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THE POTENTIAL ROLE OF ECOLOGICAL CORRIDORS FOR HABITAT CONSERVATION IN IRELAND: A REVIEW

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The purpose of this report is to review current literature on the subject of ecological corridors and their potential applicability to Ireland in the context of the EU Flora, Fauna and Habitats Directive. Conclusions are derived from the available literature. They solely represent the opinion of the author at the time of writing and with contemporary information, and do not represent policy of Dúchas the Heritage Service (National Parks and Wildlife). These conclusions are open to changes as new information becomes available. The user of this report assumes full responsibility for any policy decisions and for any action taken as a result of the conclusions contained in this report. Neither the author nor Terrascope Environmental Consultancy may be held liable for the outcome of any policy decision or action taken by users of this report.

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Executive Summary

- The literature on ecological corridors is reviewed with regard to their potential for habitat conservation in Ireland for habitats and species listed in the EU Flora, Fauna and Habitats Directive. There is considerably more information on corridors in agricultural landscapes and for semi-pristine landscapes (continental forests) than for those relevant to listed Irish habitats and species.
- The main objective of ecological corridors is to facilitate dispersal and reduce the risk of extinction of a species due to excessive habitat fragmentation and the isolation of small fragmented populations.
- Fragmentation will often be more of a problem because of its physical, hydrological or ecological impacts than because of isolation of populations. This also applies to corridors, which can be dominated by the ecology of the surrounding habitat.
- 4. Regional corridors (linking sites by many kilometres) are distinguished from local corridors (linking habitat patches within large sites). Corridors are considered to include (1) continuous linear strips of habitat, and (2) a linear arrangement of separate stepping stone habitats, as well as linear features.
- 5. Although there is little evidence for the effectiveness of corridors, this has not been a legal obstacle to their implementation in the UK and the US. However, plans for regional corridors in Europe as part of National Ecological Networks have been more aspirational than practical, and have run into problems of public acceptance where they have reached the public enquiry stage.
- 6. River corridors have a slightly different meaning to ecological corridors, but their plans have been successfully implemented and include conservation of aquatic species. River and stream corridors have the most potential for the practical implementation of the regional corridor concept for species on the Habitats Directive.
- 7. Restored regional ecological corridors are expensive to establish and may be more expensive to maintain per hectare than core sites.

- It will be more successful to plan to retain linkages in a landscape undergoing fragmentation, than to attempt to establish them in a previously fragmented landscape.
- 9. Most of the wide ranging vertebrate species for which corridors have been frequently proposed are absent from Ireland (e.g. wolf, brown bear, lynx, forest birds), or occur in rivers (e.g. salmonids, otter). Hedgerows are valuable corridors for bats, but mainly as local corridors between feeding and roosting sites.
- 10. Ecological corridors have little potential for plants. Dispersal by livestock and mammals and birds is nevertheless important, especially in grasslands, and emphasis should be on maintaining animal movement within the landscape, especially in areas such as the Burren. Seed dispersal by adhesion to animals or man is, after wind, the second most important means of dispersal for the Burren flora.
- 11. For scarce vascular plants in isolated, recently fragmented habitats, translocation may be a preferable option, where habitat conditions are suitable and sustainable in the receiving site.
- 12. Feral goats may be important as seed dispersal agents in the Burren. The cost-benefit of increasing goat movement in the Burren needs to be estimated before active management is undertaken. In particular, it needs to be established whether rare or typical plant species are becoming extinct in patches of suitable habitat where goats do not occur.
- 13. Local corridors (within sites) are likely to be more successful and feasible than regional corridors. Road verge heathland corridors have been created in the Netherlands, and appear to work for many stenotopic heathland carabid beetles if 10m + wide, but not for some of the rarest species.
- 14. The effectiveness of regional corridors is considerably reduced by the fact that many species characteristic of, and restricted to, habitats listed in the Habitats Directive, have poor dispersal ability. These species would be unlikely to use even pristine corridors.
- 15. In theory, the reduction in barriers (e.g. wooded and scrub areas for open-ground species) in extensively managed landscapes, may be more relevant for some species, than the creation

or retention of corridors. In practice, it will be as difficult to establish that a species is not dispersing through a barrier, as it is to establish that it is dispersing through a corridor.

- 16. Enlarging small sites is generally preferable to linking them with regional corridors.
- 17. One individual per generation migrating between two populations can often be sufficient for adequate genetic exchange. This will rarely be detectable by sampling for migrant individuals. Dispersal monitoring aimed at assessing whether genetic interchange is adequate is therefore only likely to be successful at levels of interchange far above critical levels. Genetic analysis of isolated populations may be the preferred means of establishing connectivity between populations.
- 18. It is generally accepted that small, isolated populations have a higher risk of extinction due to demographic stochasticity than to genetic causes. Maintenance of connectivity is thus more important to facilitate re-colonisation following local extinction, than for ensuring genetic refreshment. It is similarly important for boosting small populations and thereby avoiding local extinctions.
- 19. Regional corridors are unlikely to have a cost-benefit advantage for most habitats and species in Ireland, in comparison with other options such as site enlargement, site buffering, maintaining hydrological processes and site management. Corridors are a comparatively high-cost, high-risk, option of limited application in comparison with other means of increasing connectivity between sites, and their potential value should be considered on a site-by-site and species-by-species basis, as part of an integrated dispersal management approach. They should not be assumed to be generally applicable in every regional conservation strategy.

THE POTENTIAL ROLE OF ECOLOGICAL CORRIDORS IN HABITAT CONSERVATION IN IRELAND : A REVIEW

Abstract

Ecological corridors are recommended as a solution to the fragmentation of European habitats. Their potential for habitat conservation in Ireland for habitats and species listed in the EU Flora, Fauna and Habitats Directive is reviewed. There is considerably more information on corridors in agricultural landscapes (i.e. non-priority habitats) and for semi-pristine landscapes (continental forests) than for priority Irish habitats. Regional corridors (linking sites separated by many kilometres) are distinguished from local corridors (linking habitat patches within sites). Local corridors of suitably wide habitat are likely to benefit invertebrates, and vertebrates such as bats, but the value of regional corridors is considerably less for habitat specialist species. Regional corridors have little potential for plants. Diaspore dispersal by livestock and wild mammals and birds is nevertheless important, and emphasis should be on maintaining animal movement within the landscape, especially in areas such as the Burren. The effectiveness of regional corridors is considerably reduced by the fact that many species characteristic of, and restricted to, habitats listed in the Habitats Directive, have poor dispersal ability. These species would be unlikely to use even pristine corridors. On a cost-benefit balance, regional corridors are unlikely to be a priority for most habitats and species in Ireland, compared to other options such as site enlargement and buffering, maintaining hydrological processes and site management. Corridors need to considered on a siteby-site and species-by-species basis, as part of an integrated dispersal management approach, including other options such as translocation, regional site management coordination, habitat enlargement, etc.

Introduction

Ecological corridors, or strips of habitat allowing movement of plants and animals between isolated protected areas, have been predicted to be an important feature of the future Irish landscape, mitigating the effects of landscape and habitat fragmentation (Aalen 1997). Corridors, and also 'stepping stones' (patches of habitat between protected sites), are currently an important component of European biological conservation strategies (Bennett and Wolters 1996). All Member States of the EU are required to designate a network of sites (Special Areas of Conservation or SACs) under the Flora, Fauna and Habitats Directive (CEC 1992), which was legally adopted in the Republic of Ireland in 1997 (S.I. 94 of 1997). This network of sites is referred to as the Natura 2000 network (CEC 1992). Article 10 of the Directive specifically refers to linear landscape features and stepping stone habitats:

"Member States shall endeavour, where they consider it necessary, in their land-use 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 as 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."

The Local Government (Planning and Development) Act, 1963 (Third Schedule, Part IV, Paragraph 8A) was amended as a result of adoption of the Habitats Directive, and local authorities can now refuse planning permission without compensation, for developments which threaten functioning ecological corridors or stepping stones. The amendment cites the:

"Protection of features of the landscape which are of major importance for wild fauna and flora in accordance with the Habitats Directive." (S.I. 94 of 1997, 26(c)).

The concept of a European network of protected areas has been further developed by the Pan-European Biological and Landscape Diversity Strategy, which was endorsed by the European Ministers of the Environment at Sophia in October 1995 (Prillevitz 1996). It has as its first Action Theme the development of a Pan-European Ecological Network, to be established by 2005 (ECNC 1996):

"The network will be built up from the following elements: core areas to conserve ecosystems, habitats, species and landscapes of European importance; corridors or stepping stones, where

these will improve the coherence of natural systems; restoration areas, where damaged elements of ecosystems, habitats and landscapes of European importance need to be repaired or certain areas completely restored; buffer zones, which support and protect the network from adverse external influences ...

The coherence of the network will be ensured through the provision where appropriate of continuous corridors or discontinuous "stepping stones" which will facilitate the dispersal and migration of species between the core areas. In many cases the connectivity function of corridors and stepping stones will be compatible with appropriate forms of economic activity in the respective areas."

