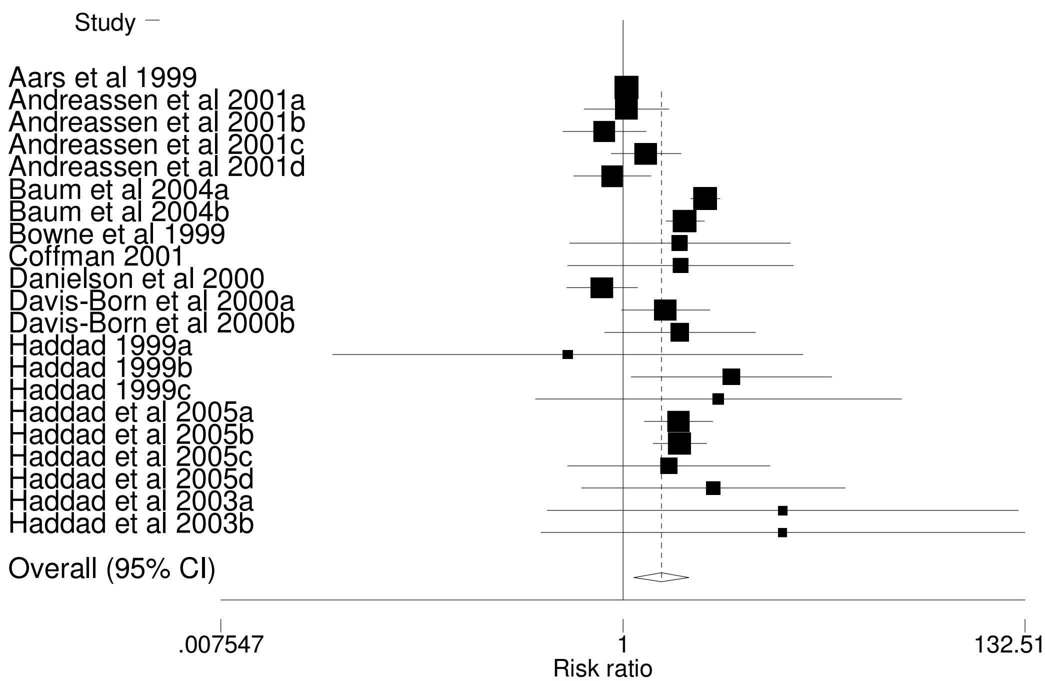


**Figure 4**. Risk ratios for comparing individual movement between patches with and without corridors. Solid boxes represent data points with the size of the box proportional to sample size. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches in a corridor than across matrix. Letters indicate multiple data points from the same study.

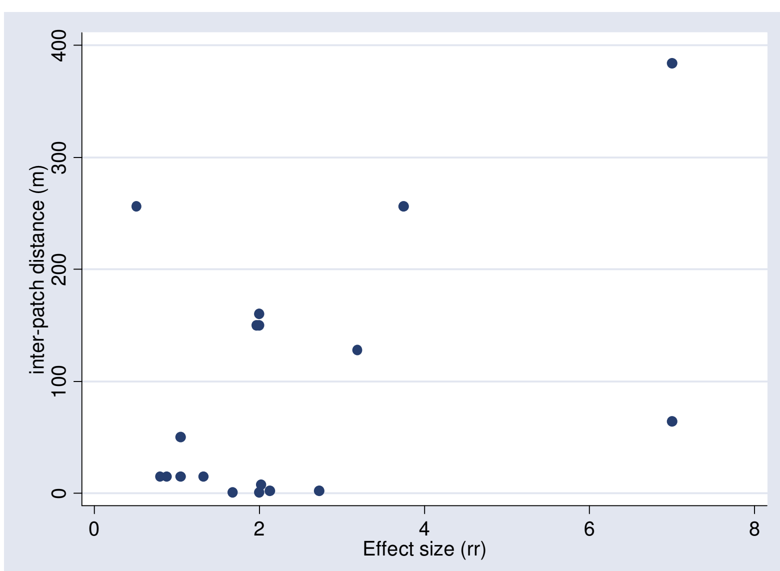


**Figure 5**. Relationship between corridor length and risk ratio based on disaggregated data.

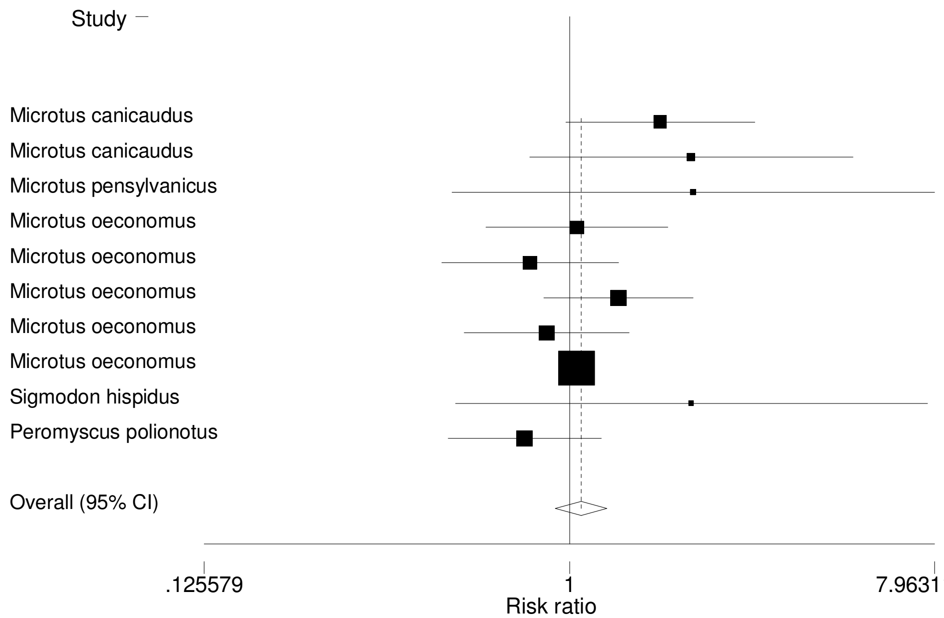


**Figure 6**. Risk ratios for the rodent subgroup in the corridor analysis. Solid boxes represent data points. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches in a corridor than across matrix.

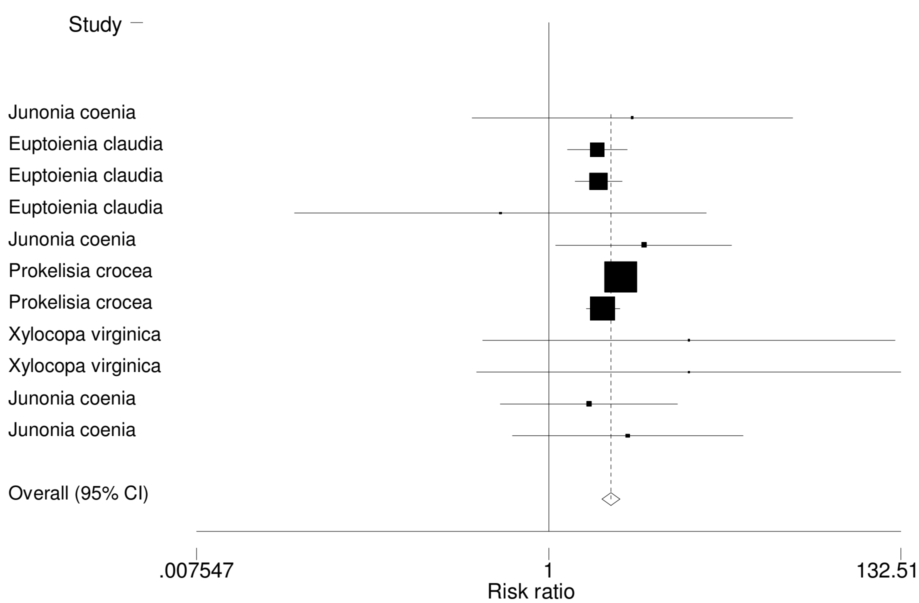


**Figure 7**. Risk ratios for the insect subgroup in the corridor analysis. Solid boxes represent data points. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches with a corridor than without a corridor.

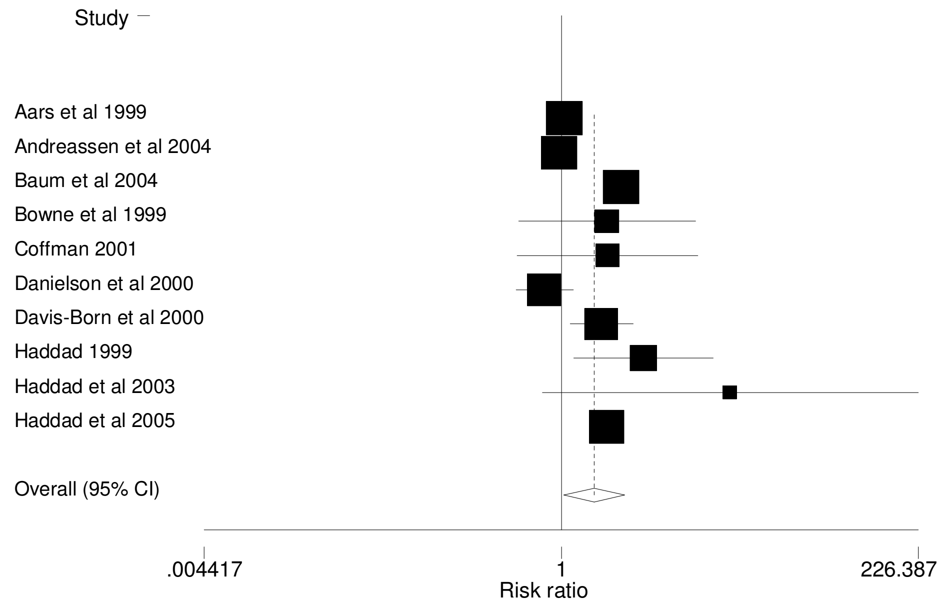


**Figure 8**. Risk ratios for corridor data aggregated within independent studies. Solid boxes represent data points. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches with a corridor than without a corridor.

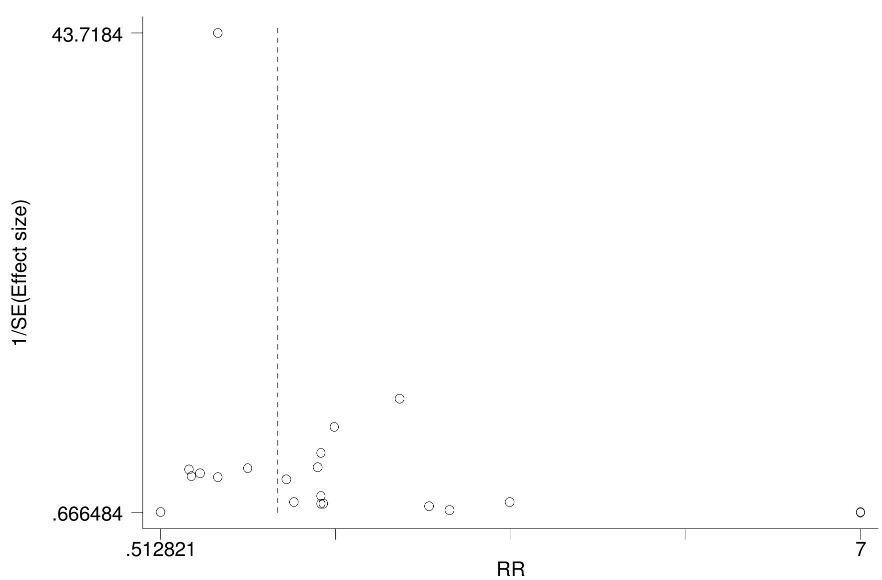


**Figure 9**. Funnel plot of data points included in the corridor meta-analysis. This shows the inverse variance of the risk ratios in relation to the magnitude of the risk ratio (RR). Negative studies including a large study are present (although small positive studies are more numerous) suggesting that the pooled effect is not distorted by publication bias. The hatched line represents the pooled effect (risk ratio = 1.598).

*4.2.2. Matrix-matrix comparison meta-analysis results*

The pooled risk ratio for disaggregated data is 1.336 (95% CI 1.075 to 1.661) indicating that individuals are more likely to move between patches across favourable than unfavourable matrix (Figure 10). The pooled confidence interval does not cross the line of "no effect" (where risk ratio equals one) indicating that the overall pooled effect is statistically significant ($p < 0.009$). Number needed to treat (NNT) indicates that overall one additional individual will successfully move between patches for every 96 individuals in more favourable matrix habitat compared to less favourable matrix habitat.

As expected there is significant variation between the individual data points (Cochran's Q = 229.50, d.f. = 17, $p < 0.001$) indicating that populations do not have a uniform response to matrix composition.

There was a weak negative correlation between risk ratio and inter-patch distance (meta-regression coefficient -0.0261, z = 2.84, n = 17, $p < 0.004$, Figure 11) although experiment duration was not related to risk ratio (meta-regression coefficient -0.0011, z = 0.76, n = 18, $p < 0.448$). This variation could not be explored in relation to taxon as one study concerns rodents (Russell *et al.*, 2007), one fish (Schaefer *et al.*, 2003) one birds (Desrochers & Hannon, 1997) leaving only 4 studies regarding insects (Baum *et al.*, 2004; Bhattacharya *et al.*, 2003; Goodwin & Fahrig, 2002; Haynes & Cronin, 2003; Figure 12).

The pooled odds ratio (odds ratios compare how likely an event is between two groups) was similarly positive and statistically significant, suggesting that choice of relative effect size metric was not critical.

Controlling for quasi-replication by aggregating data within studies increased the magnitude of the pooled effect but decreased the statistical significance although it remains above the 0.05 threshold (pooled RR 1.438, 95%CI 1.009 to 2.05, $p < 0.044$; Figure 13). A further sensitivity analysis was performed eliminating the data from Desrochers & Hannon (1997) where data had been imputed (zeros substituted by ones) for the disaggregated analysis. The pooled effect remained positive and significant ($p = 0.05$). Although a random effects model was used, the relationship between risk ratio and precision was explored using disaggregated data, to assess the potential for publication bias. Small sample size hinders the interpretation of the funnel plot but there is no compelling evidence of funnel plot asymmetry and therefore of publication bias (Figure 14).

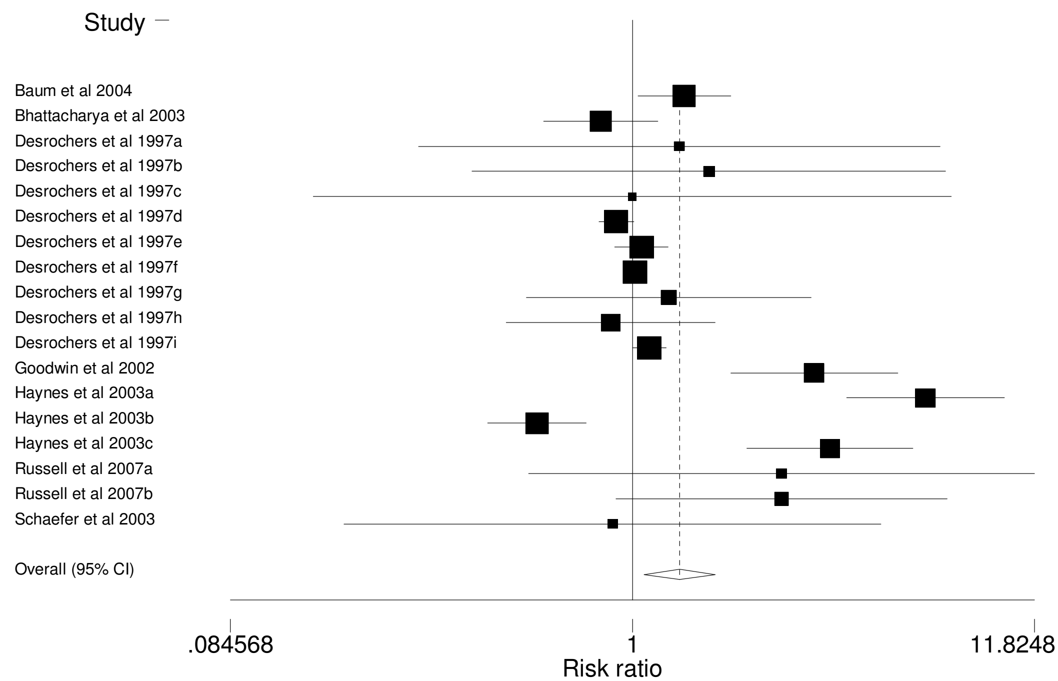


**Figure 10**. Risk ratios for comparing individual movement between patches separated by more favourable or less favourable matrix. Solid boxes represent data points. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line marks the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches with more favourable matrix than with less favourable. Letters indicate multiple data points from the same study.

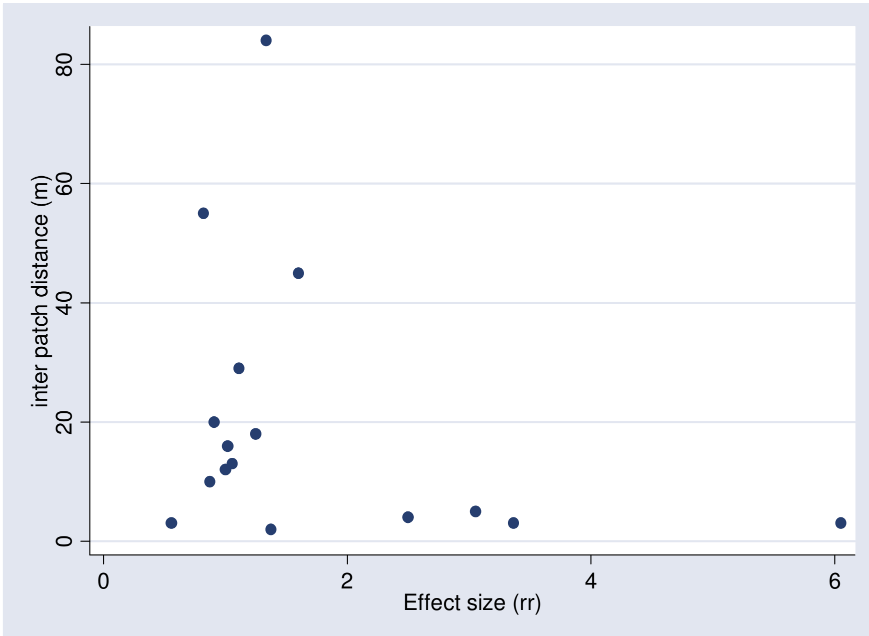


**Figure 11.** The relationship between inter-patch distance and risk ratio (within pool 1b: direct matrix comparisons) based on disaggregated data.

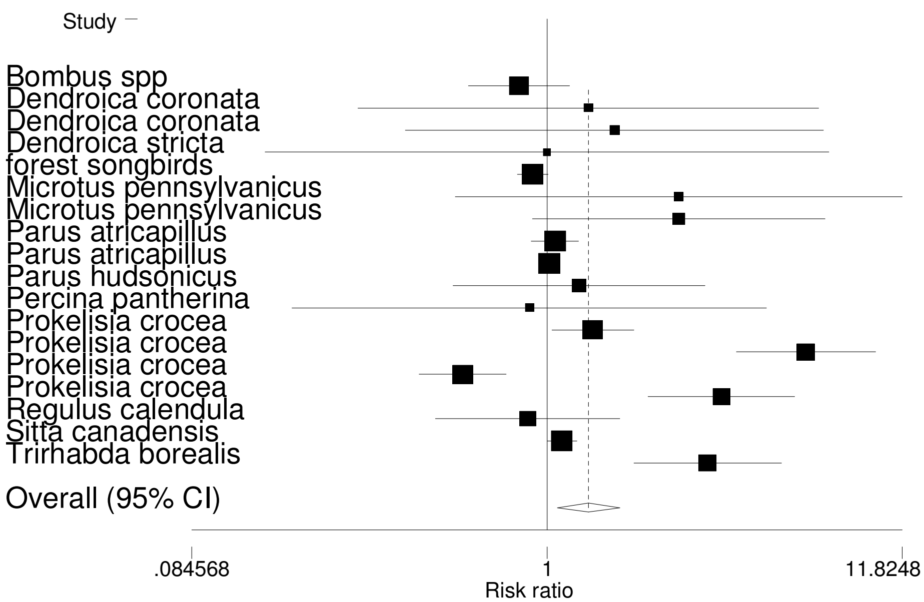


**Figure 12.** Figure 10 expressed by species. (Risk ratios for comparing individual movement between patches separated by more favourable or less favourable matrix). Solid boxes represent data points. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line marks the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches with more favourable matrix than with less favourable).

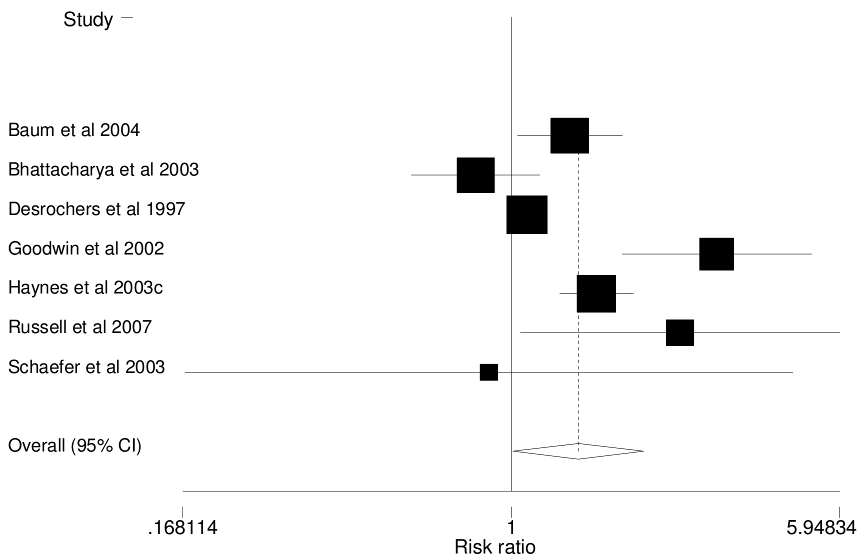


**Figure 13**. Risk ratios for comparing individual movement between patches separated by more favourable or less favourable matrix, aggregated into each study (c.f. Figure 10 where studies were divided by species). Solid boxes represent data points. Horizontal lines are 95% confidence intervals. The solid vertical line marks the line of no effect (risk ratio = 1) and the dashed vertical line marks the mean risk ratio. Where the risk ratio is > 1 the species is more likely to move between patches with more favourable matrix than with less favourable.

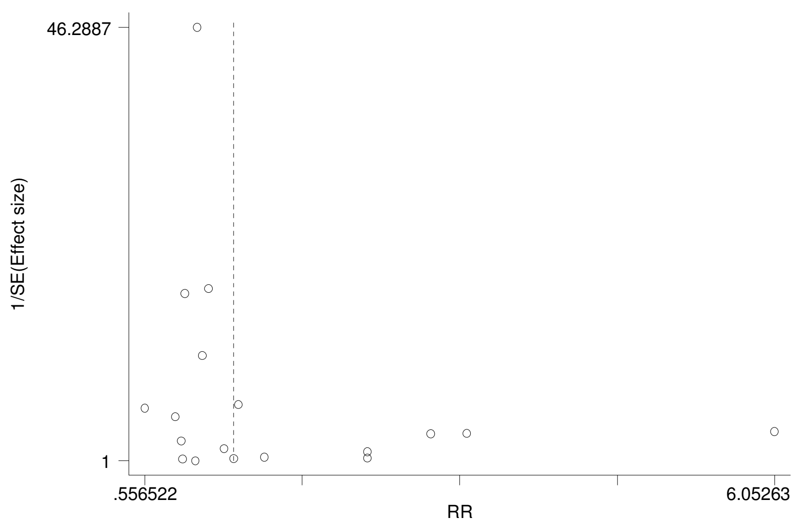


**Figure 14**. Funnel plot of studies directly comparing inter-patch movement between matrix types, showing inverse variance of the risk ratios in relation to the magnitude of the risk ratio (RR). Negative studies (including large studies) are more numerous than positive studies suggesting that the pooled effect is not distorted by positive publication bias. The hatched line represents the pooled effect (risk ratio = 1.336).

### 4.3 Summary of meta-analyses

There is evidence from the first meta-analysis that corridors facilitate movement. The evidence comes from a limited range of studies on winged insects (butterflies, planthoppers and bees) and rodents performed in simplified experimental landscapes, which allowed an explicit comparison of inter-patch movement with and without a corridor. These studies show the potential impact of corridors on movement but do not demonstrate the relative importance of these landscape features to other factors that may be present in more complex landscapes. Much heterogeneity related both to species attributes (e.g. age, sex) and landscape features remains unexplained.

The meta-analysis was robust to decisions on the methodology of the analysis (choice of effect size metric, aggregation, and quasireplication) and there was no evidence of publication bias. There is therefore reasonable evidence that corridors facilitate inter-patch movement although variation in effectiveness and the general applicability of results are not fully understood.

The second analysis examined studies in which different pairs of suitable habitat patches were separated by different matrix types, e.g. grass compared to bare ground. There is evidence that matrix type influences movement of individuals, with greater movement through habitat more structurally similar to the organism's habitat patches. The effect, while significant, is however very small (less than one in 90). This evidence comes from eight studies on a wider range of taxa over up to 160 m and four of the studies were performed in simplified experimental landscapes.

Comparing the risk ratios and NNT values of the two meta-analyses, corridor and matrix, is not appropriate as the two sets of studies are not comparable. Spatial scales, taxa included, and durations all varied. It also remains unknown if the observed magnitude of the increase would have a significant impact on populations.

# 5. Qualitative synthesis of studies on UK species

## 5.1 Introduction

Qualitative assessment can be used to complement quantitative analyses within systematic review. In this study, such an approach was used to consider a broader set of topics than were possible through meta-analysis within the time available. Qualitative analysis is used in this section to examine the effects of different matrix features on the movement of species currently present in the wild in the UK. Available information was summarised by habitat type and landscape feature. The synthesis was based on outcomes as reported by authors; unlike meta-analysis, therefore, this qualitative synthesis does not consider effect sizes nor is there an assessment of study quality.

The work aimed to:

i. Exploit pools of literature measuring common outcomes to supplement the meta-analyses and to highlight potential for future analysis.
ii. Examine the spatial and temporal scales of evidence.
iii. Provide a preliminary synthesis by landscape features

This section starts with a characterisation of the pool of included studies with particular reference to scale. The second sub-section characterises the species used in included studies, partly to aid species-based decision making and partly to show the boundaries of the evidence base. Finally, the available information is summarised by habitat type and landscape feature.

Of the 313 studies accepted at full-text, 67 included UK species. Each study was separately summarised including species information (e.g. conservation designation, common name), experimental design (including scale and replication) and reported outcome. The tables are large and so are included in Appendix 2. Table 1 summarises the numbers of studies by pool (see Figure 2 in Section 4 for details of pooling) and by taxonomic group. Study pool (which was based on experimental strategy) and taxonomic group were related (contingency coefficient 0.768, $p < 0.001$) with pool 1b dominated by birds, and pool 2 dominated by butterflies and moths.

