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ABSTRACT

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Cañada is the Spanish word for a route used for transfer of domestic animals between grazing sites and there is a major network present throughout Spain. There is much public interest in these routes, not only as historical monuments, but also because of their potential value for the maintenance of biodiversity. The current review was undertaken to assess the scientific evidence of their role as corridors and fits into the wider perspective of ecological networks in Europe. Empirical and experimental studies only are reviewed rather than theoretical models The review demonstrates that *cañadas* undoubtedly acted as corridors in the past, but further research is required to determine their current and future role because of the widespread disruption that has taken place in the network.

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Contents

Preface

Cañada is the Spanish word for a drove road, which is a route used for driving domestic animals between locations where seasonal grazing is available. Such movements may be over short distances (10-20 km), where the animals over-winter in the valleys and move to the high pastures in summer (*trasterminancia*), or long distances (300-1000 km) where the animals are moved to follow the season northwards (*trashumancia*). Spain has a network of *cañadas*, of different character, quality of cover and degree of preservation. The *Cañadas Reales* (royal drove roads) are 75.22 m wide but other classes vary in width according to the terrain and their historical importance (*Cordeles*: 37.61 m; *Veredas*: 20.89 m and Coladas: narrow ways without a stablished width, according to the new *Reglamento Español de Vías Pecuarias*, 1944; García Marín 2004). The network was designed to serve a strategic wool industry, as described by Gomez-Sal and Lorente (2004), and was developed in the Middle Ages Although they persist today, they are facing many problems such as urbanization, use as roads and for tipping, as shown in the photographs presented in this volume. Further information on the network and their relationship with transhumance is provided by Gomez-Sal and Lorente and other papers on their role in Spain are also included in Bunce et al (2004).

There is now much interest in maintaining the network, not only for their historical importance, but also for recreation and tourism. However there is a lack of information not only as to their current status, but also concerning their extent, as many have been destroyed even although they are technically in public ownership. The current report was initiated to examine their role as corridors, both past and present, in order to asses their actual and potential contribution to the maintenance of biodiversity.

Because *Cañadas* provided traditional linkages between comparable grassland habitats in Spain they can also fulfil an important role in the ecological network of Europe. Maintenance of the network would provide links between the major mountain systems of Spain and the intervening lowlands. The main mountain systems in Spain are orientated in an east-west direction, whereas the main *cañadas* are primarily north-south, the two networks are therefore complementary. The review also contributes to the underlying concept of ecological networks.

This report has been produced at Alterra in the framework of the Project *Ecologische Hoofdstructuur* (BO 02-005) Development of an Indicative map for the West-European part of the Pan-European Ecological Network

Rob Jongman, Bob Bunce,
Wageningen 12-12-2006

Summary

Cañadas are the ancient routes in Spain for moving domestic animals between summer and winter grazing land. The review was undertaken to determine what evidence was available on their role as ecological corridors because of the current policy interest in their maintenance. The recent literature on connectivity is so extensive that the present review concentrated only on those papers which contained empirical evidence relevant to the role of *cañadas* as corridors, as opposed to comprehensive coverage.

Several reviews published on the 1990's emphasized that the role of corridors as dispersal routes was unproven, especially because of the lack of experimental and empirical evidence. Nevertheless, a series of policy initiatives have been set up to promote ecological networks and the current interest in promoting the maintenance of *cañadas* could have comparable benefits. The present review summarises the current scientific evidence relating to *cañadas* but also has implications for wider initiatives.

The review first discusses the direct evidence for the use of corridors by plants and animals and secondly relevant information on dispersal. Some observations from recent field excursions in Spain are also included, as well as some final general conclusions.

Examination of the evidence for the use of corridors by plants mainly involves statistical analysis of empirical data rather than experiments but there are also now some important examples of the latter. There is now strong evidence for the movement of plants along corridors that supports strongly the historical importance of *cañadas* in this respect.

Representative examples only were included of similar studies for animals. Although the inherent character of the corridor as a habitat cannot always be separated from its use as a conduit, many faunal species have been shown to use corridors. The structure and quality of the corridor are invariably important, as is the ecological character of the species involved.

Whilst the adaptations of plant seeds for dispersal have been widely studied, the actual modern means of dispersal e.g. car tyres, often do not involve such mechanisms. The literature shows that historically *cañadas* would have certainly have been major routes for dispersal of propagules. Studies have shown that both wild and domestic animals disperse seed both between locations and within habitats and the movement of animals along *cañadas* would therefore been of importance. However studies of the current situation are required to determine their present status.

Studies of animal dispersal indicate that large animals can disperse independently of corridors, although they still frequently use them. Smaller species however are often

dependent on corridors partly due to the threat of predation but also because the animals may use the habitat for feeding.

In conclusion, therefore, it is often difficult to separate the inherent character of the corridor from it function as a dispersal route. However, this is not as imperative for policy formulation as the overall function of corridors in connecting fragmented elements is the primary reason for setting up ecological networks rather than partitioning scientific explanations. Nevertheless, it is clear that attention has to be paid to the character and structure of the corridor for it to be effective as a means of dispersal.

Finally, further work is needed to confirm the present value of *cañadas* as corridors.

1 Introduction

There is now an extensive literature on connectivity as mentioned in the review by Goodwin (2003). He gave figures which showed that the number of papers increased from less than three in 1995 up to almost 60 by 2000. The present review started by following up references recommended by colleagues, many of which were in the recognised landscape ecological literature. However, the number of papers was so overwhelming that the review had to restrict the search to these that were not only relevant to the role of *cañadas* as corridors, but also only those which included empirical measurements. A division was then made between those papers that related to dispersal and those that concentrated on the role of corridors. A secondary division was made in both cases between plants and animals. Many of the papers on plants and animals respectively were not in the main landscape and ecological journals; which shows that many authors either did not consider that their work was landscape ecology, or alternatively, published in journals that were familiar to them.

