

**The influence of linear landscape features on
pollinator behaviour**

**Thesis submitted in partial fulfilment for the degree of
Doctor of Philosophy at the University of Leicester**

Louise Cranmer

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The influence of linear landscape features on pollinator behaviour

Louise Cranmer

Abstract

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Linear landscape features such as hedgerows are important wildlife habitats but their functional role in improving connectivity in fragmented habitats remains uncertain. This thesis studied the influence of both natural and artificial linear features on pollinator behaviour at medium and landscape scales. Observations along 30m transects, perpendicular to eight different hedgerows revealed that non-foraging pollinators were far more likely to exhibit linear flight next to the hedgerow than they were further out in the field. Using a medium-scale experimental design, three patches of potted *Phacelia tanacetifolia* (Hydrophyllaceae) were arranged equidistantly with two of the patches being connected by an artificial linear feature. Results demonstrated that there was significantly greater inter-patch movement by bumblebees (*Bombus* spp.) between the connected patches than the isolated patch even after the position of the feature was changed. The isolated patch, in contrast, was not approached from the other two patches. Bumblebees demonstrated high patch fidelity but their abundance in the connected patches was not necessarily greater than the isolated patch. There were no significant differences in hoverfly (Syrphidae) abundance between patches. Later, the same experimental array was scaled up to fit within the farm landscape structure, using an existing hedgerow as the connection. A similar pattern of flight directions emerged. In a landscape investigation, the reproductive success of *Salvia pratensis* (Labiatae) growing in patches with a high number of connecting hedgerows was compared with those plants growing within poorly connected patches. Pollinator abundance, pollen grains per stigma and seed yield, were greater in highly connected patches compared with patches with fewer connecting hedgerows. The overall connectedness of a landscape may therefore be important to both pollinator movement and those plants which depend on them for greater reproductive success. Linear landscape features might represent navigational aids with which pollinators orient themselves.

For my Mother and late Father for inspiring a love of natural history by getting me out of bed as a child to look at hedgehogs or pretty moths...

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Preface

Pollinators are an important functional group within all terrestrial communities and play a key role in maintaining plant populations (Rathcke & Jules, 1993; Fisher, 1998), in energy flow between trophic levels (Watt *et al.*, 1974; Proctor *et al.*, 1996) and are required by many agricultural crops and most wild plants for seed and fruit production (Free, 1993). Landscape structure is a major determinant of movement of certain invertebrates and may play a role in the survival of populations in the increasingly fragmented landscape of lowland Britain (Forman & Baudry, 1984; Burel, 1989; Merriam, 1991). Linear features such as hedgerows, road verges, canals and railway embankments are important artificial habitats in their own right (Kirby, 1995). However, there has been some debate as to the function of these landscape elements as corridors between larger expanses of semi-natural habitat separated by urban and agricultural habitats (Simberloff & Cox, 1987; Simberloff *et al.*, 1992; Rosenberg *et al.*, 1997). Few studies have specifically studied insect behavioural responses to linear landscape elements examining whether such structures can elicit an oriented flight response along them and therefore facilitate insect movement through the landscape.

Chapter 1: Landscape structure in lowland Britain: fragmentation and species movement

Agricultural intensification, landscape change and habitat fragmentation

Insect mediated pollination of plants is a fundamental and vital service within healthy ecosystems (Kearns *et al.*, 1998). The majority of angiosperms require pollination to set seed and most of these pollen vectors are insects (Buchmann & Nabhan, 1996). Although pollination alone is insufficient to guarantee long-term plant population persistence, it is a necessary first step (Rathcke & Jules, 1993). The transfer of pollen between separate plants helps to maintain adequate levels of plant genetic variation and ultimately facilitates evolutionary adaptations to shifting environmental conditions (Osborne & Williams, 1996). Pollination systems throughout the world have suffered from various anthropogenic perturbations stemming from agricultural intensification and increasing urbanisation. The primary cause of most of these declines is attributed to habitat loss (Osborne *et al.*, 1991; Hanski, 1998; Kearns *et al.*, 1998). There is also evidence to suggest that climate change is affecting the distribution of many pollinators (Hill *et al.*, 2001; Kerr, 2001). Pollinator diversity, distribution and abundance have declined for the majority of European species (Williams *et al.*, 1991; Pollard & Yates, 1993; Banaszak, 1996) and with them, many interactions have also been lost (Rathcke & Jules, 1993; Kearns *et al.*, 1998). As natural resources are continually depleted via non-sustainable operations, more and more plant-pollinator interactions will be affected by habitat loss, degradation or fragmentation (Young & Clarke, 2000).

Urban expansion and the move towards large-scale agriculture have resulted in an increasingly fragmented landscape in lowland Britain (Kirby, 1995; Sutcliffe & Thomas, 1996; Saville *et al.*, 1997). A typical farmland environment is dominated by large arable or pasture fields, demarcated by narrow field boundaries. These linear features, such as hedgerows, drainage ditches and roads, intersect fields in a grid-like array and are often interconnected (Burel, 1996).

Agricultural land accounted for approximately 18.5 million ha (75% of the land area) in Britain in 2001 (DEFRA, 2003). As a result of intensive farming practices, landscape structure has changed dramatically over the past 55 years, altering the relationships and

ecological processes which operate between the primary landscape characteristics of size, shape, diversity, density and spatial pattern of various landscape components. The spatial arrangement of habitat patches within the landscape is naturally dynamic and continually changing, but the changes brought about by agricultural intensification have amplified this (Jonsen & Fahrig, 1997). Habitat fragmentation, as a result of agricultural intensification, has been identified as one of the most important factors threatening biodiversity (Hanski, 1998). Habitat size, quality and the spatial arrangement of patches within a complex mosaic, affect the distribution of resources in the landscape, influencing population dynamics and community structure (Dunning *et al.*, 1992; Pulliam *et al.*, 1992; Jonsen & Fahrig, 1997; Thomas & Kunin, 1999).

The numerous detrimental effects of fragmentation serve to weaken the stability of plant and animal populations (Fahrig & Merriam, 1994). Increased isolation may reduce gene flow and ultimately result in inbreeding depression such that smaller populations are at an increased risk of population extinction (Dudash & Fenster, 2000; Eisto *et al.*, 2000; Kéry *et al.*, 2000; Young *et al.*, 1996, 2000). Pollination systems have not escaped such perturbations; mutualists and habitat and food plant specialists can be particularly susceptible to reductions in habitat patch size and increased distances between habitat fragments (Rathcke & Jules, 1993; Kearns *et al.*, 1998; Krauss *et al.*, 2003; Steffan-Dewenter, 2003). It is important to consider the knock-on effects in an ecological system rather than merely the effect on a single species. For example, a loss of pollinators could initiate a negative loop of decline of dependent plants, their associated insect communities and all the other species which rely on them (Olesen & Jain, 1994).

Structural change

Large-scale mechanisation has led to the removal of hedgerows, creating larger fields to accommodate modern farm machinery. Since 1945, one quarter to one third of the total length of hedgerows within the United Kingdom have been removed. Of those, 23% disappeared between 1984 and 1990 in England and Wales (Barr *et al.*, 1993). Landscape diversity has diminished nationally as arable and pastoral farming have diverged to the east and west of the country, respectively. There has also been a reduction in smaller, mixed farms resulting in an increase in larger, more specialised holdings with fewer areas of non-cropped land (Potts, 1991; Robinson & Sutherland, 2002). This restricts the

numbers of habitats available to species which require a mosaic of habitats for different stages of their life cycle (Westrich, 1996; Appelqvist *et al.*, 2001).

Biotic change

As well as structural change, the land has sustained differing degrees of drainage, cultivation, fertilisation, irrigation, pesticide applications and pollution (Robinson & Sutherland, 2002). This can affect the local biota. For example, changes in the status of plant species have been attributed to changes in soil nutrient status in Northamptonshire since 1930 (McCollin *et al.*, 2000). In addition, the move to autumn-sown arable crops resulting in the loss of winter stubble is one of the many factors which has led to the decline of some of the once common specialist farmland birds (Baillie *et al.*, 1997).

In an attempt to ameliorate such negative effects, financial incentives such as the Countryside Stewardship Scheme have encouraged many farms to adopt a more sympathetic approach to farming practice. Field margin management, the incorporation of conservation headlands (Sotherton, *et al.*, 1989), set-aside (Corbet, 1995; Sparkes *et al.*, 1998), wild flower strips integrated with pest management strategies (Hickman & Wratten, 1996; Frank, 1999; Ullrich, & Edwards, 1999; Sutherland *et al.*, 2001) and the creation of new habitat attractive to wildlife (Carreck & Williams, 1997, 2002) have all improved matters to greater and lesser extents. Other farming strategies such as the planting of cover crops and green manure have proved attractive to some beneficial insects, albeit unintentionally (Wyland *et al.*, 1996; Rüegg *et al.*, 1998). Such proactive measures to improve biodiversity on agricultural land may be enhanced depending on their proximity to different biotypes and the connectivity of the local ecological infrastructure (Fahrig & Merriam, 1994; Fry, 1994; Visser, 2000; Baudry & Bunce, 2001).

Species movement in fragmented landscapes: perceptual range and scale

Populations living within such isolated fragments are at an increased risk of extinction unless they can disperse across land to interact with other suitable patches and maintain long-term dynamic interactions (Merriam, 1991; Fahrig & Merriam, 1994; Malanson & Cramer, 1999). The ability to disperse depends on the permeability of the landscape to individual species, including perceptual range, movement capabilities and resource accessibility (Taylor *et al.*, 1993; Mauremooto *et al.*, 1995; Farina, 1998). For example,

Schtickzelle & Baguette (2003) demonstrated that the bog fritillary butterfly (*Proclossiana eunomia*) was less likely to disperse to other patches within a highly fragmented landscape than in a more aggregated one. The insects exhibited boundary perception and modified their behaviour at patch edges by making U-turns significantly more often in the fragmented network. The surrounding matrix within the highly fragmented system consisted of unsuitable conifer plantations and fertilised pastures whereas the aggregated study area contained more natural undisturbed peat bog. Higher mortality rates of individuals dispersing from the fragmented habitat due to an unsuitable matrix probably exert a strong selection pressure for the evolution of behavioural evasion of patch boundaries, explaining the lower emigration rates recorded in the fragmented area.

Landscape permeability may be improved if fragmented habitats are physically connected by landscape elements such as hedgerows or other suitable habitat. This structural degree of 'connectedness' is distinct from the 'connectivity' of a landscape, which refers to the functional role of species specific movement within the landscape (Baudry & Merriam, 1988). Such landscape connectivity can increase immigration and emigration rates between populations (Merriam, 1991).

Assessing the spatio-temporal scale at which individual species perceive the environment is crucial to understanding population dynamics and the interaction between behavioural phenomena and the fragmented landscape (Lima & Zollner, 1996; Brandt, 1998). Behavioural responses to landscape elements will differ between species and the landscape cannot be viewed simply as intrinsically fragmented or connected (Jonsen & Fahrig, 1997; Davidson 1998; Steffan-Dewenter *et al.*, 2001; Krauss *et al.*, 2003). A decrease in landscape connectivity on vertebrate movement abilities was found to be species-specific in British Columbian forests. Small, less vagile species were adversely affected by decreasing landscape connectivity whereas the larger, more mobile species were able to withstand such perturbations (D'Eon *et al.*, 2002).

The ability of an animal to detect differing landscape components will influence its dispersal success and population dynamics within fragmented landscapes (Lima & Zollner, 1996). Animals with low perceptual ranges are at an increased risk of mortality due to prolonged searching for suitable habitat where they are vulnerable to predators or

lack of resources (Farina, 1998). Nocturnal white-footed mice (*Peromyscus leucopus*) displaced from their natural habitat of woodland displayed very poor perceptual range and were unable to locate woodlots from 30m away when placed in bare fields, and 10m away when in crop fields (Zollner & Lima, 1997). However, illumination by moonlight or dusk increased the perceptual range to 60m and 90m, respectively (Zollner & Lima, 1999).

Steffan-Dewenter *et al.* (2001) found that different groups of insects perceived the landscape at different scales in Germany. In 15 landscapes differing in complexity, the authors tested the effects of scale on pollinator and seed predator abundance. The correlation coefficients of these relationships were analysed at eight spatial scales. Changes in seed predator abundance of *Centaurea jacea* plants responded to scales of up to 2.5km whilst the correlation between changes in pollinator numbers and landscape structure decreased at larger scales. When the pollinators were analysed separately, the relationship between bumblebee (*Bombus* spp.) numbers and landscape structure positively increased at increasing spatial scales (up to 3km). Solitary bees (Apidae) appeared to respond to much smaller spatial scales between 0 - 500m. Honeybee (*Apis mellifera*) abundance exhibited a negative correlation with increasing landscape complexity at increasing spatial scales. Krauss *et al.* (2003) found similar results for butterflies in calcareous grasslands in Germany. Although landscape context exerted only marginal effects on species abundance for generalists, the surrounding matrix exerted the strongest effect on species richness at small spatial scales (within 250m radius). Habitat isolation alone had no effect on butterfly species richness. Habitat area was the most important factor affecting butterfly abundance with the species richness of specialist species being more sensitive than that for generalists. Thies *et al.* (2003) investigated the effects of the surrounding matrix on plant-herbivore-parasitoid interactions at different spatial scales in German agricultural landscapes. Low herbivory rates by the pollen beetle (*Meligethes aeneus*) and higher mortality rates as a result of parasitism occurred in the more structurally complex landscapes and the strongest correlations were detected at a scale of 1.5km. Clearly different insect taxa respond to habitat complexity at different spatial scales. These scales might be difficult to detect amongst the 'noise' of a variety of other variables affecting insect behaviour within the landscape.

Agricultural intensification affecting pollination: economic and conservation implications

Habitat destruction, disturbance and fragmentation pose major threats to both crop and wild plant pollination systems in Europe (Corbet *et al.*, 1991; Osborne *et al.*, 1991; Williams *et al.*, 1991; Rathcke & Jules, 1993; Westrich, 1996; Williams, 1996; Kearns *et al.*, 1998; Corbet, 2000) and at the global scale (Kremen & Ricketts, 2000; Paton, 2000; Roubik, 2000, 2001). Smaller, fragmented patches, by virtue of their decreased area, support fewer plants which may attract fewer pollinators and affect their foraging behaviour. A decrease in plant gene flow might result and a negative feedback loop may occur, ultimately reducing plant and insect biodiversity in that location (Dramstad & Fry, 1995; Kwak *et al.*, 1998; Kevan, 1999; Oostermeijer, *et al.*, 2000; Steffan-Dewenter *et al.*, 2001; Goverde *et al.*, 2002).

Most plant-pollinator interactions in northern Europe are very generalised (Waser *et al.*, 1996). Memmott (1999) suggested that the community might best be understood by composing interaction diagrams similar to conventional food webs. Since most pollination studies have focused on just a few of these interactions, there is little information available when trying to obtain the bigger picture of entire pollinator communities. Understanding plant-pollinator food webs has an essential application to a variety of research areas, such as the maintenance of diversity (Bascompte *et al.*, 2003), genetically modified crop pollen flow and community evolution of mutualisms (Memmott, 1999). The plant-pollinator food web can provide a powerful tool for analysing pollinator complexes. Corbet (2000) draws attention to conserving the compartments within such plant-pollinator food webs, in particular, the 'longer-tongued-bumblebee/deep corolla flower' compartment. The compartment is a sub-section of the food web which contains more interactions within its section than with species in other compartments in the web (Dicks *et al.*, 2002). This compartment has suffered losses of both the longer-tongued bumblebee species and many of the deep-flowered perennials due to annual ploughing, leaving *B. hortorum* and *B. pascuorum* as the only effective pollinators within the compartment.

Conservation efforts focusing upon dominant species, which have many interactions, will help to ensure the survival of the 'longer-tongued-bumblebee/deep corolla flower' compartment. This may be preferable to diverting all energy toward one particular rare

species which has fewer interactions than keystone species (Corbet, 2000). Dicks *et al.* (2002) found evidence of the compartmentalisation of pollination systems within Norfolk hay meadows, yet failed to find the 'long-tongued bee' compartment proposed by Corbet (2000). However, recent work by Bascompte *et al.* (2003) has cast doubt on the existence of compartments. By analysing 52 plant-animal mutualistic networks, they have demonstrated that the webs are highly nested, whereby a nucleus of generalist species provide the foundation upon which more specialist species are reliant. This nestedness conveys a more steadfast and robust system when coping with disturbance than if it was compartmentalised or randomly assembled. The endurance of rare species is buffered from stochastic events because of the highly asymmetrical organisation of the community where specialist species interact only with generalists. Ollerton *et al.* (2003) argue that this nested arrangement is the result of medium-term climate change filtering out specialist-specialist interactions.

The three most important groups of pollinating insects in the UK are the bees (Apoidea: Hymenoptera), butterflies (Rhopalocera: Lepidoptera) and the hoverflies (Syrphidae: Diptera). Their biology, ecology and relative effectiveness as pollinators vary greatly both between and within guilds and are therefore discussed separately.

Bees

It is widely recognised that bumblebees fulfil an essential function as pollinators, although their role is frequently underestimated. Their fundamental contribution to agricultural production lacks serious acknowledgement by both the general public and policy makers in Britain and the European Union (Williams, 1995). Remarkably, the reason for this is the lack of data on the pollination requirements of many crops and quantitative information on the role of bumblebees in this context. For example, in the European Union only sketchy information is known about the pollination requirements of one third of crops grown there (Williams, 1995). Kearns *et al.* (1998) put the importance of pollinators in perspective, stating that one third of the food consumed by humans is dependent either directly or indirectly on pollination. As well as being necessary for seed and fruit production, insect pollination helps to synchronise an even ripening of seed. It also affects the quantity and quality of seed and fruit produced, and is needed for hybrid seed set (Corbet *et al.*, 1991).

The decline of bees could have serious economic implications. In Europe and the USA, crop pollination may suffer due to forecasts in bee shortages (Torchio, 1990; Osborne *et al.*, 1991). In the European Union, about two thirds of 264 plant species have had their pollen vectors investigated. Of these, 83% are entomophilous. These species belong to around 60 plant families and possess widely varying flower form, which in turn, require a large diversity of pollinators (Williams, 1994).