This European Ecological Network (EECONET) was endorsed by the IUCN Action Plan for protected areas in Europe in 1994 (Bennett and Wolters 1996). Maps of existing and potential areas of conservation status, including ecological corridors, have been prepared for all EU Member States (Bischoff and Jongman 1993), and many European countries have produced plans for National Ecological Networks (Ministry of Agriculture, Nature Management and Fisheries 1990, Ministerkonferenz für Raumordnung 1992, Ministere van de Vlaamse Gemeenschap 1994, Liro 1995, Peterken et al. 1995, Kavaliauskas 1996, Sabo et al. 1996).

The ecological corridor concept, however, is dependant on two critical provisos. The first is that species of plant and animal of conservation value will actually move through them. The second is that investment of limited resources in corridors has a better cost-benefit balance than investment in other conservation activities such as site acquisition, management or restoration. Ecological corridors have been criticized as failing on both these criteria in many cases where they have been proposed (Simberloff and Cox 1987, Simberloff et al. 1992, Bonner 1994).

The aim of this report is to review the literature relating to the relevance of ecological corridors to the protection of habitats (Annex I) and species (Annex II) listed in the EU Flora, Fauna and Habitats Directive, as it applies to Ireland (CEC 1992, Romao 1996; see Appendix 1), taking into account the biological evidence, feasibility and cost-benefit considerations, and alternative options. A similar review of ecological corridors in Great Britain was carried out by Dawson (1994). The reader should refer to this work for a review of the theoretical aspects of corridors, which are not discussed here.

Corridors were legally defined in the U.S. (Ninth U.S. Circuit Court of Appeals (1990), cited in Walker and Craighead (1997)) as :

"...avenues along which wide-ranging animals can travel, plants can propagate, genetic interchange can occur, populations can move in response to enviromental changes and natural disasters, and threatened species can be replenished from other areas."

As used in the literature, the concept of a corridor can vary from a 5 m wide roadside strip (see Keals and Majer 1991) to a kilometres-wide landscape (Felton 1996). For the purposes of this report, an ecological corridor is considered to be a linear landscape feature (Figs. 1 & 2B), and ecological stepping stones are similarly considered to be a linear arrangement of habitat patches. Broad areas of habitat, either continuous or discontinuous, connecting relatively closely spaced core sites (referred to as a corridor by Noss (1987)), are considered a form of site expansion or site coalescence, or as the maintenance of landscape permeability (Fig. 2A). Examples of ecological corridors proposed in the literature are river valleys (Burkhardt et al. 1996), drove roads (M£gica et al. 1996), treeline forests, riparian forests and forests at the base of large mountains (Peterken et al. 1995), hedgerows, the banks of streams, canals and rivers and roadsides (Lammers and van Zadelhoff 1996), and small ponds, hedgerows and field margins (Jedicke 1990, Felton 1996). It is worth noting that nearly all these examples refer to river/stream, forest or farmland features.

To improve clarity, it is useful to distinguish different types of ecological corridors. An ecological corridor of any length will rarely be of uniform soil and vegetation composition, and what to larger more mobile species may be a linear feature may become a series of stepping stones to a smaller species.



FIG. 1. Illustration of what is defined as an ecological corridor for the purposes of this report, as a linear feature (above), or as a linear series of habitat patches ('stepping stones') (below).



FIG. 2. Different concepts of regional corridors: A (top) is a broad short linkage between sites close to each other. linking the Swiss National Park to the Stelvo National Park (Italy) (from Harris and Scheck 1991); B (bottom) is a series of thin long linkages between more distant, as proposed for Scotland by Peterken *et al.* (1995). The scale of the two figures is similar.

Long-distance corridors linking sites separated by at least several kilometres (regional corridors) (e.g. EECONET proposals; see Fig. 3) are different from local corridors linking habitat patches within a site, or between sites which are relatively close together. Regional corridors may have higher costs but lower chances of success because of their relative length.

It is important to distinguish ecological corridors as physical features, which provide connectedness in the landscape by physically connecting core habitats, and the biological attribute of landscape connectivity which is the ability of the target species or assemblages to disperse across a landscape (Baudry and Merriam 1988). The former does not imply successful dispersal, where the latter does.

The planning and management of corridors is much easier where they already exist, or at the beginning of the fragmentation process. For example, most Australian work on corridors is based on strips of remnant forest on roadsides, river banks, etc. (Saunders and Hobbs 1991). These remnant corridors are also important in South Africa, where for instance the Greater Cape Town corridors have high densities of threatened plants (McDowell et al. 1991). However, many of the European corridor proposals (e.g. Liro 1995, Peterken et al. 1995, Batten et al. 1996, Sidaway and Philipsen 1996) include substantial habitat restoration, and these need to be distinguished as restored corridors.



FIG. 3. Sketch map of the tentative ecological network proposed for Ireland, from Bischoff and Jongman (1992).

The main objective of ecological corridors is to facilitate dispersal and reduce the risk of extinction of a species due to excessive habitat fragmentation and the isolation of small fragmented populations. The adjective 'excessive' is used here because habitat patches are usually fragmented in natural ecosystems to begin with, due to ecological and geomorphological processes creating patches of different successional stages and different soil and sediment types (e.g. Pinay et al. 1990). The problem of the survival of small isolated populations occurs where these patches become much scarcer and more isolated in the landscape, as a result of human modification and replacement of natural processes by more uniform land management. Small isolated remnant sites are characteristic for many habitats in Ireland, such as oak woodland (Tomlinson 1997), raised bogs (Cross 1987), coastal lagoons (Carter et al. 1984), etc.

Although there are cases of small populations successfully persisting over many decades (Curtis and McGough 1988, Simberloff et al. 1992, Wid,n and Svensson 1992), there are others of small populations becoming extinct (Forney and Gilpin 1989, de Vries and den Boer 1990). These differences relate to ecological and reproductive strategies. For instance, plant species with a long-term seed bank in the soil may still survive even with very few visible plants in any one year (see Oostermeijer et al. 1996), whereas habitat-specialist invertebrates with poor dispersal ability may require large areas for populations to survive (Speight 1992, de Vries and den Boer 1990).

Sedentary species, with low mobility and specific habitat requirements, are most likely to be adversely affected by fragmentation (Wynhoff et al. 1996). Top predators are also particularly susceptible to extinction in fragmented habitats (Burkey 1997), as are other species which require large territories, and which occur at low densities (Saunders et al. 1991). Many of these 'high risk' categories are 'interior' species, in that they occur within habitat patches, but actively avoid edges of the patch (Bennett 1991).

Habitat fragmentation also detrimentally impacts ecological processes such as seed dispersal (Santos and Teller_ia 1994) and pollination (Jennersten 1988). Lack of pollinator visits may result in self-pollination by autodeposition, which can also lead to large decreases in seed-set (Oostermeijer et al. 1996).

The negative effects of habitat fragmentation may take many years to show their full impact, with species being lost steadily or intermittently over the intervening period (Saunders et al. 1991). Frequently, the processes responsible for the decline of a species (e.g. wetland drainage) will be different from those responsible for the local extinction of small populations (e.g. extreme weather) (Caughley 1994). Habitat fragmentation can lead to a loss of genetic variation in small populations

by the processes of random genetic drift, inbreeding depression (reduction in fitness), and reduction in gene flow (see Ellstrand and Elam 1993, Wid,n and Svensson 1992, Young et al. 1996). In some self-pollinating plant species, inbreeding may have little effect because they have already purged their genetic load, whereas in other species inbreeding will have detrimental effects (Oostermeijer et al. 1996, Young et al. 1996). However, it is generally excepted that small isolated populations have a higher risk of extinction due to demographic stochasticity than to genetic and other causes (Lande 1988, Shafer 1987, Hansson et al. 1992, Celada et al. 1994, Bolger et al. 1997).

It has been pointed out that potential climate changes will radically alter the suitability of currently protected sites to the species that they contain (Peters and Darling 1985, White 1996, Department of the Environment 1996). Ecological corridors and stepping stones have also been proposed as landscape features which might enable plants and animals to escape the effects of climate change (see Hill et al. 1994). This type of corridor, however, is more applicable to continental than insular countries. The comparatively uniform climatic conditions throughout Ireland mean that some susceptible species may be unable to survive on the island if a large-scale climatic change does occur, even if functioning corridors are in place. Furthermore, a study in the UK has concluded that corridor networks are unlikely to facilitate survival after rapid climatic change (Hill et al. 1994).

It has been estimated that plant species with narrow latitudinal ranges would need to move northwards at a rate 10 times faster than during the post-glacial period (Davis 1989). It has also been suggested that corridors themselves are likely to be the first habitats detrimentally affected by climate change (Blyth 1991). Habitat corridors ascending mountain ranges have been suggested for species may be able to move altitudinally (Blyth 1991). However, altidudinal range in Ireland is relatively small and decreases in temperature are complicated by increases in rainfall.