Apart from Goodwin there has been a series of reviews on connectivity and the role of corridors, starting with Dawson (1994) and then Hobbs (1992), Hobbs & Wilson (1998) and Beier & Noss (1998). These reviews, whilst containing detailed discussions, often concentrate on theoretical scientific aspects of the subject and do not provide practical help with defining the role of *cañadas*. For example, the separation of whether the corridor is only a conduit as opposed to its status as a habitat is not relevant to a stake-holder who only wishes to assess the cultural background to *cañadas* and their potential role as modern corridors. Nevertheless, these discussions have stimulated some outstanding experimental studies as well as undertaking empirical records to demonstrate the characteristics of corridors.

The most recent review (Murphy & Lovett-Doust 2004) discusses corridors as "stepping stones". The following statement encapsulates much of the discussions on the role of *cañadas* and includes "Corridors linking patches in fragmented landscapes may improve connectivity between patches and hence dispersal for some species. The use of corridors enabling movement in the matrix has received considerable attention". The review below provides the empirical evidence behind this statement.

Individual papers were reviewed that contain information directly relevant to the role of *cañadas* as corridors, both past and present and key papers are summarised at some length. The separation between past and present use is important because the majority of *cañadas* are now either not used at all by domestic animals, or only for local cattle or sheep movement. The routes of the *Cañadas Reales* are show in Figure 1 with two examples of their appearance in figure 2 and 3. Figures 4 -6 provide examples of *cañadas* disrupted by modern pressures. Figures 7-10 are examples of *cañadas* protected for recreation.

Several reviews; e.g., Dawson (1994) and Hobbs (1992) emphasise that the role of corridors on dispersal routes is unproven. Concerns have been expressed that there was an inadequate scientific core for policy initiatives e.g. those described by Jongman & Pungetti (2003). Furthermore, many of the models; e.g., LARCH (Pouwels et al (2003) are largely based on expert knowledge and contain little detailed information about the empirical basis of the parameters that are included. Discussions in some conservation agencies, e.g., English Nature in the UK, have also thrown doubt upon the value of basing policy initiatives on corridors, because of their unproven value, and suggest that money would be better allocated to proven conservation policies. However, as mentioned above, the empirical studies now available demonstrate conclusively the role of corridors in providing dispersal and connectivity, although not in all landscapes and for all organisms. Whilst the majority of the papers contain empirical evidence, there are some items of categorical information and observations made during field visits that have been used in the paper to support the value of *cañadas* for biodiversity. Within the context of the *cañadas* it is also useful to point out at this stage that the modern literature does much to support the opinions of ecologists, who have based their assessment of the importance of transhumance routes as corridors largely on expert judgement. In addition, at the meeting on Vias Pecuarias (livestock roads) in Cadiz, southern Spain in 2001 discussions on the value of *cañadas* for both recreation and biodiversity concluded that further evidence was required to support such assertions. The present review was undertaken to assess the current evidence and to identify where further work is required.

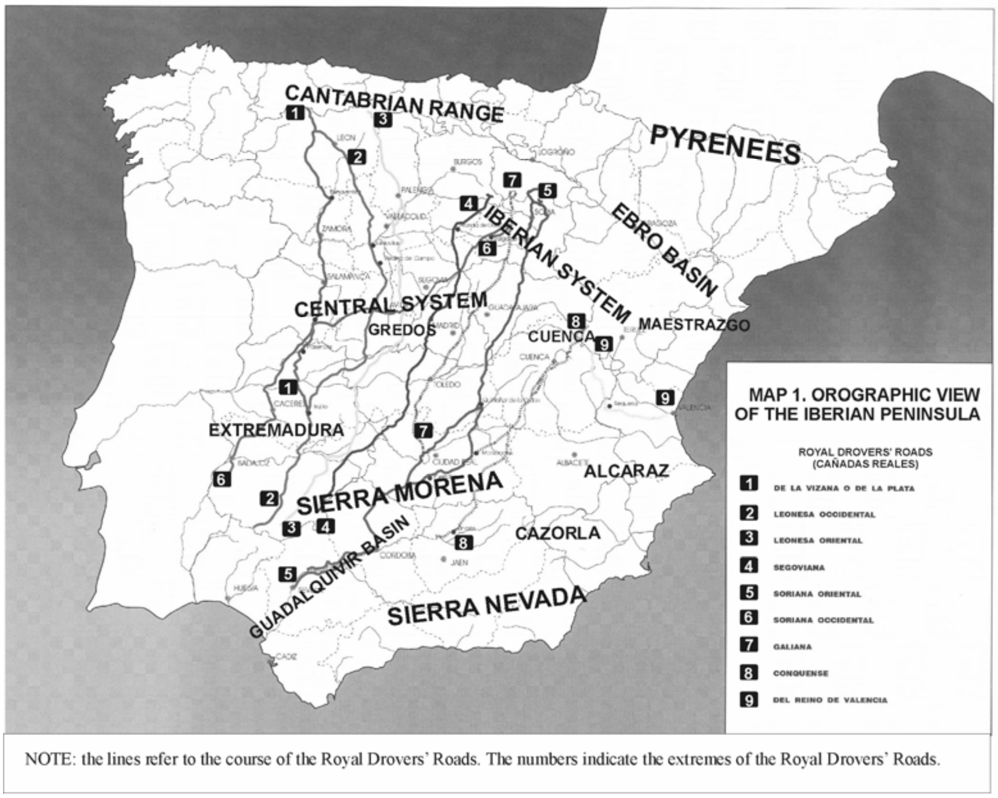

Figure 1. Orographic view of the Iberian Peninsula showing the routes of the Canadas Reales (royal drove roads, from Gomez-Sal & Lorente (2004).