There are dangers with qualitative synthesis and tabulation, in particular the temptation to vote count (simply contrasting the number of studies that do or do not show an effect of interest). This introduces subjectivity that the systematic method seeks to avoid and can cause two problems. First, problems occur if subjective decisions or statistical significance are used to define ‘positive’ and ‘negative’ studies (Cooper & Rosenthal, 1980; Antman *et al.*, 1992); statistical significance is affected by both effect size and sample size. Second, unlike meta-analysis, vote counting does not give differential weights to each study and hence does not take into account the variation in the reliability of information each study provides. Vote counting is therefore only used in evidence-based frameworks in situations when standard meta-analytical methods cannot be applied (due to limitations of data or resource). Inclusion of critical appraisal is strongly advocated as part of vote counting and methods for presenting such syntheses are currently under development (Ogilvie *et al.* 2008). Here qualitative analysis (including vote counting) was used to address the breadth of the project objectives and to provide preliminary insights in topic areas where further research may be merited.

## 5.2 Scale

A key objective of this project was to look at spatial and temporal scales of evidence. Scale is a critical factor in the design of ecological networks (Jongman & Pungetti, 2004; Tischendorf & Fahrig, 2000) and may go some way to explaining reported outcomes as indicated in section 4.2 for corridors. However, it is important to avoid confusion between the scale of a study and a species dispersal distance (Franzen & Nilsson, 2007), here we describe the range of scales over which the studies were conducted with *no implication that these are actual dispersal distances or times*.

The longest study retrieved involving UK species was over five years (Berggren *et al.*, 2001), the median 22 days and in the shortest study each experiment lasted only two minutes (Stevens *et al.*, 2004; Table 2). The range in temporal scale is in many cases explained by the purpose of the study – many of the short scale studies (Stevens *et al.*, 2004; Rühe, 1999; St Clair, 2003) examine behaviour at boundaries and are not intended to look at inter-patch movements. Experimental or methodological issues may also impact upon temporal scale; for example, five of the seven studies longer than one year were radio-tracking studies, using mammals (particularly deer) as these are large enough to carry radio transmitters with longer-life batteries.

The largest spatial scale was reported in a large mammal tracking study covering 15,800 $km^2$ (Frair *et al.* 2005). Excluding such large mammal tracking studies (pool 4) the largest spatial scale was Poysa & Paasivaara's (2006) study of goldeneye ducks which used re-sighting of bird rings over 75$km^2$. The median size was 45 hectares. The smallest spatial scale was Stevens *et al.*, (2004) using 0.03 $m^2$ arenas to study how fast natterjack toads move over different surfaces. The six smallest studies were all experimental arenas 0.03 $m^2$ – 16 $m^2$, and the smallest study in a 'natural' landscape was 560 $m^2$ (Hofe & Gerstmeier, 2001) with no studies of intermediate size. Spatial scale of studies may to some extent be related to the body size and dispersal distance of organisms (not tested in this project), though less so for the experimental arenas. Dispersal studies are often smaller than they need to be to capture intermediate distance dispersal events (Franzen & Nilsson, 2007).

Studies over larger areas tended to be of longer duration (where this information was provided, in 56 of the 67 studies; Spearman rho = 0.540, $p < 0.001$). However, this correlation is not significant if controlled for either taxonomic group (Figure 15) or pool, bearing in mind that taxonomic group and pool are confounded. The spatial scale was significantly affected by pool and taxonomic group, and the temporal scale was significantly affected by pool but not by taxonomic group (Kruskall-Wallis, pool $\chi^2_5 = 14.99$, $p = 0.010$; taxonomic group $\chi^2_8 = 8.31$, $p = 0.404$). With the exception of Rühe (1999), herbivorous mammals were studied at the largest temporal and spatial scale (Figure 15). Studies in pool 4 also included the largest spatial and temporal scale (pool 4 being dominated by large herbivore studies).

**Table 2.** The temporal and spatial ranges of studies by taxonomic group and by pool.

| | | Temporal range | Spatial range |
|---|---|---|---|
| Taxonomic group | 1. Carnivorous mammals excluding rodents | 4 - 120 days | <1 - 2600ha |
| | 2. Herbivorous mammals excluding rodents | 5 minutes - 4 years | <1ha - 15800km$^2$ |
| | 3. Rodents | 7 hours – 3 years | 750m$^2$ - 2km$^2$ |
| | 4. Birds | 6 minutes - 4 years | 4ha - 75km$^2$ |
| | 5. Fish | 100 days - 1 year | 607m - 97km |
| | 6. Reptiles | - | - |
| | 7. Amphibians | 2 minutes - 9 months | 0.03m$^2$ - 4km$^2$ |
| | 8. Butterflies and moths | 1 hour - 2.5 months | 3600m$^2$ - 1.9km$^2$ |
| | 9. Other flighted invertebrates | 1.3 - 60 days | 16m$^2$ - 6km$^2$ |
| | 10. Flightless terrestrial invertebrates | 1 hour - 6 months | 4m$^2$ - 350ha |
| | 11. Freshwater invertebrates | 56 days | 0.5km |
| Pool | 1a Corridor presence/absence | 5 hours ( 1 study) | 67m$^2$ |
| | 1b Direct comparisons of 2 matrix types | 6 minutes - 3 months | 16m$^2$ - 67ha |
| | 1c Corridor structure | - | - |
| | 2 Inter-patch movement in heterogeneous landscape | 6 hours – 5 years | 185m$^2$ - 75km$^2$ |
| | 3 The effects of barriers and barrier crossings | 3 - 120 days | <1 ha - 3 ha |
| | 4 Movement around resource patches | 5 minutes - 4 years | 10 ha - 1580km$^2$ |
| | 5 Remainder | 2 minutes - 4 years | 0.03m$^2$ - 6km$^2$ |

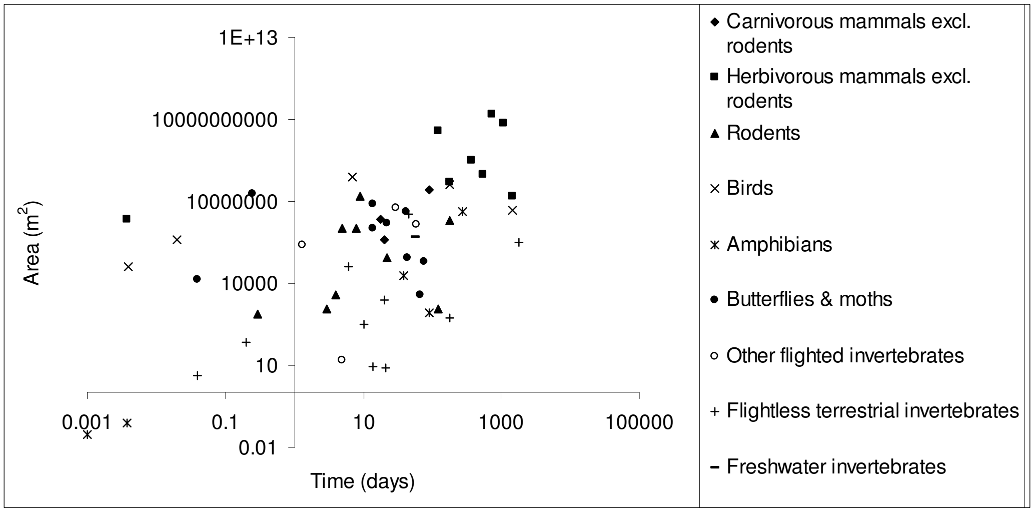


**Figure 15**. The relationship between the temporal and spatial scale of studies, split by taxonomic group, for the 56 studies where this information could be extracted from the article.

## 5.3 Species

Studies remaining after the application of the inclusion criteria included only animals.

The taxonomic group with the greatest number of studies was butterflies and moths (Lepidoptera; Table 4). This may reflect the ease with which butterflies can be observed in the field. Similarly, carabid beetles and crickets were commonly studied as they are easily marked. Among the mammals, rodents were widely studied, as they are easy to keep in experimental populations. Many groups (for example freshwater invertebrates) appear under-investigated. There were no studies retrieved on UK reptiles despite most being BAP priority species, and in the case of smooth snakes and sand lizards also being protected at a European level.

Studies concerning carnivorous mammals included those on the use of road crossings (Veenbaas & Brandjes,1998; Clevenger *et al.*, 2001) and also home-range studies that showed use of linear features for movement by foxes (MacDonald *et al.*, 2004) and weasels (Frey & Conover, 2006). Studies concerning non-rodent herbivorous mammals are dominated by radio-tracking studies of species utilising complex resource mosaics (e. g. forage, cover, and seasonal pasture in deer; Forester *et al.*, 2007).

Fish were included in three studies (Lucas & Batley, 1996; Mellina *et al.*, 2005; Carlsson *et al.,* 2004); each study was very different and none provided a controlled test of two different matrix features. The closest to a controlled test was Lucas & Batley (1996) who reported that Barbel (a European protected species) movement is limited by boulder, concrete and flow gauge dams. This was also the only fish study carried out in the UK.

Some studies contain data from more than one taxon or more than one pool – each species in each study made 1 ‘data point’ for the purposes of this review. Seventy-three data points out of 149 represented species associated with woodland, 30 points represented species associated with grassland, 12 represented species associated with ponds and waterways and two heathland, as well as mosaic species and those associated with specific tall herbs.

The 18 BAP priority species and nine non-native species included in this section are listed in Table 3. The numbers of studies including BAP species, by pool and taxonomic group, are summarised in Table 5.

**Table 3.** List of BAP priority species and non-native UK species included in papers subject to qualitative analysis.

| BAP priority species | Study |
|---|---|
| *Arvicola terrestris* (Water vole) | Veenbaas & Brandjes (1998) |
| *Asilus crabroniformis* (Hornet robberfly) | Holloway *et al.* (2003) |
| *Bufo calamita* (Natterjack toad) | Miaud & Sanuy (2005), Stevens *et al.* (2004), Stevens *et al.* (2006) |
| *Chrysolina graminis* (Tansy beetle) | Chapman *et al.* (2007) |
| *Emberiza schoeniclus* (Reed bunting) | Bellamy & Hinsley (2005) |
| *Erinaceus europaeus* (Hedgehog) | Doncaster *et al.* (2001), Veenbaas & Brandjes (1998) |
| *Fabriciana adippe* (High brown fritillary) | Dover & Fry (2001) |
| *Lepus europaeus* (Brown hare) | Veenbaas & Brandjes (1998), Rühe (1999) |
| *Melitaea athalia* (Heath fritillary) | Dover & Fry (2001) |
| *Melitaea cinxia* (Glanville fritillary) | Kuussaari *et al.* (1996) |
| *Muscardinus avellanarius* (Hazel dormouse) | Bright (1998) |
| *Mustela putorius* (Polecat) | Veenbaas & Brandjes (1998) |
| *Parus montanus* (Willow tit) | Rodriguez *et al.* (2001) |
| *Parus palustris* (Marsh tit) | Bellamy & Hinsley (2005) |
| *Salmo trutta* (Brown trout) | Carlsson *et al.* (2004) |
| *Sciurus vulgaris* (Red squirrel) | Andren & Delin (1994), Veenbaas & Brandjes (1998) |
| *Triturus cristatus* (Great crested newt) | Jehle & Arntzen (2000) |
| *Tyria jacobaeae* (Cinnabar moth) | Brunzel *et al.* (2004) |
| **Non-native species (Non-native as defined by Hill *et al.*, 2005):** | |
| *Abax parallelus* (a carabid beetle) | Hofe & Gerstmeier (2001) |
| *Branta canadensis* (Canada goose) | St Clair (2003) |
| *Bucephala clangula* (Goldeneye) | Poysa & Paasivaara (2006) |
| *Cervus nippon* (Sika deer) | Sakuragi *et al.* (2003) |
| *Oncorhynchus mykiss* (Rainbow trout) | Mellina *et al.* (2005) |
| *Oryctolagus cuniculus* (European rabbit) | Veenbaas & Brandjes (1998) |
| *Pacifastacus leniusculus* (Signal crayfish) | Light (2003) |
| *Rattus norvegicus* (Brown rat) | Veenbaas & Brandjes (1998) |
| *Sciurus carolinensis* (Grey squirrel) | Goheen *et al.* (2003) |

## 5.4 Study Pools

*Pool 1 – Direct comparisons: matrix type, corridor presence vs. absence*

Of the 67 studies including UK species that populate the data pools, only one tested the presence or absence of corridors on immigration or emigration (Table 4). Berggren *et al.* (2002) reported that Roesel's bush cricket (*Meterioptera roeseli*) was more likely to leave a long-grass patch through a corridor (of long grass) than through short grass.

Eight studies in pool 1b (direct comparisons of matrix types) included UK species. Of these, only Malmgren (2002), Bellamy *et al*. (2005), and St. Clair (2003) were carried out in natural landscape using natural populations. Seven reported an effect of matrix, four of which reported species preferring habitat structurally similar to their home or 'breeding' habitat. In the fifth of those six studies, there was no clear starting assumption as to which habitat would be more permeable; newts preferred woodland to field (Malmgren, 2002). The final study reported that adonis ladybirds had increased immigration rates in leek vs. alfalfa 'matrix' with the paper beginning with the assumption that ladybirds would find alfalfa more permeable (Grez & Prado, 2000). The studies reporting 'no effect' were on grey squirrels and fence-rows with and without trees (Goheen *et al*., 2003) and meadow brown butterflies and crop vs. field (Conradt, 2000). All the studies in pool 1b were on relatively mobile animals: squirrels, birds, newts and winged insects.

There were no studies on the effect of the structure of corridors on immigration or emigration (Pool 1c), though see Bright (1998) for an example of intact vs. gappy linear features in pool 5 – hazel dormice do not cross hedgerow gaps.

*Pool 2 – Interpatch movement in heterogeneous landscapes*

Sixteen studies looked at the role of the matrix in movement to or from patches within a heterogeneous landscape. Half the studies were conducted on relatively large flying insects. Three papers were on flightless insects, one on newts, one on birds, two on rodents and one on hedgehogs. Matrix effects were reported in a slightly lower proportion of studies than for pool 1b (10 of 16). Of these ten studies, nine reported a positive response to matrix features more similar to their home habitat; the exception was a study reporting that natterjack toads preferred woodland to open field (with no starting assumption provided about which habitat would be preferable; Jehle & Arntzen, 2000) in a similar manner to Malmgren (2000) in pool 1. Papers reporting 'no significant effect' outcomes were not restricted to a particular species group; two of these reported that permeable features are used if present but did not affect dispersal rate (Poysa & Paasivaara, 2006; Ockinger & Smith, 2008).

*Pool 3 – Anthropogenic barrier features*

Four studies looked at roads and road crossings, mostly in relation to mammals. Veenbaas & Brandjes (1998) looked at a range of vertebrates using different road-crossing tunnels. Some mammals (e.g. badgers, deer, hares and rabbits) were found to never use tunnels while others such as stoats and foxes, were found to use wide tunnels more frequently than narrow tunnels. Amphibians were affected by substrate, preferring sand or concrete to wood. In contrast, Clevenger *et al.* (2001) found that stoats prefer narrow culverts. Two papers by Rico *et al.* (2007 a and b) reported conflicting results of the impacts of road width on rodent road crossing frequency. In addition to road studies, Lucas and Bately (1996) reported that boulders, concrete and flow-gauge weirs all restrict barbel movement within river systems.

*Pool 4 – Movement around complex landscapes*

The majority of the 21 studies in pool 4 were conducted on mammal and bird species such as red deer and tawny owls. Frequently, within a mosaic landscape, home ranges extended to incorporate and increase area of preferred habitat type, as reported in Dixon (2001) for red kites, Cargnelutti & Reby (2002) for roe deer, and Anderson & Forester (2005) for red deer. In contrast, Andren & Delin (1994) reported that red squirrels do not adjust home range sizes according to the amount of preferred or avoided habitat available to them.

Seven studies identified species including hares, toads and polecats moving extensively along linear features such as hedgerows and ditches, with foxes utilising anthropogenic features such as roads in preference to areas of wetland. Sakuragi & Igota (2003) however, found sika deer avoid areas with high densities of roads. Mellina *et al.* (2005) reported that streamside clearfelling did not affect rainbow trout movement in streams in British Columbia. Overall, within heterogeneous landscapes urban areas were avoided or generally frequented less than other habitat types (e.g. Blandford 1986, and Dixon 2001).

*Pool 5 – The remainder*

Eleven of the twenty papers in pool five were based on insect species, of which six showed a negative response to less permeable matrix features such as slower movement or avoidance of the matrix habitat altogether. A high affinity toward remaining within the same or similar habitat as breeding patches when moving through the landscape was observed in these studies. For example, Mauremooto *et al.* (1995) reported that three species of ground beetle, whose patch habitat is arable field, moved faster through stubble and barley matrix than hedges. Similarly, Kuussaari *et al.* (1996) reported that open landscape surrounding patch habitats increased the emigration rate of Glanville fritillaries, a grassland butterfly species.

Of the remaining five papers in pool 5, four reported a positive outcome to movement through the matrix habitat. For example, Dennis & Hardy (2001), found butterflies utilised areas outside of their ‘breeding’ habitat for other resources and did not therefore avoid the matrix habitat, whilst Hein *et al.*

(2003) reported crickets moved faster through the matrix. Chapman *et al.* (2007) reported a neutral response of tansy beetles, as movement through the matrix was faster than tansy patch habitat but variability of this movement was high.

Three studies in pool 5 represented bird species and each reported birds avoiding the matrix habitat, with the matrix actually restricting the rate of bird movement (Rodriguez & Andrew 2001) or increasing the distance of movement from such features, i.e. roads (Foppen & Reijnen (1994). Both studies of amphibians and one of invertebrates also found matrix habitat restricted species movements. Fried *et al*. (2005) was the only study retrieved examining the impact of patch shape and four studies included species responses to edges.

Pool 5 included the only study found on a freshwater invertebrate – the signal crayfish (Light, 2003) and one of the three studies relating to fish (Carlsson *et al*., 2004). The only study including mammals in pool 5 reported both negative and positive responses to more permeable matrix features, whereby dormice were reluctant to cross gaps in hedges but moved quickly through fields if released there (Bright, 1998).

**Table 4**. The number of papers and data points (each species in each study is a data point) by pool (as described in Figure 2) and taxonomic grouping.
* NB column makes 69 as some papers contain more than one taxon.

| | 1a | 1b | 2 | 3 | 4 | 5 |
|---|---|---|---|---|---|---|

**Table 5**. The number of papers and data points (each species in each study is a data point) by pool and taxonomic grouping for BAP priority species.

| | Number of data points for BAP species | Number of BAP species studied in group | Number of papers in group including at least one BAP species |
|---|---|---|---|
| Taxonomic group | | | |
| 1. Carnivorous mammals excluding rodents | 3 | 2 | 2 |
| 2. Herbivorous mammals excluding rodents | 2 | 1 | 2 |
| 3. Rodents | 4 | 3 | 3 |
| 4. Birds | 3 | 3 | 2 |
| 5. Fish | 1 | 1 | 1 |
| 6. Reptiles | - | - | - |
| 7. Amphibians | 4 | 2 | 4 |
| 8. Butterflies and moths | 4 | 4 | 3 |
| 9. Other flighted invertebrates | 1 | 1 | 1 |
| 10. Flightless terrestrial invertebrates | 1 | 1 | 1 |
| 11. Freshwater invertebrates | 0 | 0 | 0 |
| Pool | | | |
| 1a Corridor presence/absence | 0 | 0 | 0 |
| 1b Direct comparisons of 2 matrix types | 3 | 3 | 3 |
| 1c Corridor structure | 3 | 3 | 3 |
| 2 Inter-patch movement in heterogeneous landscape | 5 | 5 | 5 |
| 3 The effects of barriers and barrier crossings | 3 | 3 | 3 |
| 4 Movement around resource patches | 8 | 8 | 9 |
| Total for column across all groups | 24 | 18 | 18 |

## 5.5 Effects of landscape features

In order to make this report more useful to land managers, broad synthesis of the findings related to landscape features was attempted. This is similar to the ‘pools’ used in the rest of this section. The different features were divided according to the list below, and papers assigned to each feature according to their methods section.

**Corridor**: a corridor in this project was defined as a linear element of the same vegetation type as the habitat patch (see glossary) and *not capable of supporting a breeding population* (according to the study text)

**Barrier**: Studies examining the impact of a linear, anthropogenic ‘hard engineering’ feature e.g. road, weir, or a structure built specifically to overcome that feature e.g. tunnel.

**Linear permeable**: Studies where any linear feature was tested as a movement route as opposed to a barrier.

**Patch edge**: Studies that reported how species responded to boundaries in their home habitat type.

**Matrix direct comparison**: Studies where results were reported about two different kinds of matrix in situations where confounding was low.

**Matrix composition**: Studies in which the amount of each land cover type in a landscape was tested with potential confounding and no exploration of how patches were arranged

**Matrix heterogeneity**: Studies examining the spatial arrangement of the matrix, most studies referring to the degree of fragmentation.

Studies were first summarised within groups according to the ‘home’ habitat; these tables are included in Appendix 3. Coverage of habitats is patchy and there are few studies of wetland and marshy habitats in particular. Much of the data is about simple, controlled comparisons of individual features for woodland or grassland species.

The tables were then summarised by landscape feature (Table 6). This is a very simplified synthesis of a complex range of papers and the reasons for different outcomes (e.g. study robustness, scale, taxonomic group) have not been explored. However, three broad conclusions stood out from the summarisation:

1. Mostly positive (increasing movement/dispersal) but also some neutral responses to landscape elements of similar structure to the patch habitat were reported (e.g. linear features, tunnels under roads). It is hard to elicit patterns underlying why some outcomes were positive and some neutral. Important exceptions where features less similar to the home habitat had a positive

impact on movement included where linear features increased movement through being used for cover (four studies of amphibians) or as visual cues (e.g. two studies on butterflies).

2. Negative (decreasing movement or dispersal) or neutral responses to anthropogenic barriers were reported. Most species with neutral responses to small roads are those common in European landscapes which have many small roads. Roads may have a cumulative effect, or a greater effect if larger. The use of road tunnels depended on species, with more generalist species more likely to use tunnels (one study including 14 taxa).

3. Speed of movement (including distance travelled over a set time period, e.g. Dzialak, 2005) may not be a good indicator of permeability. Most papers examining speed found species moved faster in more open habitats. Stevens (2004) suggests this is because physically the landscape is easier to move within. It may also be a predator avoidance strategy in response to greater exposure to predators (e.g. Chapman *et al*., 2003; Hein *et al*., 2007).

**Table 6**. Outcome synthesis of limited evidence from papers including UK species (outcome reported in this table is only for UK species), arranged by landscape feature. Tables arranged by habitat are included in Appendix 3, and incorporate some simple evaluation of study quality.

| **Landscape feature** | **Outcome summarisation** |
|---|---|
| Corridor | Positive outcomes reported (fewer studies but all well controlled). |
| Barriers | Roads – negative impacts on movement more likely for larger/multiple roads.<br>Tunnels – Often avoided; type preferred depends on species.<br>Weirs – negative impact. |
| Linear permeable | Mostly positive outcomes over a range of studies. Some species seem to follow linear elements to navigate (this includes elements of a dissimilar structure to their home habitat). |
| Patch edge | Little evidence found in this review. Edge impacts on dispersal have been reviewed elsewhere, e.g. Parker et al. (2005). |
| Matrix direct comparison (not including linear features) | Positive responses to matrix types more similar to the home habitat reported for butterflies and amphibians. Preferences may be based on protection from predation. Localised movement of mammals less impacted by matrix. Evidence for other invertebrates is a mixture of positive and neutral. |
| Matrix composition | Animals making large-scale movements respond to matrix – evidence from deer and birds. These movements may be related to resource availability. |
| Matrix heterogeneity | Less evidence. Deer and bush crickets moved further and were more likely to move in more fragmented landscapes. |

## 5.6 Section summary

A qualitative approach has enabled synthesis of papers relating to UK species, but caveats regarding study quality and the potential contrast between reported outcomes and effect sizes must be kept in mind. The literature suggests that matrix elements more structurally similar to breeding habitats of species do provide increased likelihood of movement or dispersal. Exceptions occur, in particular where the species:

- is very mobile and does not react to the matrix
- uses more permeable features if present but still disperses at the same rate
- uses less structurally similar features for cover or because they do not impede physical locomotion.

Few or no studies were found for some taxonomic groups, for example reptiles, fish and freshwater invertebrates, and also species of low mobility. Study scales were frequently short or small, with very large studies restricted to large mammal telemetry. Further research is required to refine our understanding of spatial and temporal patterns of use of landscape features by different species and taxa, and options for this are outlined in section 7.

# 6. Data limitations

The data retrieved relating to directly-measured movement in response to matrix features have some clearly-defined limitations.

- Three of the five kingdoms: Fungi, prokaryotes and protists were missed out entirely (but see Walser, 2004 and Werth *et al.,* 2006 for examples of lichen movement distance without reference to matrix features).
- Large mammal species tend to have mosaic home ranges without a specific home patch, and it is harder to extract empirical, direct tests of responses to specific landscape features in these situations.
- Most fish studies either had no comparator or no clear definition of matrix and habitat (though Schaefer *et al.,* 2003 is an exception). Some fish studies were performed on barriers with comparator/controls, of such Carlsson *et al.* (2003) and Lucas & Batley (2006) included UK species and fulfilled inclusion criteria after full-text assessment.
- There were few tests of different species responding to the same features. One example is the Savannah River Experimental Forest (providing four studies to the corridor meta-analysis; Table 1) but that has been so far restricted to rodents, butterflies, birds, wasps and pollen (Haddad *et al.,* 2003). Also, some road-crossing experiments test many species (e.g. Veenbaas & Brandjes, 1998; Clevenger *et al*., 2001).
- No marked seeds were followed over varying matrix features except ‘lift-hitching’ (e.g. Gomez, 2003; Kollmann & Schill, 1996; Lu & Zhang, 2004). No marked seeds were followed along watercourses except one without a control or comparator (Johansson *et al.,* 1993, followed rhizome fragments of *Ranunculus ligna*, and found that a lake formed a barrier but did not compare to a river without a lake).
- There was no tracing of clonal dispersal except in those studies where there was no reference to the matrix.
- There was no tracing of natal dispersal by genetic identification of parents.
- Only four before/after designs were found: tracking wolf movements inside and outside an area undergoing restoration as a wildlife ‘corridor’ (Shepherd & Whittington, 2006), vole movement before and after destroying meadow vegetation (Andreassen & Ims, 1998), seasonal movements of rainbow trout with clearfelling (Mellina *et al*., 2005) and comparing vole movement before and after creating corridors between some patches (Coffman *et al*., 2001).

The analyses presented here included 313 studies, and only 84 studies have been tabulated in this report. Although some studies contain multiple species, this still reflects a tiny proportion of all known species. Studies which were included were largely on highly mobile species, as these are easier to observe within the limited timescale of most ecological studies.

It is also pertinent here to highlight a review limitation with respect to study capture. A number of decisions as to the inclusion and exclusion of retrieved studies from the final review were made in response to resource availability and time constraints, and to their apparent potential usefulness (see Box 2). Whilst these choices were clearly-stated and rationalised, a combination of these (most notably the exclusion of studies relating to pollen dispersal, seed movement via animal vectors, and invasion/colonisation events with an unknown source) may have together acted to inadvertently exclude a body of potentially relevant studies examining the movement of plant species in relation to landscape features. Before abstract assessment, there were 509 references in the library file that included the fragment 'zoochor' (e.g. endozoochory, ectozoochorous – meaning seed dispersal by animals) or the word 'seed'. Of the 13 remaining after abstract assessment all were rejected as they considered, for example, animals dispersing seeds or colonisation where the source was not known (both explicit exclusion criteria).