Whilst farmland is not the ideal habitat for pollinators (Kearns *et al.*, 1998), large numbers of bumblebees can be found in many agroecosystems (Banaszak, 1983; Goulson, 2003). Although there have been national declines in bumblebee species and abundance (Williams, 1986) six species remain common and widespread (*Bombus hortorum*; *B. lapidarius*; *B. lucorum*; *B. pascuorum*; *B. pratorum* and *B. terrestris*). They may be scarce early in the year due to their annual colonies: they are, however, very effective pollinators and a number of characteristics make them more efficient than honeybees and other insects. Their large size provides insulation and some thermoregulation via muscle activity. This translates into an ability to work for longer periods of time and in poor weather conditions. This attribute makes them important pollinators in northern Europe (Corbet *et al.*, 1993; Kwak *et al.*, 1996; Williams, 1996). Bumblebees are generalist pollinators, but different species have varying tongue lengths and therefore tend to visit differing flower shapes for which they are adapted (Brian, 1954; Prÿs-Jones & Corbet, 1991; Fussell & Corbet, 1992; Proctor *et al.*, 1996). Nectar feeders spend the majority of their time searching for food and wild bees are dependent upon a constant supply of nectar since they store little food (Brian, 1954; Carreck & Williams, 1997). The need to move in search of food will depend on floral abundance and, as food availability declines, pollinators must travel further (Banaszak, 1996). Bumblebees are capable of flying substantial distances (Osborne *et al.*, 1999; Goulson & Stout, 2001; Dramstad *et al.*, 2003) transporting pollen across the landscape and helping to alleviate the deleterious effects of habitat fragmentation on gene flow (Jennersten, 1988; Saville *et al.*, 1997; Kwak *et al.*, 1998).

Temporal fluctuations in the abundance of the native bee community means that a high diversity of bees is required to provide adequate crop pollination services. However, isolation from floral and nesting resources contained within natural habitats was identified as a key factor reducing the diversity and abundance of native bees, negating the use of

this 'free' service in California (Kremen *et al.*, 2002). As another example, bumblebees require a range of landscape types to satisfy their varying habitat preferences for establishing nests (Svensson *et al.*, 2000) and for forage (Edwards, 1996; Saville *et al.*, 1997).

Some crops such as oilseed rape provide abundant nectar and pollen resources, but only temporarily (Williams & Carreck, 1994; Corbet, 2000). Bees need a constant supply throughout the colony's life-cycle to maintain adequate populations (Osborne *et al.*, 1991; Corbet, 1995). However, Westphal *et al.* (2003) found that bumblebee densities increased at the landscape-scale as a result of forage found in mass-flowering entomophilous crops, at the time of colony founding. The spatio-temporal heterogeneity of resources affects different species in different ways, depending on their foraging range (Walther-Hellwig & Frank, 2000). Forage found in areas such as set-asides, roadsides, hedgerows, ditches, and field margins provides floral resources in low amounts but over a long period (Westrich, 1996).

Butterflies

The habitat requirements of butterflies vary depending on whether the species belongs to an 'open' or 'closed' population. Open population species, which include migrants such as the red admiral (*Vanessa atalanta*), are highly mobile and will colonise any new suitable habitat. Closed population species only rarely colonise new habitats and individuals will complete their entire life cycle within one locality; they are consequently more susceptible to habitat degradation and fragmentation (Corke, 1997). Although the pollination behaviour of the order is poorly understood, Bronstein (1995) places the Lepidoptera as the second most important group of insect pollinators. There is wide variation in proboscis lengths of different butterfly species allowing a great diversity of flowers to be probed by the order. Butterflies feed on a wide range of British flowers but there are no examples of specialist plant-butterfly interactions within the British Isles (Proctor *et al.*, 1996).

Of the 61 butterfly species resident or regular migrants to the UK, 64% have been recorded from hedgerows although none are exclusive to hedges (Thomas & Lewington, 1991; Dover & Sparks, 2000). Compared with unimproved grassland, relatively few butterfly species are found on agricultural land. The use of herbicides, pesticides and

fertilisers has had a detrimental effect on butterfly habitats (Sparks & Parish, 1995; Kearns *et al.*, 1998) such that many butterfly species are therefore restricted to areas of non-cropped land, field boundaries and hedgerows (Sparks *et al.*, 2000). These areas receive less disturbance and support an increased abundance of larval and adult food plants (Smart *et al.*, 2001; Leimar *et al.*, 2003). Dover *et al.* (1992) cited a number of studies which suggested that butterfly abundance and diversity increased in field margins where pesticide applications had been reduced within the outer 6m of cereal fields. These so called ‘conservation headlands’ supported increasing populations of satyrid butterfly species when compared with south and south-east England regional trends. However, more and more marginal land is being cultivated particularly in the last 50 years, as food production has increased, exacerbating the situation (Kearns *et al.*, 1998). Conservation measures need not necessarily involve huge effort. Minor changes, such as more conservative use of chemicals and making the most of already existing habitats can improve abundance and diversity of many animals as well as pollinators (Dover *et al.*, 1990, Dover, 1996; Sparks & Parish, 1995; Edwards, 1996; Feber *et al.*, 1999). Sparks & Parish (1995) found that floral species richness, large hedgerows and grassy areas in field boundaries positively influenced butterfly populations in Cambridgeshire. Clearly, the existing evidence suggests that less intensive management of field margins creates a more suitable habitat for butterflies and many other pollinators, boosting the land area available for movement via a network of linear strips.

Hoverflies

Hoverflies have received much attention as biological control agents, since the larvae are voracious predators of aphids (Hickman & Wratten, 1996; Bowie *et al.*, 1999; Frank, 1999). The sowing of wild flower strips either to enhance biodiversity or to augment pest management strategies is gaining popularity and is frequently being incorporated into modern farming practices. The strips have been very successful in enhancing aphidophagous hoverfly diversity and abundance (Hickman & Wratten, 1996; Frank, 1999; Colley & Luna, 2000; Sutherland *et al.*, 2001). Linear features such as road verges and conservation headlands may have similar properties to wild flower strips in facilitating hoverfly dispersal across the landscape. If linear features contain suitable floral resources, it is then possible that the findings from wild flower strips can be applied to them in extending hoverfly distribution within the arable landscape. Yet Harwood *et al.* (1994) warn that these strips may act as sinks, depleting the surrounding landscape of

the more natural distribution of hoverflies. This is significant, as their role as pollinators has often been overlooked (Goulson & Wright, 1998; Kearns, 2001). They are the second largest pollinator group after the bees and comprise nearly 250 species in the British Isles (Proctor *et al.*, 1996). Some hoverfly species specialise on either pollen or nectar, whilst others appear to feed on both.

The management of field margin flora to enhance biological control was discussed by Cowgill *et al.* (1993). They assessed the use of floral resources by the hoverfly *Episyrphus balteatus* in UK farmland field margins. Between June and August, a sequential change of floral use was noted of the 27 plant species studied, whilst a few flowers provided constant forage. A study of insect visitation to three rare plants (*Scabiosa columbaria*, *Phyteuma nigrum* and *Salvia pratensis*) revealed that hoverflies, especially *Eristalis tenax*, were the most important pollinators for *S. columbaria* (Kwak *et al.*, 1996). They are important because they carry large pollen loads and they visit in high numbers. *E. tenax* is very common in northwest Europe, and has increased in numbers (Bankowska, 1980).

Hoverflies are very good organisms to study at the landscape scale because adults are highly mobile. With a widespread distribution, it has also been suggested that they would make good bioindicators particularly because different species have varying environmental requirements as larvae (Sommaggio, 1999; Morris & Ball, 2002).

Remnant semi-natural habitat patches

In the arable landscape, relatively small patches of semi-natural habitat remain at field corners, around disused buildings or ponds and other areas of non-cropped land. These patches fit into the agricultural matrix with varying degrees of connectedness with linear landscape features such as hedgerows, and are important areas for the maintenance of pollinator populations (Hobbs, 1992; Edwards, 1996). These patches generally suffer little anthropogenic disturbance, allowing vegetation to die down naturally after each growth season. The cyclical growth and decay of different plant species creates a mat of decaying plant material which may accumulate over time (Crawley, 1986; Begon *et al.*, 1990). This heterogeneous structure provides suitable nest sites for bumblebees and solitary bees as well as nectar sources for many insects, and larval food plants for butterflies and hoverflies (Banaszak, 1983; Kearns & Inouye, 1997; Saville *et al.*, 1997;

Tscharntke *et al.*, 1998). A succession of flowering plants along with nest sites is crucial within the landscape to support a species-rich bee community (Calabuig, 2000; León-Cortés *et al.*, 2000; Steffan-Dewenter *et al.*, 2001).

The wild flowers present in these ‘islands’ represent something of an oasis for wildlife, particularly pollinators, when compared with the surrounding monoculture so typical of arable farms in lowland Britain. There is no doubt that these patches support pollinator populations which have direct benefits to nearby entomophilous crops (Banaszak, 1983; 1996; Edwards, 1996; Westrich, 1996). Crop fields with uncultivated land nearby receive greater numbers of bumblebees. For instance, Scott-Dupree & Winston (1987) found that commercial orchards surrounded by areas of non-cultivated land received more bumblebee visits.

These fragments become all the more important in the light of recent declines in species distributions of bumblebee populations, as well as documented contractions of range of some of the rarer butterfly species, resulting from agricultural disturbance and habitat fragmentation (Williams, 1986; Prŷs-Jones & Corbet, 1991; Pollard & Yates, 1993; Rathcke & Jules, 1993; Hill *et al.*, 2001; Goulson, 2003). Species declines have been attributed to human activities such as changes in land use practices, introduction of non-native species and increased chemical applications in agriculture (Kwak *et al.*, 1996; Kearns *et al.*, 1998). Habitat degradation, either via complete loss, lower quality or fragmentation, is the single most important cause of worldwide population extirpation and species extinction (Hanski, 1998).

For populations to persist in the environment, theoretical studies have pointed to habitat spatial heterogeneity as being important if insular patches are to have a greater chance of being re-colonised (Fahrig & Paloheimo, 1987). Fahrig & Paloheimo (1988b) developed a simulation model, backed up by fieldwork, for adult females of the Large White butterfly (*Pieris rapae*) by looking at their movement behaviour in patchy habitats. Their results suggested that the effect that spatial arrangement of habitat patches has on local population sizes diminishes as the dispersal distance increases (Fahrig & Paloheimo, 1988a). Turchin (1991) reported that female *Euphydryas anicia* butterfly movement was affected by two factors when locating oviposition sites: host plant density and male

presence. Female rate of movement was increased and could lead to their emigration from the host patch following male harassment.

For species susceptible to local extirpation, colonisation of new patches is vital to their population dynamics. Successful colonisation is dependent upon the dispersal ability of enough individuals to establish a population. The Bay Checkerspot butterfly (*Euphydryas editha bayensis*) is capable of moving several kilometres. However, if they were within 50m of a suitable patch, they moved in an oriented fashion; random movement was more likely if they were further away. Patches surrounded by hills were less likely to be colonised than those surrounded by flat land (Harrison, 1989). Evidence that the landscape affected the population genetic structure of the alpine butterfly (*Parnassius smintheus*) was reported by Keyghobadi *et al.* (1999) using microsatellite DNA markers.

As the landscape has become more fragmented and its physical architecture has changed, so the flow of nutrients and energy within the landscape has altered, with the distance between semi-natural habitats increasing (Fry, 1994). The importance of non-cultivated linear landscape features within a mosaic of intensively managed cereal fields has probably never been more significant (Svensson *et al.*, 2000). As they are often field boundaries, they are frequently the only connection between the remaining fragments of once extensive semi-natural habitat (Burel, 1996; Baudry & Bunce, 2001; Boots, 2001).

Linear landscape features

Linear features can be simple, such as a fence line, or complex, such as an ancient hedgerow (Rosenberg *et al.*, 1997). Their structural and biological variety stems from their intended purpose; to contain stock, as planted shelter-belts, drainage ditches, roads, ownership boundaries or remnants of woodland (Baudry & Bunce, 2001). They facilitate functional landscape-level processes such as the flow of energy, materials and species along and between them, although this is never uniform along the entire length (Forman & Baudry, 1984; Burel, 1996; Baudry & Bunce, 2001). The various functions they make possible are determined by their network pattern within the landscape and their connectedness (Forman & Baudry, 1984). Features such as hedgerows, roadside verges and ditches can extend the distribution of wild flowers in an otherwise unfavourable farm environment (Sutcliffe & Thomas, 1996). In lowland Britain, hedgerows and roads

comprise the most dominant type of linear features (Marshall *et al.*, 2001) and these are discussed in turn.

Hedgerows

The familiar patchwork landscape of fields bordered by hedgerows is a characteristic feature of lowland Britain and reflects socioeconomic, political and historical modifications to the land (Pollard *et al.*, 1974; Chapman & Sheail, 1994; Doubleday *et al.*, 1994; Congreve, 2001). Hedgerows form grid-like networks connecting otherwise isolated habitat patches within the large-scale field environment (Burel, 1996; Barr & Gillespie, 2000). Linear features serve to break up and infiltrate large open spaces by providing more or less contiguous extensions of habitat patches and conduits (Forman & Baudry, 1984; Turner, 1989; Merriam, 1991). Conversely, they can also interrupt air fluxes and represent barriers to seed dispersal and species' movement (Burel, 1996; Bhattacharya *et al.*, 2003).

There are numerous definitions of what constitutes a hedgerow, reflecting their varying origins and intended purposes. The terms 'hedge' and 'hedgerow' are often used interchangeably although there are subtle differences between the two. The 'hedge' refers strictly to the vertical woody species whereas 'hedgerow' often incorporates other associated features such as the presence of a ditch and herbaceous species growing at its base (Forman & Baudry, 1984). The Countryside Survey defines a hedgerow as “a more or less continuous line of woody vegetation that has been subject to a regime of cutting in order to maintain a linear shape” (Barr & Gillespie, 2000). Clements & Tofts (1992b) defined hedgerows as “a line or narrow belt of closely-spaced woody shrubs, retained and/or managed so as to form a more or less continuous barrier”. Most definitions include the importance of management in maintaining the characteristic dense and linear shape, reflecting their most common function as a barrier. There were approximately 449,000km of hedgerows in England and Wales in 1998 (Countryside Survey, 2000). Hedgerows have great ecological importance within the landscape despite the relatively recent losses due to hedgerow removal discussed earlier,

The hedges occurring in Britain today originated either spontaneously, through direct planting or as a result of clearance of surrounding woodland (Forman & Baudry, 1984). Spontaneous hedges occur along existing linear features such as fence lines, where birds

may perch and deposit shrub seeds via their droppings. Immature plants might establish along such fences where there is less agricultural disturbance. The majority of Britain's hedgerows arose from deliberate planting; either to enclose stock or to provide shelter or to demarcate ownership boundaries (Pollard *et al.*, 1974; Helps, 1994). Although many hedges were planted as a result of the Enclosure Acts of the eighteenth and nineteenth centuries, there are also significant numbers of ancient hedgerows that are several centuries old. Remnant hedges represent woodland edges and are the only remaining vegetation left as the rest of the woodland was cleared to create new fields (Clements & Tofts, 1992a).

There is great variation in the physical structure of hedgerows ranging from immature planted hedges using one species, which may be thin, sparse and relatively uniform, to ancient hedges with a high species richness of both woody and herbaceous vegetation, of great width and height (Burel, 1996). Various other attributes may also contribute to the hedge's ecological value, such as the density of the herb layer, existence of ditches or hedgebanks, the number of gaps and standard trees present and the type of management regime the hedge is subjected to. Differing animal communities favour differing combinations of these physical attributes. Greater heterogeneity of the hedge structure has been linked to high animal diversity, especially where there are prominent vertical strata (Forman & Baudry, 1984). The hedge provides suitable habitat for a wide range of organisms, particularly those species naturally occurring at the woodland edge. The narrow linear shape mimics the woodland edge, having a much greater peripheral to interior area ratio. Hedgerows existing in areas with few woodlots or scrub cover are therefore particularly valuable in extending the natural habitat of woodland edge species (Clements & Tofts, 1992a).

The wildlife attributes of hedges can be divided into intrinsic and extrinsic features. Intrinsic attributes refer to the characteristics of the hedge, such as physical structure and species diversity. Extrinsic traits are those where wildlife benefits from the hedges' interaction with other landscape features, such as its proximity to woodland and connectedness to other hedgerows (Clements & Tofts, 1992a). These extrinsic factors are discussed in 'Linear features as extensions of habitat: wildlife corridors?', within this chapter.

Hedgerows can provide an extension of some of the benefits of remnant semi-natural habitats. Compared with the surrounding arable land, hedges generally suffer less disturbance and escape most direct chemical treatments although spray drift and herbicide treatments to the hedgerow base may be a problem in some cases (Dover & Sparks, 2000). As a result, there is generally greater plant species diversity, often with a positively correlated higher faunal diversity. Although no single species is restricted to hedgerows (Bunce *et al.*, 1994) a high percentage of species existing within arable landscapes occur within them (Burel, 1996). Over 500 vascular plant species have been documented from hedges, as well as more than 60 species of nesting birds (Ratcliffe, 1977). Small mammals such as dormice (*Muscardinus avellanarius*), bank voles (*Clethrionomys glareolus*) and wood mice (*Apodemus sylvaticus*) (Bright, 1998; Bellamy *et al.*, 2000), together with a high diversity of invertebrates including many pollinator species (Pollard *et al.*, 1974; Dover & Sparks, 2001; Croxton *et al.*, 2002) are all well represented within hedgerows. The hedgerow therefore represents a refuge for plants and their associated insect communities, which in turn support many bird and other vertebrate assemblages (Pollard *et al.*, 1974; Muir & Muir, 1987; Clements & Tofts, 1992a; Hinsley & Bellamy, 2000). It is not only the diversity of floral resources which are of significance to pollinators, but also the microclimate heterogeneity necessary for egg-laying and larval development, larval host plants and nest sites. Moreover, green lanes, where parallel hedgerows border trackways, have been found to provide favourable habitat for an increased numbers of bumblebees and butterflies (Sparks *et al.*, 1999; Dover *et al.*, 2000; Dover & Sparks, 2001; Croxton *et al.*, 2002). Clearly, it is not only the multitude of niches provided by the great diversity of hedgerows that are ecologically significant, but also the way in which these hedgerows interact with the surrounding landscape.

Roads

Urban expansion has also affected the spatial pattern of the landscape. Along with habitat-loss for private dwellings and commercial industries, increasing numbers of roads are being built to service such communities. In Great Britain, the total land area covered by all roads in 2001 was approximately 3,300km² with numbers increasing annually (DfT, 2001). Not only do they have a direct impact on wildlife, such as road kills and disturbance or destruction of habitat during construction, but the infrastructure fragments habitat and also acts as a barrier which impedes some animal movement (Bhattacharya *et*

al., 2003). However, numerous studies have demonstrated that road verges can provide suitable habitat for the maintenance of some populations, can be species-rich and can contain high densities of plants (Hogbin *et al.*, 1998; Auestad *et al.*, 1999), insects (Munguira & Thomas, 1992; Vermeulen, 1994; Svensson *et al.*, 2000) and small mammals (Bellamy *et al.*, 2000).