There is now much interest in maintaining the network, not only for their historical importance, but also for recreation and tourism. However there is a lack of information not only as to their current status, but also concerning their extent, as many have been destroyed even although they are technically in public ownership. The current report was initiated to examine their role as corridors, both past and present, in order to asses their actual and potential contribution to the maintenance of biodiversity.

Because *Cañadas* provided traditional linkages between comparable grassland habitats in Spain they can also fulfil an important role in the ecological network of Europe. Maintenance of the network would provide links between the major mountain systems of Spain and the intervening lowlands. The main mountain systems in Spain are orientated in an east-west direction, whereas the main *cañadas*, as shown in Figure 1, are primarily north-south, the two networks are therefore complementary. The review also contributes to the underlying concept of ecological networks.

Figure 2. Cattle on the Segoviana Cañada Real (royal drove road) of Figure 1.(Photograph: Rob Jongman)

Figure 3. Perspective view of the Segoviana Cañada Real (royal drove road) of Figure 1, showing the 75 metre width of the road enclosed with walls. (Photograph: Rob Jongman)

Figure 4. View of a cañada in Segovia, central Spain with all ground cover destroyed by vehicular traffic. (Photograph: Ramon Elena-Rossello)

Figure 5. Blockage of a cañada in Segovia central Spain. Fencing has taken place within the Cañada as well as tipping of refuse. (Photograph: Ramon Elena-Rossello)

Figure 6. Disturbance in a Cañada in central Spain. A truck is parked across the route, and an electricity pylon has also been built within it. In the foreground some relatively undisturbed grazed grassland remains. (Photograph: Ramon Elena-Rossello)

Figure 7. Cañada with grassland along the route and a retaining wall to separate the animals from the surrounding land. Madrid Province, Central Spain. (Photograph: Ramon Elena-Rossello)

Figure 8. Cañada with in its centre a track constructed primarily for recreation as for example the mountain biker in the centre of the picture. Madrid Province, Central Spain. (Photograph: Ramon Elena-Rossello)

Figure 9. Cañada now used for recreation but with an information notice about its past use as a route for livestock. Madrid Province, central Spain. (Photograph: Ramon Elena-Rossello)

Figure 10. Canada leading to the mountain chain in the background where summer pastures are located, although some animals would have traversed passes in these mountains to travel further north, as shown in Figure 1. Madrid Province, Central Spain.(Photograph: Ramon Elena-Rossello)

2 Corridors for plants

Dawson (1994) could find only one paper that satisfied his scientific criteria of proof for plants using corridors, in this case a species moving along a hedgerow. Similarly in the wider context of connectivity, Goodwin (2003) could only find four papers relating directly to plants, but none of these were relevant to *cañadas*.

Other evidence has been found in the review and the outstanding paper on the subject is an experimental study by Tewksbury *et al.* (2002). Otherwise the majority of evidence discussed below is either from statistical analysis of plant records or direct observation. Tewksbury *et al.* (2002) pointed out that previous corridor studies had neglected the inherent difficulty of separating the effects due to corridor facilitated movement from effects due to patch size and shape that accompany the addition of a corridor. Accordingly they created corridors in eight experimental landscapes. Movement from the centre patch to peripheral patches connected by corridors was higher than movement between unconnected patches for all taxa studied. Seeds of a target species were than twice as likely to be found in connected patches as in isolated patches. The results provided a large-scale experimental demonstration that habitat corridors facilitate movement between otherwise isolated habitat-patches, a conclusion which is of importance to the previous role of *cañadas* as corridors because, especially in the lowlands, they formed corridors of semi-natural vegetation linking grazing areas. The *Cañadas Reales* (royal drove roads) were over 75 m wide and were designed to provide grazing in transit.

As discussed in the section below on dispersal, there is abundant evidence of seed transfer in the Mediterranean, so the increases in fruit set and seed movement in connected patches, involving a diverse set of pollinators and seed dispersers, can be directly related to the original role of *cañadas*, although recent human disturbance and abandonment may have affected this function at the present time.

Only three other papers were found that directly showed the role of corridors. Tikka *et al.* (2001) demonstrated the ability of grassland plants to spread along roads and railways. Dispersal was tested by spatial dependence. The conclusion was that grassland plants use rail and road corridors for dispersal. Kirchner *et al.* (2003) investigated the role of corridors in seed dispersal by using population genetics and demographic structure. They showed that a given pond is more likely to be colonised by the species studied when it was connected by corridors to other ponds. Verkaar (1990) and Van Dorp *et al.* (1997) also support the role of rivers as corridors for seed dispersal, although experimental evidence is not given. However, the expansion of aquatic species, e.g., *Acorus calamus* and the movement of *Impatiens glandulifera* all provide direct evidence of the importance of water corridors for dispersal. Nováková (1998) concluded that the corridor type and vegetation structure are critical in its role in species movement, which is supported by some of the literature quoted in the disposal section which relates to the historical use of *cañadas*. A paper by Campbell & Gibson (2001) showed the indirect effect of corridors used by horses and deer. Dung was collected and 23 species were germinated in the greenhouse, although only one was found in the field. The historical use of *cañadas* is therefore likely to have been of significance for seed disposal by dung deposition. However, retention time in the gut is also important, because deposition may take place in unsuitable habitats.