Similarly, genetic studies where movement was inferred from, for example, microsatellite frequencies were explicitly excluded as not measuring movement directly. Gene flow can be a useful indicator of movement (Sunnucks, 2000) but is affected by other factors than dispersal (Garant *et al.*, 2005), accuracy of assignment tests may be as low as 65% (Berry *et al.*, 2004) and Type I error high (Paetkau *et al.*, 2004). Our criteria excluded a range of genetic studies including some testing 'permeability' (resistance) values for different matrix types (e.g. Michels *et al.*, 2001; Vignieri, 2005). Storfer (2007) provides a traditional literature review of genetic evidence for landscape effects, listing 19 studies since 1997 of which about half seem to fit the other inclusion criteria for this study.

There is a range of methodological issues associated with meta-analyses. Firstly, there is potential for different effect sizes, in this case risk ratios, to be calculated from the data presented in an article. In the early Savannah River Experimental Forest corridor studies (Bowne *et al.*, 1999; Danielson & Hubbard, 2000; Haddad, 1999; Haddad *et al.*, 2003), one of the study areas contains a range of patches and the number of possible inter-patch movements is unequal for corridor and non-corridor patches and confounded by distance. Details of how data were extracted from each of these studies in contained in Appendix 4, but we explicitly acknowledge this as a limitation in this analysis.

Finally, all reviews must be considered in the light of possible publication bias, including investigation bias. Evidence for bias toward publication of studies with positive outcomes was not found. However, species included tended to be relatively mobile, or charismatic, or both. It is probably unusual for researchers to seek and gain funding to test something they know will not have an effect.

# 7. Knowledge gaps

## 7.1 The size of the gap

With such a broad research question ("Which landscape features affect species movement?"), the knowledge gaps are, perhaps unsurprisingly, very large. It is not possible to describe them entirely and not sensible to suggest all knowledge gaps should be filled by research as an immediate priority.

## 7.2 What are the immediate research priorities?

Possible areas to focus on include:

- Gaps based on experimental designs and scales
- Gaps based on taxonomic groups
- Gaps based on UK conservation priority species
- Smaller gaps in knowledge based on combinations of the above, e.g. flightless invertebrates and corridor experiments, BAP priority butterflies and road crossing structures
- Reasons for the heterogeneity in outcomes between species from similar experiments
- How results from one species can or cannot be applied to whole groups of species.

There is a balance between furthering fundamental species-based information and furthering research synthesis. Prioritisation should be based on policy needs highlighted by groups such as BRAG (Biodiversity Research Advisory Group, a part of the UK Biodiversity Action Plan process). If we are to enable the widest biodiversity to survive and adjust to environmental change, landscape management needs to meet the demands of different organisms simultaneously.

## 7.3 How can we meet some of the research priorities?

*Species based*: Looking at less mobile species, especially plants and invertebrates, over longer timescales would be of most relevance to UK conservation. One way of doing this could be to use maps of changes in species distributions to monitor range expansions over years or decades, but this method comes with significant 'health warnings' about repeatability of study methods, pseudo-absences and other confounding factors such as variation in recorder effort. The use of studies from other continents may also introduce confounding due to differences in evolutionary history and realised niche.

*Synthesis*: Multi-species or multi-landscape experiments, testing landscape features at realistic scales necessary for populations to track climate change and habitat or resource distribution, with appropriate reference to matrix features, is a potential research direction. It is unwise to suggest that the scales species have been studied at are the scales they disperse at (Franzen & Nilsson, 2007). Simple studies which try and test how the presence of a specific landscape feature integrates with other factors affecting dispersal also help draw out the relative significance of landscape features (e.g. Samways & Lu, 2007). Increased rigour in examination of the impacts of landscape changes using full before/after+control/intervention (BACI) designs would permit clear hypothesis testing of the impact of particular interventions. It allows the evaluation of whether the restoration of connectivity in currently highly fragmented landscapes will work, as well as the impacts of adding less permeable elements to the landscape (which apply to many parts of the UK and many of the stakeholder organisations for this report).

Although some quantitative analyses are reported here, it is recommended that the potential for further quantitative analyses of the data is fully explored. For example, twenty-two of the abstracts in the library after full-text inclusion assessment also contain the words 'population persistence', and 176 contain 'range' (although this may not refer to species distributional ranges). These could be a potential source of information in the next step from individual movement to population range shift. This subset of the library may be an important source of further information without having to perform search and filter procedures again, but the original keywords must be examined in the context of any new question and modified accordingly.

The potential use of systematic review and meta-analysis to address these knowledge gaps is illustrated by the large numbers of such syntheses already undertaken in landscape ecology (Box 3). Stakeholders must consider the importance of the question and the amount of information available to decide which questions have high priority.

Genetics has a great deal to contribute, but is a relatively specialist subject with a large literature base for which a separate review may be needed. Any such analysis should be carried out by a specialist in ecological genetics, who is able to address issues regarding mutation rate of markers and delineation of populations by genetic analysis (Waples & Gaggiotti, 2006).

**Box 3**. List of data syntheses undertaken relating to wider issue of landscape ecology.


Batary, P. and A. Baldi (2004). "Evidence of an edge effect on avian nest success." Conservation Biology **18**(2): 389-400.

Bender, D. J., T. A. Contreras, *et al.* (1998). "Habitat loss and population decline: A meta-analysis of the patch size effect." Ecology **79**(2): 517-533.

Chalfoun, A. D., F. R. Thompson, *et al.* (2002). "Nest predators and fragmentation: a review and meta-analysis." Conservation Biology **16**(2): 306-318.

Clergeau, P., J. Jokimaki, *et al.* (2001). "Are urban bird communities influenced by the bird diversity of adjacent landscapes?" Journal of Applied Ecology **38**(5): 1122-1134.

Davies, Z.G. and Pullin A.S. (2007). Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landscape Ecology* 22, 333-351.

Delin, A. E. and H. Andren (1999). "Effects of habitat fragmentation on Eurasian red squirrel (Sciurus vulgaris) in a forest landscape." Landscape Ecology **14**(1): 67-72.

Driscoll, M. J. L. and T. M. Donovan (2004). "Landscape context moderates edge effects: Nesting success of wood thrushes in central New York." Conservation Biology **18**(5): 1330-1338.

Gorresen, P. M., M. R. Willig, *et al.* (2005). "Multivariate analysis of scale-dependent associations between bats and landscape structure." Ecological Applications **15**(6): 2126-2136.

Long, E. S., D. R. Diefenbach, *et al.* (2005). "Forest cover influences dispersal distance of white-tailed deer." Journal of Mammalogy **86**(3): 623-629.

Monkkonen, M., M. Husby, *et al.* (2007). "Predation as a landscape effect: the trading off by prey species between predation risks and protection benefits." Journal of Animal Ecology **76**(3): 619-629.

Parker, T. H., B. M. Stansberry, *et al.* (2005). "Edge and area effects on the occurrence of migrant forest songbirds." Conservation Biology **19**(4): 1157-1167.

Storch, I., E. Woitke, *et al.* (2005). "Landscape-scale edge effect in predation risk in forest-farmland mosaics of central Europe." Landscape Ecology **20**(8): 927-940.

Venier, L. A. and L. Fahrig (1998). "Intra-specific abundance-distribution relationships." Oikos **82**(3): 483-490.

Frankham, R. (1999). "Resolving conceptual issues in conservation genetics: the roles of laboratory species and meta-analyses." Hereditas **130**(3): 195-201.

Moilanen, A. and M. Nieminen (2002). "Simple connectivity measures in spatial ecology." Ecology **83**(4): 1131-1145.

# 8. Discussion and conclusion

## 8.1 Discussion

This report highlights the extent and diversity of available information on the impacts of landscape features on species movement. There were 313 studies included in the review after full-text assessment but the most homogenous group (impact of corridor presence on number of individuals making a successful inter-patch movement in a controlled test) included only ten studies.

This diversity is largely because dispersal is a complex process that varies widely between different species, and can be affected by different types of landscape features. There was therefore wide variation in experimental design (including marking methods and sampling strategies), landscape features under study (e.g. corridors, matrix features, linear elements) and the measurement of dispersal. However, even within relatively consistent designs, there was variation in the effectiveness of landscape features among studies.

When examined by quantitative synthesis using meta-analyses, both corridors and direct matrix comparisons had an impact on inter-patch movement rates. Although the meta-analysis was robust to analytical decisions, the detected impacts were of low magnitude.

Corridors may affect movement by changing the likelihood and also direction of dispersal, as well as the survival cost during movement. Interpreting the ecological significance of a given risk ratio is not straightforward but the number needed to treat (NNT) indicated that one additional individual will successfully move between patches for every 15 animals in habitat patches connected by a corridor compared to unconnected habitat..

There is limited evidence from the meta-analyses that individual movement is greater through matrix more similar to their preferred habitat than more structurally different habitat. There were considerable differences in movement rates with some variation explained by the distance moved. The evidence is based on a limited range of studies and the results are clearly heavily dependent on the definitions of favourable and unfavourable habitat. The matrix-matrix comparisons include multiple landscape element comparisons studied both experimentally and by direct observation in natural populations.

In the qualitative analysis of reported outcomes, direct and empirical comparison studies (pool 1) reported positive responses to matrix features structurally more similar to the home habitat in the majority of cases, which is consistent with the results from the meta-analysis. In experiments with less controlled experimental designs, the proportion of neutral outcomes reported increased. Few negative outcomes (where species were more likely to use features less structurally similar to their home habitat) were reported, but those exceptions were important. For example, linear features provided visual cues for navigation, 'highways' where movement is physically easier, or increased cover.

One hundred and nine UK animal species (including 18 BAP species and nine non-native species) have been included in 66 studies included in the review (approximately one quarter of the 313 total studies). While this severely under represents the British fauna, UK species may be somewhat over represented in the evidence pool.

The variability in spatial and temporal scales of studies that were included must be considered in relation to the original purpose of each study and the dispersal ability of the species involved. The largest studies involving UK species encompassed scales at which climate change impacts might be expected to operate (e.g. the Climatic Birds Atlas suggests approximately 550 km for 3°C rise, Huntley *et al.*, 2007). The smallest studies were not relevant to successful inter-patch dispersal but rather examined behaviour at boundaries, which can still be relevant for the initial stage of the dispersal process.

## 8.2 Recommendations for good landscape design

A key output from this study was to provide evidence to support proposed climate change adaptation strategies (Hopkins *et al.* 2007), identifying both good and poor landscape design features, which may enhance permeability, at a range of scales.

The outcome of the meta-analyses suggested that, over the small distances studied, matrix habitat of the same (i.e. a corridor) or similar structure as the patch habitat will increase movement. However, the qualitative analyses show that this is not always the case, and over larger distances or more complex landscapes, responses become less predictable. This recognises that habitat connectivity and permeability is species and landscape-specific. Therefore, the information in this report cannot be used to provide steer on specific elements of permeable landscape or ecological network design, while also not directly contradicting current and proposed adaptation strategies.

Those involved in land use planning and management may wish to accept the basic proposed principles (Hopkins *et al.*, 2007), within an adaptive management framework along with local habitat and species priorities, to maintain effective decision making. In the face of uncertainty, adaptive management intends to reduce uncertainty by monitoring, learning and refining management over time through an iterative process.

## 8.3 Summary against key objectives of project specification.

Page 4 of the project specification set out 8 specific objectives (in italics). Here we report on how we were able to address each objective:

*1. To undertake a consultation amongst key policy customers at the project outset to refine the key research questions to be addressed by the study.*

The consultation was held between 3rd December and 24th January using the steering group listed in the front pages of the report. Scoping of keywords was included, and the question 'Which landscape features affect species movement and dispersal' was agreed on 24$^{th}$ January 2008.

*2. Undertake a literature review and consultation with experts and stakeholders, to:*

*a. Provide a succinct summary of the empirical evidence demonstrating the importance and role of landscape permeability or connectivity for dispersal of a wide range of different species, including UK BAP Priority Species, migratory species and selected non native species.*

In depth quantitative and qualitative analyses form the bulk of this report. A succinct summary is provided in the policy brief.

*b. Define key terms used to describe physical and functional connectivity (habitat connectivity or permeability, corridors, networks, stepping stones, patch mosaics etc).*

Glossary provided within this report (Section 9).

*c. Categorise the spatial and temporal scales at which such connectivity works for different species, guilds, or groups of organisms.*

Section 4 (qualitative analysis) categorises the spatial and temporal scales of studies. This does not necessarily relate to the scales organisms operate at.

*d. Identify and investigate any studies of genetic evidence of historical dispersal patterns and where possible relate these to change in landscape, and habitat connectivity.*

No genetic studies were included in the review as no studies with identification of parents also fulfilled the inclusion criteria. Other genetic tests such as using microsatellites infer, rather than directly measure, movement.

*While focussed on the UK, literature and materials from other countries should be considered where relevant*

The quantitative section included all species in order to find a homogenous group for meta-analysis. The qualitative section is focussed on UK species, with sections on BAP and non-native species. Libraries of pooled articles provide a base for further study of non-UK species.

*3. Identify characteristics of the landscape that facilitate or hinder movement of native species and non native species.*

Positive and neutral outcomes are reported for a range of landscape features for a range of UK species.

*4. Indicate the time scales involved for dispersal patterns and distances travelled by a range of species, including common species as well as those on the BAP Priority Species list.*
See Comment on Objective 1c.

*5. Taking account of the strength of evidence and uncertainty, identify 'good design features' of permeable landscapes at a range of suitable scales for practical management- perhaps also contrasting these with poor design features (features that make habitats impermeable at a landscape scale).*
There is some limited evidence that corridors and patches of more permeable habitat increase species movement.

*6. Liase with the concurrent project (CR0398) which is developing an indicator for UK and country level reporting and review evidence underpinning the use of the proposed indicators.*
Matrix impacts described within this report support the use of indicators which include 'effective distance' or 'least cost' methods. However, this may not be relevant for all species.

*7. Identify gaps in the evidence base and literature and recommend areas for further work.*
See Section 7. The gaps in the evidence base should be prioritised with reference to existing policy on land management.

*8. Provide recommendations based on the review of evidence for policy development - especially in respect of methods of enhancements of habitat connectivity to accommodate the needs of species and enable them to respond to climate change, by dispersal to more favourable climatic space.*
The breadth and heterogeneity of outcomes of empirical studies mean that specific management recommendations cannot be made. Rather, land managers may need to take a species based approach. Land managers will need to consider how a permeable element for one species group may be a barrier for another. The evidence present here does not contradict current policy and practice. See section 8.5.

## 8.4 Relation to development of connectivity indicator

A Defra funded project to develop a national connectivity indicator ran parallel to this project (CR0388, Habitat Connectivity – Developing an indicator for UK and country level reporting). It used permeability values based on structural and compositional similarity to inform potential indicators of functional connectivity. The meta-analysis of matrix comparisons provides some support to this approach. However, the information found by this systematic review does not permit us to work out the relative difference in permeability value, i.e. is a road twice, ten times or fifty times less permeable than a grassland to woodland species? The relative permeability of a range of land uses, directly measured, is still not known for any UK species.

## 8.5 Concluding Remarks

Landscape features outside of habitat patches are clearly important for some species as they can impact on functional connectivity for even quite mobile groups such as butterflies, birds and large herbivores. There is some quantitative and qualitative evidence that structurally more similar matrix habitat and habitat corridors is moved through in preference. For these species, providing habitat networks based on corridors and matrix elements with similar structure to the habitat should increase dispersal and may promote longer distance movement. There is also evidence to support the use of road-crossing structures to reduce mortality rates (Veenbaas & Brandjes, 1998).

However, there are also a large number of studies in which impacts of matrix features were not shown to have a positive or a negative effect on dispersal. For species and situations where this is the case, measures to reduce mortality across the wider landscape or increase the number of emigrants from a given patch may be important.

The strength of evidence-base derived from meta-analysis to suggest development of connectivity will improve species movement is low because of the limited number of relevant studies. However, the review found no convincing evidence that commonly advocated ‘connectivity interventions’ do not work. Comparing the costs of investment in interventions to promote connectivity with the potential costs of inaction should be undertaken with this evidence-base in mind.

The breadth of the review needs placing in context of the broader question of the effectiveness of ‘connectivity interventions’. The review sought a relatively narrow slice of the potential full range of evidence that could be brought to bear on this question. Further reviews, either of the evidence pool gathered here or addressing new questions with a new search would help build a more complete picture.

Other interventions to increase species’ resilience to impacts on their existing habitat may be as important as interventions to increase their speed of response to climate envelope movement (Mitchell *et al.,* 2007). Protected areas, varied and functional ecosystems and good habitat quality are features that can promote resilient populations (Hopkins *et al.,* 2007, Mitchell *et al.,* 2007). Larger populations can produce more dispersing individuals (Matthysen, 2005), increasing the likelihood of chance, long-distance dispersal events which appear vital to keeping pace with climate change for many species (Higgins & Richardson, 1999; Brooker *et al.*, 2007). Given the magnitude of the threat posed by climate change, a precautionary approach would indicate that measures to enhance functional connectivity should be a priority. It is suggested that such activities take place within the context of adaptive management at a scale matched to the need.

# 9. Glossary

The purpose of this glossary is to provide definitions for terms used in the systematic review. In many cases different sources provide contrasting definitions which can confuse ideological debates and undermine management efforts (Colautti & MacIsaac, 2004). This glossary does not attempt to list or reconcile all published definitions. Instead, examples of the range of possible definitions are given and the one used for this report given in non-italicised text.

| Word | Definition | source |
|---|---|---|
| Adaptation | Adjustment in natural or human systems to a new or changing environment | http://glossary.eea.europa.eu/EEAGlossary |
| | *(Climate change context) Initiatives and measures to reduce the vulnerability of natural and human systems against actual or expected climate change effects. Various types of adaptation exist, e.g. anticipatory and reactive, private and public, and autonomous and planned. Examples are raising river or coastal dikes, the substitution of more temperature-shock resistant plants for sensitive ones, etc.* | IPCC Fourth Assessment Report Synthesis, 2007 |
| | *(Policy context) Policies, practices and projects which can either moderate damage and/or realize opportunities associated with climate change* | Piper *et al.*, 2006 |
| | *(Evolutionary context) Characteristics of organisms evolved as a consequence of natural selection in its evolutionary past which result in a close match with features of the environment* | Begon, Harper & Townsend 1996 |
| Aggregation (statistical context) | Systematic aggregation of separate data points (e.g. those divided by sex, species or location) in order to prevent quasi-replication | |
| Barrier | A physical, chemical or biological feature between two landscape elements that prevents the flow of individuals, genetic material, energy etc. | Forman & Godron 1986 p 298 |
| Biodiversity/ Biological diversity | The variability among living organisms from all sources including, inter *alia*, terrestrial, marine and other | Convention on Biological Diversity: http://www.cbd.int/c |

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| | aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems | onvention/articles.shtml?a=cbd-02 |
| Buffer zone | The region near the border of a protected area; a transition zone between areas managed for different objectives. | http://www.unep-wcmc.org/reception/glossaryA-E.htm |
| | *Zone / area around the network (i.e. around core areas and, if necessary, around linkage elements) which protects the network from potentially damaging external influences and which are essentially transitional areas characterized by compatible land uses* | Kettunen *et al.*, 2007 (IEEP glossary) |
| Catchment / catchment area | (1) An area from which surface runoff is carried away by a single drainage system. (2) The area of land bounded by watersheds draining into a river, basin or reservoir | http://glossary.eea.europa.eu/EEAGlossary/C/catchment_area |
| Climate change | A change of climate which is attributed directly or indirectly to human activity that alters the composition of the global *atmosphere* and which is in addition to natural climate variability observed over comparable time periods'. | *United Nations Framework Convention on Climate Change (UNFCCC)* |
| | *Climate change refers to a change in the state of the climate that can be identified (e.g., by using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer. Climate change may be due to natural internal processes or external forcings, or to persistent anthropogenic changes in the composition of the atmosphere or in land use.* | IPCC Fourth Assessment Report Synthesis, 2007 |
| Colonisation | The entry and spread of a species into an area, habitat or population from which it was previously absent | Begon, Harper & Townsend 1996 |
| Configuration | The location and juxtaposition of different landscape elements | Forman & Godron 1986 |
| Connectedness /structural connectivity | Structural connectivity is equal to habitat continuity and is measured by analysing landscape structure, independent of any attributes of | Kettunen *et al.*, 2007 (IEEP glossary) |

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| | organisms. | |
| | *The physical distance between elements of the same type (e.g. forest patches)* | Farina 2000 |
| | *(Mathematical context) A space is completely connected if it is not divided into two open wholes (i.e. is not crossed by a boundary whose ends join the perimeter of the space).* | Hocking & Young 1961 |
| Connectivity | The functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to the landscape structure. | With *et al.,* 1997 |
| | *The degree to which the landscape facilitates or impedes movement among resource patches.* | Taylor et al, 1993 |
| | *Functional connectivity is the response of the organism to the landscape elements other than its habitats (i.e. the non-habitat matrix).* | Kettunen *et al.,* 2007 (IEEP glossary) |
| Core areas | The main places within the landscape where the species/habitats that are the target of the network reside – they may support particular plants or animals, vegetation types, habitats, structural or others features, and can vary in terms of their size, composition, condition, seasonal usage, designation, degree of protection, etc. (and may be graded accordingly) – although it is convenient to delimit a core area within a single site boundary, in reality the situation is likely to be more complex because of variation in composition, condition, etc., within the core area and the supporting role played by external features, in supply food to animals that nest/roost within the core area. | Ed Mountford pers. comm. |
| Corridor | A continuous or near continuous link of suitable habitat through an inhospitable environment | Bennett, 1999 |
| | *Landscape elements which serve to maintain vital ecological or environmental connections by providing physical ([continuous] though not necessarily linear) linkages between the core areas* | Bennett, 2004 |

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| | *(1) A linear strip of land identified for present or future location of transportation or utility rights-of-way within its boundaries. (2) A thin strip of vegetation used by wildlife and potentially allowing movement of biotic factors between two areas.* | http://glossary.eea.europa.eu/EEAGlossary/C/corridor |
| | *A narrow strip of land that differs from the matrix on either side* | Forman & Godron 1986 |
| Dispersal | One-way permanent movement away from an established home range or natal area | Ricklefs, 1990 |
| | The spreading of individuals away from each other, e.g. of offspring from their parents or from regions of high population density to regions of lower density | Begon, Harper & Townsend 1995 |
| | ***Animal dispersal*** *– A one-way movement of an individual from one home range to a new home range* ***Plant dispersal*** *– A process of plant propagule movement that results in establishment of the species at a new site* | Forman & Godron 1986 (rejected because some animals do not have home ranges, and there are three other biological kingdoms) |
| Disturbance | A discrete event, either natural or human induced, that causes a change in the existing condition of an ecological system. | Kettunen *et al.*, 2007 (IEEP glossary) |
| | *An event that causes a significant change from the normal pattern in an ecological system* | Forman & Godron 1986 |
| Ecological coherence | Sufficient representation of habitats and features of the landscape essential for the migration, dispersal and genetic exchange of wild species are maintained | Adapted from http://www.bfn.de/fileadmin/MDB/documents/themen/natura2000/conclusions.pdf (Workshop on Article 10 Habitats Directive 9-12 May 2005 – Conclusions) |
| | *Such features are those which, by virtue of their linear and continuous structure (such as rivers with their banks or the traditional systems for marking field boundaries) or their function as stepping stones (such as ponds or small woods), are essential for the migration, dispersal and* | European Habitats Directive article 10 |

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| | *genetic exchange of wild species.* | |
| | *Sufficient representation of habitats / species to ensure favourable conservation status of habitats and species across their whole natural range. 'Sufficient representation' is a function of patch quality, total patch area, patch configuration and landscape permeability* | Kettunen *et al.,* 2007 (IEEP glossary) |
| Edge effect | A different species composition, relative abundance, species interaction or fitness in the outer part of a patch compared to the interior | Ries *et al*., 2004 |
| | *The existence of more species in a region of overlap between two ecosystems than occur in either of those systems* | Oxford Dictionary. Of Ecology |
| Effect size | (In meta-analysis) A statistical standardisation of study findings, in a way that means resulting values are interpretable in a consistent fashion across all the variables and measurements involved. | Lipsey & Wilson 2001 |
| Element | The smallest spatial units of ecological community that make up a landscape (habitat patches, matrix patches, barriers, corridors, etc) | Forman & Godron 1986 |
| Emigration | The movement of individuals out of a population or from one area to another | Begon, Harper & Townsend 1996 |
| Establishment | The arrival of immigrant individuals and subsequent successful life cycle of a viable population | |
| Fragmentation | *The breaking-up of continuous tracts of ecosystems creating barriers to migration or dispersal of organisms and reducing the size of homogenous areas. Fragmentation may be induced by human activities (e.g. road infrastructures, dams) or by natural processes* | http://glossary.eea.europa.eu/EEAGlossary/F/fragmentation |
| Habitat | The environment in which an animal or plant lives, generally defined in terms of vegetation and physical features | http://www.unep-wcmc.org/reception/glossaryF-L.htm |
| | *An association of species that have a strong spatial association that is quantifiable* | Roger Catchpole pers. Comm. |
| | *The place or type of site where an organism or population naturally* | http://www.cbd.int/convention/articles.s |

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| | *occurs* | html?a=cbd-02 |
| Heterogeneity (landscape context) | Landscapes' quality or state of being heterogeneous, e.g. being composed of parts of different habitats. | Kettunen *et al.,* 2007 (IEEP glossary) |
| | *Differences in the spatial distribution of species, energy and materials,* | |
| Heterogeneity (statistical context) | Differences in either the value or the variation about the value between different data points. Data which are statistically heterogeneous should frequently not be compared by traditional parametric statistical methods. | Zar, 1999 |
| Immigration | Entry of organisms into a population [or area] from elsewhere | Begon, Harper & Townsend 1996 |
| Intensive land use | A combination of cultivation and fertiliser addition | McIntyre & Martin, 2002 |
| Invasive species | Species that heavily colonise a particular habitat with adverse effects | Colautti & MacIsaac, 2004 |
| | *Non-native species which threaten ecosystems, habitats or species* | http://glossary.eea.europa.eu/EEAGlossary/I/invasive_species |
| Isolation | The [geographical] prevention of random reproduction among individuals of a population, generally leading to genetically different subpopulations | Forman & Godron 1986 |
| Landscape | The traits, patterns, and structure of a specific geographic area, including its biological composition, its physical environment, and its anthropogenic or social patterns. An area where interacting ecosystems are grouped and repeated in similar form | http://glossary.eea.europa.eu/EEAGlossary/L/landscape |
| Links/Linkages | General term for an arrangement of habitat (not necessarily continuous or linear) that enhances the movement of animals or the continuity of species processes throughout the landscape | Bennett 1999, (IUCN) |
| Matrix | The interstitial habitat / environment between habitat patches in a habitat mosaic, typically comprising the most extensive habitat /environment type in a landscape | Kettunen *et al.,* 2007 (IEEP glossary) |
| | *The most extensive and most connected landscape element type present, which plays the dominant role in landscape functioning. Also, a landscape element surrounding a* | Forman & Godron 1986 |