Dispersal Ecology and Corridors : Fauna

The corridor concept has been most frequently proposed for large forest vertebrates, in particular carnivores such as cougars (Felis concolor), bears and wolves, and for forest vertebrates with large area requirements such as woodpeckers, the North American spotted owl (Strix occidentalis caurina), etc. (Simberloff and Cox 1987, Beier 1995). Most of the limited evidence for use of corridors involves carnivores, rodents, birds and other vertebrates, mostly in hedgerows and forest strips (Arnold & Weldenburg 1990, Dmowski and Kozakiewicz 1990, Lorenz & Barrett 1990, Merriam and Lanoue 1990, Zhang and Usher 1991, La Polla and Barrett 1993, Beier 1995, Dunning et al. 1995, Sabo et al. 1996). Ecological corridors were included in the Dutch National Network to facilitate migration by wide-ranging mammals such as otter (Lutra lutra), badger (Meles meles) and red deer (Cervus elaphus), and fish such as sea and river trout (Salmo trutta), and salmon (Salmo salar) (Lammers and van Zadelhoff 1996). Constricted marine corridors may be important for species like harbour porpoise (Phocaena phocaena) and bottle-nosed dolphin (Tursiops truncatus) (Ozturk and Ozturk 1996).

However, most of these examples are not relevant to the Irish fauna. Most European terrestrial mammals with large home ranges are either absent (e.g. bison (Bison bonasus), lynx (Lynx lynx)), extinct (e.g. wolf (Canis lupus), brown bear (Ursus arctos), wild cat (Felis sylvestris), wild boar (Sus scrofa) or semi-managed (e.g. red deer) in Ireland (see Woodman et al. 1986). Ireland does not possess 'interior species' like the spotted owl and other forest species (e.g. willow tit (Parus montanus), nuthatch (Sitta europaea), Pallas' warbler (Phylloscopus proregulus) (Bourski 1996)). In the Killarney woodlands, for instance, only the redstart (Phoenicurus phoenicurus) could be regarded as a species possibly dependant on woods. All other breeding species recorded by Wilson (1977) are able to disperse through and breed in farmland.

A further source of practical experience in wildlife corridors relates to hedgerow linkages between small woodlands and ponds in agricultural landscapes. However, with the exception of bats (see below), these are not habitats considered in Annex II of the Flora, Fauna and Habitats Directive as it applies to Ireland, and therefore not directly related to the scope of this review. Also the small mammal and amphibian species with which many of these studies have been concerned are also absent in Ireland; but bats are a possible candidate group which would potentially benefit from farmland corridors.

Racey and Swift (1985) found that pipistrelle bats (Pipistrellus pipistrellus) moved between foraging sites on regular routes, and Walsh and Harris (1996) recommended preservation of linear corridor habitats within the UK landscape for vespertilionid bats. In the Czech Republic, regional

corridors have been cited where several bat species disperse between the southern Moravian lowlands to the Bohemian basin (Weidinger 1994). Clearly, the role of both regional and local corridors for bats requires more investigation, and in particular, potential barriers to long-distance dispersal by bats need to be identified.

As mentioned above, the corridor concept naturally applies to rivers and streams, and the management requirements of river corridors for salmonids are well established (e.g. Barton et al. 1985). It may also usefully apply to lampreys.

While Ireland has considerably fewer invertebrate species than Central, Southern and Eastern Europe, it has even less stenotopic species with poor dispersal ability. This is clear even in comparison to the fauna of Great Britain (see Table 1). However, even species of intermediate dispersal ability may benefit from habitat linkages in the form of stepping stones, and if it were possible to calculate dispersal rates, then some idea of which species would benefit from stepping stones and corridors might be possible.

% in Ireland	
90	
53	
37.5	
	% in Ireland 90 53 37.5

 TABLE 1. Percentages of British butterfly species of different dispersal abilities occurring in Ireland. Data from

 Pollard and Yates (1993).

Dispersal rates have been calculated for several invertebrate species. For instance, the average daily rate of dispersal of the fruit-fly *Drosophila subobscura* along a woodland/grassland margin was estimated to be 150 m by Walter and B,,chli (1987). Examples of maximum life-time distances covered by terrestrial snails (simulated, but based on field data) are 13.1 m for *Trochoidea geyeri* and 19.5 m for *Candidula unifasciata* (Bahl et al. 1996). However, there are a number of practical problems with monitoring dispersal and calculating dispersal rates, especially over short periods of only a few years. Many animal species, normally non-migratory, can migrate in years with suitable weather conditions and when population density is high or when breeding habitats become unfavourable (Hansson et al. 1992, Pollard and Yates 1993). On the other hand, even apparently mobile species, if they depend on scattered and ephemeral resources, can become temporarily

isolated and suffer genetic bottlenecks, as was found for whirligig beetles which breed in ponds (Nuernberger 1996).

In the absence of reliable estimates of dispersal ability, it would be incorrect to simply classify species according to whether they can or cannot fly. In a genetic study of leaf-mining flies of the genus *Phytomyza* in Germany, Switzerland, France and Andorra, Frey et al. (1990) found that the level of genetic variation between populations several kilometers apart was similar to that of populations up to 1000 km apart. The host plants of these species (umbellifers) were generally patchily distributed in space and time, and they concluded that local extinction and recolonization was probably common in many of these fly populations. Many natural populations of the species of *Phytomyza* studied are likely to live in small populations and undergo chromosomal mutations due to founder effects more frequently than species with higher dispersal abilities.

For marine invertebrates which disperse passively as planktonic larvae, the question of dispersal relates to the movements of currents. Even for specialists in isolated sites such as coastal lagoons, dispersal by sea appears to be more important than carriage by waterbirds, for instance (Barnes 1988). Little appears to have been published concerning corridors for invertebrates in the marine environment.

The following examples consider corridors in more detail as they apply to a listed vertebrate and invertebrate species, and assemblages of invertebrates characteristic of listed habitats.

Case Study : The Otter (*Lutra lutra*)

The otter is a listed species in Annex II of the Habitats Directive (CEC 1992), and a species for which corridors have been proposed in Central Europe (Liro 1995, Reuther 1996). These proposals relate specifically to establishing connectivity in areas where otter populations have declined and become isolated due to water pollution, etc. However, there is no evidence from recent distribution surveys of the species in Ireland (Lunnon 1996) that any Irish populations are isolated or likely to be so in the immediate future. Otters can readily cross dryland watersheds (Corbet and Southern 1977), and have even been recorded in Dublin city centre (Lunnon 1996; J.D. Reynolds, pers. comm.). The priority for the conservation of this species relates to the impact of river maintenance schemes and to water pollution (Lunnon and Reynolds 1991, O'Sullivan 1996). However, O'Sullivan (1996) emphasises the need to consider wetland/river corridors between protected areas, because the latter are insufficient to maintain sustainable populations. While there does not yet appear to be a requirement for corridors to protect dispersal of this species in Ireland, if

deterioration of river water quality and river margin habitat is expected to continue, a contingency plan for this species would need to consider aquatic corridors at the regional level.

Case Study : The marsh fritillary (Eurodryas aurinia)

Eurodryas aurinia, a species listed in Annex II of the Habitats Directive, appears to occur in metapopulations (the sum of local populations connected by dispersal) (Warren 1994), as do many other butterflies (Hanski and Thomas 1994) and other taxonomic groups (Fahrig and Merriam 1994).

E. aurinia shows large population fluctuations (Ford and Ford 1930, Lavery 1993), and, because of its likely metapopulation structure, may become extinct in a region where suitable habitat is declining, but well before all suitable patches of habitat are removed (Kareiva and Wennergren 1995). Warren (1994) considers populations in small (< 10 ha) but good quality habitat to have a high risk of extinction. Effective conservation of this species is likely to require a landscape network which encompasses a number (ideally tens) of colonies relatively close to each other (Warren 1994).

Most Irish colonies are isolated (Lavery 1993), exceptions being several large colonies in calcareous grassland. However, the distance travelled (which can be up to 20 km (Warren 1994)) over different types of habitat and land use is not known. When designing a landscape management plan for this type of species it may be more important to be able to recognise barriers to dispersal, rather than identify corridors.

Landscape management priorities for a related species, *Maculinea alcon*, in the Netherlands, included the establishment of 200-500 m wide corridors of unfertilized grassland, or heathland, rich in flowering plants (Wynhoff et al. 1996). Wet areas with *Geranium pneumonanthe* within the corridors may act as stepping stones (Wynhoff et al. 1996). The distances covered by *M*. *alcon* are relatively small on a regional scale, but this example is considered to show the benefit of remnant local corridors within large sites which are becoming more intensively managed.

Linking small populations by stepping stone habitats may be much less effective than linking large populations because of the reduced probability of successful dispersal from small populations (Harrison et al. 1988). It is also useful to distinguish between mainland-island populations, and patchy populations where dispersal rates are high enough to make the metapopulation behave as a single population (Harrison 1991). Creating or maintaining habitat corridors in the latter case

deflects attention from the connectivity of the whole landscape. The identification of and removal of barriers may be a more effective approach in this case.

Case Study : Ground Beetles (Carabidae)

Dispersal of carabid beetles has been relatively well studied in the Netherlands (den Boer 1990), and provides an insight into the role and limitations of ecological corridors for invertebrates with poor dispersal ability. Stenotopic species with poor dispersal ability are more likely to become extinct in small sites (de Vries and den Boer 1990). The ability of heathland carabids to utilize heathy road verges as corridors between heathland fragments in the Netherlands was studied by Vermeulen (1993, 1994) and Vermeulen and Opdam (1995). Width of the road-verge corridor was a critical factor for its effectiveness (Vermeulen 1993). Nearly all carabid species which occurred in the border zone of the heathland also occurred at least 100 m into the corridor if it was 10 m + wide. However, only a third of the species (and none with poor dispersal ability) occurred where the corridor was < 6 m wide.