Roadsides can be suitable habitats for pollinators (Auestad *et al.*, 1999). In the Netherlands, bumblebees and flies were the most frequent visitors to plants in roadside verges (Kwak *et al.*, 1996). Banaszak (1983) studied the occurrence of wild bees on roadsides in Poland between April and August. Varying from 2 - 4m wide, verges differed in vegetative structure and composition from short swards to overgrown vegetation, containing shrubs. Generally, the more plant species-rich verges supported a greater diversity of wild bees. However, all verges were good habitats, comparable to permanent reserves, as they provided abundant nest sites and a sequential food source throughout the season for wild bees. Although the normal flight distance of wild bees appears relatively short, shelter-belts, roadsides, boundary paths and refuge habitats nearby did enhance their movement into crops (Banaszak, 1983).

As fragmentation of the landscape increases, many conservation strategies have focused upon the functional importance of linear landscape features in ameliorating the adverse effects of increasing patch isolation. Linear features connecting discrete habitat patches may improve the functional connectivity of the ecological landscape by facilitating faunal movement along them to occupy otherwise isolated patches (Hobbs, 1992; Rosenberg *et al.*, 1997; Beier & Noss, 1998). Linear features acting as wildlife corridors have received much attention in the past couple of decades. Although this study does not directly assess the validity of hedgerows as *corridors* for pollinator movement between insular patches, the topic of wildlife corridors is worthy of discussion in the broader context of animal movement in the landscape.

Wildlife corridor definition

The definition of a corridor at first appears quite straightforward: a strip of land with differing vegetation to that of adjacent land, connecting a minimum of two insular patches which may formerly have been one larger patch (Saunders & Hobbs, 1991). The word 'corridor' should only be used in the context of species movement (Beier & Noss, 1998).

‘Linear landscape feature’ is a more appropriate term when describing strips of land, where no facilitation of movement is being implied. Simberloff *et al.* (1992) detected six interpretations of the word ‘corridor’ within the conservation literature. For example, a corridor can be a distinct habitat which does not necessarily facilitate movement. Riparian habitats, for instance, physically resemble corridors, and are undoubtedly important habitats for certain species, but do not always enhance movement. Yet a linear habitat does not have to be a conduit to be ecologically important (Rosenberg *et al.*, 1997).

Upon further examination, corridors can vary considerably in origin, structure and function. They can be man-made, such as drainage ditches, roadside verges or hedgerows, or created indirectly by the clearance of adjacent vegetation. Corridors can also be natural, for example riparian habitats. The word ‘corridor’ has also been used misleadingly in studies to infer that linear features facilitate faunal movement when this assumption was not directly tested. When constructing arguments for the preservation of habitat strips, proponents have failed to make fundamental distinctions between their functions, which make it difficult to assess whether they should be saved (Rosenberg *et al.*, 1997).

The wildlife corridor debate

The use of linear features as movement corridors for organisms has recently been the subject of contention (Hobbs, 1992; Andrews, 1993; Mann & Plummer, 1995; Gilbert *et al.*, 1998). It has been suggested that populations occupying habitat patches might utilise linear features either to maintain existing populations, or to colonise patches which are otherwise detached from each other (Dunning *et al.*, 1995; Sutcliffe & Thomas, 1996). Many studies have claimed that linear features are used as conduits (Table 1.1) yet, very few investigations have actually observed individuals moving along these landscape features (Hobbs, 1992; Rosenberg *et al.*, 1997; Beier & Noss, 1998). Studies of linear features as corridors have concentrated on animals from a diverse range of taxa and Table 1.1 summarises a selection of these studies.

Table 1.1 Summary of research papers which have aimed to measure organism movement via habitat corridors.

Authors	Year	Subject	Title
Andreassen <i>et al.</i>	1996	Male root voles	Optimal width of movement corridors for root voles: not too narrow and not too wide.
Bright	1998	Arboreal dormice	Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps.
Corbit <i>et al.</i>	1999	Forest herbs	Hedgerows as habitat corridors for forest herbs in central New York, USA.
Dunning <i>et al.</i>	1995	Sparrow	Patch isolation, corridor effects and colonisation by a resident sparrow in a managed pine woodland.
Gilbert <i>et al.</i>	1998	Micro-arthropods	Corridors maintain species richness in the fragmented landscapes of a microecosystem.
Haas	1995	Birds	Dispersal and use of corridors by birds in wooded patches on an agricultural landscape.
Ims & Andreassen	1999	Root voles	Effects of experimental habitat fragmentation and connectivity on root vole demography.
La Polla & Barrett	1993	Meadow vole	Effects of corridor width and presence on the population dynamics of the meadow vole (<i>Microtus pennsylvanicus</i>).
Micheli & Peterson	1999	Benthic macro-invertebrates	Estuarine vegetated habitats as corridors for predator movements.
Ruefenacht & Knight	1995	Deermice	Influences of corridor continuity and width on survival and movement of deermice.
Spackman & Hughes	1995	Plant species richness	Assessment of minimum stream corridor width for biological conservation – species richness and distribution along mid-order streams in Vermont, USA.

Many previous investigations have generally failed to demonstrate animal movement using linear landscape features as conduits. The methodology of such studies has also been criticised for using either unnatural experiments or merely *assuming* that organisms use linear features as corridors (Hobbs, 1992; Rosenberg *et al.*, 1997; Beier & Noss, 1998). Even when movement along linear features is evident, the permeability of the surrounding matrix is often not described, therefore preventing evaluation of the potential benefits of the linear feature for facilitating movement (Ruefenacht & Knight, 1995; Andreassen *et al.*, 1996, Table 1.1).

It is clear from current literature that linear features cannot be viewed as corridors for all species. They appear to facilitate movement for *some* species, but impede it for others. It is therefore incorrect to assume that the creation of corridors between insular patches will result in facilitating movement for all species using those patches (Malanson & Cramer, 1999).

The value of linear features, especially hedgerows, to wildlife is well documented (Pollard *et al.*, 1974; Muir & Muir, 1987; Clements & Tofts, 1992a). However, it is uncertain whether such features are used by animals as conduits to reach patches of semi-natural habitat which would otherwise be isolated (Hobbs, 1992). It is widely agreed that numerous studies have demonstrated the benefits of linear features to particular species, in some areas, as extensions of habitat. However, dispute arises when these studies then infer animal movement along such corridors without evidence (Beir & Noss 1998).

Modern day conservation measures are less species-specific. They take a more holistic view and tend towards blanket protection rather than focusing on single species needs (Young & Clarke, 2000). This can only benefit pollinators and their inherent interactions. However, in the corridor literature it suggests that the target species will determine the environment required in a linear feature in order for it to be used as a corridor although this may restrict the number of species that will benefit from it (Tewksbury *et al.*, 2002). A landscape cannot be considered inherently connected or fragmented as this depends on the dispersal abilities of the species in question and the scale at which it perceives the connectivity of the landscape (Jonsen & Fahrig, 1997; Davidson 1998; Steffan-Dewenter *et al.*, 2001; Krauss *et al.*, 2003).

The justification for corridors, expressed by their proponents, is that they can help alleviate problems caused by fragmentation. They can also help to preserve threatened species by positively influencing population processes and by decreasing the effects of demographic stochasticity. They can reduce extinction rates, allow natural movement over a larger area and enhance gene flow thus preventing inbreeding depression (Simberloff *et al.*, 1992). Despite the lack of evidence in support of corridors, there has been widespread acceptance that they are beneficial, resulting in their incorporation in many reserve designs and conservation management schemes. This has been justified by reasoning that the possibility of local extinction in insular habitats will be reduced with the addition of a linking corridor (Hobbs, 1992).

The movement function of corridors can also be disadvantageous. Movement of predators, pests, exotic and invasive species and disease vectors may be increased. The corridor may also act as a barrier if it intersects land that was formerly open habitat and prevents other animals from crossing (Hobbs, 1992; Mann & Plummer, 1995).

One of the arguments against the extensive use of corridors is the assumption that every situation is a metapopulation. Demographic stochasticity is a frequent occurrence in populations, but will not necessarily reach equilibrium with recolonisation rates balancing extinction rates (Mann & Plummer, 1995).

Metapopulations

The concept of connectivity has been around for a long time, but has become popular more recently as a result of metapopulation theory. This mathematical model proposes that species, which exist in discrete populations in separate patches, may survive by a series of immigrations and emigrations between connected patches. Reference is frequently made to the pool frog (*Rana lessonae*) to exemplify metapopulation theory. The pools in which the frog lives may sometimes dry up, causing local extinction. However, because dispersal movements functionally connect the pools, individuals from other pools can re-populate the pond when conditions become more favourable (Sjögren-Gulvë, 1994). Thus numbers in any one patch may continually fluctuate, but the species maintains its existence as a metapopulation and remains relatively stable (Mann & Plummer, 1995).

Linear features as extensions of habitat: wildlife corridors?

As already discussed, in addressing the problem of animal movement within fragmented landscapes, wildlife corridors have been widely implemented in many conservation strategies, despite little evidence of their effectiveness for multiple species (Hobbs, 1992; Andrews, 1993; Mann & Plummer, 1995; Gilbert *et al.*, 1998). The objective of implementing corridors is that they can link otherwise isolated patches of suitable habitat and facilitate movement between favourable habitats across unsuitable areas of land.

Although there is some evidence of animals using linear features as a dispersal aid (Table 1.1), much of the debate lies in the different interpretations of the corridor concept. The

temporal scale at which movement occurs may vary widely. The journey may be of short duration of just a few minutes travelling between patches or over a period of several years as the population slowly colonises the length of the linear feature and eventually, almost by chance, reaches the other patch (Rosenberg *et al.*, 1997). This latter concept implies that the entire length of the corridor is acting as an extension of the species' habitat or home range, of high enough quality to support populations in its own right. Lima & Zollner (1996) raised the important behavioural question of whether wildlife corridors are even perceived as movement routes between patches, or whether the organism merely strays into the corridor on a passive basis.

For hedgerows to function as habitat extensions, they must possess those habitat characteristics favourable to the species' requirements. McCollin *et al.*, (2000) suggested that the hedgerow environment was analogous to wood edges rather than the woodland interior. Hedgerows could therefore potentially only facilitate movement of those woodland plant species which did not require the more shaded, damper and nutrient poor conditions of the woodland interior.

The internal hedgerow structure was a significant influence for carabid (Carabidae: Coleoptera) beetle movement (Burel, 1989; Charrier *et al.*, 1997). Forest species could only utilise hedgerows as conduits when their structure mimicked their natural shady wooded habitat. Green lanes, bordered by two parallel hedgerows and nodes where hedgerows interconnect, were used as stepping stones for forest carabid dispersal. Peninsular and corridor species, however, were able to utilise more hedgerows as their habitat requirements were less specific (Burel, 1989).

The assessment of forest rides as dispersal corridors for the ringlet butterfly (*Aphantopus hyperantus*) was examined by Sutcliffe & Thomas (1996). In general, the rides did appear to facilitate dispersal. However, individual butterfly movement and information on the flora of the rides was omitted. This information would have a profound effect on whether the ringlets used the rides as movement corridors, or whether they represented extensions of habitat. The flowering phenology of food plants such as fleabane (*Pulicaria dysenterica*) and thistles (*Cirsium* spp.) differed, yet butterfly movement was not monitored over time, which might have revealed temporal movement patterns. The

study also showed that the tree-lined glades within the study area presented barriers to ringlet emigration.

Landscape structure is clearly an important factor in the dispersal and maintenance of some insect populations (Jonsen & Fahrig, 1997). Interactions with surrounding land can be highly influential as the floral composition of linear features is largely determined by adjacent land use practices (Baudry & Bunce, 2001) and the history of that locale (Burel, 1996). Dunning *et al.* (1992) described the 'neighbourhood effect' as just one of four ecological processes influencing population dynamics within complex landscapes. The attributes of contiguous patches close to a focal patch can be highly influential. Taylor *et al.* (1993) contend that it is not simply the closeness of adjacent patches which can influence animal diversity but the degree of connectivity between those patches and the land feature in question.

The importance of considering the surrounding landscape was exemplified by Dover & Sparks (2000), when surveying butterflies in agricultural land. They reported that hedgerow boundaries adjoining favourable butterfly habitat such as glades, contained more species than similar hedgerows that were situated between two cereal fields. This demonstrates that adjacent land use can exert strong influences on insect as well as plant diversity.

Linear features may ameliorate the effects of habitat fragmentation in terms of energy and materials flow by providing extensions of habitat for some species. However, for animal movement, a rudimentary distinction between the functions 'habitat extension' and 'conduit' should be highlighted. A corridor might, therefore, have two definitions: a linear feature may act as a corridor if it represents an extension of the species' usual habitat with adequate conditions and resources to support all stages of the life cycle, allowing greater species distribution within the landscape. Or, a linear feature may act as a corridor if it provides some sort of visual cue or navigational aid, or is regarded as less hostile habitat than the surrounding matrix, which facilitates species' dispersal along its length to reach another habitat (Rosenberg *et al.*, 1997).

How can landscape connectivity be measured?

Objectively investigating the use of linear features as corridors poses major methodological problems (Hobbs, 1992; Mann & Plummer, 1995). A replicated experimental design with controlled conditions is impossible to achieve since each linear feature will have its own unique combination of environmental factors such as varying species composition and complex interactions (Nicholls & Margules, 1991). However, it is argued that such a rigid experimental design is unnecessary when investigating insect behavioural phenomena under natural conditions. Direct observation and/or a 'before and after' scenario where a corridor is either created or destroyed, are methods more compatible with monitoring pollinator behaviour on a local landscape scale (Hobbs, 1992; Beier & Noss, 1998).

Obtaining experimental evidence of connectivity creates a number of difficulties. Much time and effort is required to collect data in a fragmented landscape. In assessing whether the metapopulation model applies, it would be very difficult to observe any processes such as extinction and recolonisation. A protracted study would be necessary, covering the landscape and examining each population within the supposed metapopulation (Bissonette & Storch, 2002; Beier & Noss, 1998).

Perhaps a more appropriate starting point in assessing species responses to landscape connectivity should involve more subtle questions aimed at examining insect flight behaviour to habitat boundaries or measuring behavioural responses to visual cues of landscape elements (Table 1.2). Such an approach would give clues about the appropriate spatial scale on which to determine the effect that landscape structure may have on how that species perceives the landscape.

Table 1.2 A selection of recent studies examining the influences of linear landscape features on species movement behaviour or distribution.

Authors	Year	Subject	Title	Type of linear feature	Results
Burel	1989	Carabid beetles	Landscape structure effects on carabid beetles spatial patterns in western France.	Hedgerows	Hedgerow provided species-specific extensions of habitat.
Dover & Fry	2001	Butterflies	Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape.	Artificial	Species-specific, flight behaviour modification.
Dover <i>et al.</i>	2000	Butterflies	Linear features and butterflies: the importance of green lanes.	Green lanes	Extension of habitat of particular value to closed population species.
Haddad	2000	Butterflies	Corridor length and patch colonisation by a butterfly, <i>Junonia coenia</i> .	Forest rides	Corridors had no effect on patch colonisation, but there was an interaction between corridor use and increased distance.
Haddad & Baum	1999	Butterflies	An experimental test of corridor effects on butterfly densities.	Forest rides	Corridors increased densities of habitat-restricted species.
Haddad <i>et al.</i>	2003	Diverse taxa	Corridor use by diverse taxa	Forest rides	Species-specific movement between connected patches using the corridors.
Sutcliffe & Thomas	1996	Butterflies	Open corridors appear to facilitate dispersal by Ringlet butterflies (<i>Aphantopus hyperantus</i>) between woodland clearings.	Woodland rides	The rides provided more favourable habitat to move between woodland clearings.
Tewksbury <i>et al.</i>	2002	Plants & butterflies	Corridors affect plants, animals and their interactions in fragmented landscapes	Forest rides	Increased exchange of butterflies, pollen and seed dispersal between connected patches.
Vermeulen	1994	Carabid beetles	Corridor function of a road verge for dispersal of stenotopic heathland ground beetles, Carabidae.	Roadside verge	Verge provided species-specific extensions of habitat. No evidence of verge facilitating movement.

Pither & Taylor (1998) assert that the method chosen to measure landscape connectivity must take into account both the intricate relationships and the interactions between landscape structure and individual animal behaviour. Apart from studies which have used successful techniques such as individual tracking, mark-release-recapture, habitat or individual manipulation, there is a lack of empirical data that specifically isolate those important aspects of landscape connectivity such as the movement sequences of organisms, speed of movement, and how they respond in different habitats. Even more scarce are data on animal movement behaviour in two or more different habitat structures. Little information exists that examines certain species' population dynamics in relation to their movement in the spatial dimension.

There is a lack of data on insect behavioural responses to landscape elements, particularly on agricultural land (Sparks & Parish, 1995; Dover, 1996), and at the landscape scale (Bronstein, 1995; Lima & Zollner, 1996). However, this is steadily being redressed (Jonsen & Fahrig, 1997; Steffan-Dewenter *et al.*, 2002; Krauss *et al.*, 2003; Thies *et al.*, 2003; Schtickzelle & Baguette, 2003; Steffan-Dewenter, 2003). Feeding behaviour, population viability and dynamics, and ultimately evolution of most animals, are influenced by patchily distributed food resources within the landscape (Taylor *et al.*, 1993) and the ability to move through the landscape to reach them (Fahrig & Paloheimo, 1988b; Fahrig & Merriam, 1994). Yet mutualistic animals such as pollinators and seed dispersers have rarely been studied in this context (Kwak *et al.*, 1996). Until relatively recently, researchers studying mutualisms were rarely concerned with varying space and time issues, or ecological scale. The focus of the majority of research concerned the natural history of specific interactions at particular times and locations (Bronstein, 1995; Memmott, 1999). More recently, a more holistic approach of how pollinators are influenced by their surroundings is being adopted, whereby landscape scale studies are integrated with behavioural interactions (Steffan-Dewenter *et al.*, 2001, 2002; Joyce & Pullin, 2003; Krauss *et al.*, 2003; Schtickzelle & Baguette, 2003; Thies *et al.*, 2003). In addition, analyses of global patterns of plant-pollinator interactions indicate that, contrary to popular consensus, there is little evidence that tropical ecological interactions, such as pollination systems are more specialised than those in temperate latitudes (Ollerton & Cranmer, 2002).