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| | *patch* | |
| Meta-analysis | A statistical technique used to summarise, combine and interpret independent, selected findings of empirical studies. Meta-analysis permits analytical examination of the relationships between study findings and provides an estimate of treatment effect | Lipsey & Wilson 2001 |
| Migration | A cyclic movement of animals between separated areas that are used during different seasons | Forman & Godron 1986 |
| | *The movement of individuals, and commonly whole populations from one region to another* | Begon, Harper & Townsend 1996 |
| Mitigation | Technological change and substitution that reduce resource inputs and emissions per unit of output. Although several social, economic and technological policies would produce an emission reduction, with respect to Climate Change, mitigation means implementing policies to reduce greenhouse gas emissions and enhance sinks. | IPCC Fourth Assessment Report Synthesis, 2007 |
| Mosaic (habitat mosaic) | Spatial configuration of habitats within a landscape, generally formed by patches arranged within a matrix. | Kettunen *et al.,* 2007 (IEEP glossary) |
| Movement | Any movement by an individual, directed or undirected, permanent or temporary (c.f. dispersal). | unreferenced |
| Network | A coherent system of natural and/or semi-natural landscape elements that is configured and managed with the objective of maintaining or restoring ecological functions as a means to conserve biodiversity while also providing appropriate opportunities for the sustainable use of natural resources (Bennett 2004) | Bennett, 2004 |
| Number needed to treat (NNT) | The expected number of individuals who need to receive the experimental rather than the comparator intervention for one additional individual to either incur (or avoid) an event in a given time frame | Centre for Evidence-Based Medicine: http://www.cebm.utoronto.ca/glossary/nntsPrint.htm |
| Patch | A particulate, invariant and homogeneous entity within an ecosystem | Kettunen *et al.,* 2007 (IEEP glossary) |
| | A non-linear surface area differing in | Forman & Godron |

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| | appearance from it's surroundings | 1986 |
| Permeability | The quality of a heterogeneous land area to provide for passage of organisms. | Kettunen *et al.,* 2007 (IEEP glossary) |
| Protected area | An area of land and/or sea especially dedicated to the protection and maintenance of biological diversity, and of natural and associated cultural resources, and managed through legal or other effective means | http://www.unep-wcmc.org/reception/glossaryM-R.htm |
| Quasi-replication | Replication within meta-analysis created by extraction of separate data points from one study which are non-independent | |
| Range | The spatial limits within which the habitat or species occurs. A natural range is not static but dynamic: it can decrease and expand. | ieep/habs directive |
| Resilience | A tendency to maintain integrity when subject to disturbance. | UNDP, 2007 |
| | *The ability of a social or ecological system to absorb disturbances while retaining the same basic structure and ways of functioning, the capacity for self-organisation, and the capacity to adapt to stress and change.* | IPCC Fourth Assessment Report Synthesis, 2007 |
| | *The ability of, or speed at which, a community or population returns to it's original state after a disturbance, or it's ability to resist the impacts of disturbance* | EBS (Mitchell *et al.,* 2007) |
| | *The magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behaviour. Or: the speed with which a disturbed system returns to equilibrium or the same general state after being changed* | Piper *et al.,* 2006 |
| Resistance | (Connectivity context) The inverse of permeability | |
| Restoration | The process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed | (http://www.ser.org/content/ecological_restoration_primer.asp#3). |
| | *Where substantial effort is needed to [restore] a site with relict features (or historically former habitat)* | http://www.ukbap.org.uk/library/brig/TargetsReview06/Final/BAPTargetDefinitionsGuidance.pdf |

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| | *The return of an ecosystem or habitat to its original community structure, natural complement of species, and natural functions* | http://www.unep-wcmc.org/reception/glossaryM-R.htm |
| | *Measures taken to return a site to pre-violation conditions* | http://glossary.eea.europa.eu/EEAGlossary/R/restoration |
| Risk ratio | The multiplication of the risk that occurs in the experimental group relative to the control group. | Lipsey & Wilson, 1999 |
| Semi-natural | (Vegetation/habitat context) Communities consisting predominantly of native species that have not been planted but have arisen from natural regeneration, i.e. from seed or clonal regrowth. | Adapted from Spencer & Kirby, 1992 |
| | *Both natural and semi-natural vegetation may be found in upland and lowland situations, including wetland, woodland, grassland, moor and heathland habitats, and are described as being made up of self-seeded or self propagated vegetation characteristic of the area in which the land is situated* | http://www.crosscompliance.org.uk/faqsGAEC9.htm |
| | *Land that has been subject to past human intervention that has reverted to a more natural state either through recolonisation or expansion of native species* | Roger Catchpole pers. Comm. |
| Stepping stone | A patch that allows species to move incrementally across an otherwise hostile landscape (most often associated with migratory [or dispersing] species) | Roger Catchpole pers. Comm. |
| | *A spot that is colonised by a species* | Forman & Godron 1986 |

# 10. References

Aars, J. & Ims, R.A. (1999) The effect of habitat corridors on rates of transfer and interbreeding between vole demes. *Ecology*, **80**(5), 1648-55.

Anderson, D.P., Forester, J.D., Turner, M.G., Frair, J.L., Merrill, E.H., Fortin, D., Mao, J.S. & Boyce, M.S. (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*, **20**(3), 257-71.

Andreassen, H.P. & Ims, R.A. (1998) The effects of experimental habitat destruction and patch isolation on space use and fitness parameters in female root vole *Microtus oeconomus*. *Journal of Animal Ecology*, **67**(6), 941-52.

Andreassen, H.P. & Ims, R.A. (2001) Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography. *Ecology*, **82**(10), 2911-26.

Andren, H. & Delin, A. (1994) Habitat Selection in the Eurasian Red Squirrel, *Sciurus vulgaris*, in Relation to Forest Fragmentation. *Oikos*, **70**(1), 43-48.

Antman, E., Lau, J., Kupelnick, B., Mosteller, F. & Chalmers, T. (1992) Treatments for myocardial infarction: A comparison of results of meta-analyses of randomized control trials and recommendations of clinical experts. *Journal of the American Medical Association*, **268**, 240-8.

Aviron, S., Kindlmann, P. & Burel, F. (2007) Conservation of butterfly populations in dynamic landscapes: The role of farming practices and landscape mosaic. *Ecological Modelling*, **205**(1-2), 135-45.

Bates, A., Sadler, J.P., Fowles, A.P. & Butcher, C.R. (2005) Spatial dynamics of beetles living on exposed riverine sediments in the upper River Severn: Method development and preliminary results. *Aquatic Conservation-Marine and Freshwater Ecosystems*, **15**(2), 159-74.

Baum, K.A., Haynes, K.J., Dillemuth, F.P. & Cronin, J.T. (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology*, **85**(10), 2671-76.

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, Populations and Communities*, 3rd edn. Blackwell, Oxford.

Bellamy, P.E. & Hinsley, S.A. (2005). The role of hedgerows in linking woodland birds populations. In *Planning, People and Practice* (eds D. McCollin & J.I. Jackson), pp. 99-106. International Association for Landscape Ecology (IALE(UK)), Aberdeen UK.

Bennett, A.F. (1999) *Linkages in the Landscape* IUCN, Gland, Switzerland & Cambridge, UK.

Bennett, G. (2004) *Integrating Biodiversity Conservation and Sustainable Use: Lessons Learned From Ecological Networks* IUCN, Gland, Switzerland, and Cambridge, UK.

Berggren, A., Birath, B. & Kindvall, O. (2002) Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). *Conservation Biology*, **16**(6), 1562-69.

Berggren, A., Carlson, A. & Kindvall, O. (2001) The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets *Metrioptera roeseli*. *Journal of Animal Ecology*, **70**(4), 663-70.

Berry, O., Tocher, M.D. & Sarr, S.D. (2004) Can assignment tests measure dispersal? *Molecular Ecology*, **13**, 551-61.

Bhattacharya, M., Primack, R.B. & Gerwein, J. (2003) Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation*, **109**(1), 37-45.

Bonte, D., Lens, L., Maelfait, J.P., Hoffmann, M. & Kuijken, E. (2003) Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia*, **135**(2), 227-33.

Bowne, D.R., Peles, J.D. & Barrett, G.W. (1999) Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). *Landscape Ecology*, **14**(1), 53-65.

Bright, P.W. (1998) Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Animal Behaviour*, **56**, 1485-90.

Brooker, R., Travis, J., Clark, E. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245**(1), 59-65.

Brunzel, S., Elligsen, H. & Frankl, R. (2004) Distribution of the Cinnabar moth *Tyria jacobaeae* L. at landscape scale: use of linear landscape structures in egg laying on larval hostplant exposures. *Landscape Ecology*, **19**(1), 21-27.

Bullock, J.M., Kenward, R.E. & Hails, R.S. (2001) *Dispersal Ecology* Blackwell, Oxford.

Cant, E.T., Smith, A.D., Reynolds, D.R. & Osborne, J.L. (2005) Tracking butterfly flight paths across the landscape with harmonic radar. *Proceedings of the Royal Society B-Biological Sciences*, **272**(1565), 785-90.

Cargnelutti, B., Reby, D., Desneux, L., Angibault, J.M., Joachim, J. & Hewison, A.J.M. (2002) Space use by roe deer in a fragmented landscape some preliminary results. *Revue D Ecologie-La Terre Et La Vie*, **57**(1), 29-37.

Carlsson, J., Aarestrup, K., Nordwall, F., Naslund, I., Eriksson, T. & Carlsson, J.E.L. (2004) Migration of landlocked brown trout in two Scandinavian streams as revealed from trap data. *Ecology of Freshwater Fish*, **13**(3), 161-67.

Catchpole, R.D.J. (2007) *England Habitat Network Information Note* Natural England Internal Briefing Note

Chapman, D.S., Dytham, C. & Oxford, G.S. (2007) Landscape and fine-scale movements of a leaf beetle: The importance of boundary behaviour. *Oecologia*, **154**(1), 55-64.

Charrier, S., Petit, S. & Burel, F. (1997) Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: A radio-tracing study. *Agriculture Ecosystems & Environment*, **61**(2-3), 133-44.

Clevenger A.P., C.B.G.K. (2001 Y) Drainage culverts as habitat linkages and factors affecting passage by mammals. *Journal of Applied Ecology, 38, 1340-1349*.

Coffman, C.J., Nichols, J.D. & Pollock, K.H. (2001) Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches. *Oikos*, **93**(1), 3-21.

Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Diversity & Distributions*, **10**, 135-41.

Conradt, L., Bodsworth, E.J., Roper, T.J. & Thomas, C.D. (2000) Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**(1452), 1505-10.

Conradt, L. & Roper, T.J. (2006) Nonrandom movement behavior at habitat boundaries in two butterfly species: Implications for dispersal. *Ecology*, **87**(1), 125-32.

Cooper, H. & Rosenthal, R. (1980) Statistical versus traditional procedures for summarizing research findings. *Psychology Bulletin*, **87**, 442-49.

Danielson, B.J. & Anderson, G.S. (1999). Habitat selection in geographically complex landscapes. In *Landscape Ecology of Small Mammals* (eds G.W. Barrett & J.D. Peles). Springer-Verlag, New York.

Danielson, B.J. & Hubbard, M.W. (2000) The influence of corridors on the movement behavior of individual *Peromyscus polionotus* in experimental landscapes. *Landscape Ecology*, **15**(4), 323-31.

Davies, A.A. & Maclean, G.L. (1997) Avian response to landscape elements (tesserae) in an upland grassland habitat. *Ostrich*, **68**(1), 1-7.

Davis-Born, R. & Wolff, J.O. (2000) Age- and sex-specific responses of the gray-tailed vole, *Microtus canicaudus*, to connected and unconnected habitat patches. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **78**(5), 864-70.

Debinski, D.M., Ray, C. & Saveraid, E.H. (2001) Species diversity and scale of the landscape mosaic: do scales of movement and patch size affect diversity? *Biological Conservation*, **98**, 179-90.

Defra. (2002). Working with the grain of nature: A biodiversity strategy for England. In. Department for Environment, Food and Rural Affairs, London.

Dennis, R.L.H. & Hardy, P.B. (2007) Support for mending the matrix: resource seeking by butterflies in apparent non-resource zones. *Journal of Insect Conservation*, **11**(2), 157-68.

DerSimonian, R. & Laird, N. (1986) Meta-analysis in clinical trials. *Controlled Clinical Trials*, **7**(177-188).

Desrochers, A. & Hannon, S.J. (1997) Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology*, **11**(5), 1204-10.

Diekotter, T., Speelmans, M., Dusoulier, F., Van Wingerden, W., Malfait, J.P., Crist, T.O., Edwards, P.J. & Dietz, H. (2007) Effects of landscape structure on movement patterns of the flightless bush cricket *Pholidoptera griseoaptera*. *Environmental Entomology*, **36**(1), 90-98.

Donald, P.F. & Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, **43**(2), 209-18.

Doncaster, C.P., Rondinini, C. & Johnson, P.C.D. (2001) Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology*, **70**(1), 33-46.

Dover, J.W. & Fry, G.L.A. (2001) Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape. *Entomologia Experimentalis Et Applicata*, **100**(2), 221-33.

Dzialak, M.R., Lacki, M.J., Larkin, J.L., Carter, K.M. & Vorisek, S. (2005) Corridors affect dispersal initiation in reintroduced peregrine falcons. *Animal Conservation*, **8**(4), 421-30.

Edwards, P., Clarke, M., DiGuiseppi, C., Pratap, S., Roberts, I. & Wentz, R. (2002) Identification of randomized controlled trials in systematic reviews:

accuracy and reliability of screening records. *Statistics in Medicine*, **21**, 1635-40.

EEC. (1992). Council Directive 92/43/EEC of 21st May 1992 on the conservation of natural habitats and of wild flora and fauna. In. HMSO, London.

Farina, A. (2000) *Landscape Ecology in Action* Kluwer Academic, Dordrecht, The Netherlands.

Foppen, R. & Reijnen, R. (1994) The Effects of Car Traffic on Breeding Bird Populations in Woodland .2. Breeding Dispersal of Male Willow Warblers (*Phylloscopus trochilus*) in Relation to the Proximity of a Highway. *Journal of Applied Ecology*, **31**(1), 95-101.

Foppen, R.P.B., Bouwma, I.M., Kalkhoven, J.T.R., Dirksen, J. & van Opstal, S., eds. (2000) *Corridors of the Pan-European Ecological Network: Concepts and examples for terrestrial and freshwater vertebrates (ECNC Technical report series)* European Centre for Nature Conservation, Tilburg, The Netherlands.

Forester, J.D., Ives, A.R., Turner, M.G., Anderson, D.P., Fortin, D., Beyer, H.L., Smith, D.W. & Boyce, M.S. (2007) State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, **77**(2), 285-99.

Forman, R.T.T. & Godron, M. (1986) *Landscape Ecology*, 1st edn. John Wiley & Sons, Chichester.

Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L. & Morales, J.M. (2005) Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, **20**(3), 273-87.

Frampton, G.K., Cilgi, T., Fry, G.L.A. & Wratten, S.D. (1995) Effects of Grassy Banks on the Dispersal of Some Carabid Beetles (Coleoptera, Carabidae) on Farmland. *Biological Conservation*, **71**(3), 347-55.

Franzen, M. & Nilsson, S. (2007) What is the required minimum landscape size for dispersal studies? *Journal of Animal Ecology*, **76**(6), 1224-30.

Frey, S.N. & Conover, M.R. (2006) Habitat use by meso-predators in a corridor environment. *Journal of Wildlife Management*, **70**(4), 1111-18.

Fried, J.H., Levey, D.J. & Hogsette, J.A. (2005) Habitat corridors function as both drift fences and movement conduits for dispersing flies. *Oecologia*, **143**(4), 645-51.

Garant, D., Kruuk, L.E.B. & Wilkin, T.A. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature*, **433**(7021), 60-65.

Goheen, J.R., Swihart, R.K., Gehring, T.M. & Miller, M.S. (2003) Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos*, **102**(1), 95-103.

Gomez, J.M. (2003) Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography*, **26**(5), 573-84.

Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. & Evans-Freke, I. (1998) Metapopulation dynamics, abundance and distribution in a microecosystem. *Science*, **281**, 2045-47.

Goodwin, B.J. & Fahrig, L. (2002) How does landscape structure influence landscape connectivity? *Oikos*, **99**(3), 552-70.

Grez, A.A. & Prado, E. (2000) Effect of plant patch shape and surrounding vegetation on the dynamics of predatory coccinellids and their prey *Brevicoryne brassicae* (Hemiptera : Aphididae). *Environmental Entomology*, **29**(6), 1244-50.

Gutierrez, D. & Thomas, C.D. (2000) Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni Ecological Entomology*, **25**(2), 165-70.

Haddad, N.M. (1999) Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications*, **9**(2), 612-22.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S. & Spira, T. (2003) Corridor use by diverse taxa. *Ecology*, **84**(3), 609-15.

Haddad, N.M. & Tewksbury, J.J. (2005) Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications*, **15**(1), 250-57.

Hanski, I. (1999) *Metapopulation Ecology* Oxford University Press, Oxford.

Hanski, I. & Gaggiotti, O. (2004). Metapopulation biology: past, present, and future. In *Ecology, Genetics, and Evolution of Metapopulations* (eds I. Hanski & O. Gaggiotti), pp. 3-22. Academic Press, San Diego, USA.

Haynes, K.J. & Cronin, J.T. (2003) Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology*, **84**(11), 2856-66.

Hein, S., Gombert, J., Hovestadt, T. & Poethke, H.J. (2003) Movement patterns of the bush cricket *Platycleis albopunctata* in different types of habitat: matrix is not always matrix. *Ecological Entomology*, **28**(4), 432-38.

Higgins, J.P.T. & Spiegelhalter, D.J. (2002) Being sceptical about meta-analyses: A bayesian perspective on magnesium trials in myocardial infarction. *International Journal of Epidemiology*, **31**, 96-104.

Higgins, S. & Richardson, D. (1999) Predicting plant migration rates in a changing world: The role of long-distance dispersal *American Naturalist*, **153**(5), 464-75.

Hocking, J.G. & Young, G.S. (1961) *Topology* Addison Wesley.

Hofe, H.v. & Gerstmeier, R. (2001) Ecological preferences and movement patterns of carabid beetles along a river bank. *Revue d'Écologie (la Terre et la Vie)*, **56**(4), 313-20.

Holloway, G.J., Dickson, J.D., Harris, P.W. & Smith, J. (2003) Dynamics and foraging behaviour of adult hornet robberflies, *Asilus crabroniformis*: implications for conservation management. *Journal of Insect Conservation*, **7**(3), 127-35.

Hopkins, J.J., Allison, H.M., Walmsley, C.A., Gaywood, M. & Thurgate, G. (2007) *Conserving biodiversity in a changing climate: guidance on building capacity to adapt* Department for the Environment, Food and Rural Affairs.

Hughes, C.L., Dytham, C. & Hill, J.K. (2007) Modelling and analysing evolution of dispersal in populations at expanding range boundaries. *Ecological Entomology*, **32** 437-45.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007) *A Climatic Atlas of European Breeding Birds* Lynx Edicions.

IPCC. (2007). Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In, p 104. Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.) IPCC, Geneva, Switzerland.

Jehle, R. & Arntzen, J.W. (2000) Post-breeding migrations of newts (*Triturus cristatus* and *T. marmoratus*) with contrasting ecological requirements. *Journal of Zoology*, **251**, 297-306.

Johansson, M.E. & Nilsson, C. (1993) Hydrochory, Population-Dynamics and Distribution of the Clonal Aquatic Plant Ranunculus-Lingua. *Journal of Ecology*, **81**(1), 81-91.

Jongman, R.H.G. & Pungetti, G., eds. (2004) *Ecological Networks and Greenways: Concepts, Design, Implementation* Cambridge University Press, Cambridge.

Kettunen, M., Terry, A. & Tucker, G. (2007) *Preparatory work for developing the guidance on the maintenance of landscape connectivity features of major importance for wild flora and fauna (implementation of Article 3 or the Birds*

*Directive (79/409/EEC) and Article 10 of the Habitats Directive (92/43/EEC)) - A proposal for terms and definitions. EC Project 'Guidelines: Adaptation, Fragmentation'* IEEP.

Kollmann, J. & Schill, H.P. (1996) Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio aka Plant Ecology*, **125**(2), 193-205.

Kozakiewicz, M., Kozakiewicz, A., Lukowski, A. & Gortat, T. (1993) Use of Space by Bank Voles (*Clethrionomys-Glareolus*) in a Polish Farm Landscape. *Landscape Ecology*, **8**(1), 19-24.

Kreyer, D., Oed, A., Walther-Hellwig, K. & Frankl, R. (2004) Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). *Biological Conservation*, **116**(1), 111-18.

Kupfer, J.A., Malanson, G.P. & Franklin, S.B. (2006) Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global ecology and biogeography*, **15**(1), 8-20.

Kuussaari, M., Nieminen, M. & Hanski, I. (1996) An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology*, **65**(6), 791-801.

Lamberti, P., Mauri, L., Merli, E., Dusi, S. & Apollonio, M. (2006) Use of space and habitat selection by roe deer *Capreolus capreolus* in a Mediterranean coastal area: how does woods landscape affect home range? *Journal of Ethology*, **24**(2), 181-88.

Larkin, J.L., Cox, J.J., Wichrowski, M.W., Dzialak, M.R. & Maehr, D.S. (2004) Influences on release-site fidelity of translocated elk. *Restoration Ecology*, **12**(1), 97-105.

Light, T. (2003) Success and failure in a lotic crayfish invasion: the roles of hydrologic variability and habitat alteration. *Freshwater Biology*, **48**(10), 1886-97.

Lipsey, M.W. & Wilson, D.B. (2001) *Practical meta-analysis* Sage, Thousand Oaks.

Lu, J. & Zhang, Z. (2004) Effects of habitat and season on removal and hoarding of seeds of wild apricot (*Prunus armeniaca*) by small rodents. *Acta Oecologica*, **26**(3), 247-54.

Lucas, M.C. & Batley, E. (1996) Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: Implications for river management. *Journal of Applied Ecology*, **33**(6), 1345-58.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography* Princeton University Press, Oxford.

MacDonald, D.W., Tew, T.E. & Todd, I.A. (2004) The ecology of weasels (*Mustela nivalis*) on mixed farmland in southern England. *Biologia*, **59**(2), 235-41.

Malmgren, J.C. (2002) How does a newt find its way from a pond? Migration patterns after breeding and metamorphosis in great crested newts (*Triturus cristatus*) and smooth newts (*T. vulgaris*). *Herpetological Journal*, **12**(1), 29-35.

Mauremooto, J.R., Wratten, S.D., Worner, S.P. & Fry, G.L.A. (1995) Permeability of Hedgerows to Predatory Carabid Beetles. *Agriculture Ecosystems & Environment*, **52**(2-3), 141-48.

McIntyre, S. & Martin, T.G. (2002) Managing intensive and extensive land uses to conserve grassland plants in sub-tropical eucalypt woodlands. *Biological Connservation*, **107**(2), 241-52.

Mellina, E., Hinch, S.G. & MacKenzie, K.D. (2005) Seasonal movement patterns of stream-dwelling rainbow trout in north-central British Columbia, Canada. *Transactions of the American Fisheries Society*, **134**(4), 1021-37.

Miaud, C. & Sanuy, D. (2005) Terrestrial habitat preferences of the natterjack toad during and after the breeding season in a landscape of intensive agricultural activity. *Amphibia-Reptilia*, **26**(3), 359-66.

Michels, E., Cottenie, K., Neys, L., De Gelas, K., Coppin, P. & De Meester, L. (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Molecular Ecology*, **10**(8), 1929-38.

Mitchell, R.J., Morecroft, M.D., Acreman, M., Crick, H.Q.P., Frost, M., M.Harley, Maclean, I.M.D., Mountford, O., Piper, J., Pontier, H., Rehfisch, M.M., Ross, L.C., Smithers, R.J., Stott, A., Walmsley, C.A., Watts, O. & Wilson, E. (2007) *England Biodiversity Strategy- Towards adaptation to climate change. Final Report to Defra for contract CR0327.* Defra, London.

Murphy, H.T. & Lovett-Doust, J. (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos*, **105**, 3-14.

NHS Centre for Reviews and Dissemination. (2001) *Undertaking systematic review of research on effectiveness.* NHS CRD, University of York.

Ockinger, E. & Smith, H.G. (2008) Do corridors promote dispersal in grassland butterflies and other insects? *Landscape Ecology*, **23**(1), 27-40.

Ogilvie, D., Fayter, D., Petticrew, M., Sowden, A., Thomas, S., Whitehead, M., Worthy, G. (2008) The harvest plot: A method for synthesising evidence about the differential effects of interventions. *BMC Medical Research Methodology*, **8**, 8.

Paetkau, D., Slade, R., Burden, M. & Estoup, A. (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology*, **13**(55-65).

Parmesan, C. (2006 ) Ecological and evolutionary responses to recent climate change *Annual Review of Ecology Evolution and Systematics*, **37** 637-69

Pearson, R.G. & Dawson, T.P. (2005) Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation*, **123**(3), 389-401.

Piper, J.M., Wilson, E.B., Weston, J., Thompson, S. & Glasson, J. (2006) *Spatial planning for biodiversity in our changing climate. English Nature Research Reports Number 677* English Nature.

Poysa, H. & Paasivaara, A. (2006) Movements and mortality of common goldeneye *Bucephala clangula* broods in a patchy environment. *Oikos*, **115**(1), 33-42.

Pryke, S.R. & Samways, M.J. (2001) Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation*, **101**(1), 85-96.

Pullin, A.S. & Stewart, G.B. (2006) Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, **20**, 1647-56.

Purse, B.V., Hopkins, G.W., Day, K.J. & Thompson, D.J. (2003) Dispersal characteristics and management of a rare damselfly. *Journal of Applied Ecology*, **40**(4), 716-28.

Redpath, S.M. (1995) Habitat Fragmentation and the Individual - Tawny Owls *Strix Aluco* in Woodland Patches. *Journal of Animal Ecology*, **64**(5), 652-61.

Rico, A., Kindlmann, P. & Sedlacek, F. (2007a) Barrier effects of roads on movements of small mammals. *Folia Zoologica*, **56**(1), 1-12.

Rico, A., Kindlmann, P. & Sedlacek, F. (2007b) Road crossing in bank voles and yellow-necked mice. *Acta Theriologica*, **52**(1), 85-94.

Ries, L., Fletcher, R., Battin, J. & Sisk, T. (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and Systematics*, **35**, 491-522.

Rodriguez, A., Andren, H. & Jansson, G. (2001) Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos*, **95**(3), 383-96.

Rühe, F. (1999) Effect of stand structures in arable crops on brown hare (*Lepus europaeus*) distribution. *Gibier Faune Sauvage*, **16**(4), 317-37.

Russell, R.E., Swihart, R.K. & Craig, B.A. (2007) The effects of matrix structure on movement decisions of meadow voles (*Microtus pennsylvanicus*). *Journal of Mammalogy*, **88**(3), 573-79.

Sakuragi, M., Igota, H., Uno, H., Kaji, K., Kaneko, M., Akamatsu, R. & Maekawa, K. (2003) Seasonal habitat selection of an expanding sika deer *Cervus nippon* population in eastern Hokkaido, Japan. *Wildlife Biology*, **9**(2), 141-53.

Samways, M.J. & Lu, S.S. (2007) Key traits in a threatened butterfly and its common sibling: implications for conservation. *Biodiversity and Conservation*, **16**(14), 4095-107.