Hedgerows have often been considered as corridors for plants but Smart *et al.* (2001) showed that they were of no value for Ancient Woodland Indicators, which have very specific habitat requirements. However, Hooper's law, as described in Pollard et al (1974); i.e. the accumulation of one woody species per century in hedgerows; is in itself strong indirect evidence on the role of hedges as corridors where dispersal is taking place. The long term study of changes in the distribution of the species of the British flora between 1957 and 2000 Preston (2002) has several examples of the spread of species along transport routes, especially trunk roads e.g. *Cochlearia danica* and *Senecio squalidus* providing empirical evidence of a corridor function. Whilst modern vehicles are very different from the historical movement of animals along *cañadas* dispersal linked to movement along the narrow route is undoubtedly taking place. Wrbka (personal communication) has also indicated that it is well known that the distribution of some sub-Mediterranean species in Austria follows the drove roads.

From observation of *cañadas* and their role in the surrounding landscape there are still many unanswered questions, both in relation to the relict distribution of species from previous movement of animals and also the current situation. Many former *cañadas* are either completely destroyed; e.g., by urban development or roads; or are so highly disturbed by off-road vehicles, that they are unsuitable for any assessment. Other *cañadas* pass through forest and no distinction is present between the vegetation on the ancient route and that of the surrounding forest. Some major routes (*Cañadas Reales – royal drove roads)* are however sufficiently well preserved to make studies worthwhile – specially detailed records of the land cover, vegetation and plant species in the *cañada* in comparison with the surrounding land. A further source of study would be the role of modern transport, e.g., mountain bikes and quad bikes, in dispersing propagules along the *cañadas* used for recreation.

After the report was completed, an important paper was published. The paper, by P.Manzano and J.E.Malo, is entitled 'Extreme long-distance seed dispersal by sheep' (Ecol. Environ, 2006.(4) 244-248). Experimental studies established that large numbers of seeds with different morphologies were transported for distances of upto several hundred kilometres. These results are set in the context of transhumance and support the importance of the movement of animals in the dispersal of seeds and hence the main conclusions of the present report relating to corridors.

3 Corridors for animals

The literature on the use of corridors by animals is extensive, that complete coverage was not attempted, and instead representative examples have been taken. The section commences with mammals and then moves to other groups, before discussing some general points. The separation from the dispersal section is arbitrary, with some papers overlapping. It is recognised that not all papers answer the strict criterion for the separation of the inherent value of the corridor as habitat from its use for linking patches, but this is academic in relation to the historic use of *cañadas*, which were designed to provide grazing whilst the animals were in transit, especially the *Cañadas Reales*.

Hilty & Merenlender (2004) collected empirical evidence of the use of riparian corridors by mammalian predators in vineyards in Northern California. Cameras were used in the corridors as well as areas close to core habitats. Mammalian predator rates were 11-fold higher in riparian study areas than vineyards. More matrix predator species were found in wide corridors than in narrow or denuded creek corridors. In relation to *cañadas*, this conclusion emphasises the likely importance of the *Cañadas Reales*, and also fits with intuitive judgement, and personal experience of animals moving through the landscape.

Although Laurence & Laurence (1999) studied tropical wildlife corridors, this study is relevant to *cañadas*, as they also showed the importance of width. They used systematic spotlighting to sample arboreal mammals in 36 linear rainforest remnants in Queensland, Australia. The effects of corridor width, height, isolation and elevation were assessed with multiple regression models. It was shown that floristically diverse and wide corridors can function as habitat and probably movement corridors for most arboreal mammals in the region. The character of the *cañada* is therefore likely to be important in its role as a corridor.

Bjornstad *et al.* (1998) used a factorial experimental design to look at patch configurations and corridor links for the root vole. This paper confuted previous conclusions in that narrow lines of grass are perceived by voles as corridors – they move through them more readily than across barren ground but less readily than through wider habitats. Increased patchiness increased the aggregation of individuals with connectivity reducing isolation.

Interestingly, Andreassen *et al.* (1996) had previously shown that the same species did not respond to gaps until a critical limit was reached. A similar effect is well known for bat movement along hedgerows. This type of effect could have major implications for wider *cañadas* because the progressive break up of the network and the frequent short, isolated sections could destroy their current role for linkage, regardless of their historical values.

Bolger et al. (2001) examined the role of corridors for birds and small mammal species in an agricultural landscape. They estimated that species were likely to use linear landscape features as habitat and were thus likely to use them as corridors. They found it useful to differentiate two types of corridors: habitat linkages and movement corridors. A habitat linkage supports resident individuals whereas a movement corridor does not need to support residents. They studied roads as corridors with the strips of adjacent habitat, as a surrogate for true corridors – a situation almost homologous with *cañadas*. They concluded that some species are more sensitive to fragmentation than others and that the quality of the corridor was important for many species. The remnant strips of habitats and re-vegetated roads were able to serve as habitat linkages for fragmentation tolerant species, but only remnant habitat strips were suitable for sensitive species, again emphasising the contrast between species.

Bright (1998) also studied a small mammal, the dormouse, and how it was affected by gaps in corridors. Translocated dormice were clearly averse to crossing even narrow gaps in hedgerows and preferred to remain there, rather than moving into the surrounding habitat. Although they preferred the arboreal habitat, non-corridor habitat did not represent a complete barrier to movements of 100 m. A complete network of hedges will therefore favour dormice by acting as links to new patches. Again, in relation to *cañadas,* the character of the habitat in the *cañada* and its continuity are both of importance.