Large-scale studies of the plant-pollinator landscape are necessary because extrapolations from plant-herbivore studies are invalid due to fundamental differences between the two systems (Bronstein, 1995). In both scenarios, herbivores (predominantly insects) and pollinators feed on plants existing in patches and make decisions about shifts in food choice and inter-patch movements. Yet pollinators and herbivorous insects differ in their responses to the environment, the consequences of which can alter the way in which each group moves and functions within the environment. Landscape scale studies of pollinators can be justified by considering the following major differences: pollinators differ from herbivorous insects in that they are more likely to utilise a greater diversity of plants. However, pollinators feed on flowers which are only available for short periods of time relative to vegetation and pollinator life span. Entomophilous plants have evolved to be available to their pollinators in space and time. Yet plants are under pressure to escape herbivorous insects both spatially and temporally. Bronstein (1995) argues that these two scenarios are different because they have been subjected to different selection pressures. A better understanding of flowering phenology in relation to pollinators may be the key to understanding pollinator movement within the landscape.

Thesis Overview

This thesis begins by introducing the current themes and sets the context around which this project is based. The introductory chapter reviews the literature and highlights the main knowledge gaps, which are that little is known about how insects move through the landscape or how landscape elements might influence insect flight behaviour. In reviewing the literature relevant to this project, Chapter 1 has considered three main areas: landscape structure and change; pollinators and pollination and possible functions of linear landscape features. The literature review generated many questions regarding insect movement within the landscape. These were refined to form the main aims and objectives of this project.

Aims and objectives

The general aims and their related objectives of the thesis are:

Aim 1. Do linear features influence pollinator flight behaviour?

Objective: Categorise the flight directions of pollinators at different distances away from the hedgerow.

Objective: Compare the number of pollinator visits made to flower patches connected by an artificial linear feature with those visits made to an isolated flower patch.

Aim 2. Do pollinators travel along linear features to move between otherwise separate habitats?

Objective: Categorise the flight directions of pollinators arriving at and departing from flower patches connected by an artificial linear feature and compare them with those flights made to and from an isolated flower patch.

Aim 3. Do linear features influence or facilitate pollinator movement through the landscape?

Objective: Within the farm landscape, compare the number of pollinator visits made to flower patches connected by a hedgerow with those visits made to an isolated flower patch.

Aim 4. Can this, in turn, influence plant reproductive success through increased pollen dispersal?

Objective: Measure the reproductive success of a plant growing in patches with a high number of connecting hedgerows and compare it with those plants growing within poorly connected patches.

Chapter breakdown

Following on from this general introduction (Chapter 1) it is important first to establish whether linear features have any observable effect on pollinator behaviour. This first aim is addressed in Chapter 2 where the movements of non-foraging pollinators are observed along 30m transects, perpendicular to eight different hedgerows. The results demonstrate that linear flight is far more likely to occur adjacent to the hedgerow than it is further out into the field.

As non-foraging flights of butterflies and bumblebees appear to be concentrated along the hedgerows, the importance of linear features within the landscape is considered in Aims 2 and 3. Might these hedgerows facilitate pollinator movement between otherwise separate habitats? What was particular about the hedgerow that elicited such linear flight? Could the same effect be generated along an artificial linear feature?

Chapter 3 sets out to examine if the linear flight observed along hedgerows in Chapter 2 could be recreated at the medium-scale, in an experimental arena. An artificial linear feature is created in an experimental design containing three equidistant patches of potted *Phacelia tanacetifolia* (Hydrophyllaceae). The linear feature connects two of the patches. Different artificial features varying in their structure and material are constructed and observations repeated. The results show that although the connected patches are not necessarily visited more than the isolated patch, flight directions between the connected patches are concentrated along the artificial feature. These flight patterns occur even when the position of the linear feature is changed to connect a different pair of patches. This experiment is scaled up to fit within the farm landscape, using an existing hedgerow as the connecting feature. Although flight directions cannot physically be monitored for their duration, bumblebees marked on either of the two connected patches are far more likely to be reobserved on both the connected patches rather than the isolated patch. Bumblebees exhibit high patch fidelity.

The fieldwork results from Chapter 2 and 3 suggest that artificial linear features do influence pollinator flight behaviour and that hedgerows appear to facilitate pollinator movement across the landscape. Linear features might not only facilitate the movement of these insects across the landscape but the plants, which receive pollination service by

these insects, might also benefit. Therefore, plants located in semi-natural habitat patches possessing numerous hedgerow connections, might receive greater pollinator visitation than those patches with few or no connecting hedgerows (Aim 4). Chapter 4 takes a bioindicator approach and studies the relationship between seed yield of *Salvia pratensis* (Labiatae) growing in patches with high connectedness and compares it with those plants growing within poorly connected patches. The results show that pollinator abundance, pollen grains per stigma and seed yield is greater in highly connected patches compared with patches with fewer connections. The overall connectedness of a landscape might therefore be important to both pollinators and those plants that depend on them for greater reproductive success.

The concluding chapter (Chapter 5) consolidates the findings from this entire study and places them within the context of the current knowledge base. The chapter discusses some of the limitations of the investigations and suggests possible improvements and proposals for future study.

Chapter 2: The influence of hedgerows on non-foraging pollinator flight behaviour

Introduction

An understanding of inter-patch movement by insects through the landscape is crucial in order to conserve such populations and the plant communities with which they interact (Bronstein, 1995; Kwak *et al.*, 1996; Fisher, 1998; Osborne *et al.*, 1999). Knowledge of the spatial scale of pollinator movements is also highly relevant to global agricultural production (Corbet *et al.*, 1991; Williams, 1995; Saville *et al.*, 1997; Allen-Wardell *et al.*, 1998; Kevan & Phillips, 2001; Kremen *et al.*, 2002). Bond & Pope (1974) and Free & Williams (1976) reported that inadequate pollination toward the centre of field bean (*Vicia faba*) fields exceeding 12ha contributed to seed yield decline. Furthermore, reductions in pollinator services to water melons (*Citrullus lanatus*) by native bee (Apidae) communities in California were evident when crop fields were located in areas of poor biodiversity (Kremen *et al.*, 2002).

Typical foraging distances of bumblebees (*Bombus* spp.) are still unknown, as is the influence that landscape structure has on their foraging decisions (Osborne *et al.*, 1999). Knowledge of pollinator foraging ranges over the landscape is vital to conserve plant-pollination systems, as habitat fragmentation increases and the distance between fragments expands (Kearns *et al.*, 1998). The perceptual range of individual species will have a significant impact on how pollinators interact with various landscape elements and to what extent species are affected by habitat fragmentation (Lima & Zollner, 1996). For pollinators with low mobility, large-scale habitat fragmentation may not be perceived if the insect completes its entire life cycle within one particular patch. However, insects with greater perceptual ranges will detect fragmentation at larger scales which might prove detrimental to successful life cycle completion and fecundity (Jonsen & Fahrig, 1997; Davidson 1998; Steffan-Dewenter *et al.*, 2001; Krauss *et al.*, 2003).

Bees are the most important group of insect pollinators followed by butterflies and moths (Lepidoptera) (Bronstein, 1995). Their pollination service is significant, both economically for crop pollination and for ecosystem functioning (Williams *et al.*, 1991; Williams, 1995; Kearns *et al.*, 1998). Examining pollinator behaviour in relation to the

landscape elements they encounter is important when attempting to redress the recent declines of many pollinator species abundance and distributions (Williams, 1986; Pollard & Yates, 1993; Banaszak, 1996). The habitat requirements, motility and pollination efficiency of species can vary tremendously within the pollinator guild. Some species are extremely localised, whilst others are more mobile (Proctor *et al.*, 1996; Stubbs & Falk, 2000; Pollard & Yates, 1993). Hoverflies (*Syrphidae*), bumblebees and butterflies are all generalist pollinators (Kwak *et al.*, 1996) able to forage from a wide range of plant species.

Pollinators must move between patches in search of food and to maintain populations. Food availability is an important factor determining the distribution of pollinators within the landscape (Banaszak, 1996; Appelqvist *et al.*, 2001). However, it is not known how this movement relates to the spatial arrangement of the respective patches (Rathcke & Jules, 1993). It has been reported that a few temperate-zone bees specialise in particular patch sizes (Sih & Baltus, 1987; Sowig, 1989). Dramstad (1996) made a clear distinction between 'in transit' flights between forage patches and 'foraging flights' between plants. 'In transit' flights are relatively direct and straight with the bee demonstrating knowledge of the location of forage patches from the nest; bees are not searching for food *en route*. A hierarchical scale of bumblebee flight distances can be described ranging from interflower movements, inter-patch movements and landscape scale flights (Figure 2.1). Their movement behaviour within fragmented farm systems can only be understood if inter-patch movement is studied (Saville *et al.*, 1997).

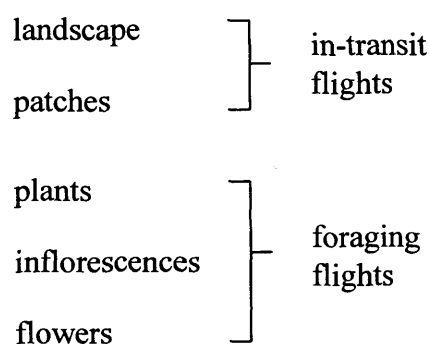


Figure 2.1 Hierarchical categorisation of pollinator flight movements from small to large-scales.

The way in which pollinators respond to spatial and temporal variation of floral resources across the landscape is poorly understood. Pollinators have tended to be studied at a population level and the influence of the landscape in which they exist has largely been ignored (Cushman & Beattie, 1991; Bronstein, 1994). Observations of non-foraging insects recorded and compared within different habitats may reveal whether landscape structure is the main factor exerting any effect on pollinator movement.

There have been many studies investigating the flight movements of pollinators at the small-scale such as between flowers and plants (Hodges & Miller, 1981; Galen & Plowright, 1985; Schmid-Hempel, 1985; Goulson *et al.*, 1997; Stout *et al.*, 1998; Cresswell, 2000). Yet studies of landscape scale movements of pollinators are insufficiently represented in the research literature due to the inherent difficulties of tracking relatively small individuals at larger scales. Although recent techniques such as harmonic radar have made it easier to track individual movements (Osborne *et al.*, 1999), the method is still in its infancy, is largely unavailable and the cost is prohibitive. Many years of research have contributed new developments in aiding the understanding of insect visual processing and discrimination between visual cues and how this relates to their behaviour in the natural environment (for reviews see Dafni *et al.*, 1997; Srinivasan *et al.*, 1999; Egelhaaf & Kern, 2002). Much of this work has focused on small-scale honeybee (*Apis mellifera*) learning, memory, landmark and pattern recognition in relation to food rewards (Lehrer, 1990; Horridge, 1996; Zhang, *et al.*, 1999 and Horridge, 2003).

From the insects' perspective, the predominant visual cues in lowland agricultural landscape are hedgerows which most frequently border crop or pasture fields (Burel, 1996; Barr & Gillespie, 2000). Although hedgerows can vary dramatically in structure and woody species content, they are narrow enough to mimic the woodland edge and contain many, though not exclusive, flowering species attractive to pollinators (Forman & Baudry, 1984). Some of the flowering plants once common in semi-natural, species rich meadows may now be found within the hedgerow herb layer (Robinson & Sutherland, 2002).

Despite the lack of studies of insect movement behaviour at the landscape scale, a few carefully designed studies have realistically addressed the problem of measuring landscape connectivity using appropriate spatial scales and produced some interesting

results (Steffan-Dewenter *et al.*, 2001; Krauss *et al.*, 2003; Thies *et al.*, 2003). Pither & Taylor (1998) focused on the habitat-specific movement patterns of two ecologically similar species of damselflies. Using mark-release-recapture and displacement techniques in both pasture and forest habitats, they concluded that habitat structure did affect the insects' ability to move through the landscape. Whilst *Calopteryx aequabilis* displayed no difference in movement ability through both landscapes, *C. maculata* moved more readily through pasture than forest. The study was particularly useful, because the scale was specific to the insects' flight range.

Although there is much debate as to whether such linear features can act as movement corridors for animals to move from one patch to another (Simberloff *et al.*, 1992; Mann & Plummer, 1995; Rosenberg *et al.*, 1997; Chapter 1), perhaps a more subtle question to ask is whether linear features can influence and therefore modify faunal responses. Many studies have addressed the issue of whether linear features act as movement corridors for various taxa (Vermeulen, 1994; Sutcliffe & Thomas, 1996; Bright, 1998; Haddad, 1999; Tewksbury *et al.*, 2002; Haddad *et al.*, 2003). Such studies are very difficult to conduct and the resulting evidence is species-specific and often equivocal (Beier & Noss, 1998). A less complicated first step would be to focus on whether the landscape feature can actually elicit an oriented movement along it. Dover & Fry (2001) demonstrated that artificial linear structures could alter the flight behaviour of some species of butterfly in Norway. Direct butterfly movements between the two patches using the linear features were not observed yet there was evidence that the structures could educe an oriented movement along the structure, which is discussed later.

This chapter addresses the issue of whether such linear features act as landmarks assisting insect navigation, when making non-foraging flights, through the landscape and whether the visual cue of a rectilinear feature can promote movement along it. Linear features may not simply represent an extension of a pollinator's natural habitat in which individuals may merely stray into. Landscape features such as hedgerows may perform a more functional purpose of providing orientation indicators within the landscape.

An observational strategy was devised which aimed to gain 'snapshots' of pollinator flight behaviour in relation to hedgerow orientation. Because of their relatively small size and flight speed, it is impossible to follow individuals for very long before they are lost from

view. Butterflies can be followed to a certain extent (Kearns & Inouye, 1993; Pollard & Yates, 1993; Goulson *et al.*, 1997) but this would make quantification of their distance and their overall orientation in relation to the hedgerow difficult to record. One of the main objectives of this study was to investigate the influence of the hedgerow, as a three dimensional landscape structure, on pollinator flight behaviour. The distances from the hedgerow were therefore very important data points. Instead of actively following individuals, a more passive, stationary observation method was employed in which all pollinator guilds could be observed simultaneously. By observing in one location at four different distances from the hedgerow, for an hour each, the observation area was kept constant and observation points were standardised.

Methods

Study site

All observations and experiments were conducted at Purston Manor Estate, Great Purston, Brackley, Northamptonshire, England (OS Landranger Map 151, grid reference: 518395). The estate is situated in a rural area, approximately 8km to the east of the nearest town. This mixed arable farm has an area of 209ha, two thirds of which are arable, and one third permanent pasture for sheep and cattle. The site is typical of many agricultural landscapes in lowland Britain, with large fields frequently bordered by hedgerows. There are relatively few areas of woodland and the field site has an undulating topography with a maximum height of 122m above mean sea level.

Hedgerows

Eight different hedgerows within the same farm were selected for their accessibility, structure and orientation (Figure 2.2, Table 2.1). All hedgerows were dominated by hawthorn (*Crataegus monogyna*) and blackthorn (*Prunus spinosa*) and, unless otherwise stated, were regularly managed as stockproof field boundaries. The age of the hedgerows was unknown but previous surveys (Cranmer, unpublished) revealed a number of clues suggesting that the hedges were centuries rather than decades old. These included the number of woody species per 30m lengths and the presence of standard trees together with evidence of thick, multi-stemmed woody species indicating previous management practices such as coppicing and hedge laying (Clements & Tofts, 1992a). Table 2.1 provides a brief habitat description of the fields and hedgerows. The lengths of the hedgerows ranged from 169 - 405m with mean heights of between 2.2 - 4.6m. Most hedgerows bordered wheat and pasture fields, were relatively dense and stockproof. At each hedgerow, 30m transects were marked out, perpendicular to the axis of the hedgerow. No grazing stock were present during the investigation.

The observation point along the hedgerow was chosen at random, for each separate sampling day, by dividing the hedgerow into 10m intervals which were each assigned unique numbers, and selected using random numbers generated by MS Excel 97 (Microsoft Corp., 1997). The direction of transects and observations was decided by tossing a coin (i.e. which side of the hedgerow, where accessibility permitted, and in which direction). Observation points were 0m, 10m, 20m and 30m from the hedgerow

(Figure 2.3). At each observation point, only non-foraging flight behaviour of bumblebees and butterflies was observed for 15 minute periods. The observation area was approximately 0.5m either side of the observer. The flight direction of each individual was categorised in relation to the orientation of the hedgerow into either linear; perpendicular; diagonal or irregular (referred to as 'random') (Figure 2.3). Each hedgerow was sampled for between 4 - 6 days each in June 2000 (Table 2.1). Insects were identified to species level, where possible but otherwise grouped to family or order level, e.g. *Bombus* sp. and *Pieris* sp. etc. Because of the difficulty in distinguishing certain bumblebee species in the field, *B. terrestris* and *B. lucorum* were grouped and recorded as *B. terrestris*; *B. lapidarius* and *B. ruderarius* were combined and referred to as *B. lapidarius*. Hoverflies were not counted, as they were less conspicuous.

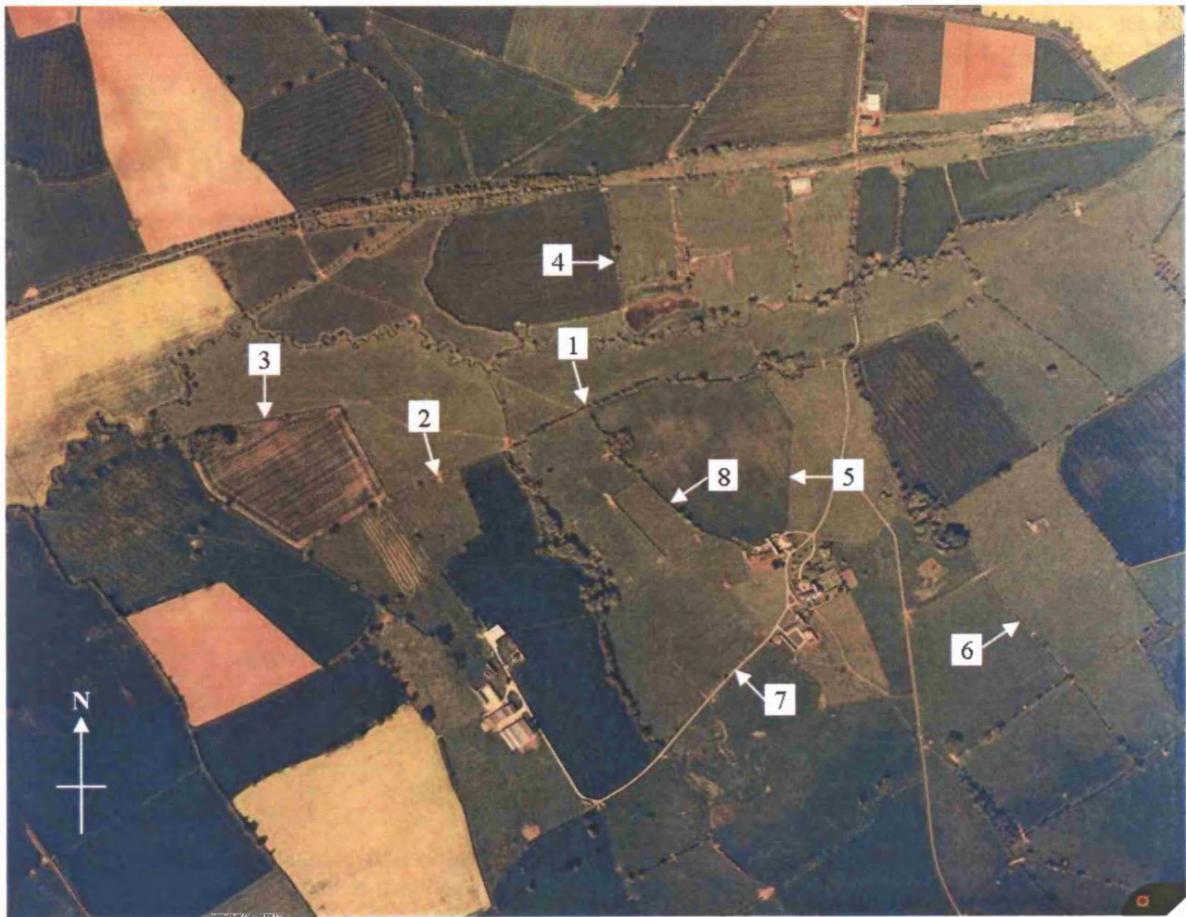


Figure 2.2 Location of hedgerows with hedge numbers. The arrows indicate the side of the hedgerow the observations occurred. Scale: 1:10,000. Photograph taken: May 1990, reproduced with permission from NRSC Ltd.