Schaefer, J.F., Marsh-Matthews, E., Spooner, D.E., Gido, K.B. & Matthews, W.J. (2003) Effects of barriers and thermal refugia on local movement of the threatened leopard darter, *Percina pantherina*. *Environmental Biology of Fishes*, **66**(4), 391-400.

Sharp, S. (1998) Meta-analysis regression: statistics, biostatistics, and epidemiology. *Stata Technical Bulletin*, **42**, 16-22.

Shepherd, B. & Whittington, J. (2006) Response of wolves to corridor restoration and human use management. *Ecology and Society*, **11**(2).

Shirley, S.M. (2006) Movement of forest birds across river and clearcut edges of varying riparian buffer strip widths. *Forest Ecology and Management*, **223**(1-3), 190-99.

Spencer, J.W. & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, **62**, 77-93.

St Clair, C.C. (2003) Comparative permeability of roads, rivers, and meadows to songbirds in Banff National Park. *Conservation Biology*, **17**(4), 1151-60.
Sterne, J.A., Egger, M. & Smith, G.D. (2001) Systematic reviews in health care: Investigating and dealing with publication and other biases in meta-analysis. *British Medical Journal*, **323**(101-5).

Stevens, V.M., Leboulenge, E., Wesselingh, R.A. & Baguette, M. (2006) Quantifying functional connectivity: experimental assessment of boundary permeability for the natterjack toad (*Bufo calamita*). *Oecologia*, **150**(1), 161-71.

Stevens, V.M., Polus, E., Wesselingh, R.A., Schtickzelle, N. & Baguette, M. (2004) Quantifying functional connectivity: experimental evidence for patch-specific resistance in the Natterjack toad (*Bufo calamita*). *Landscape Ecology*, **19**(8), 829-42.

Stewart, G.B., Pullin, A.S. & Tyler, C. (2007) The effectiveness of asulam for Bracken (*Pteridium aquilinum*) control in the U.K: A meta-analysis. . *Environmental Management*, **40**, 747-60.

Storfer, A., Murphy, M., Evans, J., Goldberg, C., Robinson, S., Spear, S., Dezzani, R., Delmelle, E., Vierling, L. & Waits, L. (2007) Putting the 'landscape' in landscape genetics. *Heredity*, **98**, 128-42.

Sunnucks, P. (2000) Efficient genetic markers for population biology. *Trends in Ecology & Evolution*, **15**(5), 199-203.

Szacki, J. (1999) Spatially structured populations: how much do they match the classic metapopulation concept? *Landscape Ecology*, **14**(4), 369-79.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity as a vital element of landscape structure. *Oikos*, **68**(3), 571-73.

Thomas, C., Franco, A. & Hill, J. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, **21**(8), 415-16.

Thomas, C.D. & Kunin, W.E. (1999) The spatial structure of populations. *Journal of Animal Ecology*, **68**, 647-57.

Thompson, S.G. & Sharp, S.J. (1999) Explaining heterogeneity in meta-analysis: a comparison of methods. *Statistics in Medicine*, **18**, 2693-708.

Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7-19.

Travis, J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 467-73.

UK Biodiversity Partnership. (2007) *Conserving Biodiversity - The UK Approach* Defra, London.

UNDP. (2007) *Fighting climate change: human solidarity in a divided world* United Nations Development Program, New York.

Valtonen, A. & Saarinen, K. (2005) A highway intersection as an alternative habitat for a meadow butterfly: effect of mowing, habitat geometry and roads on the ringlet (*Aphantopus hyperantus*). *Annales Zoologici Fennici*, **42**(5), 545-56.

Vanreusel, W. & Van Dyck, H. (2007) When functional habitat does not match vegetation types: A resource-based approach to map butterfly habitat. *Biological Conservation*, **135**(2), 202-11.

Veenbaas, G. & Brandjes, G.J. (1998). The use of faunapassages along waterways under motorways. In *Key concepts in landscape ecology. Proceedings of the 1998 European Congress of the International Association for Landscape Ecology,* (eds J.W. Dover & R.G.H. Bunce). International Association for Landscape Ecology (IALE(UK)), Aberdeen, Myerscough College, UK, 3-5 September 1998.

Vignieri, S.N. (2005) Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (*Zapus trinotatus*). *Molecular Ecology*, **14**(7), 1925-37.

Walmsley, C.A., Smithers, R.J., Berry, P.M., Harley, M., Stevenson, M.J. & Catchpole, R.E. (2007). Modelling Natural Resource Responses to Climate Change: a synthesis for biodiversity conservation. UKCIP, Oxford.

Walser, J.C. (2004) Molecular evidence for limited dispersal of vegetative propagules in the epiphytic lichen *Lobaria pulmonaria*. *American Journal of Botany*, **91**(8), 1273-76.

Waples, R.S. & Gaggiotti, O. (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, **15**, 1419-39.

Warren, M., Hill, J., Thomas, J., Asher, J., Fox, R., Huntley, B., Roy, D., Telfer, M., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S., Greatorex-Davies, J., Moss, D. & Thomas, C. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change *Nature*, **414**(6859), 65-69.

Werth, S., Wagner, H.H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J.M. & Scheidegger, C. (2006) Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology*, **87**(8), 2037-46.

With, K.A. & King, A.W. (1997) The use and misuse of neutral landscape models in ecology. *Oikos*, **79**, 219-29.

Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Prentice Hall, New Jersey.

# Appendix 1. Review protocol (including scoping searches)

**CENTRE FOR EVIDENCE-BASED CONSERVATION**

**SYSTEMATIC REVIEW No. 43**

**WORKING TITLE: WHAT IS THE EVIDENCE FOR THE DEVELOPMENT OF CONNECTIVITY TO IMPROVE SPECIES MOVEMENT, AS AN ADAPTATION TO CLIMATE CHANGE?**

**CONSULTATION DRAFT REVIEW PROTOCOL**


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## COVER SHEET

| | |
|---|---|
| Title | **Working title: What is the evidence for the development of connectivity to improve species movement, as an adaptation to climate change?** |
| Systematic review | **N$^{o.}$43** |
| Reviewer(s) | **Amy Eycott, Kevin Watts, Lisette Buyung-Ali, Gavin Stewart, and Andrew Pullin** |
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| Contact address | **Rural & Urban Landscape Ecology Group, Ecology Division, Forest Research, Alice Holt Lodge, Farnham, Surrey. GU10 4LH. UK.** |
| Sources of support | **Defra, Scottish Natural Heritage, Countryside Council Wales, Woodland Trust, Forestry Commission** |
| Conflicts of interest | **None** |

## 1. BACKGROUND

### 1.1 Policy context and need for review:

In the context of commitments to halt the loss of biodiversity and meet other targets in the UK Biodiversity Action Plan, there is a need to consider the impacts of climate change on species, for understanding of their response and provision of potential adaptation measures (UK Biodiversity Partnership 2007). This is in addition to commitments in place which require reduction of the impacts of fragmentation. The EU Habitats Directive (EEC, 1992; transposed into law as the Habitats Regulations 1994) obliges the UK to endeavour to improve the ecological coherence of Natura 2000 sites (see Box 1) and maintain or restore favourable conservation status to species of community importance, many of which have been adversely affected by fragmentation. The England Biodiversity Strategy (EBS) Climate Change Adaptation workstream is currently engaged in promoting adaptation, and developing an adaptation strategy across all sectors of the EBS in recognition of the threat of climate change to meeting their biodiversity objectives.

### 1.2 Connectivity and climate change

There is a growing body of evidence of impacts of climate change on biodiversity, which include:

- Changes in phenology, which may lead to loss of synchrony between species (e.g. Visser *et al.*, 1998)
- Changes in species distribution (including arrival of non-native species and potentially loss of species for which suitable climate conditions disappear, e.g. Wilson *et al.*, 2005)
- Subsequent changes in community composition and interspecific interactions (e.g. Klanderud, 2005)
- Changes in ecosystem function (e.g. Fay *et al.*, 2008)
- Loss of physical space due to sea level rise and increased storminess (e.g. Desantis *et al.*, 2007)

Projected shifts in suitable climate space may force species to adjust their ranges if they are to survive (Walmsley *et al.*, 2007) and many species groups are already showing range margin movement (Parmesan, 2006). Many species may not be able to move rapidly enough to track their future climate space and this problem is further compounded by fragmentation (Travis, 2003).

Habitat isolation, urbanisation and agricultural intensification may all inhibit species movement. Dispersal can become energetically more costly and have higher mortality risks (Pearson & Dawson, 2005; Warren *et al.*, 2001; Thomas *et al.*, 2006). Even mobile species such as butterflies have been shown to encounter difficulty moving quickly enough in response to climate change (Gutierrez & Thomas, 2000).

A contrasting impact of climate change is that invasive species may be able to spread further. In order to protect native species assemblages, conservation interventions may be required to reduce connectivity for invasive species (Manchester & Bullock, 2000).

**Box 1**

Article 10 of the Habitats directive
'*Member States shall endeavour, where they consider it necessary, in their landuse planning and development policies and, in particular, with a view to improving the ecological coherence of the Natura 2000 network, to encourage the management of features of the landscape which are of major importance for wild fauna and flora. Such features are those which, by virtue of their linear and continuous structure (such as rivers with their banks or the traditional systems for marking field boundaries) or their function as stepping stones (such as ponds or small woods), are essential for the migration, dispersal and genetic exchange of wild species.*'

Article 3 of the Birds directive
'*…Member States shall take the requisite measures to preserve, maintain or re-establish a sufficient diversity and area of habitats for all the species of birds referred to in Article 1. 2. The preservation, maintenance and re-establishment of biotopes and habitats shall include […] (b) upkeep and management in accordance with the ecological needs of habitats inside and outside the protected zones…*'

### 1.3 (Re)Building connectivity as an adaptation measure

Measures to increase species' resilience and their speed of response are both important to limit the consequences of climate change (Hannah *et al*., 2002; Hulme, 2005; Pearson & Dawson, 2005). Measures proposed to increase resilience in the face of biodiversity threats include protected areas, varied and functional ecosystems and good habitat quality (Hopkins *et al*., 2007; Mitchell *et al*., 2007).

However, a key measure for increasing the speed at which species are able to respond to climate change is probably ensuring landscapes are permeable to species movement. There are a number of complex links and feedback processes in moving from increasing individuals' movement to predicting changes in the ranges of populations as a climate response. The link between increased species movement and (meta) population persistence has strong foundations in ecological theory (Hanski & Gaggiotti, 2004) but the importance of dispersal on population dynamics can vary with the spatial structure of the population (Thomas & Kunin, 1999).

Landscape scale interventions such as the development of functional ecological networks are often proposed as a measure to limit the consequences of habitat fragmentation and so help species adapt to the impacts of climate change. Functional ecological networks are based on functional connectivity, as contrasted to networks based purely on structural connectedness. For individual species, a landscape is functional if it allows a species to carry out all its ecological functions including movement for foraging, mate finding and dispersal. For all but the most immobile and most mobile species, functional connectivity will be affected by the availability and spatial arrangement of habitat and the composition and arrangement of intervening landscape (Tischendorf & Fahrig, 2000; Murphy & Lovett-Doust, 2004). A basic principle of functional connectivity is that some land covers or land uses are more permeable than others (Donald & Evans, 2006). The implication of this definition of connectivity is that different species will respond in different ways so connectivity can only be defined from each species viewpoint (Tischendorf & Fahrig, 2000).

Management, expansion, restoration and creation of suitable habitat, provision of buffer zones around habitat, provision of corridors and stepping-stones between habitats and improving matrix permeability, are the ‘building blocks’ for functional ecological networks. From a practical perspective, in the UK there may be limited potential for creation of structural networks based on large core areas and corridors of near-continuous habitat applied elsewhere in the world (e.g. North and South America and Europe; Jongman & Pungetti, 2004). This is due to the limited scale of land tenure, current landscape use and the current species composition (Bennett, 2004). However, each kind of network aims to incorporate core breeding areas with permeable elements between them.

Functional ecological network models have already been used throughout the UK to target and evaluate conservation options at various spatial scales (Catchpole *et al*., 2007; Watts *et al*., 2007). This reflects recognition of a potential limitation of site-based conservation systems. For example, the recent UK Biodiversity Partnership publication ‘*Conserving Biodiversity in a changing climate: guidance on building capacity to adapt*’ advocates provision of ecological networks as one of several measures that can be taken to encourage adaptation (Hopkins *et al*., 2007, p.18).

Functional ecological networks are based on first principles derived from ecological theory (e.g. island biogeography, MacArthur & Wilson 1967; metapopulation dynamics, Hanski 1999). However some authors have noted that there is little supporting empirical evidence to demonstrate the practicality and effectiveness of ecological networks in general (e.g. Jongman & Pungetti, 2004) or to guide design features such as size, shape, spacing, or structure.

With the current focus on evidenced-based policies, it is important to test links between general principles of functional connectivity and specific species-based studies. This systematic review will help ensure that any further development and application of ecological networks as an adaptation to climate change would be:

- Based on the best available evidence
- Refined and applied, to benefit species or groups of species
- Accepted by the wider policy, planning and conservation communities.

## 2. OBJECTIVE OF THE REVIEW

The overall objective is to review evidence that supports (or does not support) the principles of landscape functional connectivity. This is in order to help ensure that policies and actions taken in the UK to increase (or decrease) species movement by changing landscape connectivity are supported by robust scientific evidence. A key secondary objective is to identify knowledge gaps.

### 2.1 Primary question

Which landscape features affect species movement and dispersal?

This question can be broken into components based on potential subjects, interventions, outcomes, and study format and design.

As the question begins 'what landscape features…' (the intervention component) a broad range of landscape features and characteristics associated with connectivity will be searched initially, a list of which is given in section 3.1.1. However, there are options to broaden or narrow the scope of each of the subject, outcome, study format and study design aspects, depending on the evidence available, which are given in Table 1.

The breadth of studies included will be decided upon when initial searches and title filters have been performed and the amount of evidence becomes clear. If a large number of articles are obtained by the search, the review will be limited to subjects, interventions and outcomes ranked higher in the table. Different levels of analytical detail may be applied to narrower and broader search scopes. The review is intended to support conservation policy and activity in the UK, so there will be a focus on UK studies and species, where possible, as results from other species or biogeographic regions may be misleading.

**Table 1. Options for scope of question: Subject, outcome, study format and design**

| Subject | Intervention | Outcome | Study format | Study design |
|---|---|---|---|---|
| 1. UK species<br><br>2. Defra potential invasives<br><br>3. Temperate Europe species<br><br>4. Other species in comparable landscapes[1]<br><br>5. All species | See section 3.1.1 for comprehensive list | 1. Change in dispersal rate<br><br>2. Change in movement distance<br><br>3. (Re)colonization of vacant patches (inc. increase in proportion of patches occupied)<br><br>4. Increased range<br><br>5. Genetic evidence of dispersal/ isolation | 1. Empirical evidence of movement<br><br>2. Genetic evidence<br><br>3. Anecdotal or qualitative evidence<br><br>4. Modelling/ simulations | 1. Land use/habitat change(before and after/control and intervention designs - BACI)<br><br>2. Habitat change without BACI design but including a spatial OR a temporal comparator<br><br>3. Comparison between different landscape structures or compositions |

[1]Similarity of landscape structure for this analysis will refer to studies with patches of semi-natural habitat within a primarily agricultural and/or urban matrix.

[2]Habitat creation or restoration is used in this instance broadly to include creation, re-creation, restoration, regeneration, and reclamation (see section 2.2).

### 2.2. Evidence: restoration, degradation, creation and destruction of habitats

Habitat creation or restoration may not have the exact opposite impact of degradation, therefore it is important to keep evidence from creative/positive changes and destructive/negative intervention separate. This does raise the issue of 'what is a negative change?' which will be defined by reference to the species being studied.

Habitat restoration, re-creation, reclamation, regeneration and creation are all used within the literature, in many cases interchangeably. The Society for Ecological Restoration defines restoration as "*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*" (http://www.ser.org/content/ecological_restoration_primer.asp#3). This implies the location of a habitat defines whether it is being restored or created.

For simplicity, in this document 'habitat creation and restoration' is used as a broad phrase which encompasses restoration, re-creation, reclamation, regeneration and creation, as there is no consistently used definition of a starting point between restoration and re-creation (see Glossary in Appendix 1). The UK BAP targets define restoration as "*where substantial effort is needed to [restore] a site with relict features (or historically former habitat)*." However, the differences between systems where restoration activities have different starting points will be an important consideration when reviewing evidence.

Similarly, there is a lack of clearly defined boundaries between habitat disturbance, degradation, disruption and destruction (see Glossary). It is however, important to note the difference between landscape degradation (increased fragmentation and isolation of patches) and habitat degradation (loss of quality of an area of habitat), although each will have impacts on the other. Specifically, we use 'degradation' to refer to loss of condition or destruction of the quantifiable ecological communities that make up habitats.

## 3. METHODS

### 3.1 Search strategy

#### *3.1.1. General sources*

The search will include general computerised/web databases such as:
1) ISI Web of Science
2) Directory of Open Access Journals
3) Index to Theses Online
4) CAB Abstracts
5) Conservation Evidence.com

Potential keywords will be grouped into four categories for efficiency of searching as follows:

Interventions - barrier, bridge, [difference in] connectivity, connectedness, connection, corridor, stepping stone, network, links or linkages, spatial patterns, highways, habitat mosaics, [difference in] permeability, buffer zone, edge, heterogeneity, patches

Outcome - movement, dispersal, isolation, migration, colonisation, invasion, immigration, emigration

Spatial context - habitat, landscape, matrix, fragmentation,

Subject context – population, metapopulation, species, conservation, biodiversity

A wild card term will be used when appropriate. Search terms are inclusive; for example searching for 'dispersal' will also detect 'long-distance dispersal'.

Examples from scoping searches are provided in Appendix 2 (Tables 2 and 3).

In addition, web searches will be performed using the search engines: www.alltheweb.com, www.scirus.com, and www.google.com. The first 50 hits (.doc .txt .xls and .pdf documents where this can be separated) from each data source will be examined for appropriate data. No further links from the captured website will be followed unless to a document/pdf file.

### *3.1.2 Specialist sources*

Searches for data published by statutory and non-statutory organisations will be included: Natural England (English Nature), Scottish Natural Heritage, Countryside Council for Wales, Environment and Heritage Service Northern Ireland, JNCC, CEH, Alterra, IALE, CSIRO (Australian national science agency) and the US Nature Conservancy.

Once electronic and bibliography searching is complete, recognised experts, practitioners and authors (including the project steering group) will be contacted for further recommendations and for provision of relevant unpublished material or missing data.

## 3.2 Study inclusion criteria

Study inclusion criteria will be based on the outcome of the initial search and title filter, so may be further limited by subjects, interventions and outcomes ranked higher in Table 1 depending on the number of articles obtained of each type. Marine studies are excluded at the outset, as are those without a control or comparator.

### *3.2.1 Potential reasons for heterogeneity:*

This is a (not exhaustive) list of the factors that could cause different studies of the same question or organism to have different results.

- Spatial scale of the study (considered with respect to degree of habitat fragmentation, nearest neighbour etc; dispersal distance of the organism, including rare and chance long distance dispersal; scale of matrix changes).
- Temporal scale of the study (considered with respect to the generation time of the organism; probability of dispersal; time lags for species responses; time for species to establish following initial colonisation).
- The way the effect has been measured, and in some cases analysed.
- Patch (or population) size (of both donor and recipient patches where available), also taking into account impact of edge effects.
- Landscape history (e.g. recent fragmentation or natural/long-term fragmentation).
- The different use of the terms restoration, recreation, creation.
- Habitat type.
- Landscape composition.
- Geographical location.
- Physical factors: Altitude, topography, climate (macro and microclimate; variability), geology, soil.

### 3.3 Study quality assessment

To determine the level of confidence that may be placed in selected data sets, each one must be critically appraised to assess the extent to which its research methodology is likely to prevent systematic errors or bias (Khan *et al*. 1996). Data quality assessment will be undertaken using a simple but discriminatory list of desirable characteristics e.g. control for biases such as baseline confounding, parameter estimation inaccuracy, inappropriate spatio-temporal scales, and pseudoreplication, using an explicit score system and recorded in spreadsheets. Sensitivity analyses may then be undertaken to assess the extent to which results are consistent for studies which do and do not employ methodologies that control for these biases.

### 3.4 Data extraction and synthesis

The quantity, quality and type of information available to address the subcomponents of this review are currently unknown. Inclusion and exclusion criteria, and methods for extraction and synthesis are therefore imprecise and will be the subject of amendment prior to commencing this phase of the work. Where limited information is available, or data types too diverse for quantitative synthesis, studies will be categorised according to landscape feature and species type to facilitate qualitative synthesis of outcomes. Consideration will be given to study scale and validity. Meta-analysis will be undertaken on any sufficiently homogeneous pool of data where effect sizes can be derived. Particular consideration will be give to the ecological meaningfulness of any effect size calculated.

## 4. Potential Conflicts of Interest and Sources of Support

This project was commissioned by Defra and is funded by the Forestry Commission, Countryside Council for Wales, Defra , Scottish Natural Heritage and the Woodland Trust.

## 5. Protocol References

Begon, M., Harper, J.L. & Townsend, C.R. (1996) *Ecology: Individuals, populations and communities (Third Edition)* Blackwell Science, Oxford.
Bennett, A.F. (1999) *Linkages in the Landscape* IUCN, Gland, Switzerland & Cambridge, UK.
Bennett, G. (2004) *Integrating Biodiversity Conservation and Sustainable Use: Lessons Learned From Ecological Networks* IUCN, Gland, Switzerland, and Cambridge, UK.
Bullock, J.M., Moy, I.L., Pywell, R.F., Coulson, S.J., Nolan, A.M. & Caswell, H. (2002). Plant dispersal and colonisation processes at local and landscape scales. In *Dispersal Ecology* (eds J.M. Bullock, R.E. Kenward & R.S. Hails), pp. 279-302. Blackwell Science, Oxford.
Catchpole, R.D.J. (2007) *England Habitat Network Information Note* Natural England Internal Briefing Note
Desantis, L., Bhotika, S., Williams, K. & Putz, F. (2007) Sea-level rise and drought interactions accelerate forest decline on the Gulf Coast of Florida, USA. *Global Change Biology*, **13**(11), 2349-60.
Donald, P.F. & Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, **43**(2), 209-18.
EEC. (1992). Council Directive 92/43/EEC of 21st May 1992 on the conservation of natural habitats and of wild flora and fauna. In. HMSO, London.
Farina, A. (2000) *Landscape Ecology in Action* Kluwer Academic, Dordrecht, The Netherlands.
Fay, P., Kaufman, D., Nippert, J., Carlisle, J. & Harper, C. (2008) Changes in grassland ecosystem function due to extreme rainfall events: implications for responses to climate change
*Global Change Biology*, **14**(7), 1600-08.
Forman, R.T.T. & Godron, M. (1986) *Landscape Ecology*, 1st edn. John Wiley & Sons, Chichester.
Gutierrez, D. & Thomas, C.D. (2000) Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni Ecological Entomology*, **25**(2), 165-70.
Hannah, L., Midgley, G. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global ecology and biogeography*, **11**, 485-95.
Hanski, I. (1999) *Metapopulation Ecology* Oxford University Press, Oxford.
Hanski, I. & Gaggiotti, O. (2004). Metapopulation biology: past, present, and future. In *Ecology, Genetics, and Evolution of Metapopulations* (eds I. Hanski & O. Gaggiotti), pp. 3-22. Academic Press, San Diego, USA.
Hocking, J.G. & Young, G.S. (1961) *Topology* Addison Wesley.
Hopkins, J.J., Allison, H.M., Walmsley, C.A., Gaywood, M. & Thurgate, G. (2007) *Conserving biodiversity in a changing climate: guidance on building capacity to adapt* Department for the Environment, Food and Rural Affairs.

Hulme, P. (2005) Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, **42**(5), 784 - 94.
IPCC. (2007). Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. In, p 104. Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.) IPCC, Geneva, Switzerland.
Jongman, R.H.G. & Pungetti, G., eds. (2004a) *Ecological Networks and Greenways: Concepts, Design, Implementation* Cambridge University Press, Cambridge.
Jongman, R.H.G. & Pungetti, G. (2004b). Introduction: Ecological networks and greenways. In *Ecological Networks and Greenways: Concept, Design, Implementation* (eds R.H.G. Jongman & G. Pungetti). Cambridge University Press, Cambridge.
Kettunen, M., Terry, A., Tucker, G. & Jones, A. (2007) *Guidance on the maintenance of landscape connectivity features of major importance for wild flora and fauna (Guidance on the implementation of Article 3 of the Birds Directive (79/409/EEC) and Article 10 of the Habitats Directive (92/43/EEC))* Institute for European Environmental Policy (IEEP), Brussels.
Khan, K.S., Daya, S. & Jadad, A. (1996) The importance of quality of primary studies in producing unbiased systematic reviews *Archives of Internal Medicine*, **156**, 661-66.
Klanderud, K. (2005) Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, **93**(1), 127-37.
Lipsey, M.W. & Wilson, D.B. (2001) *Practical meta-analysis* Sage, Thousand Oaks.
MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography* Princeton University Press, Oxford.
Manchester, S.J. & Bullock, J.M. (2000) The impacts of non-native species on UK biodiversity and the effectiveness of control. *Journal of Applied Ecology*, **37**(5), 845-64.
Mitchell, R.J., Morecroft, M.D., Acreman, M., Crick, H.Q.P., Frost, M., M.Harley, Maclean, I.M.D., Mountford, O., Piper, J., Pontier, H., Rehfisch, M.M., Ross, L.C., Smithers, R.J., Stott, A., Walmsley, C.A., Watts, O. & Wilson, E. (2007) *England Biodiversity Strategy- Towards adaptation to climate change. Final Report to Defra for contract CR0327.* Defra, London.
Murphy, H.T. & Lovett-Doust, J. (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos*, **105**, 3-14.
Parmesan, C. (2006 ) Ecological and evolutionary responses to recent climate change *Annual Review of Ecology Evolution and Systematics*, **37** 637-69
Pearson, R.G. & Dawson, T.P. (2005) Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation*, **123**(3), 389-401.
Piper, J.M., Wilson, E.B., Weston, J., Thompson, S. & Glasson, J. (2006) *Spatial planning for biodiversity in our changing climate. English Nature Research Reports Number 677* English Nature.
Ries, L., Fletcher, R., Battin, J. & Sisk, T. (2004) Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and Systematics*, **35**, 491-522.
Spencer, J.W. & Kirby, K.J. (1992) An inventory of ancient woodland for England and Wales. *Biological Conservation*, **62**, 77-93.
Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity as a vital element of landscape structure. *Oikos*, **68**(3), 571-73.