Clevenger et al. (2001) studied the role of drainage culverts as habitat linkages in Banff, Canada. Several species were shown to be using an array of culvert types as corridors, with contrasting species favouring different types; e.g., heights and degree of openness. Such culverts can provide vital habitat linkages and justify the expenditure on their construction. Similar conclusions were recorded by Veenbaas & Brandjes (1998) although not in such detail.

Dover & Fry (2001) reviewed the literature relating to corridors and concluded that an experimental route could be followed that would allow large scale replicated and manipulation studies that could address the concerns expressed in the literature. Accordingly, model structures were used to simulate different attributes of hedges for their potential role in initiating corridor movement. All the species studied were strongly affected by a visual link, although in different ways. A corridor effect was detected with an increased proportion of butterflies moving along the wind break compared with the control. Simple structures can therefore modify the behaviour of species moving through the landscape, with individual species reacting in different ways to the same structure. This conclusion supports the evidence from several studies discussed above and emphasises the likely importance of the character of the *cañadas* which differs between those with scrub as apposed to more grassy conditions in the mountains. Fry (2003) also discussed the role of hedgerows as corridors for butterflies and concluded that there was evidence for the use of hedges as conduits and as links between habitat patches. He stated that for the scarce copper butterfly "suitable habitat connected to other habitats by hedges and supporting grassland, showed that a suitable habitat connected to other habitats by hedges had twice the probability of supporting a population".

Haddad (1999) used empirical studies and simulation to demonstrate how simple behaviours can be used in lieu of detailed studies to predict the effects of corridors on inter-patch movements. The experiments were designed to overcome the points raised in previous studies. Movements of three butterfly species were measured in large experimental patches of open habitats, some of which were connected by corridors. Some butterflies emigrated from patches through corridors at higher rates than expected by random movement. Models predicted that corridors have proportionally greater effects as their width increases and that conduit effects decrease as patch size increases. The study suggested that corridors direct movements of habitat restricted species. It was concluded that corridors need not support an animal population to act as conduits but that there were differences between species. However, for corridors to be effective for species that need to establish and reproduce within them, the corridor quality must be as high, or higher, than the quality in larger patches. Furthermore, forest and threatened species that are often native to stable habitats are more likely to be restricted in their movements. This conclusion helps to explain the restricted movement of plant Ancient Woodland Indicators in Britain and their limited recurrence in hedgerows as described by McCollin et al. (2000).

Haddad (2000) further tested whether corridors increased patch colonization by a butterfly regardless of its original distance from a patch. An important conclusion was that inter-patch distance may determine the relative effectiveness of corridors. The value of corridors is highest relative to other habitat configurations when larger distances separate patches in fragmented habitats. The latter case is likely to have applied to many *cañadas* in lowland agricultural landscapes.

Conradt et al. (2000) also released individual butterflies and showed that when released within range of their normal dispersal distance, the butterflies orientated towards suitable habitat at a higher rate than expected at random. They also returned to a familiar habitat patch rather than a non-familiar one. Thus, *cañadas* with extensive habitat patches are likely to maintain their population of species and the butterflies are likely to move along them preferentially. A comparable pattern was observed in the field in a *cañada* near Linares in southern Spain, where butterflies moved along the line of *Cirsium* species and did not venture into the surrounding hostile landscape of olive groves.

Carabid beetles have been much studied in the landscape ecological literature because of the relative ease of following their movements. In general, the literature supports the importance of corridors for these taxa and only two examples are given here to demonstrate the type of results. Petit & Burel (1998) showed that for a carabid beetle using linear wooded elements as corridors between local populations, the mean distances covered by individuals per unit of time differ according to the quality of the wooded habitat. Euclidean distance proved the best measure of functional connectivity of hedgerows, but integrating the structure and the quality slightly improved the correlation. As with some of the papers on birds discussed below, the character of the corridor cannot be strictly separated from its use by the animals, as discussed by Dawson (1994), but for practical considerations of the value of *cañadas* this is immaterial. Charrier et al (1997) had previously used radio-tracing to trace individual beetles. This study showed that the movement of the carabids decreased in parallel to the decline of vegetation cover – emphasizing the importance of the quality of the corridor and the necessity of some species to use it as a preferred habitat for movement.

Turning to birds, Hinsley et al. (1995) noted that hedges acting as corridors may facilitate movement out of woods as well as into them. Bellamy & Hinsley (2005) later provided a summary of the relevant literature and stated that most birds use a mixture of field boundaries and cross field movements. The mean number of birds moving between woods along boundaries was greater than that seen flying across open fields. There was also a strong relationship between the proportion of observed individuals which flew across open fields and the mean body size for that species. More birds also moved between woods when there was woody cover along the field boundaries. The results provided clear evidence that birds used hedges as corridors for moving between woods, probably to reduce predation risk. Therefore it was again shown that the quality of the habitat was important, but also that larger animals are better able to cross open spaces

Clergeau & Burel (1997) examined tree creepers in polders where hedgerows linked the recently planted dykes to historic woodlands. Tree creepers were only present in new woods where linear rows of trees provided a high degree of connection to traditional landscapes, providing an example of a species using its own habitat as a corridor to move between patches.

4 Dispersal of plants

The adaptations of plants for seed dispersal have been the subject of descriptive studies since the inception of botanical science in the 19th century. Books are available, e.g., Forget *et al.* (2005), which provide a wealth of information on seed fate and dispersal. This volume covers the range of dispersal mechanisms in a variety of biomes with seed removal being affected by factors such as hunting, logging and habitat fragmentation.