Vermeulen (1995) and Vermeulen and Opdam (1995) conclude that corridors longer than several (100-500) metres will need to have areas of heathland broad enough (> 25 m) to facilitate breeding, as non-flying stenotopic carabids will be unlikely to extend beyond this distance in one generation.

Suitably broad heath road margins have been shown to support reproductive populations of stenotopic carabids in Britain (Eversham and Telfer 1994). In Brittany, lanes bordered by two hedgerows were more effective corridors between woodlots for *Abax parallelepipidus*, than single hedgerows (Charrier et al. 1997), confirming the requirement for wide corridors. The closer the ground conditions are to the natural habitat the more species are likely to use corridors (Sustek 1992).

From the above studies, it can be concluded that the shorter and wider the corridor, the more effective it is likely to be for stenotopic species with poor dispersal ability. Local corridors will, therefore, be more effective than regional corridors.

Case Study - Molluscs in fens

Small molluscs restricted to fens and other wetlands, such as several *Vertigo* species listed in Annex 2 of the Habitats Directive (Appendix 1), may be more isolated now than in the past

(Coleville 1996, Killeen 1996a,b). Isolation can be due to drainage reducing the size and connectedness of their habitat, and a decline in potential dispersal agents such as water-flow and waterfowl. Mollusc dispersal, not unexpectedly, is often very poor. For instance, many riparian land mollusc species were unable to disperse through villages in stream valleys in Germany (Martin and Roweck 1988). Only 4 out of 53 land snails were found to be capable of crossing a two-lane asphalt road in Germany, and the four that did were all eurytopic species (Martin and Roweck 1988). Even tall, dense vegetation can act as a barrier to grassland molluscs (Bahl et al. 1996).

Vivian-Smith and Stiles (1994) collected seeds from the feathers and feet of geese and ducks shot in a U.S. salt marsh. They recorded an average of 2.44 seeds/bird collected from the feathers and 0.39 seeds/bird from their feet. It is not inconceivable that small molluscs could also be dispersed in this way by waterfowl, although Barnes (1988) did not consider this likely in the case of coastal lagoons.

However, there have been declines in the numbers of waterfowl (e.g. white-fronted goose (*Anser albifrons*) (Ruttledge and Ogilvie 1979)) using several wetland sites as a result of drainage and disturbance. If waterfowl were an important dispersal agent, these changes may mean that small sites, which were once larger, have a highly reduced probability of dispersal for wetland molluscs.

If water flow and waterfowl are the predominant dispersal mechanisms for small molluscs in fens, then modern populations are likely to be less connected than those historically. To increase dispersal of molluscs between wetland sites, translocation of moss, litter and turf samples from an occupied to an unoccupied site could be carried out. Even if this was done infrequently (once every 10 to 20 years), it would probably be more cost-effective than maintaining a hydrologically intact regional corridor through a developed landscape. However, this assumes that wetland molluscs need to disperse because their populations have become so small to increase their risk of local extinction in isolated sites.

There is little field data on the effectiveness of seed dispersal as a means of recolonization or augmentation of isolated populations of species characteristic of the habitats or species listed in the Habitats Directive (see Appendix 1). Poschlod et al. (1996) were unaware of any experiments which had investigated the effect of dispersal on plant population viability. Nevertheless, the actual or presumed means of dispersal have been categorized for nearly all species of the Irish vascular flora, albeit from Central European data (M.C.D. Speight, pers. comm.).

Many species are adapted for dispersal by wind, but apart from spore-producing groups like bryophytes and Equisetum spp, seeds of grassland plants show poor long-distance dispersal by wind (Sorensen 1986, Strykstra 1997), and rely on dispersal by mowing machinery in meadows (Strykstra 1997) and livestock in pastures (Fischer et al. 1995). Dispersal of seeds by fruit-eating birds and mammals is well-known (e.g. Snow and Snow 1988), and particularly applies to scrub species but also to herbs like Galium spp. Dispersal of wetland diaspores on the feathers and feet of waterbirds has also been demonstrated (Gilham 1970, Vivian-Smith and Stiles 1994), but bird dispersal was found to be ineffective for four plant species studied by Primack and Miao (1992). Water dispersal (hydrochory) is also important (Nilsson et al. 1991), although vegetative propagules may often be more important than seeds because they have longer floating times (Johansson and Nilsson 1993). However, in isolated waterbodies like turloughs, seed dispersal by livestock and wild mammals may be more effective between water bodies (Johansson and Nilsson 1993). Some species may even have adaptations to avoid dispersal, because the risks of not finding suitable habitat by dispersing are outweighed by remaining in a habitat patch which has allowed successful reproduction over a long period (Zedler and Black 1992).

Poschlod et al. (1996) recommend a focus on 'moving ecological infrastructure', which includes domestic livestock, rather than on a 'static ecological infrastructure' in the form of corridors, even if livestock move along specific routes in the landscape. Connectivity and plant diaspore dispersal between limestone pastures are discussed in more detail below, especially with regard to livestock movement between discrete habitats. However, this particularly applies to movement within a landscape. In general, the likelihood that species of conservation importance will use corridors many kilometres long is low. Oostermeijer et al. (1996) concluded that "because of their highly restricted pollen and diaspore dispersal, it has been doubted that such corridors will ever be successful for most plant species". This conclusion appears to be especially valid for species with poor dispersal ability, for example, certain *Sphagnum* mosses (see below).

Case Study : Seed Dispersal by Mammals in the Burren

The importance of grassland seed dispersal by livestock was demonstrated by Fischer et al. (1995), who recorded over 8 500 diaspores of 85 species from a regular investigation of the fleece of a single sheep, and estimated that more than 3 000 000 seeds were dispersed on the fleeces of a flock of 350 sheep in one season in the Schwabische Alb (Germany). To this epizoochory (seed dispersal by adhesion to animals) must be added the potential for seed dispersal by endozoochory (dispersal in animal dung).

Work in the Netherlands has suggested that wind dispersal of seeds is relatively poor in most grassland flowering plants, and dispersal by herbivores or mowing machinery are the only efficient mechanisms for many species (Strykstra 1997, Vegelin et al. 1997). Verkaar (1990) provides an explanation for this. Prior to human modification, selection pressure on plant species of grazed areas was for survival rather than reproduction, and, even if grazed areas became isolated, the herbivores maintaining them would have acted as dispersal agents. In contrast, disturbed 'pioneer' habitats would have been scattered and ephemeral, and the selection pressure on pioneer species was for reproduction rather than survival. Because the human landscape has reversed the proportion of disturbed to undisturbed habitat, pioneer species (including aliens) can spread rapidly as weeds, whereas species typical of later seral habitats are isolated and often vulnerable to extinction due to their poor dispersal abilities. This situation is exacerbated where the movement of livestock is reduced, as it is in modern fixed-area grazing systems, compared to historical commonages (Poschlod et al. 1996).

As can be seen from Fig. 4, epizoochory (transport by adhesion to animals or man) is the second most important means of potential dispersal for flowering plants in the Burren, the first being wind. Approximately half (229 of 459) of the flowering plant species listed for the Burren hills by Webb and Scannell (1983) have the potential to be dispersed by epizoochory, according to the plant traits database (Fig. 4). However, the vast majority of species which can be dispersed by epizoochory are also dispersed by wind. Indeed, many species are likely to rely on a multiple-agent dispersal strategy, and some may even be polymorphic for adhesive or wind pollinated diaspores (Sorensen 1986).



Fig. 4. Relative frequency of potential dispersal mechanisms for 459 flowering plants occurring in the Burren hills, listed by Webb and Scannell (1983), and in the plant traits database (M.C.D. Speight, pers. comm.). This representation, however, is unlikely to represent the colonization success due to the various dispersal mechanisms (see text). The limitations of the qualitative data in the database must be recognised when interpreting Fig. 4. Actual quantitatively-important dispersal agents have only been established for a proportion of the species listed; others have been extrapolated from morphology, similarity to related species, etc. Dispersal is not directly related to colonization success in all cases, depending on the extent to which the dispersal mechanism is random or directed (see text). Also, the applicability to the Burren will differ. Ants, for instance, are likely to be of less importance in recolonization because the large colonies of seed-foraging species such as the *Messor barbara* are absent from Ireland.