Thomas, C., Franco, A. & Hill, J. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, **21**(8), 415-16.
Thomas, C.D. & Kunin, W.E. (1999) The spatial structure of populations. *Journal of Animal Ecology*, **68**, 647-57.
Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7-19.
Travis, J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 467-73.
UK Biodiversity Partnership. (2007) *Conserving Biodiversity - The UK Approach* Defra, London.
UNDP. (2007) *Fighting climate change: human solidarity in a divided world* United Nations Development Program, New York.
Visser, M., van Noordwijk, A., Tinbergen, J. & Lessells, C. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, **265**(1408), 1867-70.
Walmsley, C.A., Smithers, R.J., Berry, P.M., Harley, M., Stevenson, M.J., Catchpole, R. & (Eds.). (2007) *MONARCH - Modelling Natural Resource Responses to Climate Change - a synthesis for biodiversity conservation* UKCIP, Oxford.
Warren, M., Hill, J., Thomas, J., Asher, J., Fox, R., Huntley, B., Roy, D., Telfer, M., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S., Greatorex-Davies, J., Moss, D. & Thomas, C. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change *Nature*, **414**(6859), 65-69.
Watts, K., Ray, D., Quine, C.P., Humphrey, J.W. & Griffiths, M. (2007). Evaluating Biodiversity in Fragmented Landscapes: Applications of Landscape Ecology Tools. In. Forestry Commission Information Note 085, Edinburgh.
Wilson, R., Gutierrez, D., Gutierrez, J., Martinez, D., Agudo, R. & Monserrat, V. (2005) Changes to the elevational limits and extent of species ranges associated with climate change. *Ecology Letters*, **8**(11), 1138-46.
With, K.A., Gardner, R.H. & Turner, M.G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, **78**, 151-69.

**PROTOCOL APPENDIX 1 GLOSSARY**

(Draft glossary removed: see updated glossary in final report text)

**PROTOCOL APPENDIX 2 SCOPING STUDIES**

**PILOT SCOPING OF SEARCH TERMS**

**19TH DECEMBER 2007**

Table 2. Simple initial searches on Web of Science including only papers from 1997-2007.

| | | | Hits | Of 10 most recent, number rejected on title |
|---|---|---|---|---|
| "green bridge" | | | 8 | 7 |
| "land use" | | connectivity | 205 | 2 |
| change | dispers* | "land use" | 117 | 7 |
| "land use" | species | change | 17 | 3 |
| "patch shape" | dispers* | landscape | 10 | 3 |
| "patch size" | dispers* | landscape | 161 | 1 |
| barrier | connectivity | species | 66 | 4 |
| barrier | dispers* | connectivity | 65 | 5 |
| barrier | dispers* | landscape | 50 | 4 |
| barrier | dispers* | species | 468 | 5 |
| barrier | movement | connectivity | 25 | 3 |
| barrier | movement | landscape | 46 | 3 |
| barrier | movement | species | 152 | 3 |
| barrier | moving | landscape | 12 | 9 |
| barrier | moving | species | 37 | 7 |
| barrier | track* | connectivity | 7 | 4 |
| barrier | track* | landscape | 16 | 6 |
| barrier | track* | species | 44 | 6 |
| barrier | | connectivity | 200 | 6 |
| "land use" | barrier | species | 15 | 4 |
| buffer | coloni* | | 301 | 8 |
| connectivity | metapopulation | habitat | 260 | 1 |
| connectivity | metapopulation | | 316 | 1 |
| corridor | coloni* | habitat | 38 | 0 |
| corridor | coloni* | landscape | 30 | 2 |
| corridor | coloni* | matrix | 9 | 1 |
| corridor | dispers* | habitat | 120 | 0 |
| corridor | dispers* | landscape | 87 | 1 |
| corridor | dispers* | matrix | 32 | 2 |
| corridor | movement | habitat | 99 | 0 |
| corridor | movement | landscape | 67 | 0 |
| corridor | movement | matrix | 26 | 1 |
| green bridge | species | | 26 | 9 |
| green bridge | | | 486 | 10 |
| matrix | dispers* | distance | 384 | 7 |
| matrix | permeab* | distance | 54 | 6 |
| matrix | restor* | metapopulation | 11 | 0 |
| matrix | | metapopulation | 164 | 0 |
| network | dispers* | ecolog* | 111 | 1 |

| | | | | |
|---|---|---|---|---|
| restor* | connectivity | habitat | 187 | 0 |
| restor* | connectivity | | 430 | 2 |
| restor* | dispers* | connectivity | 71 | 0 |
| restor* | dispers* | habitat | 270 | 0 |
| restor* | dispers* | matrix | 84 | 5 |
| restor* | movement | connectivity | 32 | 1 |
| restor* | movement | habitat | 106 | 0 |
| restor* | movement | matrix | 43 | 8 |
| restor* | moving | connectivity | 6 | 1 |
| restor* | moving | habitat | 20 | 0 |
| restor* | moving | matrix | 9 | 9 |
| restor* | network | ecolog* | 84 | 4 |
| restor* | network | habitat | 73 | 3 |
| restor* | track* | connectivity | 9 | 3 |
| restor* | track* | habitat | 68 | 2 |
| restor* | track* | matrix | 20 | 7 |
| stepping stone | movement | matrix | 0 | |

Table 3. More complex search strings to encompass terms in draft question, on full Web of Science listings.

| **Search string** | **Number of hits returned (WoS)** |
|---|---|
| (habitat OR landscape) AND connectivity | 1542 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND connectivity | 810 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND corridor* | 651 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND matrix | 486 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND barrier* | 778 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND metapopulation* | 1109 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND network* | 571 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND coloni*[1] | 1,740 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND "stepping stone*" | 76 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND bridge* | 83 |
| ? (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND ("land use" OR land-use) | 635 |
| **Total hits:** | **6939** |
| **Total hits after duplicate removal:** | **4875** |

## PROTOCOL APPENDIX 2 SCOPING STUDIES

### PILOT SCOPING OF SEARCH TERMS

### 19TH DECEMBER 2007

Table 2. Simple initial searches on Web of Science including only papers from 1997-2007.

| | | | Hits | Of 10 most recent, number rejected on title |
|---|---|---|---|---|
| "green bridge" | | | 8 | 7 |
| "land use" | | connectivity | 205 | 2 |
| change | dispers* | "land use" | 117 | 7 |
| "land use" | species | change | 17 | 3 |
| "patch shape" | dispers* | landscape | 10 | 3 |
| "patch size" | dispers* | landscape | 161 | 1 |
| barrier | connectivity | species | 66 | 4 |
| barrier | dispers* | connectivity | 65 | 5 |
| barrier | dispers* | landscape | 50 | 4 |
| barrier | dispers* | species | 468 | 5 |
| barrier | movement | connectivity | 25 | 3 |
| barrier | movement | landscape | 46 | 3 |
| barrier | movement | species | 152 | 3 |
| barrier | moving | landscape | 12 | 9 |
| barrier | moving | species | 37 | 7 |
| barrier | track* | connectivity | 7 | 4 |
| barrier | track* | landscape | 16 | 6 |
| barrier | track* | species | 44 | 6 |
| barrier | | connectivity | 200 | 6 |
| "land use" | barrier | species | 15 | 4 |
| buffer | coloni* | | 301 | 8 |
| connectivity | metapopulation | habitat | 260 | 1 |
| connectivity | metapopulation | | 316 | 1 |
| corridor | coloni* | habitat | 38 | 0 |
| corridor | coloni* | landscape | 30 | 2 |
| corridor | coloni* | matrix | 9 | 1 |
| corridor | dispers* | habitat | 120 | 0 |
| corridor | dispers* | landscape | 87 | 1 |
| corridor | dispers* | matrix | 32 | 2 |
| corridor | movement | habitat | 99 | 0 |
| corridor | movement | landscape | 67 | 0 |
| corridor | movement | matrix | 26 | 1 |
| green bridge | species | | 26 | 9 |
| green bridge | | | 486 | 10 |
| matrix | dispers* | distance | 384 | 7 |
| matrix | permeab* | distance | 54 | 6 |
| matrix | restor* | metapopulation | 11 | 0 |
| matrix | | metapopulation | 164 | 0 |
| network | dispers* | ecolog* | 111 | 1 |
| restor* | connectivity | habitat | 187 | 0 |
| restor* | connectivity | | 430 | 2 |
| restor* | dispers* | connectivity | 71 | 0 |
| restor* | dispers* | habitat | 270 | 0 |
| restor* | dispers* | matrix | 84 | 5 |
| restor* | movement | connectivity | 32 | 1 |
| restor* | movement | habitat | 106 | 0 |

| | | | | |
|---|---|---|---|---|
| restor* | movement | matrix | 43 | 8 |
| restor* | moving | connectivity | 6 | 1 |
| restor* | moving | habitat | 20 | 0 |
| restor* | moving | matrix | 9 | 9 |
| restor* | network | ecolog* | 84 | 4 |
| restor* | network | habitat | 73 | 3 |
| restor* | track* | connectivity | 9 | 3 |
| restor* | track* | habitat | 68 | 2 |
| restor* | track* | matrix | 20 | 7 |
| stepping stone | movement | matrix | 0 | |

Table 3. More complex search strings to encompass terms in draft question, on full Web of Science listings.

| Search string | Number of hits returned (WoS) |
|---|---|
| (habitat OR landscape) AND connectivity | 1542 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND connectivity | 810 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND corridor* | 651 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND matrix | 486 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND barrier* | 778 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND metapopulation* | 1109 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND network* | 571 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND coloni*[1] | 1,740 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND "stepping stone*" | 76 |
| (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND bridge* | 83 |
| ? (dispers* OR move* OR migrat*) AND (habitat OR landscape) AND ("land use" OR land-use) | 635 |
| **Total hits:** | **6939** |
| **Total hits after duplicate removal:** | **4875** |

# Appendix 2. Studies retained after full-text assessment which included UK species.

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Anderson *et al.* (2005) | *Cervus elaphus* (L. 1758) - Red deer. | Wisconsin & Yellowstone, USA and Alberta, Canada | Home range sizes compared to landscape composition and metrics by telemetry of free-ranging deer. | Mosaic | 4 years | 1852 - 15800 $km^2$, 3 sites across temperate N. America. | 99 | Home ranges are larger when there is a greater percentage of forest cover |
| 2 | Andren & Delin (1994) | *Sciurus vulgaris* (L. 1758) - Red squirrel. | Sweden | Home ranges determined by telemetry and compared to landscape composition | Forest | 3 years | 15 $km^2$ | 20 | Home range size not related to the amount of preferred or avoided habitats in that landscape |
| 3 | Aviron *et al.* (2007) | *Maniola jurtina* (L. 1758) - Meadow brown butterfly. | Brittany, France | Marked butterflies recaptured in different habitat patches. | Long grass | 14 days | 1 $km^2$ | 1112 | Woodlands reduce number of inter-patch movements compared to grassland. |
| 4 | Bates *et al.* (2005) | *Bembidion atrocaeruleum* (Stephens, 1828) - Ground beetle. | Upper Severn (Caersws), UK | Marked beetles recaptured on different patches of exposed riverine sediment. | Bare | 20 days, x2 | 9 patches, 2400 $m^2$ area | 157 | More likely to move through vegetation than over water. |
| | " | *Bembidion decorum* (Zenker in Panzer, 1800) - Ground beetle. | Upper Severn (Caersws), UK | " | " | " | " | 10 | Too few inter-patch movements to compare. |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Fleutiauxellus maritimus* (Curtis, 1840) - Ground beetle. | Upper Severn (Caersws), UK | " | " | " | " | 29 | Too few inter-patch movements to compare. |
| 5 | Bellamy & Hinsley (2005) | *Parus* (*Cyanistes*) *caeruleus* (L. 1758) - Blue tit | Cambridgeshire UK | Movements of birds between pairs of woods using open or wooded routes recorded by direct observation. | Woodland | 30 mins, 3 months | Up to 625 m, 31 pairs of woods, spread over one county. | 162 | Seventy-nine boundary movements, four open field movements. |
| | " | *Fringilla coelebs* (L. 1758) - Chaffinch | " | " | " | " | " | 81 | Twenty-five boundary movements, thirty-one field movements. |
| | " | *Parus major* (L. 1758) - Great tit | " | " | " | " | " | 66 | Thirty-two boundary movements, two field movements |
| | " | *Aegithalos caudatus* (L. 1758) - Longtailed tit | " | " | " | " | " | 37 | Eighteen boundary movements, one field movement |
| | " | *Picus viridis* (L. 1758) - Green woodpecker | " | " | " | " | " | 13 | Two boundary movements, nine field movements |
| | " | *Regulus regulus* (L. 1758) - Goldcrest | " | " | " | " | " | 14 | Seven boundary movements, zero field movements |
| | " | *Turdus merula* (L. 1758) - Blackbird | " | " | " | " | " | 9 | Three boundary movements, three field movements |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Pyrrhula pyrrhula* (L. 1758) - Bullfinch | " | " | " | " | " | 10 | Four boundary movements, two field movements |
| | " | *Dendrocopus major* (L. 1758) - Great spotted woodpecker | " | " | " | " | " | 6 | Zero boundary movements, six field movements |
| | " | *Garrulus glandarius* (L. 1758) - Jay | " | " | " | " | " | 6 | One boundary movement, four field movements |
| | " | *Phylloscopus collybita* (Vieillot, 1817) - Chiffchaff | " | " | " | " | " | 10 | Five boundary movements, zero field movements |
| | " | *Erithacus rubecula* (L. 1758) - Robin | " | " | " | " | " | 7 | Three boundary movements, one field movement |
| | " | *Parus* (*Periparus*) *ater* (L. 1758) - Coal tit | " | " | " | " | " | 8 | Four boundary movements, zero field movements |
| | " | *Prunella modularis* (L. 1758) - Dunnock | " | " | " | " | " | 6 | Three boundary movements, zero field movements |
| | " | *Troglodytes troglodytes* (L. 1758) - Wren | " | " | " | " | " | 4 | Two boundary movements, zero field movements |
| | " | *Parus* (*Poecile*) *palustris* (L. 1758) - Marsh tit | " | " | " | " | " | 2 | One boundary movement, zero field movements |
| | " | *Sylvia atricapilla* (L. 1758) - Blackcap | " | " | " | " | " | 2 | One boundary movement, zero field movements |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Sylvia communis* (Latham, 1787) - Whitethroat | " | " | " | " | " | 2 | One boundary movement, zero field movements |
| | " | *Emberiza schoeniclus - Reed bunting* | " | " | " | " | " | 2 | One boundary movement, zero field movements |
| | " | *Turdus philomelos* (Brehm, 1831) - Song thrush | " | " | " | " | " | 1 | Zero boundary movements one field movement |
| | " | *Pica pica* (L. 1758) - Magpie | " | " | " | " | " | 1 | Zero boundary movements one field movement |
| 6 | Berggren *et al.* (2001) | *Metrioptera roeseli* (Hagenbach, 1822) - Roesel's Bush-cricket. | Sweden | Crickets released into previously uncolonised area and monitored. | Long grass | 5 years | 30 ha | 868 | Permeable linear landscape elements increase successful dispersal, as does the number of nodes. |
| 7 | Berggren *et al.* (2002) | *Metrioptera roeseli* (Hagenbach, 1822) - Roesel's Bush-cricket | Sweden | Crickets released in patches with a corridor and observed departing. | Grassland | 290 minutes, 2 years | 67 $m^2$, 7 plots in single field | 131 | Individuals were more likely to leave patch through corridor. Crickets moved further through the corridors but faster in the matrix. |
| 8 | Bonte *et al.* (2003) | *Pardosa monticola* (Clerck, 1757) - Wolf Spider. | Flemish dunes | Marked spiders released into different length grass communities | " | 24 hours | Not clear | 341 | Shrubs are a barrier to this species |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 9 | Bright (1998) | *Muscardinus avellanarius* (L. 1758) - Common dormouse. | Isle of Wight, UK | Dormice were translocated to intact and gappy hedges and meadow, and movement radiotracked | woodland | 7 hours | 750 $m^2$ | 12 | Dormice are reluctant to cross hedgerow gaps, but can go very fast across fields if released in them |
| 10 | Brunzel *et al.* (2004) | *Tyria jacobaeae* (L. 1758) - Cinnabar moth | Germany | Pots were placed 600m away from isolated population and monitored for colonisation. | *S. jacobaea* (calcaerous open ground) | 2.5 months x 2 | 60000 $m^2$ | Not clear but > 36 | Plants are more likely to become infected with *T. jacobae* in valleys with roads than without roads, and less likely to become infected away from valleys. |
| 11 | Cant *et al.* (2005) | *Aglais urticae* (L. 1758) - Small Tortoiseshell butterfly. | Rothamsted, Hertfordshire, UK | Radar tracking combined with direct observation in an agricultural landscape. | Grassland | Not given | 0.2 $km^2$ | 17 | Butterflies avoid dense tree lines compared to grassland. Raw data per species not present. |
| | " | *Vanessa atlanta* (L. 1758) - Red Admiral butterfly. | " | " | " | " | " | " | " |
| | " | *Polygonia c-album* (L. 1758) - Comma butterfly. | " | " | " | " | " | " | " |
| | " | *Vanessa cardui (L. 1758) - Painted lady butterfly.* | " | " | " | " | " | " | " |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Inachis io* (L. 1758) - Peacock butterfly. | " | " | " | " | " | " | " |
| 12 | Cargnelutti *et al.* (2002) | *Capreolus capreolus* (L. 1758) - Roe deer. | France | Deer radiotracked moving through heterogeneous landscape | Forest | 18 months | 100 $km^2$ | 15 | Deer in mosaics make their home ranges larger to include the same amount of wooded cover as those in forest, irrespective of spatial arrangement |
| 13 | Carlsson *et al.* (2004) | *Salmo trutta* (L. 1758) - Brown trout. | Sweden | Movement by tagged fish compared in two streams, one isolated by an impassable barrier | River | 100 days, replicated over 3 years. | 6-16km, 2 streams | 1227 | Brown trout make longer distance movements all year round, even within isolated, landlocked streams |
| 14 | Chapman *et al.* (2007) | *Chrysolina graminis* (L. 1758) - Tansy beetle. | River Ouse, York, UK | Movement compared in patch and matrix by direct observation | Tansy (tall herbs) | 1 hour | 4 $m^2$ | 45 | Movement in matrix is faster but more variable |
| 15 | Charrier *et al.* (1997) | *Abax parallelepipedus* (Piller & Mitterpacher, 1783) - Forest ground beetle. | Brittany, France | Beetles followed using harmonic radar | Forest | 46 days | 350ha | 32 | Mean speed is less around hedgerows with less vegetation cover |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 16 | Clevenger *et al*. (2001) | *Mustela erminea* (L. 1758) - Stoat. | Banff, Canada | Soot-trays in culverts under roads, compared to prints in snow nearby | Woodland/ mosaic | 4 months, Two replicates (2 winters). | Not clear - < 100m?, 36 sites. | Not given | Stoats prefer narrower passages with cover near or around the openings |
| 17 | Conradt & Roper (2006) | *Maniola jurtina* (L. 1758) - Meadow brown butterfly. | Brighton, UK | Butterfly behaviour directly observed near habitat boundaries | Long grass | not clear, < 1 day | 4750m2 | 209 | Butterflies respond to habitat boundaries within 5m |
| | " | *Pyronia tithonus* (L. 1771) - Gatekeeper butterfly. | " | " | " | " | " | 175 | Butterflies respond to habitat boundaries within 5m |
| 18 | Conradt (2000) | *Maniola jurtina* (L. 1758) - Meadow brown butterfly | Cambridgeshire fens, UK | Butterflies translocated away from home patch into short pasture or arable field. | Grassland | Not clear, < 1 day | 67500 $m^2$ | 209 | Return rates do not differ between pasture and crop matrix |
| 19 | Davies & Maclean (1997) | *Buteo buteo* (L. 1758) - Common Buzzard. | South Africa | Direct observation of flight paths | Mosaic | 15 minutes, repeated over 5 months. | 10ha | 7 | Individual species data not presented |
| | " | *Hirundo rustica* (L. 1758) - Swallow. | " | " | " | " | " | 131 | " |
| | " | *Delichon urbicum* (L. 1758) - House martin. | " | " | " | " | " | 1 | " |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 20 | Dennis & Hardy (2007) | *Pieris brassicae* (L. 1758) - Large/Cabbage White butterfly. | Northwest England & Wales | Butterfly flight types recorded in different matrix types | Brassica plants (tall herbs) | Not clear, < 1 day | Not clear, sites replicated across NW England and Wales. | 493 | Butterflies make searching flights for resources in non-breeding habitat |
| | " | *Pieris rapae* (L. 1758) - Small White butterfly. | " | " | " | " | " | 769 | " |
| | " | *Pieris napi* (L. 1758) - Green-Veined White butterfly. | " | " | " | " | " | 537 | " |
| 21 | Diekotter *et al.* (2007) | *Pholidoptera griseoaptera* (DeGeer, 1773) - Dark Bush-cricket. | Switzerland & France | Marked crickets were followed from release points in two heterogeneous landscapes. | Grassland | 10 days | 90ha, two in each country. | 200 Sw / 100 Fr | Movement distance higher in landscape with greater fragmentation. |
| 22 | Doncaster *et al.* (2001) | *Erinaceus europaeus* (L. 1758) - European hedgehog. | Oxfordshire & Berkshire, UK | Radiotracking of hedgehogs released at 5 suitable unoccupied sites. | Hedge or woodland edge near grassland | 20 days, spread over 2 years. | 40 ha, replicates spread over 90 km2. | 73 | Hedgehogs use linear landscape features more frequently than expected by random chance |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 23 | Dover & Fry (2001) | *Melitaea athalia* (Rottemberg, 1775) - Heath fritillary. | Norway, experimental arenas | Direct observation of the behavioural responses of butterflies to artificial structures representing sight-line and barrier functions of hedgerows. | Grassland | 1 hour, x8 days for Sight-line. Seven replicates over 6 days for windbreak | Site 1 = 1.410ha, Site 2 = 0.036 ha. Site 3 17-83m. Maximum recorded flight 30m. | | Butterflies fly further along linear features. 99 responded in the control, 62 responded when using tape. 54 responded in the control, 42 responded to the windbreak. |
| | " | *Fabriciana* (*Argynnis*) *adippe* (Denis & Schiffermüller, 1775) - High Brown fritillary. | Norway, experimental arenas | “. | “ | “ | As above but maximum recorded flight 60m. | | 54 responded in the control, 84 responded when using tape. 63 responded in the control, 48 responded to the windbreak. |
| 24 | Dzialak *et al.* (2005) | *Falco peregrinus* (Tunstall, 1771) - Peregrine Falcon. | Kentucky, USA | Reintroduced peregrines were radiotracked dispersing from their release site in two contrasting landscapes | " | 90 days | Not clear | 33 | Peregrines dispersed further in the forested landscape (using open areas as corridors) than the agricultural landscape |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 25 | Foppen & Reijnen (1994) | *Phylloscopus trochilus* (L. 1758) - Willow Warbler. | Netherlands | Colour-ringed males were located in their territories in successive years | Woodland/ scrub | 4 years | 4.7 $km^2$ | 222 | Breeding dispersal distances of yearling males nearer the road were larger appear to be directed away from the road |
| 26 | Forester *et al.* (2007) | *Cervus elaphus* (L. 1758) - Red deer. | Yellowstone N.P., Wyoming, USA | Radiotracking marks were compared to correlated random walks | Mosaic | 4 months | 3600 $km^2$ | 16 | Individual deer had very different space-use patterns and habitat preferences |
| 27 | Frair *et al.* (2005) | *Cervus elaphus* (L. 1758) - Red deer. | Alberta, Canada | Radiotracked deer over a wide area | Mosaic | 2 years | 15800 $km^2$ | 18 | Deer rest in areas more than 50 m from linear anthropogenic features |
| 28 | Frampton *et al.* (1995) | *Harpalus rufipes* (De Geer, 1774) - Strawberry Seed beetle. | Norway | Beetles released at one end of arenas containing different amounts of habitat and long grass matrix | Arable field | 14 days, Replicated 6 times over 2 months. | 9.2 $m^2$, Replicated over a 0.7 ha area. | 188 | Beetles reached the ends of their enclosures quicker when there was a lower proportion of matrix |
| | " | *Pterostichus melanarius* (Illiger, 1798) - Ground beetle. | " | " | " | " | " | 430 | " |
| | " | *Pterostichus niger* (Schaller, 1783) - Ground beetle. | " | " | " | " | " | 53 | " |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 29 | Frey & Conover (2006) | *Vulpes vulpes* (L. 1758) - Red fox. | Utah, USA | radiotracked home range polygons were compared to landscape composition | " | 3 months | 2600ha | 19 | Foxes use roads and levees in preference to wetland, creating oblong home ranges |
| 30 | Fried *et al.* (2005) | *Musca domestica* (L. 1758) - House fly. | Savannah, Georgia, USA | Flies released in central patch and recaptured in different shaped surrounding patches | | 32 hours | 25ha, 10 replicates | 30000 | Flies were recaptured most frequently in corridor-connected patches, then winged patches, least frequently in rectangular patches |
| | " | *Musca domestica* (L. 1758) - House fly. | Florida, USA | Flies released along edges with different vegetation structures | | 32 hours | 2.5ha | 18750 | Flies tend to cross open edges and follow closed edges |
| 31 | Goheen *et al.* (2003) | *Sciurus carolinensis* (L. 1758) - Eastern Grey Squirrel | Indiana, USA | Translocated squirrels into woody fence-rows either connected or unconnected to nearby woodland, used radio-tracking to determine how long it took them to find the woodland. | Forest | 22 days, 2 months x 2 years | 28-954m to nearest woodlot, 13 release sites in 812 km2 study area | 28 | Grey squirrels not affected by fence-row connectedness but more likely to cross fallow than cropped land. |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 32 | Grez & Prado (2000) | *Hippodamia variegata* (Goeze, 1777) - Adonis Ladybird | Chile | Marked ladybirds monitored emigrating from OR immigrating into (two separate experiments) brassica patches surrounded by 2 different matrix types. | Brassica crops | 5 days, 3 times over 2 years. | 16 $m^2$, 16 patches, 8 of each matrix type, within 1 field. | Emigration experiment 1728 individuals, immigration experiment 5440 individuals. | Raw data not presented, due to low recapture rate. |
| 33 | Hein *et al.* (2003) | *Platycleis albopunctata* (Goeze, 1778) - Grey Bush-cricket. | Bavaria, Germany | Mark recapture in different habitat or matrix patches, plus direct observation of behaviour of crickets translocated to edges | Grass | 6 days | 4000 - 40900 $m^2$, three sites. | 188 | Crickets move faster in matrix, and may enter matrix when released at an edge |
| 34 | Hofe & Gerstmeier (2001) | *Abax parallelepipedus* (Piller & Mitterpacher, 1783) - Forest ground beetle. | Northern Alps | Beetles marked and recaptured in mosaic of habitats | forest | 6 months | 560 $m^2$ | 261 | Able to move through meadow to copse |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Abax parallelus* (Duftschmid 1812) - Ground beetle. | " | " | forest | " | " | 401 | Able to move through meadow to copse |
| | " | *Carabus granulatus* (L. 1758) - Ground beetle. | " | " | meadow | " | " | 448 | Able to move into forest - hibernation site? |
| | " | *Nebria brevicollis* (Fabricius, 1792) - Ground beetle. | " | " | forest | " | " | 1060 | Able to move through meadow to copse |
| | " | *Platynus assimilis* (Paykull 1790) - Ground beetle. | " | " | forest | " | " | 544 | Able to move through meadow to copse |
| | " | *Poecilus cupreus / versicolor* (L. 1758 / Sturm 1824) - Ground beetle. | " | " | meadow | " | " | 952 | Able to move into forest - hibernation site? |
| | " | *Pterostichus burmeisteri* (Heer 1838) - Ground beetle. | " | " | forest | " | " | 188 | Able to move through meadow to copse |
| 35 | Holloway *et al.* (2003) | *Asilus crabroniformis* (L. 1758) - Hornet robberfly. | Cholsey, Oxfordshire, UK | Marked flies released and looked for in 8 possible patches. | meadows | 44 days | not clear. 1 $km^2$? | 385 | Species can cross road and garden matrix. |
| 36 | Jehle & Arntzen (2000) | *Triturus cristatus* (Laurenti, 1768) - Great Crested newt. | France | Newts leaving a pond were radiotracked moving around an agricultural landscape. | pond | 39 days | 2ha | 14 | Newts migrate more frequently through matrix containing trees than open. |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 37 | Kozakiewicz *et al.* (1993) | *Clethrionomys glareolus* (Schreber, 1780) - Bank vole. | Poland | Different coloured bait left at 5 stations in agricultural landscape. | banks, woodlands, hedgerows | 6 months, x 2 years. | 2 $km^2$ | 95 | Bank voles show no preference for moving in either alder wood, pasture or crop matrix, and are not limited by a gravel road. |
| 38 | Kreyer *et al.* (2004) | Bombus pascuorum (Latreille, 1802) - Common Carder bumblebee. | Hesse, Germany | Marked bees from natural and artificial nests observed moving around a mosaic landscape | open | 1 month | 6 $km^2$ | 568 Bt, 178 Bp | Forest matrix (<=660m) is not a limit to bumblebee dispersal distance or frequency, as compared to grassland habitat. |
| 39 | Kuussaari *et al.* (1996) | *Melitaea cinxia* (L. 1758) - Glanville fritillary. | Finland | Released marked butterflies into a network of empty patches on an isolated island | grassland | 22 days | 1.6 $km^2$ | 882 | Open landscape around the patch increased emigration |
| 40 | Lamberti *et al.* (2006) | *Capreolus capreolus* (L. 1758) - Roe deer. | Spain | Radiotracked deer home ranges in an agricultural mosaic compared to landscape composition | forest | 6 months | 48 $km^2$ | 9 | Male deer home range size is more affected by woodland density than female deer |
| 41 | Larkin *et al.* (2004) | *Cervus elaphus* (L. 1758) - Red deer. | Kentucky, USA | Released deer were radiotracked from their start patch | mosaic | 1 year | 314 $km^2$, replicated over three sites in Kentucky. | 415 | Deer most likely to leave area with lower area to edge ratio. |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 42 | Light (2003) | *Pacifastacus leniusculus* (Dana, 1852) - Signal crayfish. | California, USA | Movement of marked crayfish was studied in a stream reach | stream | 56 days | 0.5 km | 529 | More upstream movement than downstream |
| 43 | Lucas & Batley (1996) | *Barbus barbus* (L. 1758) - Barbel. | River Nidd, Yorkshire, UK | Radiotagged fish followed in a river with 3 weirs | middle-reach rivers | 1 year, 2 years. | 97km | 31 | Boulder, concrete and flow-gauge weirs all restrict movement |
| 44 | MacDonald *et al.* (2004) | *Mustela nivalis* (L. 1766) - Weasel. | Wytham Wood, Oxfordshire, UK | | | 18 days, several replicates over 2 years. | 210 ha | 9 | Weasels travel along hedges, ditches and woodland edges, rarely moving >5m from them |
| 45 | Malmgren (2002) | *Triturus* (*Lissotriton*) *vulgaris* (L. 1758) - Smooth newt | Sweden | Choice experiment: do newts move into woodland or grassland upon leaving pond? Direct observation using continuous drift fence and bucket traps. | Pond | 3 months, 3 years | 800 $m^2$ | 6647 | Newts move into woodland more often than grassland when leaving a pond. |
| 46 | Mauremooto *et al.* (1995) | *Harpalus* (*Pseudoophonus*) *rufipes* (De Geer, 1774) - Strawberry Seed beetle. | Hampshire, UK | Marked beetles released at one end of enclosures crossing a hedge or a barley field (crop, stubble or bare), and captured at the other end | arable field | 21 days | 8 $m^2$, replicated along one hedge. | 135 | Beetles reached the ends of their enclosures quicker in barley/stubble/bare than hedge |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Pterostichus (Omaseus) melanarius* (Illiger, 1798) - Ground beetle. | Hampshire, UK | " | " | " | " | 482 | " |
| | " | *Pterostichus* (*Steropus*) *madidus* (Fabrici us, 1775) - Black Garden beetle. | Hampshire, UK | " | " | " | " | 82 | " |
| 47 | Mellina *et al.* (2005) | *Oncorhynchus mykiss* (Walbaum, 1792) - Rainbow trout. | British Columbia, Canada | Fish marked on three similar streams | " | 4 months, 3 years. | 372-607m, 3 sites. | Not clear - >160 0? | " |
| 48 | Miaud & Sanuy (2005) | *Bufo calamita* (= Epidalea calamita) (L. 1758) - Natterjack toad. | Spain | Toads radiotracked dispersing away from natal ponds | pond | 9 months | 4km2 | 19 | Toads move along ditches and stone embankments and avoid arable fields |
| 49 | Ockinger & Smith (2008) | *Aphantopus hyperantus* (L. 1758) - Ringlet butterfly. | Sweden | Marked butterflies released and recaptured in different grassland patches. | Grassland | 41 days | 4 $km^2$ | 5333 | Linear grassland matrix features are used if present, but their presence (as compared to agricultural matrix) does not increase dispersal frequency. |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Maniola jurtina* (L. 1758) - Meadow brown butterfly. | " | " | Grassland | 41 days | 4 $km^2$ | 871 | " |
| | " | *Coenonympha pamphilus* (L. 1758) - Small Heath butterfly. | " | " | Grassland | 30 days | 4 $km^2$ | 421 | " |
| 50 | Poysa & Paasivaara (2006) | *Bucephala clangula* (L. 1758) - Common Goldeneye. | Finland | Broods moving around a landscape monitored using rings. | Lakes | 1 week, Repeated yearly x12. | 75 $km^2$ | 67 | Linear matrix features (ditch) are used if present, but their presence does not affect dispersal distance or frequency of movement (as compared to agricultural matrix). |
| 51 | Pryke & Samways (2001) | *Vanessa cardui* (L. 1758) - Painted lady butterfly. | South Africa | Butterflies followed using binoculars moving through afforested landscape. | Grassland | 6 hours, 16 reps over 4 months. | 1.9 $km^2$ | 246 | Movement faster in narrower grassland corridors and more frequent in corridor centre |
| 52 | Purse *et al.* (2003) | *Coenagrion mercuriale* (Charpentier, 1840) - Southern damselfly. | Preseli & New Forest, UK | Marked damselflies recaptured in different suitable patches, compared over two landscapes. | Streams over heathland | 60 days | 1.5 $km^2$ , replicated in two different landscapes. | 4935 | Scrub forms a semi-permeable barrier to movement |
| 53 | Redpath (1995) | *Strix aluco* (L. 1758) - Tawny owl. | Cambridgeshire, UK | Owls radiotracked in 2 parts of a landscape containing different woodland amounts | Woodland | 6 months, 3 years. | 40 $km^2$ | 23 | Owls use grassland more than arable land |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 54 | Rico *et al.* (2007a) | *Sorex araneus* (L. 1758) - Common shrew. | Czech Republic | Mark-recapture of mice across roads of varying widths using trap lines | Woodland | 4 nights, twice over 4 months. | 1250 - 3750 $m^2$, 4 replicates within Czech Republic. | 85 | No significant difference in crossing rates between road widths 4-13m (only one crossing recorded out of 53). |
| | " | *Clethrionomys glareolus* (Schreber, 1780) - Bank vole. | " | " | " | " | " | 194 | No significant difference in crossing rates between road widths 4m-13m. |
| | " | *Apodemus flavicollis* (Melchior, 1834) - Yellow-necked mouse. | " | " | " | " | " | 275 | Significantly fewer crossings of wider roads (11-13m) than narrower roads (4-9m). |
| 55 | Rico *et al.* (2007b) | *Clethrionomys glareolus* (Schreber, 1780) - Bank vole. | Czech Republic | Voles marked and recaptured in trap lines across roads | Woodland | 4 months | 1125 $m^2$, 4 replicates within Czech Republic. | 178 | Voles did not cross roads (but see below). |
| | " | *Apodemus flavicollis* (Melchior, 1834) - Yellow-necked mouse. | " | Mice marked and recaptured in trap lines across roads | " | " | 1125 $m^2$, 4 replicates within Czech Republic. | 581 | 0% crossed 50m highway, 3% crossed 19m country road. |
| | " | *Clethrionomys glareolus* (Schreber, 1780) - Bank vole. | " | Voles marked, translocated across road and recaptured in trap lines on 'start' side | Woodland | 3 nights | 1125 $m^2$, 2 replicates within Czech Republic. | 33 | 33% of voles returned across 19m country road, 0% across 50m highway. |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Apodemus flavicollis* (Melchior, 1834) - Yellow-necked mouse. | " | Mice marked, translocated across road and recaptured in trap lines on 'start' side | " | " | 1125 $m^2$, 2 replicates within Czech Republic. | 99 | 50% of mice returned across 19m country road, 13% across 50m highway. |
| 56 | Ries & Debinski (2001) | *Danaus plexippus* (L. 1758) - Monarch butterfly | Iowa, USA | Butterflies in plots located on prairie patch - matrix boundary were directly observed and paths plotted. Four matrix types. | Grassland | 68 days, 2 months | 3600 $m^2$, 9 sites with 30 plots total | 436 | Monarch butterflies more likely to enter field matrix than woodland matrix. Raw data per species not present. |
| 57 | Rodriguez *et al.* (2001) | *Regulus regulus* (L. 1758) - Goldcrest. | Sweden | Birds were directly observed responding to playback at forest-matrix edges | woodland | 20 mins, replicated in 2 month periods over 3 years | Not clear, Replicated over 840k $m^2$. | not clear | Open matrix restricted the rate of bird movement |
| | " | *Parus* (*Lophophanes*) *cristatus* (L. 1758) - Crested tit. | Sweden | " | " | " | " | not clear | " |
| | " | *Parus* (*Poecile*) *montanus* (Conrad von Baldenstein, 1827) - Willow tit. | Sweden | " | " | " | " | not clear | " |
| | " | *Parus* (*Periparus*) *ater* (L. 1758) - Coal tit. | Sweden | " | " | " | " | not clear | " |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 58 | Rühe (1999) | *Lepus europaeus* (Pallas, 1778) - Brown hare. | Germany | Hares radiotracked or visually observed in different arable crops | Open (arable/grass) | 5 minutes, several replicates over 11 years. | 220ha | 41 | Hares use tractor lines, and rarely pass through crops of fully grown winter wheat |
| 59 | Sakuragi *et al.* (2003) | *Cervus nippon* (Temminck, 1838) - Sika deer. | Hokkaido, Japan | Deer radiotracked moving through heterogeneous landscape | Mosaic | 3 years | 7466 $km^2$ | 53 | Deer use agricultural land less frequently than expected from a random distribution, and avoid roads |
| 60 | Shirley (2006) | *Sturnus vulgaris* (L. 1758) - Common starling. | | Birds were directly observed crossing forest-matrix edges | | 15 mins, replicated over two months | Not clear, Replicated over very large area. | 2 | Too few birds to make conclusion |
| | " | *Troglodytes troglodytes* (L. 1758) - Wren. | " | " | " | " | " | 7 | 5 birds crossed into clear-cut, 2 into stream |
| | " | *Melospiza melodia* (Wilson, 1810) - Song Sparrow. | " | " | " | " | " | 11 | 8 birds crossed into clear-cut, 3 into stream |
| 61 | St Clair (2003) | *Melospiza melodia* (Wilson, 1810) - Song sparrow. | Banff, Canada | Playbacks of bird mobbing calls were used to compare the response rate across three barrier types: roads, rivers and meadows, of songbirds. | Forest | 6 minutes, 1 month x 2 years | 80m gaps, playback audible 250m either side, ? | Data not presented. | Forest dependent song birds less likely to cross rivers than roads or meadows. Individual species data not presented |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | " | *Loxia curvirostra* (L. 1758) - Common crossbill | " | " | " | " | " | " | " |
| | " | *Branta canadensis* (L. 1758) - Canada goose | " | " | " | " | " | " | " |
| | " | *Gallinago gallinago* (L. 1758) - Common snipe | " | " | " | " | " | " | " |
| | " | *Pandion haliaetus* (L. 1758) - Osprey | " | " | " | " | " | " | " |
| | " | *Pica pica* (L. 1758) - Magpie | " | " | " | " | " | " | " |
| | " | *Corvus corax* (L. 1758) - Raven | " | " | " | " | " | " | " |
| | " | *Sturnus vulgaris* (L. 1758) - Common starling | " | " | " | " | " | " | " |
| 62 | Stevens *et al.* (2004) | *Bufo calamita* (= *Epidalea calamita*) (L. 1758) - Natterjack toad. | Belgium | Toadlets released into different arenas and induced to move were directly observed | Pond | 2 minutes | $0.03m^2$, One arena for each of five treatments. | 9 | Movement more efficient in sand/tarmac than leaf litter |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 63 | Stevens *et al.* (2006) | *Bufo calamita* (= *Epidalea calamita*) (L. 1758) - Natterjack toad. | Belgium | Toadlets were presented with choices of different boundary types in Y shaped arenas and directly observed | Pond | 5 minutes | 0.075 $m^2$ | 50 | Toadlets showed a preference for bare environments and forests, whereas they avoided the use of agricultural environments. |
| 64 | Szacki (1999) | *Apodemus flavicollis* (Melchior, 1834) - Yellow-necked mouse. | Poland | Radiotracking to record inter-patch movement around an agricultural landscape with different roads. | woodland | 8 days, Repeated 5x over 11 months. | 1 $km^2$ | 42 | One inter-patch movement recorded across a gravel road but mice made forays out of wood across 10m paved road |
| | " | *Apodemus flavicollis* (Melchior, 1834) - Yellow-necked mouse. | " | Capture mark recapture to record inter-patch movement around an agricultural landscape with different roads. | woodland | 5 days, Repeated 11x over 11 months. | 1 $km^2$ | 2339 | 39 mice recorded moving across fields and roads (e.g. 300m of field plus one 10m paved road and one 5 m gravel road in one move) |
| | " | *Clethrionomys glareolus* (Schreber, 1780) - Bank vole | " | " | woodland | " | 1 $km^2$ | 2236 | 23 voles recorded moving across fields and roads (e.g. 300m of field plus 1 10m paved road and 1 5 m gravel road in one move) |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| 65 | Valtonen & Saarinen (2005) | *Aphantopus hyperantus* (L. 1758) - Ringlet butterfly. | Finland | Marked butterflies recapture in different grassy sections surrounding a road interchange. | Grassland | 44 days | 8.6ha | 2113 | Single roads are not absolute barriers but series of roads may be |
| 66 | Vanreusel & Van Dyck (2007) | *Callophrys rubi* (L. 1758) - Green hairstreak butterfly. | Belgium | marked butterflies released and recaptured in different heathland patches. | heathland | 14 days | 784 ha | 1148 | Butterflies released in forest fly straight to open areas and rarely (<0.01 % of events) enter forest |
| 67 | Veenbaas & Brandjes (1998) | *Mustela putorius* (L. 1758) - Polecat. | Netherlands | Infrared detectors, sandbox prints and ink prints were used to monitor numbers crossing roads through a range of fauna underpasses | Woodland, hedges | 12 weeks | not clear - < 100m?, 28 replicates throughout Netherlands. | not given | Prefer wider passageways |
| | " | *Mustela erminea (L. 1758)* - Stoat. | " | " | Woodland, hedges | 12 weeks | " | " | Prefer wider passageways |
| | " | *Vulpes vulpes* (L. 1758) - Red fox. | " | " | Woodland, hedges | 12 weeks | " | " | Only used wide passageways |
| | " | *Erinaceus europaeus* (L. 1758) - European hedgehog. | " | " | Woodland and hedgerow | 12 weeks | " | " | Rarely used passages |
| | " | *Talpa europaea* (L. 1758) - Mole. | " | " | Grassland | 12 weeks | " | " | Never used passages despite local presence |
| | " | *Mustela nivalis* (L. 1766) - Weasel. | " | " | Woodland, hedges | 12 weeks | " | " | Never used passages despite local presence |