Data bases have been set up, e.g., Thompson (1997), of the mechanisms of seed dispersal, although, as emphasised below, the adaptation of a given seed may not be that by which it has been dispersed. As in much of the literature on connectivity, the original stimulus was from island biogeography theory. Freckleton & Watkinson (2002) presented a theoretical discussion of metapopulation theory in relation to the spatial dynamics of plants and concluded that the concept of patches of a suitable habitat in a matrix of unsuitable conditions is not always true, and that metapopulation theory might not be applicable. Ehrlen & Eriksson (2003) discuss and dispute these conclusions but, although such theoretical discussions are important background, it is rather the practical situation within *cañadas* that is the subject of the present paper.

Ehrlen & Eriksson (1999) had also previously examined dispersal and patch occupancy in forest herbs by using experimental transport of seeds and bulbils. The availability of seed was found to limit recruitment, with the size of the seed being important. It was concluded that the distribution of species can be perceived as the result of processes operating among and between patches. However, the literature described below, as elsewhere in this review, centres on the role that *cañadas* may have played in dispersal and therefore, especially deals with transport of seed by animals. A general thread running through the literature is that the dispersal strategies evolved by plants are often not those that are actually involved. This is not surprising since the evolutionary process has been going on for far longer than the mechanisms at work in modern times and recent historical landscapes.

The outstanding paper in relation to *cañadas* is the paper by Fischer *et al.* (1993) who examined a transhumant flock of sheep in southern Germany for evidence of dispersal. Over 8,500 diaspores, from a wide range of species, were found on a single sheep grazing in relict calcareous grasslands embedded in a hostile matrix of managed forest grasslands and roads. Species were from a range of habitats, both in passage and from the habitats in which the sheep grazed. They were quite evenly spread over the body of the sheep but because most were on the breast the surface structure and height of the donor plants was critical in determining the likelihood of being picked up – an important factor when considering the character of the *cañadas*. Although most species had hooks, many species without contrivances were found. Therefore the common assumption that only diaspores with special structures can stay on sheep is no longer viable. However, the total burden of seeds is still dominated by those with adaptations. Apart from vegetation height the wallowing of sheep is also important in picking up species – fourteen species were found after a single wallow. This conclusion is especially important for *cañadas* as it emphasises the importance of the resting places as both dispersal and receiving points for seeds. Many seeds were retained over seven months and more than 100 kilometres had been travelled, suggesting that this mechanism is more important than the deposition through dung, discussed below.

Almost all plant species from grasslands can be transported – a conclusion which fits with the general observations reported in the section on corridors. Animal behaviour is very important; it is likely to be true for goats and cattle as it is with the sheep in this study. Furthermore there will be a difference between traditional and modern breeds because the former move more widely through the landscape. The dispersal pathway will depend on the number of diaspores produced by each species, on their morphological structure and the height of the plant. However, the character of the resting places is likely to be different from the habitats crossed in the intervening movement of animals, but because the sheep tend to graze in similar grasslands the end plants are likely to be similar.

Couvreur *et al.* (2004) examined the fur of domesticated large herbivores; i.e., Galloway Cattle, donkeys and horses, after transport between nature reserves. 6,385 seeds from 75 species were found, probably as a transient seed bank. There was gradual turnover in the vegetation season and seed dispersal took place both within, and outside, the different reserves. Domesticated large herbivores were considered as models of wild animals and are therefore important dispersers; i.e., they are "mobile link organisms" and can connect isolated nature reserves. As instruments in fragmented landscapes they relate directly to *cañadas*. Cosyns et al (2005) studied seed establishment in the dung of horse and cattle in sand dunes. 117 species were found with up to 158 germinating seeds per sample. Deposition was from 10 to 100 seeds per metre and as so many animals were moving during transhumance, dung transfer along the route must been a major source of dispersing seeds.

Kiviniemi & Telenius (1998) also looked at the attachment of seeds to animals, especially wood mice. They found potential dispersal distance of up to 300m and concluded that, in comparison with fallow deer and domestic cattle, wood mice were surprisingly effective as seed dispersers. They considered that the mice enhanced the probability of occasional propagules reaching suitable sites in a fragmented landscape.

Bulloch & Primach (1977) carried out an experimental study of seed dispersal on people and showed a mean dispersal from five metres up to 2.4 kilometres. The settlement of seeds was selective and depended upon the structure of the existing vegetation. As in the study by Fischer (1993), plant height was considered to be a crucial factor. Dispersal by animals was shown to be a continuous process. Therefore, because during transhumance the shepherds moved with the animals, they have also to be considered as significant agents of dispersal – as would horses in taller vegetation.

The subject of dispersal of seeds in mammals has been the subject of many papers and there is a great deal of evidence about the numbers of seeds and the way different grazing animals may increase viability. Malo *et al.* (2000) studied dispersal by animals in Mediterranean systems. They recorded high seed densities in the Mediterranean and also summarise the extensive literature. Rabbits, fallow deer, red deer and cattle all dispersed seeds, but goats and sheep must also have been important. The spatial variability was high but there were accumulations of thousands of seeds, with effects at various scales. Seed deposition took place throughout the year and in terms of *cañadas* would therefore be linked to the seasonal movement of animals. The differential uptake and germination of seeds can change interspecific competition as well as local disturbance and colonisation. These effects were considered to increase the diversity of *dehesas,* the open savannah-like systems widespread in Spain. Malo has also published a range of papers on related topics e.g. in Manzano et al (2005) the passage and survival of shrub seeds in the guts of sheep is described.