Table 2.1 Brief summary of hedgerow characteristics and observation dates.

Hedge no.	Aspect	Length (m)	Mean height (m)	Mean width (m)	Adjacent field use		Observation dates (June, 2000)	Description
					Survey side	Opposite side		
1	NNW	440	4.6	3.5	Pasture	Pasture	7, 23, 26 - 28	Ditched, less managed, interspersed with occasional mature oaks & ash
2	NNW	169	3.2	1.8	Pasture	Wheat	7, 13, 26 - 28	Dense, managed, stockproof
3	NNW	192	3.6	2.0	Pasture	Wheat	7, 12 - 13, 15, 26 - 27	Steep-sided, ditched, managed
4	W	177	2.9	2.1	Silage	Pasture	12, 15, 19, 23, 28	Dense, managed, stockproof
5	E	290	2.9	1.9	Pasture	Wheat	12, 15, 19, 23, 29	Newly planted, more sparse, circa 10yrs old
6	WSW	405	2.6	2.2	Silage	Wheat	13, 20, 26, 27, 28	Steep-sided ditched, dense, managed, stockproof
7	SE	180	2.2	1.9	Pasture	Lane & pasture	13, 19, 20, 23	Dense, managed, stockproof,
8	NE	172	4.5	3.3	Wheat	Pasture	15, 20, 26, 27, 28	Ditched, interspersed with mature oaks, ash & lime

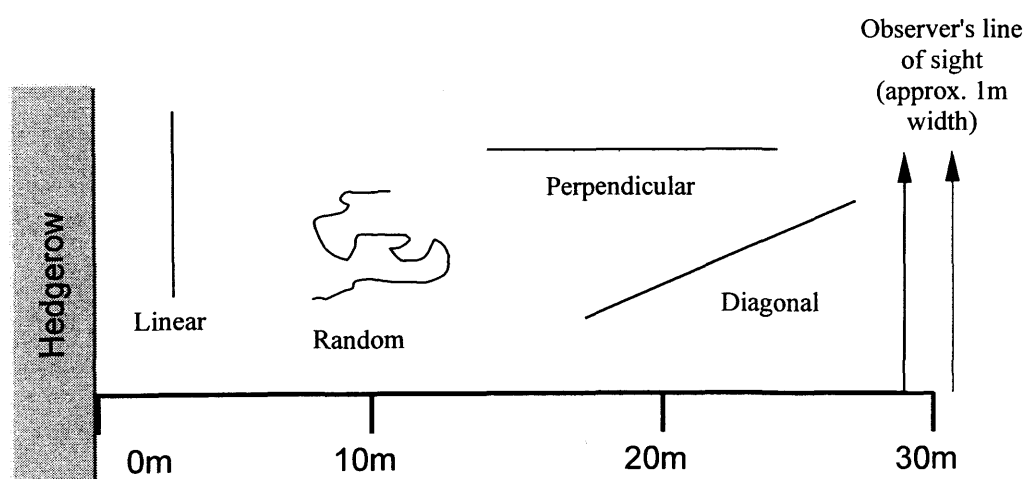


Figure 2.3. Schematic diagram illustrating the position of the observation points and examples of flight direction categories, in relation to the hedgerow.

Data analysis

The data were counts on a ratio scale and assigned to nominal categories. All observations were obtained randomly. For the bumblebees, a Kolmogorov-Smirnov test showed that the data were normally distributed and had similar variances (Levene's test). They were suitable for a univariate general linear model which provides an ANOVA for one dependent variable (*Bombus*) by one or more factors and/or variables. The interactions between factors (for example, distance*orientation) as well as the effects of individual factors could be investigated. The butterfly data were not suitable for parametric analysis (see page 45).

Results

A total of at least three bumblebee and 10 butterfly species were recorded over the entire study period (Table 2.2). Bumblebee species' abundance (1029) was greater than that of the butterflies (153). Due to the flight speed and distance away from individuals, many bumblebees could not be identified to species. *M. jurtina* and *Pieris* spp. were the most abundant butterflies. Linear flight was observed more than any other flight direction for all pollinators (540) and constituted 43.5% of the total observations (Table 2.2).

Table 2.2 Total species abundance and flight directions for all hedgerows. (UID = Unidentified)

All hedgerows	Linear	Random	Perpendicular	Diagonal	Total
<i>Bombus</i> sp.	309	150	186	170	815
<i>B. terrestris</i>	144	13	18	11	186
<i>B. lapidarius</i>	8	3	3	2	16
<i>B. pascuorum</i>	7	2	3	0	12
<i>Pieris</i> sp.	10	2	5	0	17
<i>P. brassicae</i>	18	1	10	1	30
<i>P. rapae</i>	5	2	1	7	15
<i>Aglais urticae</i>	2	3	1	0	6
<i>Inachis io</i>	1	0	1	2	4
<i>Pararge aegeria</i>	4	1	0	0	5
<i>Vanessa atalanta</i>	2	2	2	0	6
<i>Ochlodes/Thymelicus</i> spp.	3	2	4	6	15
<i>Aphantopus hyperantus</i>	9	1	1	1	12
<i>Maniola jurtina</i>	10	2	14	8	34
UID brown butterfly	0	1	7	1	9
<i>A. mellifera</i>	4	4	4	35	47
UID bee	4	2	4	2	12
Total	540	191	264	246	1241

Figure 2.4a displays the mean number of flight directions of bumblebees observed at each observation point for all eight hedgerows. Linear flight was far more likely to be observed adjacent to the hedgerow than at increasing distances away from the hedgerow. At 0m, there were just under 50 mean linear flight observations whereas at 10, 20 and 30m away from the hedgerow, linear flight observations ranged between 1.4 - 6.0. Fewer individuals were observed further out into the field than at the hedgerow interface. Random, perpendicular or diagonal flight directions were more likely to be observed as the distance away from the hedgerow increased and ranged between 1.0 - 3.3 mean flights at 0m to 5.6 - 8.8 across the other observation points (Figure 2.4a).

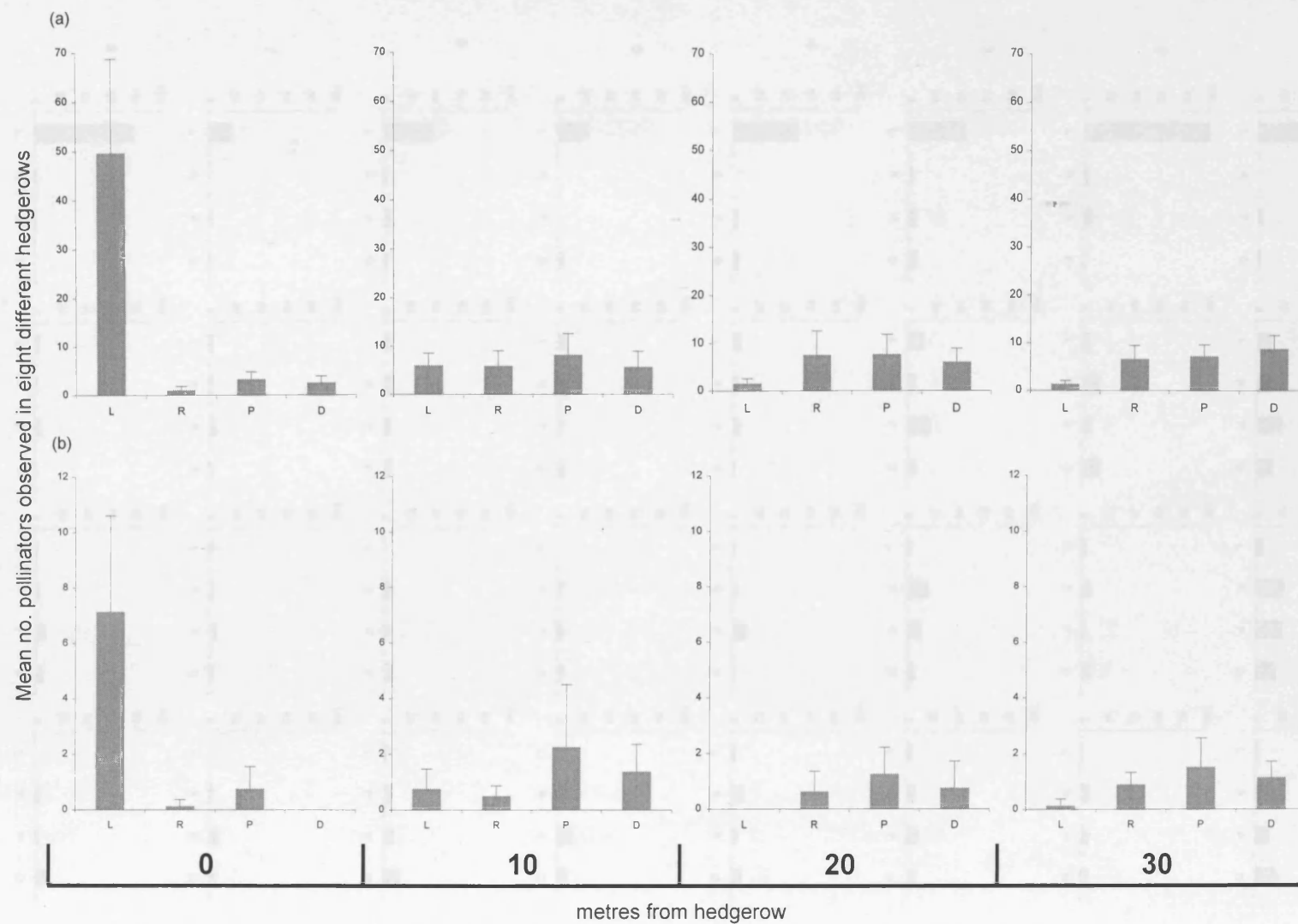


Figure 2.4 Mean no. of *Bombus* spp., (a) and butterfly spp., (b) observed in flight direction categories: L = Linear, R = Random, P = Perpendicular, D = Diagonal in relation to eight different hedgerows. Error bars indicate 95% confidence intervals. (a) and (b) are plotted on different scales because of the lower butterfly numbers.

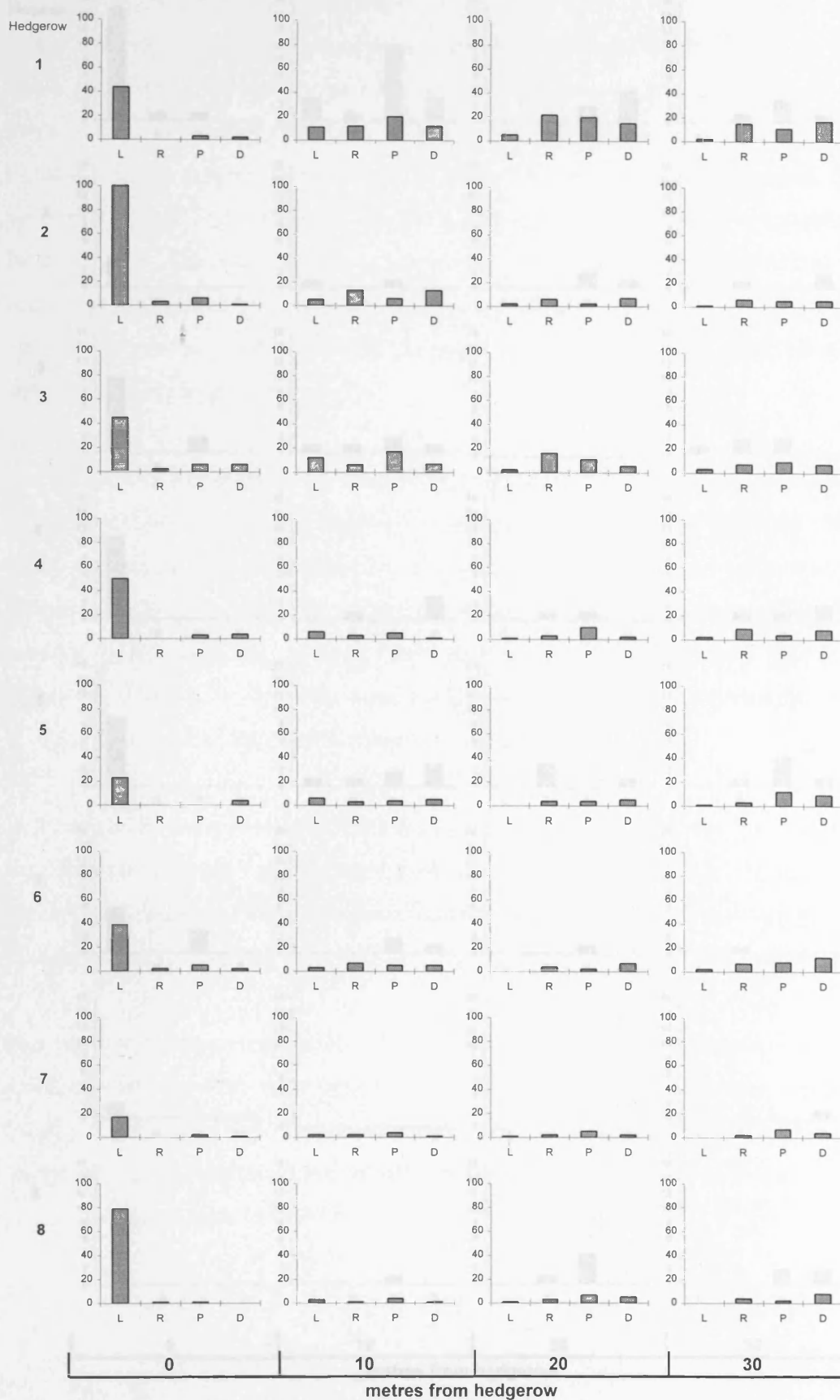


Figure 2.5 Total numbers of *Bombus* spp. observed in flight direction categories: L = Linear, R = Random, P = Perpendicular, D = Diagonal in relation to eight different hedgerows.

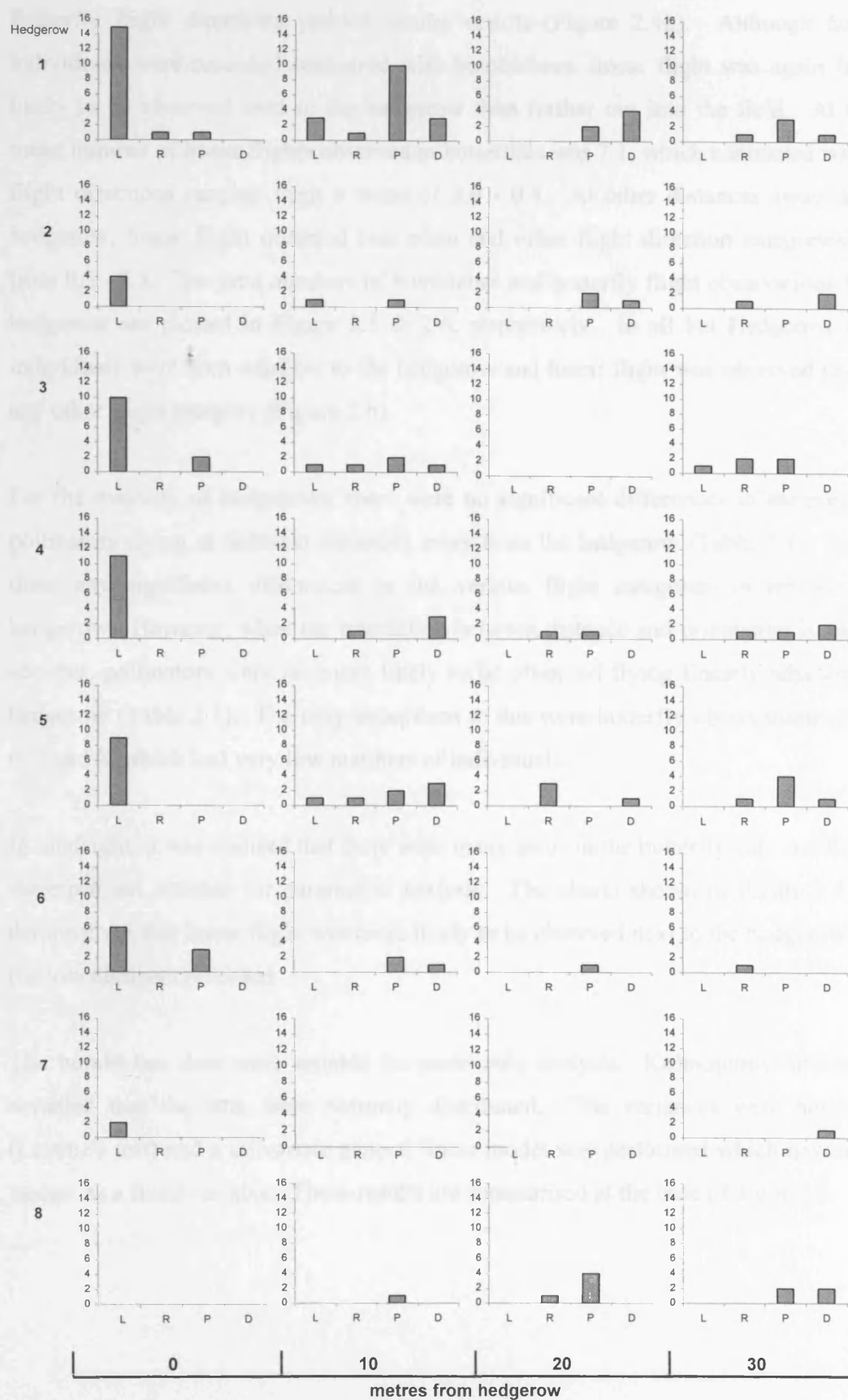


Figure 2.6 Total numbers of butterfly spp. observed in flight direction categories: L = Linear, R = Random, P = Perpendicular, D = Diagonal in relation to eight different hedgerows.