| No. | Reference | Species | Location | Experimental design | Habitat patch type | Temporal scale, replication | Spatial scale, replication | N | Outcome summary |
|---|---|---|---|---|---|---|---|---|---|
| | Veenbaas & Brandjes (1998) | *Meles meles* (L. 1758) - European badger. | " | " | Woodland | 12 weeks | " | " | Never used passages despite local presence |
| | " | *Capreolus capreolus* (L. 1758) - Roe deer. | " | " | Woodland | 12 weeks | " | " | Never used passages despite local presence |
| | " | *Lepus europaeus* (Pallas, 1778) - Brown hare. | " | " | Grassland or arable | 12 weeks | " | " | Never used passages despite local presence |
| | " | *Oryctolagus cuniculus* (L. 1758) - European Rabbit. | " | " | Grassland or arable | 12 weeks | " | " | Never used passages despite local presence |
| | " | *Rattus norvegicus* (Berkenhout, 1769) - Brown rat. | " | " | Human environments | 12 weeks | " | " | Near-ubiquitous use of all crossing types |
| | " | *Arvicola terrestris* (L. 1758) - Water vole. | " | " | Waterways | 12 weeks | " | " | Used four passageways (3 wide 1 narrow) |
| | " | *Sciurus vulgaris* (L. 1758) - Red squirrel. | " | " | Woodland | 12 weeks | " | " | Never used passages despite local presence |
| | " | *Amphibia spp.*- Amphibians. | " | " | Pond | 12 weeks | " | " | Prefer wooden passageways to sand or concrete ones |

## Appendix 3. Synthesis of papers including UK species by habitat and landscape feature. Numbers in superscript refere to row numbers of Appendix 2.

| | Wooded |
|---|---|
| **Corridor** | - |
| **Barrier** | Rodents cross fewer wide roads than narrower ones (three small studies[54, 55, 64]) and avoid tunnels [67]. Generally, mustelids and foxes will only use wider and vegetative covered tunnels[16, 67]. Weasels, badgers, hedgehogs and deer rarely enter or avoid tunnels[67]. Breeding birds disperse[25] away from roads and further where roads are present. One small study suggested localised movements of bank voles were not influenced by presence of gravel roads[37]. |
| | *Good external validity. Range of temporal scales. Spatial scales all relatively small (related to barrier size).* |
| **Linear permeable** | Large study shows woodland birds have preference for woody linear matrix feature (hedge)[5]. Carnivorous mammals[22, 29, 44] also use woody linear features for movement. Grey squirrels[31] cross hedge gaps but dormice[9] do not. |
| | *Most studies have a small sample size. Range of validities and scales.* |
| **Patch edge** | - |
| **Matrix direct comparison** | Evidence from bird[57, 60, 61] and beetle[34, 46] species. Birds do respond to the matrix, with a reluctance to cross rivers[61]. Beetles respond to the matrix but can move through e.g. meadow[34], going faster over open ground[46]. One small study suggested localised movements of bank voles were not influenced by the matrix[37]. |
| | *Bird studies had good replication but low detection for some species. Beetle studies were small-scale experiments but with good numbers of individuals.* |
| **Matrix composition** | Deer respond to matrix, [12, 40, 59] as do owls[53] both avoiding arable, red squirrels[2] less so. |
| | *Large spatial scales & temporal scales, good external validity.* |
| **Matrix heterogeneity** | - |

| | Shrub/scrub |
|---|---|
| **Corridor** | - |

| | |
|---|---|
| **Barrier** | - |
| **Linear permeable** | - |
| **Patch edge** | - |
| **Matrix direct comparison** | One paper[66]: short term, large study reports butterflies inhibited by woodland. |
| **Matrix composition** | - |
| **Matrix heterogeneity** | - |

| **Feature** | **Habitat classification** |
|---|---|
| | **Grass/Herb** |
| **Corridor** | Crickets[7] and butterflies[51] prefer corridors (crickets in preference to agriculture, butterflies in preference to woods).<br>*Both short-term behavioural studies.* |
| **Barrier** | Flighted invertebrates cross roads (two small studies[35, 65]) but not necessarily a series of roads[65]. Hares, rabbits and moles avoid road tunnels (one large study[67]).<br>*Longer experiments, survey based with good external validity.* |
| **Linear permeable** | Butterflies and moths[10, 23, 49] and crickets[6] prefer linear grass elements (and may use linear elements as a visual cue), there is conflicting evidence whether this increases actual dispersal rates[49].<br>*Good sample sizes and external validity.* |
| **Patch edge** | One small study [17]: Butterflies respond to habitat boundaries within 5m.<br>*Controlled experiment in large -scale landscape.* |
| **Matrix direct comparison** | Most evidence from butterflies[3, 11, 18, 39, 56], which are inhibited by woodland[3, 11, 56] matrix as compared to grassy. This was not found to be true for bumblebees[38]. Flightless terrestrial invertebrates will enter the matrix[8, 14, 33, 34] but may move faster in more open matrix[14, 33] and slower in more closed matrix [28].<br>*Wide range of scales and validities, good external validity for many.* |
| **Matrix composition** | - |

| | |
|---|---|
| **Matrix heterogeneity** | One paper[21]: fragmentation increases movement distance.<br>*Large scales.* |

| **Feature** | **Habitat classification**<br>**Arable** |
|---|---|
| **Corridor** | - |
| **Barrier** | - |
| **Linear permeable** | - |
| **Patch edge** | - |
| **Matrix direct comparison** | Small amount of evidence to suggest flighted invertebrates will enter other habitats[20, 32] but slowed down by structural complexity[28].<br>*Good internal validity. Short studies with high numbers of individuals.* |
| **Matrix composition** | - |
| **Matrix heterogeneity** | - |

| **Feature** | **Habitat classification**<br>**Generalist/mosaic** |
|---|---|
| **Corridor** | One paper[30]: flies utilise corridors (even dead-ends).<br>*Controlled experiment in large-scale landscape.* |
| **Barrier** | One paper[67]: rats make use of all tunnel types under roads.<br>*Good external but poor internal validity.* |
| **Linear permeable** | - |
| **Patch edge** | |

| | |
|---|---|
| | One paper[30]: Houseflies tend to cross open edges and follow closed edges. |
| **Matrix direct comparison** | - |
| **Matrix composition** | Evidence from raptors[19, 24] and red deer[1, 26, 27], both respond to matrix. Deer avoid roads[27] and adapt their home ranges to the matrix[1] but responses vary between individual deer[26]. |
| | *Large spatial scales & temporal scales, good external validity.* |
| **Matrix heterogeneity** | One paper[41]: Release site fidelity of red deer decreases with fragmentation. |
| **Feature** | **Habitat classification** |
| | **Still freshwater** |
| **Corridor** | - |
| **Barrier** | One study[67]: Amphibians avoid sand and concrete tunnels. |
| | *Longer term, good external validity.* |
| **Linear permeable** | Two studies[48, 50]: Ditches are used by birds[50] and natterjack toads[48]. |
| | *Long term studies over wide areas with good external validity.* |
| **Patch edge** | - |
| **Matrix direct comparison** | Four amphibian papers[36, 45, 62, 63]: migrating amphibians prefer wooded habitats[36, 45, 63], but move faster through bare habitats[62, 63]. |
| | *Two papers good external, longer studies[45, 36]. Two poor external, short term studies[62, 63].* |
| **Matrix composition** | - |
| **Matrix heterogeneity** | - |
| | **Moving freshwater** |
| **Corridor** | - |
| **Barrier** | Two studies[43, 67]: Water voles use some road tunnels[67]. Barbels are restricted by many kinds of weir[43]. |
| | *Longer scale with good external validity.* |

| | |
|---|---|
| **Linear permeable** | - |
| **Patch edge** | - |
| **Matrix direct comparison** | Three very different papers[42, 47, 52], two on non-native species[42, 47]. Reader referred to Appendix. *Each paper small scale with many individuals.* |
| **Matrix composition** | One paper[13]: brown trout move through the matrix all year round. *Large scale (spatial and temporal), low internal validity due to confounding but good external validity.* |
| **Matrix heterogeneity** | - |

| **Feature** | **Habitat classification Wetland/marsh** |
|---|---|
| **Corridor** | - |
| **Barrier** | - |
| **Linear permeable** | - |
| **Patch edge** | - |
| **Matrix direct comparison** | One paper[61]: outcome not given (small sample size). |
| **Matrix composition** | - |
| **Matrix heterogeneity** | - |

| **Feature** | **Habitat classification Bare** |
|---|---|
| **Corridor** | - |
| **Barrier** | - |
| **Linear permeable** | - |
| **Patch edge** | - |
| **Matrix direct comparison** | |

| | |
|---|---|
| | One small study[4]: suggests beetles inhibited by water but can move through dense vegetation. |
| **Matrix composition** | - |
| **Matrix heterogeneity** | - |

| **Feature** | **Habitat classification** |
|---|---|
| | **Buildings** |
| **Corridor** | - |
| **Barrier** | - |
| **Linear permeable** | - |
| **Patch edge** | - |
| **Matrix direct comparison** | - |
| **Matrix composition** | One paper[19]: birds of swallow family respond to matrix when foraging. |
| | *Small scale, not spatially-replicated.* |
| **Matrix heterogeneity** | - |