Wind is, nevertheless, not considered to be an efficient long distance dispersal mechanism for most species (Sorensen 1986, Strykstra 1997). Vegelin et al. (1997), for instance, demonstrated that seeds of most grassland species are dispersed only short distances by wind, but wind speeds during the period of observation were not given, and the ability of occasional late summer storms (e.g. 1 in 10-20 years) to disperse seeds long distances remains a possibility. Dixon (1982) records very few seeds of Sesleria albicans being carried more than 2 m by an air-speed of 11-14 m/s (= 39.6 - 50.4 km/h). The relative importance of wind in areas like the Burren, exposed to the Atlantic, is also likely to be higher than in sites where seed dispersal by wind has been measured. However, even in very windy environments the effectiveness of wind dispersal appears limited to a few species. Welch et al. (1990) reviewing seed dispersal in British moorland, conclude: "The evidence on wind dispersal indicates that the vast majority of seeds will be deposited close to the parent plant and the supply of seed will not be regular even a few metres from the source. Only in a few species will some seeds be carried distances of several kilometres, the numbers involved being small and the chances of colonization unpredictable." Welch et al. (1990) also draw attention to the relatively recent lack of trees from upland habitats (which also applies to the Burren (Watts 1983)) and that most plant species will have evolved in less windy parts of Europe, and may therefore not be capable of taking advantage of their modern windy habitat.

Fischer et al. (1996) pointed out that seed dispersal on sheep is directed dispersal, from one patch of pasture to another, unlike wind which is random. However, many seeds are likely to be knocked off in scrub thickets (Sorensen 1986); such conditions may not be suitable for germination of many species.

Nearly all large mammals occurring in the Burren can be implicated in seed dispersal (Table 2), but obviously some will be more important than others. The lack of sheep, one of the best proven dispersal agents for seeds in calcareous grasslands (Fischer et al. 1996), means that existing dispersal will, for most species, be effected by feral goats (with shaggy, often matted, coats), domestic cattle, hares (*Lepus timidus*) and rabbits (*Oryctolagus cuniculus*). Feral goats occur in scattered herds (D'Arcy & Hayward 1992), and there appears to be some exhange of individuals between at least some of these herds (Bonham & Fairley 1984). The diet of the Burren goats has been studied (Byrne et al. 1996), but their role in epizoochorous or endozoochorous seed dispersal is unknown, but if comparable to sheep, it may be considerable (cf. Fischer et al. 1995). Goats show less preference for grass-dominated swards than cattle, but both have a role in maintaining patch diversity by grazing (O'Donovan and Moles 1997). Hares, although smaller, groom in habitats which may be suitable as seed germination sites (Sorensen 1986), and mountain hares can travel long distances even daily (Flux 1970). Rabbits, too, may be important diaspore vectors (e.g.

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Zedler and Black 1992, Malo et al. 1995), but on a more local basis since their home range is considerably smaller (Corbett and Southern 1977).

The relative importance of endozoochory, or seed dispersal in dung, was studied in British moorlands by Welch (1985), who found that cattle dung was more effective for dispersal than that of red deer, sheep, hare, rabbit and red grouse (*Lagopus lagopus*). In a glasshouse experiment, Welch (1985) germinated 662 seedlings of 24 species from a single cow-pat, but nearly all species were common and widespread. It was concluded that dispersal by cattle dung may favour certain species preferred by cattle. This indicates that, in the Burren, cattle may be more effective seed dispersers for common species by endozoochory than goats. The possibility of poor dispersal of less palatable, and often more characteristic species of a habitat, was also shown by Zedler and Black (1992) for rabbits (*Sylvilagus* spp.) in Californian vernal pools. Only one rabbit pellet in one of the studied pools contained a seed of the endemic *Pogogyne abramsii*, compared to a seed production of more than 1600 seeds/m2 in parts of the habitat in the previous season.

Given the modern fixed-area grazing systems, the abandonment of livestock droving and the use of horses for human transport, in the Burren today, the importance of continuing to allow access to feral goats throughout the area is probably important for seed dispersal. The maintenance of the long-haired characteristics of the goat herds is also a factor ; the possible genetic effects of shorthaired domestic goats abandoned to these herds may need to be considered.

Although the surveying of animal dispersal agents (e.g. goats) for seeds and other diaspores may provide information on a range of species likely to be dispersed, it will not provide useful data on connectivity, for two reasons. Firstly, diaspore dispersal in many species is likely to be a sporadic or rare event (see Sorensen 1986, Legg et al. 1992, England 1993), with a low probability of being detected by random survey. Secondly, dispersal is only part of a series of events which allow effective recolonization; in particular, the plant has to successfully establish and survive. Measuring genetic differentiation between isolated populations may be useful for estimating effective dispersal and connectivity (Burgman et al. 1993), as long as there have not been large demographic changes in the populations of the target species in recent times (see Widén and Svensson 1992).

TABLE 2. Potential mammal seed dispersal agents in the Burren, with sources of information demonstrating their potential as dispersal agents (some references are to related species). Further information is available in Stiles (1992), Schupp (1993) and Wilson (1993). Data on goats was not found during this review, but may exist in the Mediterranean literature.

Badgers	Hernandez (1990)
Cattle	Welch (1985), Malo and Suarez (1995)
Foxes, dogs	Leon-Lobos and Kalin-Arroyo (1994)
Hares	Agnew and Flux (1970), Welch (1985)
Hedgehogs	Hernandez (1990)
Horses	Liddle and Elgar (1984)
Goats	-
Man (clothing)	Clifford (1956), Bullock and Primack (1977), Carter (1993)
Man (tents)	Good and Cullinane (1990)
Pigs	Genard and Lescourret (1985)
Pine marten	-
Rabbits	Welch (1985), Zedler and Black (1992), Malo et al. (1995)
Sheep	Welch (1985), Talbott Roche et al. (1992), Fischer et al. (1996)

Case Study : Sphagnum in peat bogs

Dispersal of *Sphagnum* occurs by wind-borne spores released from capsules, or by vegetative structures. Poor dispersal ability and rarity appear to be correlated for many species of *Sphagnum* (Fig. 5) (see also Longton 1992). Restricted gene flow is more characteristic of bryophytes than vascular plants, although, in general, risk of extinction due to population isolation can be compensated by their smaller area requirements (Wyatt 1992).

Sphagnum pulchrum (Braithw.) Warnst. is recorded from the Killarney and Connemara regions, but also from two midland bogs; it is rare in Britain (Hill et al. 1992). Capsules of this species have not been recorded in Britain and Ireland (Hill et al. 1992), and consequently its dispersal is likely to be restricted. In Britain the species shows a high level of genetic variation both within and between sites (Daniels 1982), suggesting that dispersal is poor even within sites.

Peatland corridors are unlikely to be effective for a number of the characteristic bog mosses due to their poor dispersal ability. Although peat-forming species of *Sphagnum* can be cheaply and successfully re-established where a stable water-table and ombrotrophic conditions are maintained (Rochefort and Campeau 1997, Silva et al. 1997), transplantation of rarer mosses requires some knowledge of the genetics of the populations affected (Wyatt 1992). Any plan to increase connectivity between populations must be done on a case-by-case basis (Wyatt 1992), rather than from generalizations based on a limited number of examples. The maintenance of favourable habitat conditions is therefore likely to be of greater priority for many threatened characteristic bog species (IPCC 1996, Stoneman 1997).

FIG. 5. Relationship between capsule production and distribution in Co. Donegal for 25 species of Irish *Sphagnum*. Note that species which produce capsules rarely or not at all occur rarely or are absent from Donegal. Data from Hill *et al.* (1992).



Feasibility of Corridor Proposals

Many papers proposing corridors refer to movement and connectivity without citing examples of where this has occurred relevant to the type of habitat for which corridors are being proposed, or without defining target species (see Henle and Muhlenberg 1996). Nevertheless, the absence of evidence has not necessarily been a legal obstacle to their implementation. In the U.S. several legal cases have been decided against development proposals which might affect connectivity, in the absence of scientific evidence for connectivity (Harrison et al. 1993, Russell 1994). Similarly, a public enquiry in Bristol (UK) decided that a corridor did contribute to the dispersal of wildlife, even though conclusive proof was not available (Batten et al. 1996).

Simberloff et al. (1992) criticize the conclusion that, in the absence of reliable information, corridors should be retained or created on the basis of the precautionary principle, or because action cannot wait for evidence (Noss 1987, Forman and Collinge 1996). They emphasize cost-benefit analysis of corridors in each specific situation, in comparison to other competing demands for financial resources. Alternative options may achieve conservation objectives more successfully. Corridors will not provide a 'quick fix' solution (Plummer and Mann 1995).

One of the most politically advanced ecological network plans involving corridors in Europe was produced for Flanders. It provides some insights into the potential problems associated with the implementation of networks containing ecological corridors on a national scale. The Flanders plan included corridors covering 178 000 ha (12.9 % of the country), of which 57% was under intensive agricultural management, and a further 12% was urbanized (De Blust and Kuijken 1996). De Blust and Kuijken (1996) described the political response to the network plan:

"The public inquiry took place after the round of official consultations was complete. Public hearings were organized and a questionnaire distributed. The response was overwhelming - the Department of Nature Conservation received 16,833 returned questionnaires (Ministerie van de Vlaamse Gemeenschap, 1994), revealing that the absence of clear procedures for implementation, the lack of compensation commitments and incentives, and the uncertainty about legal protection had fuelled much resistance among farmers, foresters and private landowners. This rousing of public sentiment made the Green Main Structure for Flanders a hot political item by the end of 1993; even the unity of the Flemish government was put at risk. As a result the original plan for the Green Main structure for Flanders has had to be shelved while a new procedure for its incorporation in the Structure Plan for Flanders can be found."