Levin (1995) examined the ecogenetic importance of plant outliers, many of which occur as trees and shrubs in *cañadas*. These outliers may occur from 100's of metres up to several kilometres away from core populations, but can still be linked by pollen dispersal. Many species such as *Quercus ilex* act as outliers in dehesas or as core populations in forests. The outliers may be a source of both pollen and seed and often produce proportionally more pollen than in forests. Indeed the whole management of dehesas is to encourage acorn production from the scattered trees. Contrasting patch sizes are present and even flowers on individual trees several kilometres apart may be pollinated from other trees. Outlier assemblages may also provide stepping stones for the dispersal by herbivores between populations as well as providing resting and roosting sites for birds. Any recording of c*añadas* must therefore include point features, such as trees or shrubs, because of their likely genetic importance.

Finally, Imbert & Ronce (2001) showed that in the heteromorphic species *Crepis sancta* that dispersal ability changed according to environmental stress, emphasising the complexity of dispersal mechanisms above the well known seed adaptations. In the wide range of environmental conditions in the *cañadas,* such changes are also likely to be important.

Therefore, there is sufficient empirical evidence to show that domestic and wild animals moving through *cañadas* are agents of dispersal. Nevertheless it is still necessary to carry out detailed studies of the current situation in *cañadas* to establish the extent of such dispersal at the present time. However, in recent work near Madrid, Hortal (pers comm.) has shown that animals are still dispersing seeds.

5 Dispersal of animals

As with plant dispersal there is an extensive literature, so only a few examples have been selected to show the type of results that are relevant to *cañadas*.

Poole (1997) examined the dispersal patterns of lynx in the northwest territories of Canada, using radio collars and ear-tagging. Dispersal ranges varied from 17 to 930 kilometres. The populations were both mobile and vulnerable, but eight lynx established new home ranges. It therefore seems likely that such large predators are able to move directly through the landscape to seek out new and more productive habitats with the main prey species being crucial in this respect.

Sweanor et al. (1999) looked at cougar dispersal patterns in New Mexico by tagging and radio collars and also showed that large animals can disperse independently of corridors. Protected cougar populations can contribute to metapopulation persistence by supplying immigrants to surrounding populations that are affected by fragmentation. Such results may also apply to the European Lynx.

Whittington et al. (2004) studied the spatial response of wolves to roads and trails in Canada by recording movements of two packs over two winters. Both packs avoided areas of high road and trail density – therefore avoiding highly disturbed corridors. The packs usually moved within 25 m of roads and trails. Roads and trails therefore have a cumulative effect on wolf movement and it was necessary to maintain high quality habitat corridors for wolves to move freely in the landscape and encourage dispersal.

Coulon et al. (2004) examined landscape connectivity by studying gene flow in a roe deer population in a fragmented landscape. Two geographical distances were calculated, Euclidean distance (straight line) and 'least cost distances' that maximises the used wooded corridors. The correlation was tested using the least cost distance which takes into account the distribution of wooded patches. The results suggest that in a fragmented landscape roe deer dispersal is strongly linked to wooded structures. However, the results can also be interpreted to indicate that dispersal may also take place across open areas – linking well to other studies in the corridors section and to personal observations of roe deer movement in the British Countryside. Doncaster et al. (2001) studied the dispersal of hedgehogs in Southern Britain. They used a field experiment to explore the responses by hedgehogs to normal and unfavourable terrain when dispersing between fragmented local populations. No two trajectories of any translocated hedgehogs followed the same route, and they moved substantially further and faster from the unfavourable than the favourable sites. Habitat edges acted as corridors, and the hedgehogs were capable of dispersal up to 3.8 km from a release point and up to 9.9 km in total. These animals therefore have their individual pathway, or corridor, through the landscape.

Bakker & Van Vuren (2003) studied the gap-crossing decisions of a smaller mammal, the red squirrel, in California. Individuals were released across clear cuts and routes determined subsequently. Squirrels were more likely to cross clear cuts if the detour efficiency (distance to the home crossing gap divided by distance of forest detour) was low. Detour efficiency also reportedly effects the gap-crossing decisions of some forest birds.

Belisle & Desrocheres (2002) also studied gap-crossing decisions, in this case for forest birds in *Cañada*. Birds preferred to travel under forest cover rather than across open areas, even when the forest detour conveyed a substantially longer route. Birds rarely ventured more than 25 m from the forest edge. The experiment supports the hypothesis that forest bird movements are constrained in fragmented landscapes, and links to the results of Bellamy & Hinsley (2005), discussed in the section on corridors. Although some *cañadas* pass through forest, the majority are unwooded but they have individual trees and shrubs which could act as stepping stones for birds – for example jays and wood pigeons have both been observed using individual trees for feeding and dispersal. The value of *cañadas* for dispersal of animals is likely to differ widely according to local habitats and the degree of fragmentation of the surrounding landscape.

The paper by Dover & Fry (2001), already discussed in some detail in the corridor section, is also important in describing how butterflies disperse through the landscape. Dramstad & Fry (1994) examined the foraging actuality of bumble bees in relation to flower sources. All bumble bee species had a preference for perennial herbs as a forage resource. The quantity of flower resources, their spatial pattern and temporal constancy varied among sites.