## Appendix 4. Details of studies, data extraction methods for meta-analyses of corridors & matrix impacts.

| Reference | Aars, J. and R. A. Ims (1999). "The effect of habitat corridors on rates of transfer and interbreeding between vole demes." Ecology 80(5): 1648-1655. |
|---|---|
| Subject | *Microtus oeconomus* Tundra / Root vole |
| Spatial set-up | Study plots consisted of separate enclosures for corridor and non-corridor populations. Habitat patches and corridors were imbedded within a bare matrix. |
| Temporal set-up | 2 years, over 2 recording seasons - Year One: 16 weeks, Year Two: 21 weeks |
| Location | Evenstad experimental arenas, Norway |
| Patch & corridor habitat | Long grass |
| Matrix | Bare ground |
| Reported outcome | No effect of corridor on inter-patch movement frequency |

| | Number of individuals | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Corridor | 660 | 574 |
| Control | 680 | 566 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 4 – enclosed outdoor experimental arenas, introduced laboratory-bred founder demes, mark-release-recapture. |
| Inter-patch distance | 50 m |
| Receiving patch size | 750 $m^2$ (37.5 x 20) |
| Species group | Rodents |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Emailed Ims – 9th April 2008. Reply received – 10th April, forwarding email to Aars. |
| Independence issues | |
| Tables & Figures used | Figure 15. |

| | |
|---|---|
| Extraction | Data extracted from single figure by eye, with associated reading error. |
| Miscellaneous comments | Effect on females masked by much higher male dispersal rates. |

| Reference | Andreassen, H. P. and R. A. Ims (2001). "Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography." Ecology 82(10): 2911-2926. |
|---|---|
| Subject | *Microtus oeconomus* Tundra / Root vole |
| Spatial set-up | Four replicates of three habitat configurations: The 'larger' consisted of two isolated patches; the 'corridor' plots comprised six patches connecting two sets of three patches together, and the 'small' patch plots consisted of six isolated patches. |
| Temporal set-up | 2 years, period of 17 weeks |
| Location | Evenstad experimental arenas, Norway |
| Patch & corridor habitat | Long grass |
| Matrix | Short grass |
| Reported outcome | Corridors do not increase movement frequency, rather emigration rates were affected by density-dependence |

| | | *Number of individuals* | | | |
|---|---|---|---|---|---|
| | | Northern | | Southern | |
| *Habitat type* | Sex | Marked at start | Found destination patch | Marked at start | Found destination patch |
| Corridor | Male | 90 | 22 | 49 | 18 |
| Corridor | Female | 113 | 27 | 62 | 27 |
| Control | Male | 72 | 22 | 54 | 19 |
| Control | Female | 92 | 25 | 79 | 26 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 4 – enclosed outdoor experimental arenas, mark-release-recapture. |
| Inter-patch distance | 15 m |
| Receiving patch size | 15 m (225 $m^2$) corridor and small plots and 26 m (675 $m^2$) large plots |
| Species group | Rodents |
| Life history | Iteroparous |

| | |
|---|---|
| Covariate notes | Males more likely to move if high density of females |
| Author contacted - date | Emailed Ims rolf.ims@ib.uit.no – 9th April 2008. Received reply – 10th April confirming data was correctly extracted. |
| Independence issues | |
| Tables & Figures used | Table 1. |
| Extraction | Data extracted directly from table. |
| Miscellaneous comments | |

| Reference | Baum, K. A. *et al.* (2004). "The matrix enhances the effectiveness of corridors and stepping stones." Ecology 85(10): 2671-2676. |
|---|---|
| Subject | *Prokelisia crocea* Plant-hopper |
| Spatial set-up | A total of 10 experimental landscapes (brome matrix), each with a central source patch surrounded by three vacant target patches. |
| Temporal set-up | 7 days |
| Location | Experimental arenas, North Dakota, USA. |
| Patch & corridor habitat | Cord grass |
| Matrix | Brome grass or Mud |
| Reported outcome | Corridor increases inter-patch movement. |

| Brome grass | *Number of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Corridor | 500 (per landscape) | 300 |
| Control | 500 (per landscape) | 110 |

| Mud | | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Corridor | 500 (per landscape) | 170 |
| Control | 500 (per landscape) | 80 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created open experimental landscape, release densities similar to natural population densities. |
| Inter-patch distance | 2 m |
| Receiving patch size | 0.76 $m^2$ |
| Species group | True bugs |
| Life history | Semelparous |
| Covariate notes | |
| Author contacted - date | Emailed K. Baum – 8th April 2008. |
| Independence issues | |
| Tables & Figures used | Figure 2. |
| Extraction | Data extracted from single figure by eye, with associated reading error. |
| Miscellaneous comments | Paper gives proportion and standard error (se), numbers of individuals arriving at destination patch extracted by multiplication of mean. Same start patch population measured moving to control or corridor patch. |

| Reference | Bowne, D. R. *et al.* (1999). "Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*)." Landscape Ecology 14(1): 53-65. |
|---|---|
| Subject | *Sigmodon hispidus* Cotton rat |
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two start patches selected for use were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | 2 weeks, 8 repetitions. |
| Location | Savannah River Site (SRS), South Carolina, USA. |
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Corridors more likely to be used to leave patch. |

| | *Number of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |

| | | |
|---|---|---|
| Corridor | 48 | 4 |
| Control | 96 | 4 |

| | |
|---|---|
| Internal validity | 1 – controlled experiment, problems with randomisation. |
| External validity | 3 – created experimental landscape. |
| Inter-patch distance | 64 m |
| Receiving patch size | 128 $m^2$ (1.64 ha) |
| Species group | Rodents |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Raw data presented in paper. |
| Independence issues | |
| Tables & Figures used | Text page 58, Figure 15. |
| Extraction | Extracted first and last move point, and for adjacent, equal distance patch pairs only (moves from Patch 2 to 3 or 7, and from Patch 3 to 2 or 8). |

| Reference | Coffman, C. J. *et al.* (2001). "Population dynamics of *Microtus pennsylvanicus* in corridor-linked patches." Oikos 93(1): 3-21. |
|---|---|
| Subject | *Microtus pennsylvanicus* Meadow vole |
| Spatial set-up | Four replicate study areas consisting of three grids per replicate: continuous, corridor linked and non-linked fragment, each containing a grid of trapping stations. |
| Temporal set-up | Trapping was conducted for 5 consecutive days, every 8 weeks, over 10 months. |
| Location | Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland, USA |
| Patch & corridor habitat | Old field |
| Matrix | Bare ground |
| Reported outcome | Corridors facilitate and increase movement frequency between patches. |

| | *Number of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Corridor | 185 | 6 |

| | | |
|---|---|---|
| Control | 187 | 3 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 4 – enclosed outdoor experimental arenas, mark-release-recapture of animals already existing within patches. |
| Inter-patch distance | 7.6 m |
| Receiving patch size | 2830 $m^2$ |
| Species group | Rodents |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Email sent to coffman@hsrdxail2.mc.duke – 8th April 2008, bounced. Emailed cynthia.coffman@duke.edu – 8th April 2008. Coffman replied – 10th April: checking for data permissions. Coffman replied – 25th April suggesting rates adjusted by capture probability were better to use than raw data. Emailed – 12th May: raw capture rates had been used in other extractions and giving more details about the analysis. |
| Independence issues | |
| Tables & Figures used | Table 3 & 8. Figure 2. |
| Extraction | Extracted by eye from figure, by multiplication of Table 3 & 8. |
| Miscellaneous comments | Multiplication of mean population size provides estimate only. |

| Reference | Danielson, B.J. and M. W. Hubbard (2000). "The influence of corridors on the movement behavior of individual *Peromyscus polionotus* in experimental landscapes." Landscape Ecology 15(4): 323-331. |
|---|---|
| Subject | *Peromyscus polionotus* Deer mouse |
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two start patches selected were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | |
| Location | Savannah River Site (SRS), South Carolina, USA. |

| | |
|---|---|
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Corridors do not increase movement frequency between connected patches |

| *Habitat type* | *Number of individuals* Marked at start | Found destination patch |
|---|---|---|
| Corridor | 112 | 24 |
| Control | 163 | 45 |

| | |
|---|---|
| Internal validity | |
| External validity | |
| Inter-patch distance | |
| Receiving patch size | 128 $m^2$ (1.64 ha) |
| Species group | Rodents |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Emailed Danielson – 8th April 2008: Where did the mice end up? Danielson replied – 9th April 2008: expressed concerns about whether the data being used were appropriate to the question. Conversation ongoing. |
| Independence issues | |
| Tables & Figures used | |
| Miscellaneous comments | Without the raw data, the only information available is related to those individuals leaving a patch. Final destination unknown. |

| | |
|---|---|
| Reference | Davis-Born, R. and J. O. Wolff (2000). "Age- and sex-specific responses of the gray-tailed vole, *Microtus canicaudus*, to connected and unconnected habitat patches." Canadian Journal of Zoology-Revue Canadienne De Zoologie 78(5): 864-870. |
| Subject | *Microtus canicaudus* Gray-tailed vole |
| Spatial set-up | Experimental units consisted of eight enclosures planted with alfalfa. Small isolated patches (156 $m^2$) in a 2 x 2 format with adjacent patches separated by 12.5 m matrix habitat. Within treatment enclosures, patches connected by 1m wide corridors. |

| | |
|---|---|
| Temporal set-up | 4 months |
| Location | Benton County, Oregon, USA. |
| Patch & corridor habitat | Alfalfa (*Medicago sativa*) |
| Matrix | Bare ground |
| Reported outcome | Corridors increase inter-patch movement frequency. |

| | Numbers of individuals | | |
|---|---|---|---|
| *Habitat type* | Sex | Marked at start | Found destination patch |
| Corridor | Male | 68 | 28 |
| | Female | 67 | 12 |
| Control | Male | 57 | 14 |
| | Female | 67 | 6 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 4 – enclosed outdoor experimental arenas. |
| Inter-patch distance | 1 m |
| Receiving patch size | 156 $m^2$ |
| Species group | Rodents |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted – date | Emailed J.O. Wolff: jowolff@stcloudstate.edu – 9th April 2008. Received reply – 9th April, data no longer available. |
| Independence issues | |
| Tables & Figures used | Text page 866 |
| Extraction | Extracted directly. |
| Miscellaneous comments | Experimental arena is enclosed by parameter fence. |

| | |
|---|---|
| Reference | Haddad, N. M. (1999). "Corridor and distance effects on interpatch movements: A landscape experiment with butterflies." Ecological Applications 9(2): 612-622. |
| Subject | *Junonia coenia* Common Buckeye butterfly |

| | |
|---|---|
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two subsets selected for use were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | 3 months |
| Location | Savannah River Site (SRS), South Carolina, USA. |
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Butterflies more likely to use corridor to colonise adjacent patch |

| | *Numbers of individuals* | | |
|---|---|---|---|
| *Habitat type* | Area | Marked at start | Found destination patch |
| Corridor | A2 | 137 | 14 |
| | A4 | 47 | 3 |
| Control | A2 | 110 | 3 |
| | A4 | 50 | 1 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created experimental landscape. |
| Inter-patch distance | 256 m |
| Receiving patch size | 128 $m^2$ (1.64 ha) |
| Species group | Butterflies and moths |
| Life history | |
| Covariate notes | |
| Author contacted - date | Emailed nick_haddad@ncsu.edu – 9th April 2008 requesting JC data for 1995 patch 12. Haddad replied – 11th April, would like to provide help in future but currently unable to but will respond at a later date. Received via email – May 2008: 1996 raw data taken from electronic supplementary material: http://esapubs.org/archive/appl/A009/005/default.htm. Haddad replied with raw data for 1995 on 15th May. |
| Independence issues | |
| Tables & Figures used | Appendix A. |
| Extraction | Extracted directly. |

| | |
|---|---|
| Miscellaneous comments | Extracted subsets of Areas A2 and A4 where there was one connected and one unconnected start patch within the same distance as the finish patch, and only used subsets where no other patches or corridors were within twice the inter-patch distance. |

| Reference | Haddad, N. M. (1999). "Corridor and distance effects on interpatch movements: A landscape experiment with butterflies." Ecological Applications 9(2): 612-622. |
|---|---|
| Subject | *Euptoieta claudia* Variegated fritillary |
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two subsets selected for use were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | 3 months |
| Location | Savannah River Site (SRS), South Carolina, USA. |
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Inadequate evidence |

| | *Numbers of individuals* | | |
|---|---|---|---|
| *Habitat type* | Area | Marked at start | Found destination patch |
| Corridor | A2 | 38 | 2 |
| | A4 | 2 | 0 |
| Control | A2 | 3 | 0 |
| | A4 | 4 | 0 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created experimental landscape. |
| Inter-patch distance | 256 m |
| Receiving patch size | 128 $m^2$ (1.64 ha) |
| Species group | Butterflies and moths |
| Life history | |

| | |
|---|---|
| Covariate notes | |
| Author contacted - date | Emailed nick_haddad@ncsu.edu – 9th April 2008 requesting JC data for 1995 patch 12. Haddad replied – 11th April, would like to provide help in future but currently unable to but will respond at a later date. Received via email – May 2008: 1996 raw data taken from electronic supplementary material: http://esapubs.org/archive/appl/A009/005/default.htm. Haddad replied with raw data for 1995 on 15th May. |
| Independence issues | |
| Tables & Figures used | Appendix B. |
| Extraction | Extracted directly. |
| Miscellaneous comments | Extracted subsets of Areas A2 and A4 where there was one connected and one unconnected start patch within the same distance as the finish patch, and only used subsets where no other patches or corridors were within twice the inter-patch distance. |

| Reference | Haddad, N. M., *et al.* (2003). "Corridor use by diverse taxa." Ecology 84(3): 609-615. |
|---|---|
| Subject | *Xylocopa virginica* Common Eastern carpenter bee |
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two subsets selected for use were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | Missing data |
| Location | Savannah River Site (SRS), South Carolina, USA. |
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Inconclusive results, analyses not possible. |

| | *Numbers of individuals* | | |
|---|---|---|---|
| *Habitat type* | Distance (m) | Marked at start | Found destination patch |
| Corridor | 64 | 12 | 3 |
| | 384 | 57 | 3 |
| Control | 64 | 12 | 0 |
| | 384 | 57 | 0 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created experimental landscape. |
| Inter-patch distance | 64 m and 384 m |
| Receiving patch size | 128 $m^2$ (1.64 ha) |
| Species group | Bees |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Emailed nick_haddad@ncsu.edu – 9th April 2008 requesting the number of bees marked in total. Haddad replied – 15th May 2008 providing relevant data. |
| Independence issues | |
| Tables & Figures used | |
| Extraction | |
| Miscellaneous comments | |

| Reference | Haddad, N. M. and J. J. Tewksbury (2005). "Low-quality habitat corridors as movement conduits for two butterfly species." Ecological Applications 15(1): 250-257. |
|---|---|
| Subject | *Junonia coenia* |
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two subsets selected for use were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | 2 years, 2 months |
| Location | Savannah River Site (SRS), South Carolina, USA. |
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Butterflies dispersed through corridors move frequently than between isolated patches. |

| | *Numbers of individuals* | | |
|---|---|---|---|
| *Habitat type* | Year | Marked at start | Found destination patch |

| | | | | |
|---|---|---|---|---|
| | Corridor | 2000 | 1352 | 7 |
| | | 2001 | 1599 | 6 |
| | Control | 2000 | 1325 | 4 |
| | | 2001 | 1599 | 2 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created experimental landscape. |
| Inter-patch distance | 150 m |
| Receiving patch size | 1.375 ha |
| Species group | Butterflies & moths |
| Life history | |
| Covariate notes | |
| Author contacted - date | Emailed nick_haddad@ncsu.edu – 9th April 2008 requesting the number of butterflies marked in total. Haddad replied – 15th May 2008 providing relevant data. |
| Independence issues | |
| Tables & Figures used | |
| Extraction | |
| Miscellaneous comments | |

| Reference | Haddad, N. M. and J. J. Tewksbury (2005). "Low-quality habitat corridors as movement conduits for two butterfly species." Ecological Applications 15(1): 250-257. |
|---|---|
| Subject | *Euptoienia claudia* |
| Spatial set-up | A total of ten patches: four isolated and six connected in pairs by corridors of varying width. Two subsets selected for use were only those adjacent to and of equal distance to that of an isolated and connected patch. |
| Temporal set-up | 2 years, 2 months |
| Location | Savannah River Site (SRS), South Carolina, USA. |
| Patch & corridor habitat | Clear-cuts |
| Matrix | Pine forest |
| Reported outcome | Butterflies dispersed through corridors move frequently than between isolated patches. |

| *Habitat type* | *Numbers of individuals* Year | Marked at start | Found destination patch |
|---|---|---|---|
| Corridor | 2000 | 556 | 61 |
| | 2001 | 912 | 100 |
| Control | 2000 | 556 | 31 |
| | 2001 | 912 | 50 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created experimental landscape. |
| Inter-patch distance | 150 m |
| Receiving patch size | 1.375 ha |
| Species group | Butterflies & moths |
| Life history | |
| Covariate notes | |
| Author contacted - date | Emailed nick_haddad@ncsu.edu – 9th April 2008 requesting the number of butterflies marked in total. Haddad replied – 15th May 2008 providing relevant data. |
| Independence issues | |
| Tables & Figures used | |
| Extraction | |
| Miscellaneous comments | |

| Reference | Baum, K. A. *et al.* (2004). "The matrix enhances the effectiveness of corridors and stepping stones." Ecology 85(10): 2671-2676. |
|---|---|
| Subject | *Prokelisia crocea* Plant-hopper |
| Spatial set-up | A total of 10 experimental landscapes, each with a central source patch surrounded by three vacant target patches. |
| Temporal set-up | 7 days |
| Location | Experimental arenas, North Dakota, USA. |

| | |
|---|---|
| Patch habitat | Cord grass |
| Matrix 1 (low resistance) | Brome grass |
| Matrix 2 (high resistance) | Mud |
| Reported outcome | Low resistance matrix assists higher inter-patch movement of plant-hoppers than the high resistance matrix. |

| | *Number of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Matrix 1 | 5000 | 110 |
| Matrix 2 | 5000 | 80 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 3 – created open experimental landscape, release densities similar to those of natural population densities. |
| Inter-patch distance | 2 m |
| Receiving patch size | 0.76 $m^2$ |
| Species group | True bugs |
| Life history | Semelparous |
| Covariate notes | |
| Author contacted - date | Emailed K. Baum – 8th April 2008. |
| Independence issues | |
| Tables & Figures used | Figure 2. T test data extracted from text. |
| Extraction | Data extracted from figure by eye, with associated reading error. |
| Miscellaneous comments | Paper gives proportion and se, numbers of individuals arriving at destination patch extracted by multiplication of mean. Same start patch population measured moving to control or destination patch. The landscape used is the same as that used in Haynes *et al*. with a different experimental design. |

| | |
|---|---|
| Reference | Bhattacharya, M. *et al*. (2003). "Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area?" Biological Conservation 109(1): 37-45. |

| | |
|---|---|
| Subject | *Bombus impatiens* & *B. affinis* Bumblebee species |
| Spatial set-up | A total of four wetland habitat patches within a ~1225 $m^2$ study area, each located either side of a 14 m wide road. Sites I and II exhibit similar inflorescence densities, with site I located on the opposite side of the road to the three others. |
| Temporal set-up | 4 days |
| Location | Webster conservation area, Boston, Massachusetts, USA. |
| Patch habitat | Sweet pepperbush plant (*Clethra alnifolia* L.) |
| Matrix 1 | Forest |
| Matrix 2 | Forest and road |
| Reported outcome | Natural or artificial landscape barriers do not restrict bumblebee movement where plant patchiness is comparable to habitat fragmentation. However, if plant populations become divided, bees may not readily cross the intervening area, particularly where the smaller, divided populations meet resource needs. |

| | *Numbers of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch. |
| Matrix 1 | 68 | 28 |
| Matrix 2 | 92 | 46 |

| | |
|---|---|
| Internal validity | 2 – Baseline differences commented on. |
| External validity | 1 – Natural populations, mark-release-recapture. |
| Inter-patch distance | 35 – 110 m |
| Receiving patch size | 240 – 850 $m^2$ |
| Species group | Bees |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Emailed Bhattacharya mita@bu.edu – 8th May 2008 bounced. Unable to find another address. |
| Independence issues | |
| Tables & Figures used | Table 2. |
| Extraction | Extracted directly. |

| | |
|---|---|
| Miscellaneous comments | Line 7 of table gives barrier as road and natural forest but line 6, Figure 1 and text both say site 2 and 3 assumed separated by forest. |

| Reference | Desrochers, A. and S. J. Hannon (1997). "Gap crossing decisions by forest songbirds during the post-fledging period." Conservation Biology 11(5): 1204-1210. |
|---|---|
| Subject | Forest songbirds - See Table 3 for full list of species. |
| Spatial set-up | Two rural and forested landscapes. Landscape 1: boreal forest containing 1-150 ha clear-cuts. Landscape 2: deciduous forest and open fields (pastures). |
| Temporal set-up | Each playback lasted 10 minutes, over ~40 day period. |
| Location | Southern Québec, Canada. |
| Patch habitat | Woodland |
| Matrix 1 | Clear-cut |
| Matrix 2 | Field (pastures) |
| Reported outcome | Inter-patch movements varied between species, but overall respondents preferred moving through patch habitat than either open matrix type. No preference was exhibited between matrix types for those birds moving to destination patch. |

*Total numbers of individuals for all species*

| *Habitat type* | Marked at start | Found destination patch |
|---|---|---|
| Matrix 1 | 161 | 116 |
| Matrix 2 | 492 | 391 |

| | |
|---|---|
| Internal validity | 2 – Addressed confounding factor (distance) within the study: not significant. |
| External validity | 1 – Natural populations within natural landscape. |
| Inter-patch distance | 7 – 160 m |
| Receiving patch size | Not included. |
| Species group | Birds |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | Emailed – 8th May 2008, raw data supplied by author – 13th May 2008. |

| | |
|---|---|
| Independence issues | |
| Tables & Figures used | Text page 1207. |
| Extraction | |
| Miscellaneous comments | Matrix type not significantly confounded by distance (checked using t-test with levene statistic, t219 =1.152, p = 0.250). |

| Reference | Goodwin, B. J. and L. Fahrig (2002). "How does landscape structure influence landscape connectivity?" Oikos 99(3): 552-570. |
|---|---|
| Subject | *Trirhabda borealis* Goldenrod beetle |
| Spatial set-up | Four 5 $m^2$ micro-landscapes constructed at four separate sites, each surrounded by traps. |
| Temporal set-up | 4 days |
| Location | Abandoned agricultural field, Ontario, Canada. |
| Patch habitat | Goldenrod |
| Matrix 1 (low resistance) | Cut vegetation (height 2 cm or less) |
| Matrix 2 (high resistance) | Camouflage netting |
| Reported outcome | The matrices with high resistance caused beetles to move more frequently but undirected. Low resistance matrix allowed for frequent bursts of slow, sustained and directed movements. Landscape structure determines movement behaviour of beetles. |

| | *Numbers of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Matrix 1 | 1600 | 58 |
| Matrix 2 | 1600 | 19 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 4 – enclosed, outdoor arenas. |
| Inter-patch distance | 5 m |
| Receiving patch size | 0.25 $m^2$ |
| Species group | Beetles |
| Life history | Semelparous |

| | |
|---|---|
| Covariate notes | |
| Author contacted - date | Emailed – 8th May 2008 requesting raw data and clarification of axes. Reply received – 14th May: still unclear. Emailed – 15th May looking for further clarification. Goodwin sent raw data – 10th June 2008. |
| Independence issues | |
| Tables & Figures used | Figure 5. |
| Extraction | Multiplied up from Figure 5 (which was mean per experiment) - 64 tests were run and half had 40% netting plus matrix, half had 100% matrix. Each run had a mean of 3 patches (half had two and half had four), and were multiplied both the 0.6 and 0.2 by (32*3). |
| Miscellaneous comments | |

| Reference | Haynes, K. J. and J. T. Cronin (2003). "Matrix composition affects the spatial ecology of a prairie planthopper." Ecology 84(11): 2856-2866. |
|---|---|
| Subject | *Prokelisia crocea* Prairie plant-hopper |
| Spatial set-up | Three matrix types: Periodically flooded mudflats, mixture native grass species, and mono-species-stands of smooth brome. |
| Temporal set-up | 72 hours |
| Location | Kelly's Slough National Wildlife Refuge, North Dakota, USA. |
| Patch habitat | Cord grass |
| Matrix 1 | Mudflat, bare ground |
| Matrix 2 | Native grass |
| Matrix 3 | Brome |
| Reported outcome | Connectivity among patch habitats is highest with a brome matrix than within the mudflat matrix. Patches in native grass have intermediate connectivity. |

*Numbers of individuals*

| | High permeability | | Low permeability | | |
|---|---|---|---|---|---|
| *Habitat type* | Start patch | Found destination patch | *Habitat type* | Start patch | Found destination patch |
| Matrix 2 | 4000 | 64 | Matrix 3 | 4000 | 115 |

| | | | | | |
|---|---|---|---|---|---|
| Matrix 2 | 4000 | 64 | Matrix 1 | 4000 | 19 |
| Matrix 3 | 4000 | 115 | Matrix 1 | 4000 | 19 |

| | |
|---|---|
| Internal validity | 1 – controlled, replicated experiment. |
| External validity | 4 – enclosed, outdoor arenas. |
| Inter-patch distance | 3 m |
| Receiving patch size | 0.06 $m^2$ |
| Species group | True bugs |
| Life history | Semelparous |
| Covariate notes | |
| Author contacted - date | |
| Independence issues | Used the same landscape but different experiment as Baum *et al.* (2004) |
| Tables & Figures used | Figure 2. |
| Extraction | Extracted means and standard error (se). |
| Miscellaneous comments | Each treatment has 8 reps and 8 catching patches per replicate. So the se may be compound. And total dispersed population was calculated immigrants per patch x 8 repetitions x 8 patches. |

| Reference | Russell *et al.* (2007). "The effects of matrix structure on movement decisions of meadow voles (*Microtus pennsylvanicus*)." Journal of Mammalogy 88(3): 573-579. |
|---|---|
| Subject | *Microtus pennsylvanicus* Meadow vole |
| Spatial set-up | Two experiments, each run in two enclosures, 4 $m^2$ habitat patch design. Experiment 1 had matrix corridors of different vegetation heights, Experiment 2 had matrix areas. |
| Temporal set-up | 2 weeks for each vole, spread over 2 months. |
| Location | Purdue Wildlife Area, Indiana, USA. |
| Patch habitat | Uncut grass |
| Matrix 1 | 35 – 75 cm Grass |
| Matrix 2 | 5 cm Grass or bare ground |
| Reported outcome | Voles prefer corridors with taller vegetation but will occasionally use corridors with mid-length vegetation. |

| | | | |
|---|---|---|---|
| Experiment 1 | | *Numbers of individuals* | |
| | *Habitat type* | Marked at start | Found destination patch |
| | Matrix 1 | 28 | 5 |
| | Matrix 2 | 28 | 2 |
| Experiment 2 | | *Numbers of individuals* | |
| | *Habitat type* | Marked at start | Found destination patch |
| | Matrix 1 | 25 | 10 |
| | Matrix 2 | 25 | 4 |
| Internal validity | | 1 – controlled, replicated experiment. | |
| External validity | | 4 – enclosed, outdoor arenas, mark release recapture. | |
| Inter-patch distance | | 4 m | |
| Receiving patch size | | 64 $m^2$ | |
| Species group | | Rodents | |
| Life history | | Iteroparous | |
| Covariate notes | | | |
| Author contacted - date | | Emailed – 8th May 2008 requesting for raw data or that Figure 15 be split into four matrix types. Reply received 14th May 2008. | |
| Independence issues | | | |
| Tables & Figures used | | Figure 15. | |
| Extraction | | Extracted by eye from figure with associated reading error. | |
| Miscellaneous comments | | Presented as probabilities. Potential to use number of telemetry fixes =160, or number of voles = 28. Number of voles was used to be conservative. Scope for sensitivity test here. | |

| Reference | Schaefer, J. F. *et al.* (2003). "Effects of barriers and thermal refugia on local movement of the threatened leopard darter, *Percina pantherina*." Environmental Biology of Fishes 66(4): 391-400. |
|---|---|
| Subject | *Percina pantherina* Leopard darter |
| Spatial set-up | Two narrow river channel sites, both with distinct riffle and pool structure. Within each site, 4 patches, numbered in descending order from upstream – downstream. ‘Preferred’ habitat patches separated by natural riffle, the second was separated by low water road crossing with culverts. |

| | |
|---|---|
| Temporal set-up | 2 months, over a period of 2 years (due to protective status and limitations on numbers of darters removed). |
| Location | Glover River, south-eastern Oklahoma, USA. |
| Patch habitat | Pool |
| Matrix 1 | Riffle |
| Matrix 2 | Road culvert |
| Reported outcome | Movement of darters was unidirectional (downstream) over road crossing sites. Darters moved both up and downstream over the natural riffle. |

| | *Numbers of individuals* | |
|---|---|---|
| *Habitat type* | Marked at start | Found destination patch |
| Matrix 1 | 74 | 4 |
| Matrix 2 | 35 | 2 |

| | |
|---|---|
| Internal validity | 2 – Baseline differences commented on. |
| External validity | 1 – Natural populations within natural landscape, mark-resight. |
| Inter-patch distance | |
| Receiving patch size | 700 $m^2$ |
| Species group | Fish |
| Life history | Iteroparous |
| Covariate notes | |
| Author contacted - date | |
| Independence issues | |
| Tables & Figures used | Figure 2 supported by text. |
| Extraction | Inter-patch movements extracted directly. |
| Miscellaneous comments | |