Sidaway and Philipsen (1996) consider that much of the political opposition to the implementation of this network was because the plan was too narrowly based, and did not include

cultural aspects and multi-function land-use. They suggested that the earlier involvement of farmers, foresters and private landowners in the public debate, before options were decided upon, would have increased the chances of agreement. The goal of public support, however, may be more difficult in Ireland than in the UK or in Flanders for cultural and legal reasons (e.g. the importance of private property (Hickie 1997)).

As pointed out by the IUCN Commission on National Parks and Protected Areas (1994), support of local communities is essential to the long-term success of protected areas. While a local pride in, and identity with, protected landscapes can be encouraged, the question must be asked whether a similar local attitude could be developed in the case of regional corridors, which are not unique areas in themselves, but routes to and from other more valued areas.

Corridors will have ongoing management costs such as weed control, fire control, fence repair, etc. (Panetta and Hopkins 1991). In Australia, costs of corridor management were greater per hectare than core sites (Loney & Hobbs 1991), especially for riparian corridors where access requires cooperation of adjacent landowners (Watson 1991). The type and cost of successional management to maintain habitat uniformity along the corridor needs to be considered. Habitat corridors/islands for plants and invertebrates may require more management than those for vertebrates with a wider dispersal habitat range, or for the habitat in the core sites, where successional patches will replace each other.

While wide corridors are more expensive in terms of land acquisition, it is generally recognised that broad strips of land are more effective as corridors than narrow strips (e.g. Keals and Majer 1991, Tischendorf and Wissel 1997). The latter are dominated by physical and biological 'edge effects' due to microclimate changes (especially in forests) (Margules 1996), hydrological changes, increased predation (Simberloff and Cox 1987) and competition from species invading from surrounding land (Bauer 1989). These detrimental effects can mean that corridors of poor habitat act as sinks for the population dispersing into them (Henein and Merriam 1990). In practice, stepping stones are often more feasible to implement than corridors, because the latter require a continuous strip of land with cooperative landowners (Batten et al. 1996), but here again there will be a trade-off with species of poor dispersal ability being unable to move from one 'stone' to the next (e.g. Gruttke and Kornacker 1995).

In terms of feasibility, river corridors are an exception to the above comments, in that planning, survey and management are well-developed, and integrate riparian habitat requirements with human use of rivers and riverbanks (e.g. National Rivers Authority 1992, Schaefer and Brown 1992, Baschak and Brown 1994).

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Case Study : Corridors in a potential Ecological Network in Ireland.

The EECONET proposals include a tentative ecological network for Ireland (Fig. 3). An example of one of the proposed regional corridors, from Slieve Blooms to Slieve Felim, Silvermines, etc. is examined below, using maps provided by D£chas (National Parks and Wildlife).

The Slieve Bloom mountains contain a relatively large pcSAC for blanket bog and associated habitats. The upland area of Slieve Felim, Silvermines, etc. contains three small pcSACs: (1) Keeper Hill; (2) Silvermine Mountains; and (3) Bollingbrook Hill. Monaincha raised bog (a pcSAC) lies in the low-lying saddle in between these two upland areas. This lowland area contains Roscrea to the West and Borris-in-Ossary to the east, and the two upland areas are linked by a ridge which forms the proposed EECONET corridor, and which also includes a small pcSAC at Devilsbit Mountain. The four areas with pcSACs are isolated from each other (6-17 km), and are on peat or peaty soils used for agriculture and forestry. Each area is separated from the others by extensive areas of mineral soils, mainly podzolics and gleys (Gardiner and Radford 1980).

Habitat-specialist species, which are unable to disperse medium to long distances through habitats in which they do not breed, will be unlikely to use the proposed EECONET corridor described above. If a species can disperse across the barriers in the proposed EECONET corridor, then it is likely that much of the landscape surrounding the corridor will be permeable to this species. This is because the variety of habitats, agricultural, afforested and drained, which occur along the proposed corridors also occur more widely in the landscape. The example above would seem to indicate that the proposed EECONET corridors will be of little value for the specialized flora and fauna of the habitats for which pcSAC sites have been listed, although they may be valuable for more eurytopic species which also occur in these sites.

Alternatives to Corridors

In terms of costs and benefits, effectively dealing with the ever-changing degradative pressures on habitats as they exist at present, and expanding and buffering small sites, are likely to be a greater priority for habitat conservation in Ireland, than regional ecological corridors.

Acceptance of ecological corridors may also give rise to the erroneous perception that small sites are adequate if connected (see Fahrig 1997), or are preferable to one or two large sites. Soul, and Gilpin (1991) warned against this, and pointed out that corridors have a high edge-to-habitat ratio, which makes them much more sensitive to predation and weed and pathogen invasion than broad tracts of habitat. Batten et al. (1996) also recommended site enlargement and buffering against external impacts where the surrounding landscape is developed. In the highly fragmented Dorset heathlands in England (Webb 1990), the conservation priorities adopted by English Nature are management of remnant patches to prevent further degradation, and investigation of the potential for coalescing some of these remnant patches (Batten et al. 1996). In a study of nuthatches (*Sitta sitta*) in the UK, site enlargement by the creation of new habitat was concluded to be a better long-term strategy than linking small sites with corridors (Bellamy et al. 1997).

A clear priority for the scarce financial resources available for biological conservation will be the maintenance or restoration of site hydrological and ecological processes. The marsh saxifrage (Saxifraga hirculus) is a plant listed in the Habitats Directive, and recorded by Curtis and McGough (1988) from only two sites in Ireland (Antrim and Mayo). At the Mayo site, there is a high risk of local extinction due to nearby peat extraction causing drying out of the mineral flush in which the saxifrage occurs (Curtis and McGough 1988). For many other species not so threatened by extinction at present, maintenance of disturbance processes (e.g. extensive grazing), avoidance of eutrophication (especially in oligotrophic waters), maintenance of hydrological integrity of the site (e.g. in fens and raised bogs), and maintenance of active dispersal processes within large sites (e.g. by domestic livestock), will clearly demand financial resources many times in excess of those currently available. Integrating economic productivity with these conservation objectives in a politically acceptable manner, within core sites, is a challenge which has not yet been successfully overcome (Sidaway and Philipsen 1996). Yet intensive management and abandonment are important sources of medium-term extinction risk for many species still with relatively large populations (Nilsson and Ericsson 1992). Much permeability of managed semi-natural landscapes was maintained by heterogeneous patches created before uniformity of management and economies-of-scale were adopted in local forestry and agriculture (Angelstam 1992). Thus,

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connectivity is as much a function of the sum of local management activities as it is of planned physical linkages.

If there is any principle which is useful in addressing biological problems resulting from modern land management, it is that even the best method will only be successful in some places and at some times. The development of integrated pest management, where a number of methods are combined in a site-specific manner, is an example of how an integrated approach has been successful in practice. Noss (1987) refers to an integrated landscape conservation strategy, but the concept of dispersal management has the benefit of emphasising the management of processes rather than the planning of structures, although, of course, both will be necessary. Clearly, ecological corridors are useful in certain circumstances, but they must be viewed as part of a suite of options available to maintain or enhance connectivity.

Some criteria for evaluating the suitability of ecological corridors for specific sites or habitats are given in Table 3, with the range of options for managing habitat connectivity, including regional corridors.

Even if it is accepted that ecological corridors will be cost-effective in only a few circumstances, this does not detract from the value of an ecological network approach, and the necessity for intersite, landscape planning for the conservation of Irish habitats. In particular, the integration of regional plans from different sectors is essential (Sidaway and Philipsen 1996), as is a flexible approach drawing on a range of options which can be used as circumstances change (Blyth 1991) with an emphasis on processes as well as structures.

 TABLE 3. Evaluation of integrated management options for maintaining or restoring connectivity in a landscape.

 The type of information required for corridors is indicated under the headings for corridor options.

Possible evaluation headings

- A. Target species/functional group
- B. Feasibility of option
- C. Cost of option
- D. Risk of option failing to achieve connectivity
- E. Compatibility of option with others when used together

Management options

- 1. Regional corridors : Distance between sites, types of habitat between sites, development potential of land between sites, minimum width for corridor, types of dispersal process, etc.
- 2. Local corridors : Distance between habitat patches, types of habitat between patches, land use potential of land between patches, minimum width for corridor, successional changes predicted, types of dispersal process, etc.
- 3. Site enlargement (including merging with nearby sites)
- 4. Halting habitat loss
- 5. Translocation and artificial seed dispersal
- 6. Livestock, mammal, bird and human movement
- 7. Water flow diversion
- 8. Barrier removal
- 9. Management coordination between potentially connected sites
- 10. 'Do nothing' (action unnecessary)

Conclusion

An overview of regional corridors as they apply to Habitats Directive sites in Ireland (including those tentatively proposed as part of EECONET) must reach the conclusion that they are aspirational, have little biological basis for the vast majority of specialized species occurring in listed priority and non-priority habitats, and demonstrate little practical means of being implemented in reality. However, regional corridors are likely to be more successful where they are planned for target vertebrate species which disperse in existing linear habitats (e.g. otters and salmonids in rivers, bats along hedgerows). This is in part because the maintenance of these linear features already has non-conservation human benefits. Local corridors between habitat patches within sites are also important (Table 4), but it is often preferable to consider the total permeability of the landscape rather than specific corridors, unless the latter are linear features like streams.