Butterfly flight directions yielded similar results (Figure 2.4b). Although far fewer individuals were recorded compared with bumblebees, linear flight was again far more likely to be observed next to the hedgerow than further out into the field. At 0m, the mean number of linear flights observed in butterflies was 7.1, which contrasted with other flight directions ranging from a mean of 0.0 - 0.8. At other distances away from the hedgerow, linear flight occurred less often and other flight direction categories ranged from 0.5 - 2.3. The total numbers of bumblebee and butterfly flight observations for each hedgerow are plotted in Figure 2.5 & 2.6, respectively. In all but Hedgerow 8, more individuals were seen adjacent to the hedgerow and linear flight was observed more than any other flight category (Figure 2.6).

For the majority of hedgerows, there were no significant differences in the numbers of pollinators flying at different distances away from the hedgerow (Table 2.3). Nor were there any significant differences in the various flight categories in relation to the hedgerow. However, when the interaction between distance and orientation is taken into account, pollinators were far more likely to be observed flying linearly adjacent to the hedgerow (Table 2.3). The only exceptions to this were butterfly observations at hedges 6, 7 and 8, which had very low numbers of individuals.

In hindsight, it was realised that there were many zeros in the butterfly data and they were therefore not suitable for parametric analysis. The charts shown in Figure 2.4 clearly demonstrate that linear flight was more likely to be observed next to the hedgerow despite the low numbers recorded.

The bumblebee data were suitable for parametric analysis. Kolmogorov-Smirnov tests revealed that the data were normally distributed. The variances were homogenous (Levene's test) and a univariate general linear model was performed which now included 'hedge' as a fixed variable. These results are summarised at the base of Table 2.3.

Table 2.3 Pollinator flight directions at varying distances from the hedgerow: general factorial ANOVA.
 $P < 0.01$ (++), $P < 0.05$ (+)

		No.	Distance	Orientation	Dis*Orie
		Inds	df=3 Sig	df=3 Sig	df=9 Sig
Hedge 1	Bombus	211	ns	ns	++
	Butterfly	45	ns	ns	++
Hedge 2	Bombus	181	+	+	++
	Butterfly	12	ns	ns	+
Hedge 3	Bombus	161	ns	ns	+
	Butterfly	22	++	++	++
Hedge 4	Bombus	111	ns	ns	++
	Butterfly	21	ns	ns	+
Hedge 5	Bombus	83	ns	ns	++
	Butterfly	26	ns	ns	++
Hedge 6	Bombus	110	ns	ns	++
	Butterfly	14	ns	ns	ns
Hedge 7	Bombus	52	ns	+	++
	Butterfly	3	ns	ns	ns
Hedge 8	Bombus	120	+	+	++
	Butterfly	10	ns	+	ns

Univariate general linear model: All hedges, Bombus only.

		No.	Distance	Orientation	Dis*Orie	Hedge	Hedge*	Hedge*	Hedge*
		Inds	df=3	df=3	df=9	df=7	Dis df=21	Orie df=21	Dis*Orie df=63
All hedges	Bombus	1029	++	++	++	++	ns	ns	ns

This test revealed that there were significant differences in the numbers of bumblebees flying at different distances and orientations away from the hedgerow. There were significant differences in the numbers of pollinators flying at different distances between hedges. Yet 'hedge' had no effect when the interaction between distance and orientation was taken into account. The type of hedge, therefore, did not appear to influence pollinator flight behaviour.

Discussion

Bumblebee and butterfly abundance was far greater next to the hedgerow than at increasing distances away from it (Figures 2.4a & b). Furthermore, these insects were more likely to exhibit linear flight when observed adjacent to the hedgerow (Figures 2.4a & b, Table 2.3) and this same pattern was observed in all eight hedges. Many studies have established that invertebrate abundance and species diversity are greater along hedgerows and field margins, with the higher structural and floral diversity offering suitable resources, often cited as the main explanatory factor (Forman & Baudry, 1984; Thomas & Marshall, 1999). Meek *et al.* (2002) compared invertebrate abundance in five different types of field margin. Most nectar and pollen feeding insects were found in greater abundance in the grass and wildflower treatments. Yet early-flying butterflies were observed to fly along the entire lengths of margins containing annual weeds, irrespective of treatment type. However, the results from this study contribute another dimension of insect utilisation of such landscape features in that not only was the abundance of pollinators collected, but also their non-foraging flight behaviour.

The propensity for bumblebees and butterflies to fly linearly next to the hedgerow suggested that these landscape features might be utilised as navigational aids rather than solely for forage. Osborne *et al.* (1999) found that 'in transit' flights of individual *B. terrestris*, tracked using harmonic radar, were shown to fly in relatively straight lines on both outward and return journeys at ground speeds ranging from 3.0 - 15.7ms⁻¹. Bees exhibited route constancy in both flight distance and direction from the nest to the destination forage patches over many trips and appeared to compensate for cross winds (Riley *et al.*, 1999). Most of the study area of Osborne *et al.* (1999) was in open farmland and did not contain hedges. Bee flights radiated from the nest and crossed field boundaries. It is unknown how prominent the field boundaries were but they did not appear to influence flight direction. Of the few hedges on the periphery of the study site, there was no evidence of bee flight following the length of hedgerows. However, radar visibility is reduced by buildings, trees and hedges. Tall crops, hedges and topography prevented the radar from tracking bees, most of which flew close to the ground circa 1 - 3m in height. Dover (1990) commented that even strong flying butterflies such as *Pieris* spp. were rarely observed to fly across open fields but were far more likely to follow hedgerows and field margins.

Pollinators such as bumblebees and butterflies might follow the length of hedgerows as the physical structure could provide shelter and afford protection from predators. Bumblebees have, however, few natural predators in the UK (Prŷs-Jones & Corbet, 1991) although this has been disputed by Dukas & Morse (2003). Although butterflies are frequently preyed upon by birds and spiders, predation may be higher along the hedgerow (Corke, 1997). Sparrowhawks often hunt along hedgerows and sometimes prey upon bumblebees. An insect is more conspicuous flying over open fields but the hedgerow and its associated faunal community arguably harbours more predators than would be found out in the open (Andrews, 1993; Hinsley & Bellamy, 2000; Fuller *et al.*, 2001).

The physical structure of the hedgerow can ameliorate the effects of strong winds and significant modifications to the microclimate have been recorded on the leeward side of hedgerows. Increased densities of three satyrid butterflies were recorded at hedgerow intersections (nodes) where the increased shelter, along with floral resources, was a strong explanatory factor (Dover, 1996). Such shelter effects are more pronounced within green lanes where a track is bordered by hedgerows on either side. Dover *et al.* (2000) and Dover & Sparks (2001) have recently investigated the importance of green lanes to insects. Butterfly abundance and species richness were greater within green lanes when compared with other types of hedge. Lower wind speeds, lack of disturbance and an abundance of nectar sources found in the larger surface area of uncropped land were identified as the explanatory factors. Croxton *et al.* (2002) found that bumblebee abundance was higher within the green lanes than on the field margins which was directly related to abundance of pollen and nectar resources. However, it is well established that bumblebees are able to fly during periods of inclement weather and to compensate for wind drift (Osborne *et al.*, 1999; Riley *et al.*, 1999). Migrating butterflies also display the same ability to prevent being blown off course (Wehner *et al.*, 1996). With both taxa, evidence of their navigational abilities appears to focus on their capability of orienting their position within the landscape in relation to landmarks.

The above studies have indicated that it is the conditions and resources within the linear feature which facilitate species' use and movement along them. However, little work has been conducted as to whether this is the only factor which influences insect distribution along them. What if the linear feature is devoid of resources and offers no rewards or

incentives to the animal, but flight direction is still affected? This question is addressed in Chapter 3; bumblebee flight behaviour was indeed affected by the presence of an artificial linear feature.

Dover & Fry (2001) demonstrated that artificial linear structures could modify the flight behaviour of some species of butterfly in Norway. The authors constructed artificial features which imitated two different characteristics of a hedge: the visual signal presented by forage plants along the hedgerow and the physical structure of the hedgerow (represented by a narrow red and white builders' warning tape, and by green horticultural windbreak, respectively). Individual species reacted in different ways. The high brown fritillary (*Fabriciana adippe*) and niobe fritillary (*F. niobe*) demonstrated significantly greater movement along the visual link than the control; they also flew greater distances along the linear feature than in the control. Conversely, the tape acted as a barrier to the scarce copper (*Heodes virgaureae*). The windbreak feature acted as both a 'corridor' and barrier to all three study species depending on the individual's approach. Flight movement along the windbreak was greater than for the control for all species, particularly for *H. virgaureae*. No butterflies were observed to move from one patch to another but it was concluded that this was probably due to the simplicity of the model linear features. However, there was evidence that the structures could elicit an oriented movement along the structure. The complexity of the heterogeneous constitution of a real hedgerow may be an important factor in maintaining the flight direction along its length to reach another patch. The different responses of the observed species to the linear features could be attributed to the different mate-finding strategies and varying flight heights employed by these species. Alternatively, the red and white colours may have been interpreted as flower patches, which may have been inspected and rejected.

In this study, although linear flight of insects was more likely to be observed next to the hedgerow, it is possible that no other flight category could have occurred there because of the physical presence of the hedgerow. Insect flight may have been constrained by the hedgerow structure preventing more sinuous or sideways movements. However, the hedgerows varied in their structure and height (Table 2.1) and it would have been possible for pollinators to either go through (in some cases) or over the hedges, though none were observed in this study. Although direct measurements of flight heights were not recorded, the vast majority of bumblebees and butterflies flew close to the ground, between

approximately 1 - 2m, which accord with the flight levels of bumblebees recorded by Osborne *et al.* (1999). Whether linear flight was an effect of the hedgerow restricting more meandering flight directions, or whether linear flight was adopted as the insect encountered the hedgerow as a more energy efficient way to follow it, is unclear from these observations, yet the outcome is the same. The experiments carried out in Chapter 3 suggest that the latter explanation appears more likely. Bumblebee flight directions were modified in response to three dimensional (1.2m high) and two dimensional artificial linear features (1.5m wide) which linked two patches of flowers. Bumblebees flew straight along these linear features to reach the connected patches of flowers even though the experimental array was within an open field.

In this investigation, it is also possible that specific flight directions may have been wrongly categorised in the open field away from the hedgerow. Bees may modify their flight pattern when flying along the hedge by flying more directly with few twists and turns but this may become more sinuous without the presence of the hedgerow (Figure 2.7).

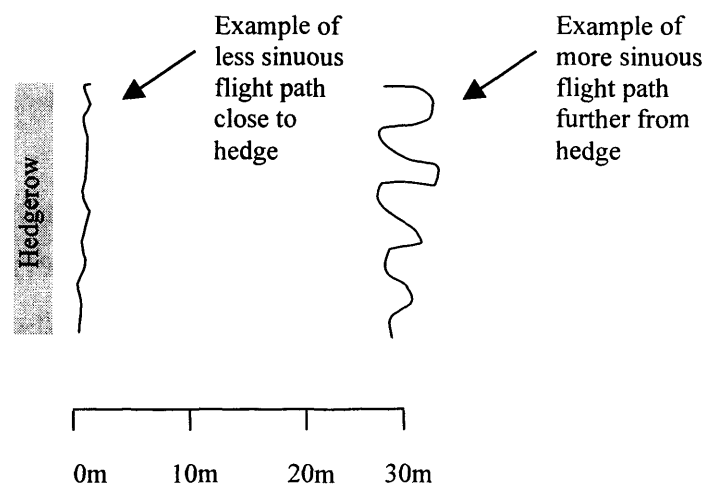


Figure 2.7 Variation in linear flight. Flight behaviour might be more sinuous at 30m without the immediate presence of the hedgerow.

The overall flight direction is linear; yet when observed over a relatively short period of time with the observer's line of vision approximately 0.5m either side of each marked point, it appears to be non-linear since it occurs on a larger scale. However, as will be seen in Chapter 3, using artificial linear features provides substantive evidence that the linear flight patterns observed in this investigation were not artefacts of the physical presence of the hedgerow.

The ease with which bumblebees and butterflies are observed in the field varies greatly between the two groups. The darker coloured and often smaller sized bumblebees, coupled with their relatively fast flight speeds, make them less visible than the slower moving, sometimes more brightly coloured butterflies, which have greater contrast within the field. It is acknowledged that bumblebees may have been less conspicuous and may therefore have been underrepresented in the results.

If hedgerows were being used as landmarks, then it could be argued that the insects do not necessarily have to fly directly along them. Linear flight might have been equally likely to occur at 10m as 0m as long as the landmark was in sight. Little information is known about the perceptual range and 360° field of vision which can be analysed simultaneously by these pollinators. Apidae do have a relatively wide visual field but the resolution is poor (Chittka, pers. comm). Distance estimation in honeybees is obtained by using retinal image flow, where the landscape structure and landmarks are assimilated as the insects fly (Esch *et al.*, 2001). This ability to estimate distance was disrupted when the bees' flight path was lined with chequered patterns, increasing the image flow. Honeybees then greatly overestimated the distance from the nest to the feeder (Esch *et al.*, 2001).

The relationship between the spatial vision of insects and spatial flower parameters were reviewed by Dafni *et al.* (1997) to examine what effects these had on foraging success. Lehrer *et al.* (1985) video-filmed honeybees in free flight and showed that they would follow the contours contained within presented black and white patterns. This 'scanning' behaviour was found to be innate and not learned.

These small-scale investigations have demonstrated that honeybees are capable of relatively sophisticated visual cue assimilation and processing. The results from this study and subsequent studies suggest that this same pattern of landmark recognition is occurring in bumblebees at the larger, landscape scale with hedgerows being used as visual markers within the habitat matrix. Landscape-scale navigation with reference to landmarks has been exhibited in migrating butterflies (Srygley, 2001), honeybees (Chittka & Geiger, 1995; Chittka *et al.*, 1995a; 1995b; Wehner *et al.*, 1996; Riley *et al.*, 1999) and bumblebees (Goulson & Stout, 2001; Osborne, pers. comm). Evidence of landmark

mediated navigation within the landscape suggests that bees are responding in the same way to striped or contrasting patterns at a larger scale as they do at a small scale.

There is increasing evidence of evolutionary responses to increased landscape fragmentation, in the form of morphological flight adaptations by insects. Heavier thorax weights have been recorded in the butterflies *Hesperia comma* and *Plebejus argus* whose populations were located in heavily fragmented habitats, compared with those in more contiguous landscapes. Since the flight muscles are contained within the thorax, it appears that there is a strong selection pressure for greater colonisation abilities on butterfly populations in more isolated patches (Van Dyck & Matthysen, 1999). Similarly, Taylor & Merriam (1995) reported that damselflies (*C. maculata*) had larger wings and heavier thoraxes when sampled in pasture landscapes, where foraging and reproduction sites were greater distances apart, than their usual forested habitat. Despite this evidence it is difficult to establish that fragmentation is the sole cause of such changing morphologies. The observed phenotypes are possibly responding to more subtle variations within the community. A changing landscape might affect the population dynamics of the target organism and also those with which it interacts. Fragmentation might influence predator-prey ratios and mate-finding strategies which could also explain the observed evolutionary adaptations (Van Dyck & Matthysen, 1999).

Conclusions

Bumblebees and butterflies were significantly more likely to fly linearly adjacent to the hedgerow than further out in the field. Abundance of these pollinators was also greater at the hedgerow interface than at increasing distances away from it. The presence of the hedgerow appeared to influence the flight behaviour of non-foraging pollinators and may represent a visual cue with which these insects might orient directed movements through the landscape. As hedgerows are one of the most dominant linear features within lowland Britain, their physical structure could have a significant influence on pollinator movement at large scales. This is particularly pertinent in view of recent evidence indicating that bumblebees do not necessarily forage on patches close to their nest (Osborne *et al.*, 1999; Dramstad *et al.*, 2003).

The influence of linear features on insect flight direction has implications for the conservation of both plants and insects. Species movement across the landscape is a critical component of a healthy ecosystem (Saunders & Ingram, 1987; Fahrig & Paloheimo, 1988b). Movement is required ultimately for gene flow, for some species to locate suitable resources, mates, nests, for pollination, seed-set and seed dispersal (Waser *et al.*, 1996 and Kwak *et al.*, 1998). Linear features may ameliorate some of the deleterious effects on isolated populations. Plants located within highly connected patches may receive the advantage of more pollinator visits than plants in poorly connected patches (Chapter 4).

The results from these observations suggested that linear landscape features did appear to influence pollinator flight directions in the field. The results also generated many questions such as: does the linear feature represent a visual cue, which some species might innately follow and might a linear feature be utilised as a navigational aid? These questions highlight the need to test explicit differences in the functional roles of linear features, which is crucial to the understanding of the propensity of some species to move along linear features and, ultimately, facilitate movement across the landscape. Further investigations were designed to elucidate the precise nature of this influence. The next chapter describes medium-scale landscape manipulations using artificial landmarks to assess the effect of visual cues on pollinator flight directionality.

Summary

Little is known of the effects of landscape structure on insect movement through the matrix of agricultural land. Linear landscape features such as hedgerows may provide visual cues, which influence insect flight direction. In this study, observations of the flight directions of non-foraging pollinators in relation to eight different hedgerows were investigated. Thirty metre long transects were marked out, perpendicular to the axis of each hedgerow. The flight directions of non-foraging pollinators were categorised as linear, irregular (random), perpendicular or diagonal, in relation to the orientation of the hedgerow at each of the observation points (0m, 10m, 20m and 30m). The presence of a hedgerow did affect pollinator flight directionality of non-foraging insects. Linear flight patterns were far more likely to occur next to the hedgerow than they were further out into the open field. It is postulated that linear features may prove important landmarks for insect orientation and navigation across the landscape.

Chapter 3: Artificial linear features and pollinator behaviour

Introduction

The importance of linear landscape features such as hedgerows to animal and plant life within the lowland arable landscape has long been recognised (Forman & Baudry, 1984; Clements & Tofts, 1992a; Burel, 1996). Not only do they support populations, providing valuable resources in a comparatively resource poor area, but they can function as an important landscape component in helping to ameliorate the effects of habitat fragmentation, connecting otherwise isolated patches and aiding dispersal (Baudry & Merriam, 1988; Burel, 1989; Merriam, 1991).