Because flowers were needed, the length of field boundary was a poor index of the value of the field boundary, presumably because the availability of suitable flowers overrode actual length. Again therefore habitat quality is the critical factor, because flowers were essential if the field boundary was to be of value for bumble bees. The use by bumble bees of the flowers as corridors is therefore primarily because of their value as a habitat, and where flowers are present the boundary will act as a link. Saville et al. (1997) also examined bumble bee movement and showed the links of individual species to particular plants, so the occurrence of plants provides the necessary habitat for the bees. Bumble bees remain on isolated patches of forage but could disperse more widely across discontinuities in the landscape. Although bumble bees have a high forage patch fidelity, a small number fly much longer distances. These animals therefore use corridors, but probably primarily for feeding rather than dispersal, although the latter may incidentally take place.

A final paper included in this section is an elegant contribution on connectivity by Schiegg (2000) who examined the effects of the spatial distribution of wood volume and connectivity on saproxylic insect species diversity in Switzerland. Saproxylic insects are dependent during some part of their life cycle on dead wood, wood-inhabiting fungi, or on the presence of other saproxylic insects. The volume and spatial distribution of dead wood species were recorded on scales ranging from 50 to

200m around the plots where the insects were collected. High dead wood connectivity enhanced the number of saproxylic Diptera and Coleoptera species collected in a plot. Hence habitat fragmentation is expressed for these species at a local scale by the arrangement of single dead wood species. In addition to the importance of a sufficient supply of dead wood for saproxylic species, short average distances between dead wood pieces are advantageous. The range of 150 m could be interpreted as the grain for Diptera and Coleoptera and relate to the home range of these groups. Dispersal over wide distances, as with other groups, is also likely to be due to chance and to take place rarely.

It was unclear how many individuals are needed to found new populations and it was considered possible that only a few individuals reaching a suitable forest by wind drift would be enough to establish the species in that location. However, the well known restricted distribution of some species restricted to old growth forests, suggests this may take place over a long period of time.

This report demonstrates that connectivity is not only important for the widely studied species but could also be for other groups such as fungi and lichens which are not so often studied. The patches within *cañadas,* as well as the habitats they pass through, are therefore likely to be important but would have to be measured through surrogates. As one moves down the size range of animals, so it appears that the dependence on corridors increases perhaps due to the threat of predation but also because they may be using the habitat in its own right for feeding. Also, as elsewhere in the review, a corridor valuable for one species may not be suitable for another. In addition, animals often use habitat edges for dispersal, so that corridors are not always features such as lines of trees or shrubs.

6 General conclusions

Early in the review it became clear that much of the connectivity literature did not relate either to *cañadas* or to corridors as such. Although the dispersal literature is also extensive an important general point is that plants and animals have evolved dispersal mechanisms over millions of years, but man has only dominated the landscape over the last two millennia. The adaptations are therefore often incidental to modern conditions, especially for plants which are frequently dispersed by means other than their evolutionary structure; e.g., the wind adapted mechanism of the genus *Taraxacum* is not involved when seeds are been picked up by car tyres and then depositing them on roadsides, often in spray under wet conditions regardless of any adaptive mechanism. Even where domestic animals are involved Fischer et al (1996) found that a significant number of seeds dispersing on wool had no adaptive mechanism.

Whilst it is theoretically important to separate the inherent character of the habitat of the corridor from its function as a dispersal conduit, this is not important for policy determination as the two are invariably inextricably linked. The identification of a potentially valuable *cañada* may therefore have a dual function which actually gives it an added value. For example, in the Sierra Morena in southern Spain, a *cañada* had vegetation with many flowering plants of *Cynara radunculus* and *Onopordum acanthium,* but was also acting as a corridor for bees, butterflies and moths which were feeding and dispersing along it. Such observations are often made by people walking in the countryside and seeing dispersal taking place; e.g., a fox moving along a hedgerow or a pigeon along a line of trees, but are inevitably anecdotal. The scientific review in the present paper provides the empirical evidence to support these observations. The character of the *cañadas* will also affect its value as corridor or habitat, for example a grass strip may be useful for mice or voles but is of no value for woodland birds.

An examination of the position of *cañadas* in the field; indicates that they follow natural lines in the landscape, in some ways comparable to the "old straight roads" described in England by Alfred Watkins. Certainly, during recent visits to *cañadas* this conclusion was readily apparent, but further modelling is required to demonstrate these observations scientifically. Likewise, the anecdotal evidence referred to in the review about the spread of species along *cañadas* needs supporting data. In this context the scarcity of well maintained *cañadas* means that representative case studies must be identified that will enable sufficient robust empirical evidence to be collected. In this respect, the ingestion by animals of plant seeds, and their subsequent deposition, may not lead to dispersal if these seeds are deposited in an unsuitable habitat. For example, seeds picked up in Almería by animals passing and grazing in *Phlomis/Thymus matorral* may subsequently be deposited on moist soils by a well used for watering animals which is not suitable for such species. Likewise the species from damper soils taken up near the well will not be able to colonise *matorral.* In addition, the current state of vegetation and habitats in the *cañada* is likely to be very different from when it was being used regularly by livestock.

In Spain there is widespread interest in *cañadas* both from professional policy makers but also the general public, not only because of their historical value as part of the national heritage, but also because of their potential for the maintenance of biodiversity. Furthermore, in southern Spain in Andalusia and near Madrid the *cañadas* have been widely developed for recreation; e.g., walking and horse riding. Work is still being undertaken to develop such uses further, but an assessment of the current status and extent of the resource would provide a framework for future action. The present review demonstrates that *cañadas* undoubtedly acted as corridors in the past but that further research is need to determine their current and future role as ecological corridors e.g. in linking Natura 2000 sites

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