The concept of ecological corridors should not be allowed to deflect attention from dispersal processes (such as seed dispersal by livestock) to landscape patterns. Habitat fragmentation and integrated dispersal management must be considered on a case-by-case basis comparing the cost-benefit of the range of available options.

TABLE 4. Summary of review of examples of corridors in Irish habitats. Examples are ticked where habitat corridors are likely to be successful.

Species or group	Local corridors	Regional corridors	
Bats	\checkmark	Very unlikely	
Otter	Can move through existing Irish landscape		
Marsh fritillary	Barrier recognition more important		
Carabid beetles	\checkmark	Very unlikely	
Fen molluscs	√ Tr	anslocation preferrable	
Wind-dispersed flora	\checkmark	No	
Burren grassland flora	Dispersal agents more important		
Bog Sphagnum	Not relevant for spp with poor dispersal ability		

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APPENDIX 1. Habitats listed in Annex I, and species listed in Annex II, of the Flora, Fauna and Habitats Directive, which occur in Ireland (CEC 1992, Romao 1996).

PRIORITY HABITATS

Coastal lagoons; Fixed dunes with herbaceous vegetation (grey dunes); Machair; Turloughs; Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia) (important orchid sites); Species-rich Nardus grasslands, on siliceous substrates in mountain areas; Active raised bogs; Blanket bog (active); Calcareous fens with Cladium mariscus and Carex davalliana; Petrifying springs with tufa formation (Cratoneurion); Limestone pavements; Bog woodland; Residual alluvial forests (Alnion glutinoso-incanae); Taxus baccata woods.

NON-PRIORITY HABITATS

Sandbanks which are slightly covered by seawater all the time; Estuaries; Mudflats and sandflats not covered by seawater at low tide; Large shallow inlets and bays; Reefs; Annual vegetation of drift lines; Perennial vegetation of stony banks; Vegetated sea cliffs of the Atlantic and Baltic coasts; Atlantic saltmarshes with Salicornia and other annuals colonizing mud and sand; Spartina swards (Spartinion); Atlantic salt meadows (Glauco-Puccinellietalia); Embryonic shifting dunes; Shifting dunes along the shoreline with Ammophila arenaria (white dunes); Eu-atlantic decalcified fixed dunes (Calluno-Ulecetea); Dunes with Hippophae rhamnoides; Dunes with Salix arenaria; Humid dune slacks; Oligotrophic waters containing very few minerals of Atlantic sandy plains with amphibious vegetation: Lobelia, Littorelia and Isoetes.; Oligotrophic waters in medio-European and perialpine area with amphibious vegetation: Littorella or Isoetes or annual vegetation on exposed banks (Nanocyperetalia); Hard oligo-mesotrophic waters with benthic vegetation of Chara formations; Natural eutrophic lakes with Magnopotamnion or Hydrocharition type vegetation; Dystrophic lakes; Floating vegetation of Ranunculus of plain, submountainous rivers; Chenopodietum rubri of submountainous rivers; Northern Atlantic wet heaths with Erica tetralix; Dry heaths; Alpine and subalpine heaths; Juniperus communis formations on calcareous heaths or grasslands; Calaminarian grasslands; Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia) (not important orchid sites); Molinia meadows on chalk and clay (Eu-Molinion); Eutrophic tall herbs; Lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis); Degraded raised bogs (still capable of natural regeneration); Blanket bog (non-active); Transition mires and quaking bogs; Depressions on peat substrates (Rhynchosporion); Alkaline fens; Siliceous scree; Eutric scree; Chasmophytic vegetation on calcareous rocky slopes; Chasmophytic vegetation on siliceous rocky slopes; Caves not open to the public; Old oak woods with Ilex and Blechnum in the British Isles.

PRIORITY SPECIES

None

NON-PRIORITY SPECIES

ANIMALS

Lesser horseshoe bat (*Rhinolophus hipposideros*) Otter (*Lutra lutra*) Grey seal (*Halichoerus grypus*) Common seal (*Phoca vitulina*) Bottle-nosed dolphin (*Tursiops truncatus*) Porpoise (*Phocoena phocoena*) River lamprey (*Lampetra fluviatilis*) Brook lamprey (*Lampetra planeri*) Sea lamprey (*Petromyzon marinus*) Atlantic salmon (*Salmo salar*) Allis shad (*Alosa alosa*) Twaite shad (*Alosa fallax ssp. fallax*) Killarney shad (*Alosa fallax ssp. killarnensis*) Freshwater crayfish (*Austropotamobius pallipes*) Marsh fritillary (*Eurodryas aurinia*) Kerry spotted slug (*Geomalacus maculosus*) Whorl snail (*Vertigo angustior*) Whorl snail (*Vertigo geyeri*) Whorl snail (*Vertigo moulinsiana*) Freshwater pearl mussel (*Margaritifera margaritifera*)

PLANTS

Marsh saxifrage (*Saxifraga hirculus*) Slender naiad (*Najas flexilis*) Floating water plantain (*Luronium natans*) Killarney fern (*Trichomanes speciosum*) Moss (*Drepanocladus vernicosus*) Moss (*Petalophyllum ralfsii*)

Genetic Effects of Isolation

Habitat fragmentation can lead to a loss of genetic variation in small populations by the processes of random genetic drift, inbreeding depression (reduction in fitness), and reduction in gene flow (see Ellstrand and Elam 1993, Wid,n and Svensson 1992, Young et al. 1996).

The genetic effects of fragmentation and isolation may not always be detrimental, however, and connecting isolated populations has been predicted in some instances to lead to 'outbreeding depression', or reduction in fitness following hybridization (Ellstrand and Elam 1993). This is due to the loss of local adaptations, and because of intrinsic coadaptation where "the genes in a local population primarily adapt to the genetic environment defined by other genes" (Templeton 1986). Although Noss (1987) stated that outbreeding depression had never been demonstrated to occur, more recent evidence from plants has shown it to occur in small populations in most cases studied (Waser 1993, cited by Ellstrand and Elam 1993).

Plant species with a restriced distribution are likely to have lower levels of genetic polymorphism than widespread species (Wid,n and Svensson 1992), but it is not always the case that genetic diversity will be less in isolated (as opposed to small) populations. Drosophila sulfurigaster had higher levels of mtDNA polymorphism in scattered isolated island populations than in connected mainland populations (Tamura et al. 1991).

Henle et al. (1996) bluntly stated that "As yet no instance of extinction by genetic malfunction has been reported." While not a direct genetic malfunction, Templeton (1986) reported the case of the successful reintroduction of Capra ibex ibex to the Tatra mountains, which subsequently became extinct when augmented by individuals of Capra ibex aegagrus and C. i. nubiana. Extinction occurred because rutting was much earlier in the year and the kids of the resulting fertile hybrids were born in cold weather in February rather than later in the spring.

The genetic effects of fragmentation depend on the reproductive system of the species and the genetic history of the population (Wid,n and Svensson 1992). In self-pollinating plant species, inbreeding in some species may have little effect because they have purged their genetic load, whereas in other species inbreeding will have detrimental effects (Oostermeijer et al. 1996, Young et al. 1996).

The objective of maintaining connectivity between sites is to reduce the risk of extinction of populations, whether they occur as non-dispersing populations in a particular site, or as metapopulations where individual sites are frequently recolonized from other sites. Connectivity is

generally of more importance for demography (i.e. boosting small populations thereby avoiding local extinction, or recolonizing after local extinction) than for genetics (i.e. maintaining genetic variability and avoiding inbreeding depression in small populations) (Shafer 1987).

Mimimum Viable Populations

The analysis of all factors that can cause extinction of a population is referred to as Population Viability Analysis (PVA), and involves the assessment of minimum viable populations (MVP) size (Gilpin and Soul, 1986). Many studies have addressed the problem of assessing MVP size, mainly for vertebrate species, and where probabilities of adverse events can be calculated (Burgman et al. 1993). However, MVPs will vary with time and location, and are not comprehensively known for any species (Lacey 1992, Burgman et al. 1993).

Population size, however, is not always a good indicator of extinction risk. Many invertebrate species are much more specialized that vertebrates, and even though they may possess large populations at a given point in time, if the resource (e.g. dead wood, microclimate) upon which they depend is depleted due to changes in successional management, they may be very susceptible to extinction (Nilsson and Ericsson 1992). Furthermore, populations cannot be viewed in isolation from other species. Burgman et al. (1993) point out that a population focus can conclude that minimum risk is associated with low environmental variability, whereas a community focus can conclude that environmental variability is essential for community persistence.

Atmar and Patterson (1993) are of the opinion that minimum habitat area is easier to assess than population size:

"While minimally-sustainable populations are very difficult to assess in a reasonable time scale by direct assessment, the area of appropriate habitat is not particularly difficult to measure. If minimum sustainable population sizes are as tightly linked to minimum habitat area as currently believed, then given a moderately well-defined extinction matrix, the determination of the habitat area alone may prove to be not only a far more easily achievable measure of minimally stable populations than direct demographic measurement, but more accurate as well. A single density measurement, even if correct, has little value without a sense of the long-term statistical variation of the species populations"

This assumes, of course, that the habitat of the species can be readily recognised, not always an easy task for plants or invertebrates with specialized and little-understood requirements, and with little or no precedent in Irish habitats.