However, little information exists on what effect, if any, the physical structure of a linear feature has on animal movement or behaviour. Animal movement along hedgerows has previously been explained as the hedgerow representing an extension of an organism's habitat (Rosenberg *et al.*, 1997). The architecture of the linear feature has rarely been the subject of investigation when ascertaining the extent to which the feature facilitates movement.

Dover & Fry (2001) experimentally simulated some of the visual and physical components of a hedge by using artificial materials. They reported that butterfly behaviour was strongly affected by such artificial constructions and this was discussed in detail in Chapter 2. Artificial linear features are simplified structures, providing a basic representation of particular hedge characteristics. They can be used to test animal responses to two- and three-dimensional structures, are relatively inexpensive and are easy to deploy.

Small-scale artificial structures, patterns and models have been employed over several decades to investigate and elicit varying responses in insect visual systems (Srinivasan *et al.*, 1999). Insect perception of the spatial arrangement of individual flower structures has been shown to affect foraging success (Dafni *et al.*, 1997) and the detection of motion (optomotor response) has proved crucial for insect orientation and navigation within the environment (Srinivasan *et al.*, 1999).

True navigation is a sophisticated mechanism where the insect is able to orient itself to a goal site despite displacement by drift. By utilising innate vector programmes or navigational maps, the insect must possess an ability to know its current position and orient toward the target destination within the landscape. Large-scale navigation has been greatly studied in birds (Alerstam, 1990; Berthold, 1993) but very little in insects (Srygley, 2001).

The importance of landmarks for navigation in migrating butterfly species was studied by Srygley (2001). Following their natural migration over the Caribbean Sea, three families of butterfly (Nymphalidae, Hesperidae and Pieridae) were able to compensate for crosswind drift using the sun or magnetic compass and landmarks. Butterflies were significantly less likely to compensate for crosswind drift in the absence of landmarks or clouds.

Social hymenopterans appear to use two different navigation mechanisms: egocentric and geocentric (Wehner *et al.*, 1996). The egocentric method appears to be most important and employs path integration, by which the individual takes into account all of its complex twists and turns, and the distance travelled on the outward journey but can then travel directly home even in unfamiliar territory. This has been studied intensively in the desert ant *Cataglyphis* spp. (Müller & Wehner, 1988). The geocentric method complements the first and is based on a map system. The individual knows its location in relation to the environment it is in by the use of landmarks (Wehner *et al.*, 1996).

Honeybees (*Apis mellifera*) exhibit path integration in their dances by giving the precise compass direction of the target, even though they might have flown many twists and turns to locate it in the first instance. Chittka *et al.* (1995a) reported that the path integration strategy was continually used during flight when the bees were in new territory. However, when in familiar territory, the compass-guided flight vector instructions took precedence.

Riley *et al.* (1999) suggested that bumblebees, like honeybees and several other Hymenopteran species, are likely to use the sun's angle in relation to their nest to navigate

around the landscape. During cloudy periods, familiar landmarks are used instead. They are able to compensate for wind drift by using optical flow, i.e. flying at the angle at which objects on the ground come into the field of vision. They are unable to take a large-scale aerial view and must obtain landscape information step by step (Wehner *et al.*, 1996). Following artificial displacement, *B. terrestris* demonstrated remarkable homing abilities (Goulson & Stout, 2001). Of the 25% confirmed returns to the nest, homing declined as the displacement distances increased. The majority of bees returned from distances between 1 - 5km, but took several days to do so. The mechanism by which bees navigate through the landscape is not truly understood although evidence is growing that landmarks are used as navigational aids (Chittka & Geiger, 1995; Chittka *et al.*, 1995a & 1995b).

Having established that pollinators were more likely to fly along hedgerows rather than in adjacent open land where no such linear features exist (Chapter 2), the question arose of whether the same effect would occur by creating a medium-scale experimental array using an artificial linear feature. Would flower patches located at the ends of artificial features be visited more frequently than similar flower patches with no connections? Could the linear flight patterns observed in the field (Chapter 2) be replicated using an artificial linear feature? Is the visual signal of the hedgerow enough to generate this flight behaviour?

The technique employed in this investigation was based in part on Dover & Fry (2001). The experiment's aim was to ascertain whether a flower patch connected via an artificial linear feature to another flower patch would receive more visits, using the linear feature, than a similar patch with no connections. The artificial features were devoid of resources. Would the structure alone elicit any change in flight behaviour?

Methods

All observations and experiments were conducted at the same farm location as described in the 'study site' section in Chapter 2.

Plant selection

Phacelia tanacetifolia (Hydrophyllaceae) was chosen for this investigation as numerous studies have demonstrated that it is highly attractive to pollinators, particularly bumblebees (*Bombus* spp.), providing a rich nectar and pollen source. It is also easy to grow, flowers in the first year and has a long flowering period of about eight weeks (Williams & Christian, 1991; Stout *et al.*, 1998; Carreck & Williams, 1997 & 2002; Carreck *et al.*, 1999).

P. tanacetifolia (Figure 3.1) is an annual herb, native to California, reaching 20 - 100cm in height. Flower colour ranges from light blue/purple to pink to white, but all the plants grown in this study, had purple flowers. Each plant can produce several inflorescences. The cymes are tightly curled which slowly unwind to reveal simple bisexual flowers which open in acropetal sequence as the stem matures. The stamens are twice the length of the petals, and radiate outward (Mabberley, 1987; Williams, 1997).



Figure 3.1 Flowering cymes of *P. tanacetifolia*. Reproduced with kind permission from Ernst Horak, Botanik im Bild.

The plant has been incorporated into wild flower strips sown in non-cropped areas such as set-aside and field margins to enhance arable farmland by attracting a greater diversity of insects (Carreck & Williams, 1997 & 2002; Carreck *et al.*, 1999; Ullrich & Edwards, 1999; Denys & Tschardtke, 2002). *P. tanacetifolia* has also been used as part of pest management strategies where the nectar and pollen rich flowers are used to attract hoverflies (Syrphidae) in an attempt to augment biological control of aphids (Lövei *et al.*, 1992; Harwood *et al.*, 1994; White *et al.*, 1995; Hickman & Wratten, 1996; Frank, 1999; Colley & Luna, 2000). *P. tanacetifolia* is also grown as a nitrogen catch crop or green manure in Europe and the USA (Wyland *et al.*, 1996; Rüegg *et al.*, 1998).

Plant cultivation

Seeds were obtained from Chiltern Seeds, Ulverston, Cumbria. Twenty 25cm diameter plastic plant pots were filled with multi-purpose compost, mixed with two teaspoons of 'Aquafeed' water storing granules. Each pot was seeded with *P. tanacetifolia* on 19 May 2000 and 17 May 2001, respectively, and later thinned to five plants. The first flowers appeared on 7 July 2000 and 10 July 2001, respectively, and when the flower density reached approximately five flowering cymes per pot, the pots were transferred to the experimental array. The mature plants reached a height of approximately 40cm and the flowers and foliage covered an area approximately 1m², per patch. Sequential sowings were made every three weeks to ensure a constant supply of flowers for later experiments and to replenish senescing patches to maintain a consistent flowering density between patches. The plants were frequently dead-headed to prolong the flowering period.

Experimental design

Three patches of flowering *P. tanacetifolia* (A, B & C) were placed 30m apart, equidistantly in an open, 7ha field which had recently been cut for silage (Figures 3.2 & 3.3a). No other floral resources were within at least 70m of the study area. Each patch consisted of six pots arranged with one central pot surrounded by the other five. Flower density of each patch was monitored throughout the investigation by counting the number of flowering cymes per patch each day. Each patch contained a mean of approximately 40 flowering stems (Table 3.3).

Artificial linear features

In all experiments, an artificial linear feature linked patches A and B (Figure 3.2). Then, excepting the first experiment (tapes) and following an observation period, the artificial feature was repositioned between patches B and C (for the three-dimensional (3D) experiment) and patches A and C (for the two-dimensional (2D) experiment) and the observations repeated for another eight and nine days, respectively (Table 3.1). The suffixes 'before' and 'after' refer to whether the experiment is being described before or after the repositioning of the linear feature. The experiment was run three times within this location, with a different linear feature used on each occasion, on non-consecutive dates.

Table 3.1 Observation dates and number of marked individuals reobserved visiting each of the experiments.

Linear feature	No. individuals marked & reobserved per patch (% reobservation rate)			Marking dates	Observation dates	No. observation days
	A	B	C			
Tapes	-	-	-	-	18-19, 21-24 July 2000	6
2D before	13 (72.2)	10 (90.9)	10 (90.9)	31 July, 1, 6-7 Aug 2001	1-3, 6-8, 10-14 Aug 2001	11
2D after †	14 (70)	12 (92.3)	12 (92.3)	31 July, 1, 6-7 & 16 Aug 2001 ‡	15-18, 20-24 Aug 2001	9
3D before	11 (64.7)	9 (52.9)	6 (35.3)	2, 4, 7-8, 12, 15 & 19 Aug 2000	25-28 July, 1, 3-12 & 14 Aug 2000	16
3D after †	5 (29.4)	4 (23.5)	6 (35.3)	2, 4, 7-8, 12, 15 & 19 Aug 2000 ‡	14-17, 19-22 Aug 2000	8
Landscape	17 (73.9)	17 (89.5)	17 (77.3)	13-16, 19-22 July 2001	17-27 & 30 July 2001	12

† Includes those individuals marked from previous marking dates before the connection position was changed.

‡ Shows the marking dates of only those individuals reobserved after the connection position was changed.

The following different types of linear feature were used: 1) five measuring tapes laid on the ground; 2) a two-dimensional structure consisting of black weed control fabric to a width of 1.5m; 3) a three-dimensional structure consisting of black weed control fabric held up with poles to a height of 1.2m.

These three different artificial features were chosen to assess whether they would have different effects on pollinator flight behaviour. All contrasted starkly with the surrounding grass for bee vision. The two-dimensional black sheet provided a broad and continuous strip of colour and contrasted with the predominantly white measuring tapes with a more broken appearance. Creating a three-dimensional structure from the weed control fabric was more akin to the physical structure of a hedge.

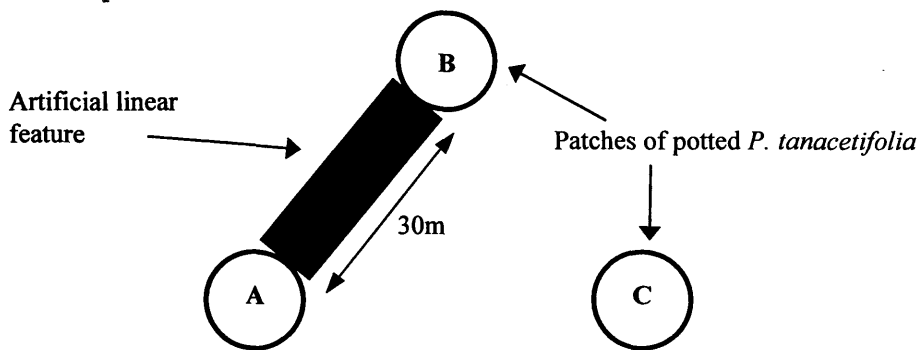


Figure 3.2 Schematic diagram illustrating the layout of the experimental array

The first linear feature was two-dimensional and consisted of five extended measuring tapes. Each tape was 30m x 2cm with black numbering on a white background. They were placed directly on the ground, parallel with each other with an approximate 10cm gap between tapes. The total width of the tapes was 50cm and connected patches A and B.

The second linear feature was two-dimensional again, but this time, black weed control fabric was used as it contrasted starkly with the surrounding environment. Several sheets of fabric were laid flat on the ground and secured with tent pegs, reaching 30m in length to connect patches A and B (1 sheet: 5m x 1.5m).

The third linear feature was three-dimensional and was constructed using the same weed control fabric tied to upright wooden stakes (0.25m x 0.25m x 1.22m), forming a triangular cross section, the sheets were tied together to reach 30m long (Figures 3a-b).

Landscape-scale experiment

The following year the experiment was run within the landscape using an existing hedgerow as the connecting linear feature (Figure 3.3a). Twelve pots of *P. tanacetifolia* were arranged in a similar triangular pattern as described above but at a larger scale using an existing hedgerow as the connecting linear feature (Figure 3.4). Patches A and B were placed on either side of the hedgerow and the isolated patch (C) was placed away from each of them. The experiment was run in the same way as the previous one.

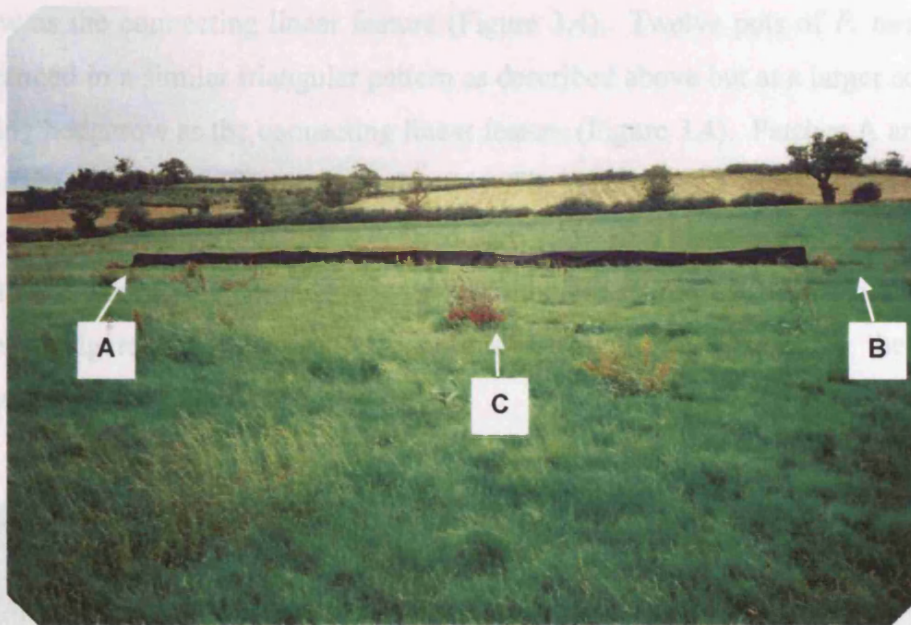


Figure 3.3a. Three-dimensional artificial linear feature showing the location of the connected patches (A & B) and the isolated patch (C).



Figure 3.3b. A view of patch B connected by the three-dimensional linear feature. This picture was taken at the end of the fieldwork season showing senescing flowers of *P. tanacetifolia*.

Landscape-scale experiment

The following year the experiment was run within the landscape using an existing hedgerow as the connecting linear feature (Figure 3.4). Twelve pots of *P. tanacetifolia* were arranged in a similar triangular pattern as described above but at a larger scale using an existing hedgerow as the connecting linear feature (Figure 3.4). Patches A and B were placed at either end of a 180m long hedgerow. The third patch, C, was placed in an area of non-cultivated land surrounding a disused barn and was a distance of 130m away from each of the patches A and B. This barn area was located in a wheat field and was isolated from any hedgerows. Observations of bees followed the format for the previous experiment.



Figure 3.4 Aerial photograph showing the location of the potted *P. tanacetifolia* patches A, B and C. Scale: 1:5,000. Photograph taken: May 1990, reproduced with permission from NRSC Ltd.

Bumblebee marking

Bees were marked to allow individuals to be recognised and to quantify re-visits, following a similar method described by Kwak (1987). Marking was carried out in all

experiments except with the measuring tapes (Table 3.1). A queen bee marking kit was obtained from EH Thorne (Beehives) Ltd., Wragby, Market Rasen, Lincs, LN8 5LA. Placing the clear perspex holding tube over the bee easily captured individual foragers. A foam-covered plunger was then placed underneath the bee whereupon it would fly upwards. The plunger was slowly pushed upwards until the insect was held, dorsal side uppermost, gently but firmly by the foam against the plastic mesh at the top of the holding tube. A small colour coded plastic disc with a unique number was then coated with a tiny amount of glue and placed onto the thorax of the bee taking care not to interfere with the area where the wings attached to the body. The insect was held in place for about 30 seconds whilst the glue dried. The plunger was then slowly pulled back and the bee released. They were then observed to ensure that they could fly normally. Such kits are widely used to mark bumblebees and, if correctly applied, cause no adverse effect to normal flight behaviour (Kwak, 1987).

For the 3D experiment, marking of individual bees did not commence until 2.8.00 and recording of these reobservations did not start until 3.8.00. There were therefore five days of observations of unmarked bees. However, marking of new bees continued throughout the duration of all the experiments, as necessary.

Observations

The abundance, tag number/species and flight direction of individual bumblebees arriving at and departing from each patch were recorded. Each patch was observed for one hour per day, the order of which was randomly assigned using MS Excel 97 (Microsoft Corp., 1997). The direction of all flights in relation to the array was sketched using arrows to indicate the course of patch arrivals and departures. For the connected patches, if an individual was observed to fly straight from one patch to the other, along the artificial feature, this was recorded as a direct flight. It was possible to observe this occurring with the naked eye. However, during busy periods, it was impossible to track all individual inter-patch movements. If the individual was last seen directly moving to the other connected patch and watched for at least two thirds of the length of the linear feature, it was recorded as a direct movement. All other individuals were recorded as 'unknown'. There were a few occasions when a bee would follow the linear feature for part of the way

and then change direction; these were categorised as 'some linear feature use'. The 'other' category was designated when a bee would arrive at or depart from the patch using any other direction. These observations were repeated after repositioning the artificial feature within the experimental array.

The number of foraging hoverflies at each patch was counted in a 'snapshot' at the end of each hourly patch observation. Due to the difficulty of following hoverfly movements, their flight directions were not recorded. Butterflies were not attracted to the flowers at all.

Identification

Bumblebees were identified to species level using Prŷs-Jones & Corbet (1991). Because of the difficulty of distinguishing certain species in the field, *B. terrestris* and *B. lucorum* are referred to as '*B. terrestris*'; *B. lapidarius* and *B. ruderarius* were combined and referred to as '*B. lapidarius*'.

Hoverflies were identified in the field to species or genus using Stubbs & Falk (2000). Prior to the experiment, numerous hoverflies were caught and preserved in alcohol and identified using a microscope.

Data analysis

Visitation rates

The number of bumblebees visiting each patch per day was totalled and then compared using a one-way ANOVA (Figures 3.5a, 3.6a, 3.7a, 3.8a, 3.9a, 3.10a, Table 3.2). A Kolmogorov-Smirnov test showed that the data had a normal distribution and an F_{\max} test showed that the variances were homogenous. In hindsight, the observations suffered from pseudoreplication (see page 83 for discussion).

Flight directions

The total number of inter-patch flight directions per experiment was compared using a G-test. If the artificial feature had no effect on the movement patterns of bees then there would be no differences between all three patches. The 3x4 G-test compared the observed frequencies of bumblebee movements with an expected null hypothesis. All observations should be random and independent of each other but suffered from non-independence (see page 83). Pie charts were generated to show the flight directions of individual bees as a proportion of the total number of flight observations per patch (Figures 3.5 – 3.10).