Hamilton and Moller (1995) concluded that PVA models have a more important role in distinguishing priorities for alternative management actions, than as predictive tools for "divining certainty from a lack of field information that may still take decades to collect."

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APPENDIX 3: Woodland Corridors

In theory and practice, ecological corridors have been mostly applied to forest and wooded habitats. Yet only three of the priority habitats listed in the Habitats Directive for Ireland (bog woodland, residual alluvial forest, and Taxus baccata (yew) woods; see Appendix 1), and only one of the non-priority habitats, are woodland (old oak woods with Ilex (holly) and Blechnum (hard fern); see Appendix 1). Intact examples (i.e. with associated biological communities) of these four types of habitat are generally small, scattered and isolated throughout Ireland (Kelly 1981, Tomlinson 1997).

Arguments for ecological corridors have mainly related to strips of wooded habitat connecting core areas of forest or woodland (e.g. Forman 1995). However, their applicability to the above types of Irish woodland is likely to be low, for the following reasons (see also general issues above):

(1) Given the relatively small size of core habitats, priority needs to be given to habitat enlargement and management, before linking small sites which are many kilometres apart. In a study of nuthatches (*Sitta sitta*) in the UK, site enlargement by the creation of new habitat was concluded to be a better long-term strategy than linking small sites with corridors (Bellamy et al. 1997).

(2) A continuous recruitment of over-mature trees, avoiding gaps due to even age structure, is essential for the supply of resources for saproxylic (dead-wood-inhabiting) invertebrates (Speight 1989, Nilsson and Ericsson 1992). This may be more important than establishing even-aged between-site linkages, where the dispersal of these specialized invertebrates is not likely to occur for 150 or so years.

(3) There are few characteristic 'interior' species in Irish woodlands, compared to European forests, and most of the species occurring here can migrate through hedgerows, wood edges, etc. In the Killarney oakwoods, the only species of breeding bird nearest to the definition of an 'interior' species is the redstart (*Phoenicurus phoenicurus*), a hole-nesting species (see Batten 1976),

(4) The landscape complexity of land-ownership by family farms in Ireland means that establishing long-term strips of deciduous forest across the landscape would be very difficult, if not impossible, to achieve in practice, without much negotiation and expenditure, as has been demonstrated for land acquisition for commercial forestry (Tomlinson 1997).

(5) Wind can have critical microclimatic effects in forest strips (Saunders et al. 1991), and although most studies of the negative effects of energy fluxes at the margins of woodland strips are

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from cleared remnants areas, the implications will also apply to recreated woodland strips. Thus woodland corridor margins may suffer from weed invasion leading to increased transpiration (Saunders et al. 1991), greater soil disturbance and nutrient enrichment (Cole and Hobbs 1991).

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APPENDIX 4: Management issues.

Conservation managers must frequently make decisions in the absence of complete data on the sites under their management. In these circumstances, scientific information will be useful where it reduces the risk of making the wrong decisions (Hobbs 1992). Although land cover classifications, such as that carried out for Northern Ireland (Murray et al. 1992), or maps of habitat patches within sites, will provide valuable information on which to base Landscape Unit plans, much information can only be usefully collected in the context of the impact of site management plans.

It is hoped that this report can provide relevant background information on ecological corridors. In practice, connectivity should be considered on a habitat-by-habitat and site-by-site basis. A possible starting point for this is the check-list of landscape question headings which can be incorporated into site management plans (Lohnes 1992, Table A4.1.

A handbook for corridor management has been produced for Australian forest corridors (Hussey et al. 1991). This may also provide useful information if ecological corridors are to be developed.

Planning data requirements for National Ecological Networks

The Slovakian National Ecological Network provides an example of the type of planning data required for ecological networks, where both inductive and deductive approaches are used (from Sabo et al. 1996):

- Deductive approach: Includes maps of original plant communities, biogeographic zones, soil maps, maps of geomorphological features, current landscape structure, protected areas, etc.
- (2) Inductive approach: A composite map of the distribution of selected threatened indicator species (flowering plants, ferns, molluscs, spiders, butterflies, damselflies, selected Hymenoptera, amphibians, reptiles, birds and mammals).

TABLE A4.1. Selected elements of landscape ecology (Forman and Godron 1986) which can be incorporated into site management plans (from Lohnes 1992). Possible questions arising from these headings are also suggested.

1. Corridor ecology

What management is necessary where corridors exist within or between sites?

2. *Stream corridors*

Where streams or rivers occur within or between sites, what management is required to maintain or restore their value for the connectivity of the site?

- Flows between different ecosystems
 What energy and species flows occur from different ecosystems within and between sites, and do these need to be maintained or curtailed?
- Animal and plant movement across the landscape
 What parts of the landscape are particularly important for animal and plant movement, and what management or planning is required to maintain or restore these?
- 5. Wind, water and nutrient fluxes across a landscape What are the fluxes of wind, water and nutrients across a landscape, and do these need to be maintained or curtailed?
- 6. The landscape as an ecosystem

What extra management requirements derive from considering the whole landscape, rather than individual sites, as a single ecosystem.

7. Landscape change

What are the likely landscape changes (e.g. due to urban development, abandonment of marginal agricultural land, new and more intensive recreational use, more frequent droughts, storms or flooding events), and are there management changes or contingencies which need to be considered now to address these in the future?

However, it is equally important to consider the processes which maintain these patterns, when considering corridor design (Flather et al. 1997).

Droving in the Burren

The following cost-benefit considerations should be mind before reinstating droving practice and droving corrridors in landscapes such as the Burren:

- (1) The potential local importance of wind (eg on steep slopes);
- (2) The low probability of rare plant seed dispersal by occasional long-distance movement of goats or livestock;
- (3) The possible disruption of local goat herds by forced long-distance movement;
- (4) The cost of paying drovers, insurance, fencing; and
- (5) The cost of gaining access to a land corridor where drove roads no longer exist.

The target benefit of re-establishing and maintaining goat droves would be the colonization of suitable habitat patches by local or rare plant species. A first step might be the comparison of areas with a recent history of being frequented and not frequented by goats, to examine whether there are fewer occupied patches in their absence, and thereby estimate benefit. If local patch extinction is occurring rapidly, this approach might prove successful, but soil, microclimate and grazing intensity would need to be similar to avoid confounding effects. It must also be kept in mind that establishment and survival are often more important than dispersal in effective recolonization (e.g. Johansson and Nilsson 1993). Maintenance of suitable conditions for germination (e.g. disturbance, plant cover, etc.) are necessary at both control and experimental sites if comparisons are to indicate dispersal rather than establishment. Some assessment of seed banks may also be necessary. At the same time, a feasibility and costing study of restablishing a drove-road in a small part of the Burren could be conducted to estimate costs. For comparison with other management options which might more effectively reduce the risk of extinction, it is worth drawing attention to the analysis of distrbution of 139 scarce vascular plants in Britain by Thompson and Hodgson (1996), which found habitat destruction to be a more important factor in distribution on a national scale, than dispersal ability. This contradicted the earlier results of Quinn et al. (1994), which were based on a less detailed classification of dispersal ability.

While drove-roads as ecological corridors are recommended in Spain (Múgica et al. 1996), the reinstatement of droving in the Burren is not comparable, either economically or ecologically, to that practiced in Spain (see Ruiz and Ruiz 1986).

Mapping and GIS

Geographic Information Systems have a great potential as landscape management tools for protected areas (e.g. Fry and Norris 1992, Veitch et al. 1995). They are much cheaper than field survey (Table A4.2). GIS and Gap Analysis have been used to locate corridor routes using 'least cost path analysis' (e.g. Walker and Craighead 1997). This 'least-cost' or optimum path would result in the greatest probability of survival for the animal moving through the landscape. The method is

limited to species for which adequate data on habitat preference, barriers, and dispersal rates are available. It has been used in the U.S. for grizzly bear, elk and cougar (Walker and Craighead 1997), and may possibly be useful for pine marten, red deer and bats in Ireland.

However, Wiens et al. (1997) have pointed out that for mobile animals which use several types of habitat, there may not be a simple correlation between where individuals of the population occur, and habitats identified by GIS or land-cover maps. This is because, they concluded, movement patterns of these species may depend on features of the surrounding landscape rather than a given habitat patch. Management for connectivity within a landscape, based purely on habitat maps, will not always be successful, it seems. Flather et al. (1997) also warn against total concentration on vegetation patterns without considering the processes behind the patterns.

TABLE A4.2. Comparative costs of various land cover survey methods cited by Veitch et al. (1995) for surveys of the Dorset heathlands. Figures in UKœ.

Remote sensing Land Cover	£ 2.50 / km2
Aerial photography	£ 18.50 / km2
Phase I habitat survey	£ 87.50 / km2
Field survey	$\pm 145.00 \ / \ km2$

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