Mean percentage reobservations

During the experiments, it was suspected that individuals were more likely to be reobserved on the patch they were marked on, than on any other. The following hypothesis was formulated:

H_1 : For bees marked on a particular patch, there will be more reobservations of those bees on that patch than for any other patch.

H_0 : There will be no differences in the number of reobservations per patch.

For example, if patches A and B are connected, then bees marked on patch A will be far more likely to be reobserved visiting patch A, fewer numbers will be reobserved on patch B and far fewer numbers will be reobserved on patch C:

For bees marked on A, the proportion of reobservations will be:

$A > B \gg C$

For bees marked on B, the proportion of reobservations will be:

$B > A \gg C$

For bees marked on C, the proportion of reobservations will be:

$C \gg (A \approx B)$

To test this hypothesis, the percentage of reobservations at each patch was recorded for each sampling day. Their means were then compared using a one-way ANOVA (Figures

3.11 – 3.13). Although a Kolmogorov-Smirnov test showed the data to have a normal distribution, each sample unit was not independent as the same bees were being counted repeatedly (see page 83).

Prior to computing the one-way ANOVAs, an F_{\max} revealed that some of the experiments contained data with non-homogenous variances. The data were transformed as follows:

2D before, Patch C (Figure 3.11c). Arcsine transformed.

2D after, Patch A (Figure 3.11d). Log transformed.

3D before, Patch C, (Figure 3.12c). Log transformed.

All results were analysed using SPSS for Windows, Version 9.0 (SPSS Inc., 1998) except for the G-tests which were computed using an MS Excel 97 spreadsheet (Microsoft Corp., 1997).

Results

A total of four bumblebee and nine syrphid species were observed visiting *P. tanacetifolia*: *B. lapidarius*, *B. pascuorum*, *B. pratorum* and *B. terrestris* (for hoverflies, see Table 3.7). Butterflies were rarely attracted and the low numbers recorded did not permit any data analysis. These recorded species concur with Carreck & Williams (2002) with the exception of the honeybee, which was seen in abundance in their study, but was absent in this investigation. The pie charts (Figures 3.5a – 3.10a) were generated from the total number of individual flight observations, showing the proportions of different flight directions. However, since one visit includes an individual arriving at and departing from that patch (two flight observations), the actual *visits* to the patch are half of this total and are displayed next to the pie charts. For instance in Figure 3.5a, there were a total of 372 visits made to all three patches, but each individual arrived at and departed from those patches making a total of 744 observations. Total visits per day per patch were compared using a one-way ANOVA. Table 3.2 summarises these ANOVA results, along with the total mean visits and number of marked individuals across all the experiments.

Table 3.2 Total mean visits per patch and number of marked individuals for all the experiments.

Experi- mental array	No. individuals	Total mean visits			No. days (year)	One-way ANOVA	Significance
		A	B	C			
Tapes	-	20.5	19.7	21.8	6 (2000)	$F_{2,15} = 1.0, p=0.39$	ns
2D before	33	37.5	39.4	31.5	11 (2001)	$F_{2,30} = 3.5, p=0.04$	+
2D after	38	36.0	25.6	34.3	9 (2001)	$F_{2,24} = 1.0, p=0.37$	ns
3D before	>26†	22.2	23.4	17.8	16 (2000) †	$F_{2,45} = 1.7, p=0.19$	ns
3D before	26 ‡	21.5	21.4	10.7	11 (2000) ‡	$F_{2,30} = 9.5, p<0.001$	++
3D after	15	10.9	17.5	20.9	8 (2000)	$F_{2,21} = 14.0, p<0.001$	++
Landscape	51	35.6	36.7	25.0	12 (2001)	$F_{2,33} = 4.3, p=0.02$	+

† Includes data for both marked and unmarked bees. The number of individuals was unknown for the first five days, but four different species, containing both workers and males were observed during this period.

‡ Data for marked bees only.

Flower status between patches

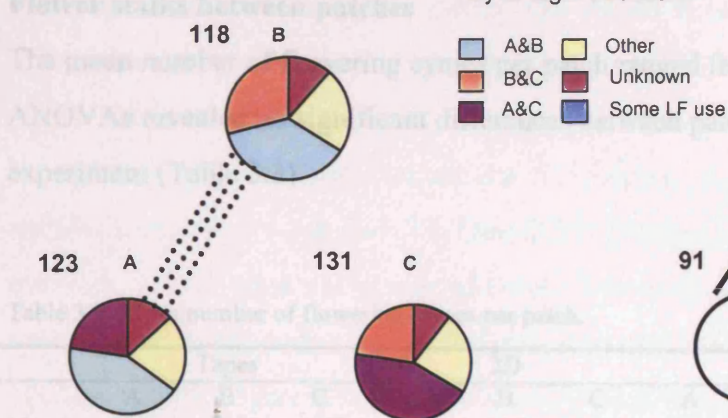


Figure 3.5a LF=Tapes. $F_{2,15} = 1.0$, $p=0.39$

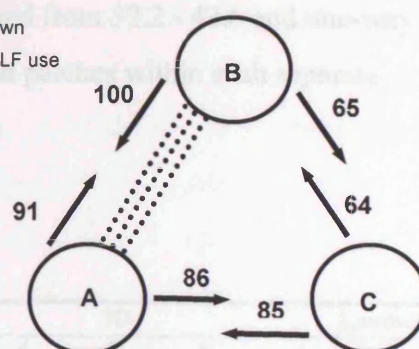


Figure 3.5b LF=Tapes. $G_6 = 11.9$, $p>0.05$

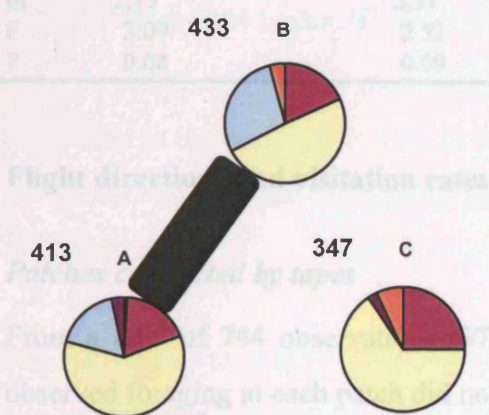


Figure 3.6a LF=2D. $F_{2,30} = 3.5$, $p=0.04$

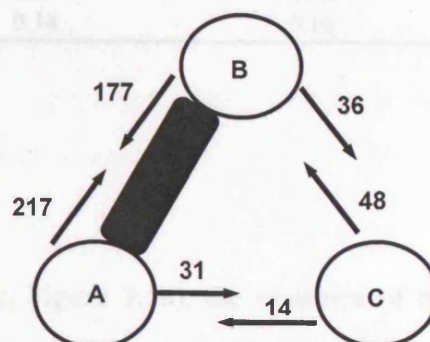


Figure 3.6b LF=2D. $G_6 = 116.5$, $p<<0.01$

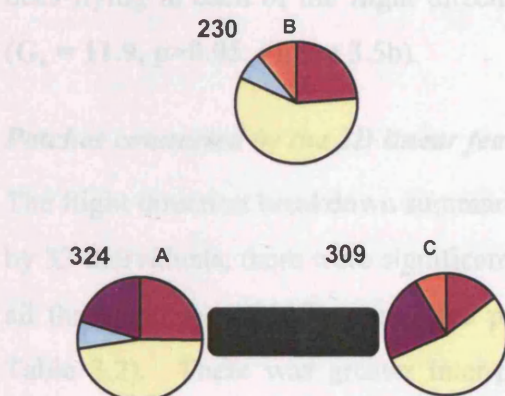


Figure 3.7a LF=2D after LF position changed.
 $F_{2,24} = 1.0$, $p=0.37$

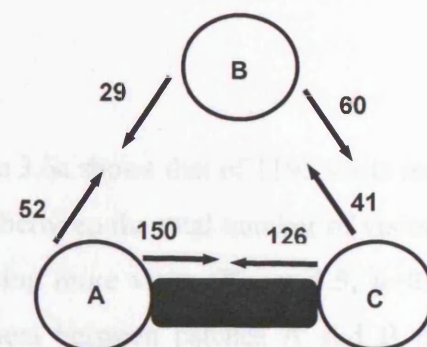


Figure 3.7b LF=2D after LF position changed.
 $G_6 = 106.2$, $p<<0.01$

Figures 3.5a-3.7a. One-way ANOVAs of total visits per patch (numbers in bold) and proportional flight direction categories per patch. LF=Linear Feature.

Figures 3.5b-3.7b. Individual inter-patch flight directions. G-tests.

Flower stalks between patches

The mean number of flowering cymes per patch ranged from 39.2 - 42.6 and one-way ANOVAs revealed no significant differences between patches within each separate experiment (Table 3.3).

Table 3.3 Mean number of flowering cymes per patch.

	Tapes			2D			3D			Landscape		
	A	B	C	A	B	C	A	B	C	A	B	C
Mean	39.2	40.2	40.7	41.0	40.8	39.7	42.2	40.0	40.6	40.6	39.8	42.6
SD	0.8	1.5	0.8	1.5	2.0	2.5	4.2	3.8	3.7	1.4	0.9	2.2
n	6			20			24			12		
df	2,15			2,57			2,69			2,33		
F	3.09			2.52			2.01			1.93		
P	0.08			0.09			0.14			0.16		

Flight directions and visitation rates

Patches connected by tapes

From a total of 744 observations (372 actual visits, Figure 3.5a), the numbers of bees observed foraging at each patch did not differ significantly (one-way ANOVA, $F_{2,15} = 1.0$, $p=0.39$, Table 3.1). Inter-patch movement accounted for approximately two thirds of all observations at each patch. There were no significant differences between the number of bees flying in each of the flight directions between connected and unconnected patches ($G_6 = 11.9$, $p>0.05$, Figure 3.5b).

Patches connected by the 2D linear feature

The flight direction breakdown summarised in Figure 3.6a shows that of 1193 visits made by 33 individuals, there were significant differences between the total number of visits on all three patches with the connected patches receiving more visits ($F_{2,30} = 3.5$, $p=0.04$, Table 3.2). There was greater inter-patch movement between patches A and B than between C. Sixty-six per cent of bees departing from and arriving at patch C came from 'other directions' with only 2% and 7% inter-patch movement with patches A and B, respectively. Figure 3.6b shows that there was far higher inter-patch movement between the connected patches, A and B, than there was for the isolated patch C ($G_6 = 116.5$, $p<<0.01$).

When the position of the linear feature was altered to connect patches A and C, (Figure 3.7b) inter-patch movement was significantly greater between the newly linked patches ($G_6 = 106.2$, $p < 0.01$). Figure 3.7a shows that of a total of 863 visits made by 38 individuals, the connected patches did not receive significantly more visits than the isolated patch ($F_{2,24} = 1.0$, $p = 0.37$, Table 3.2). The proportion of individuals flying in the direction of the connection was relatively low at patches A and C (20% and 23%, respectively), compared to the other flight categories but was still highly significant ($G_6 = 106.2$, $p < 0.01$, Figure 3.7b). The majority of individuals arriving at and departing from all three patches were categorised as either 'other' or 'unknown' directions.

Patches connected by the 3D linear feature

The pie charts and flight directions (G-tests) in Figure 3.8a & 3.8b were generated from observations including both marked and unmarked bees and are denoted by † (16 days) whilst the total number of visits for the marked bees only are given in brackets (11 days) and are denoted by ‡.

For the 16 day sample (†), the connected patches did not have a statistically significant higher visitation rate than the isolated patch ($F_{2,45} = 1.7$, $p = 0.19$, Figure 3.8a). However, Figure 3.8b demonstrates that there was a far greater number of flight directions between the connected patches than to the unconnected patch ($G_6 = 40.0$, $p < 0.01$). Approximately one third of the 729 visits made to patches A and B were made using direct movements between the connected patches. Very few direct movements were observed between patch C and the two connected patches. Of the 284 individuals seen foraging at the isolated patch, 60% arrived and departed from 'other directions' (Figure 3.8a). When the marked bees were analysed separately, (‡, 11 day sample, Figure 3.8a), the connected patches received significantly more visits than patch C ($F_{2,30} = 9.5$, $p < 0.01$). The flight directions between the connected patches were also significantly greater than the connected patch ($G_6 = 27.1$, $p < 0.01$).

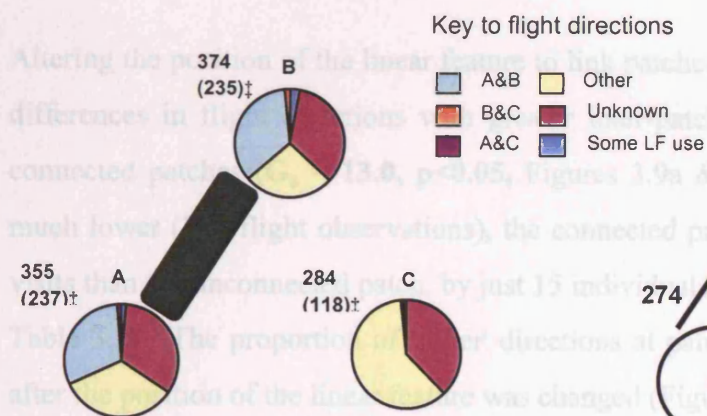


Figure 3.8a LF=3D. $F_{2,45} = 1.7$, $p=0.19$ †
 $F_{2,30} = 9.5$, $p<0.01$ ‡

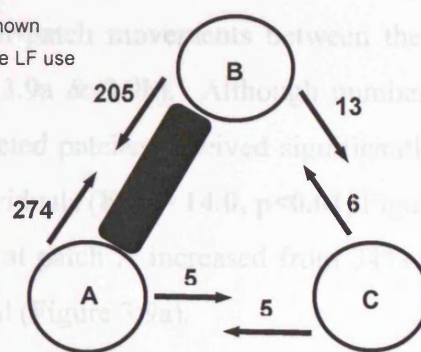


Figure 3.8b LF=3D. $G_6 = 40.0$, $p<<0.01$ †
 $G_6 = 27.1$, $p<0.01$ ‡

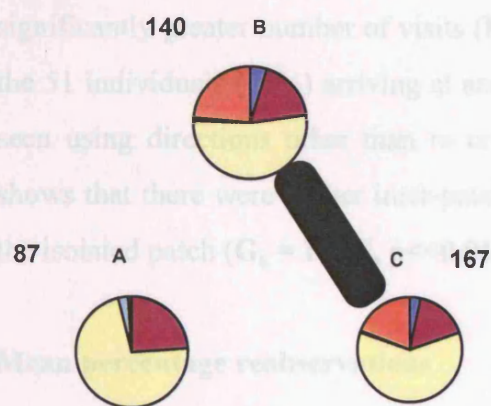


Figure 3.9a LF=3D after LF position changed.
 $F_{2,21} = 14.0$, $p<<0.01$

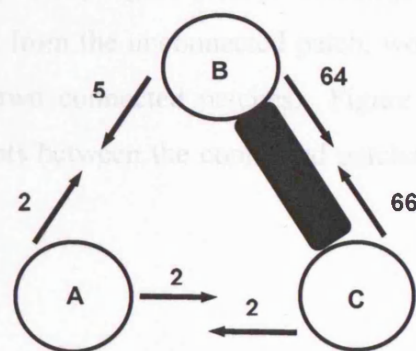


Figure 3.9b LF=3D after LF position changed.
 $G_6 = 13.0$, $p<0.05$

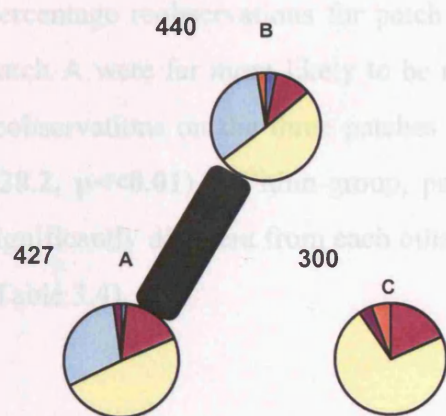


Figure 3.10a Landscape. $F_{2,33} = 4.3$, $p=0.02$

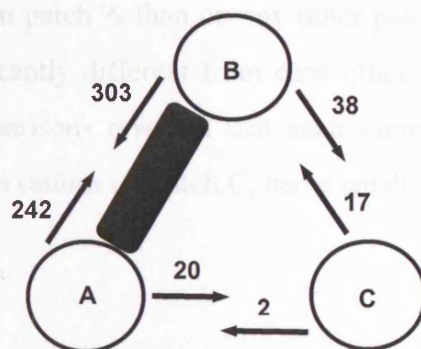


Figure 3.10b Landscape. $G_6 = 106.8$, $p<<0.01$

Figures 3.8a-3.10a One-way ANOVAs of total visits per patch (numbers in bold) and proportional flight direction categories per patch. LF=Linear Feature.
 † Includes data for both marked and unmarked bees.
 ‡ Data for marked bees only (not illustrated).

Figures 3.8b-3.10b Individual inter-patch flight directions. G-tests.
 † Includes data for both marked and unmarked bees.
 ‡ G-test for marked bees only (not illustrated).

Altering the position of the linear feature to link patches B and C still revealed significant differences in flight directions with greater inter-patch movements between the newly connected patches ($G_6 = 13.0$, $p < 0.05$, Figures 3.9a & 3.9b). Although numbers were much lower (788 flight observations), the connected patches received significantly more visits than the unconnected patch, by just 15 individuals ($F_{2,21} = 14.0$, $p < 0.01$, Figure 3.9a, Table 3.2). The proportion of 'other' directions at patch A increased from 34% to 72% after the position of the linear feature was changed (Figure 3.9a).

Landscape-scale experiment

From a total of 2334 observed flights, patches connected with the hedgerow received a significantly greater number of visits ($F_{2,33} = 4.3$, $p = 0.02$, Figure 3.10a). The majority of the 51 individuals (71%) arriving at and departing from the unconnected patch, were last seen using directions other than to or from the two connected patches. Figure 3.10b shows that there were higher inter-patch movements between the connected patches than the isolated patch ($G_6 = 106.8$, $p < 0.01$).

Mean percentage reobservations

Patches connected by the 2D linear feature

Thirty-three individual bees were reobserved in the entire experiment. The mean percentage reobservations for patch A (Figure 3.11a) show that individuals marked on patch A were far more likely to be reobserved on patch A than on any other patch. All reobservations on the three patches were significantly different from each other ($F_{2,30} = 128.2$, $p < 0.01$). Within-group, pairwise comparisons revealed that each sample was significantly different from each other, but reobservations on patch C, had a smaller mean (Table 3.4).

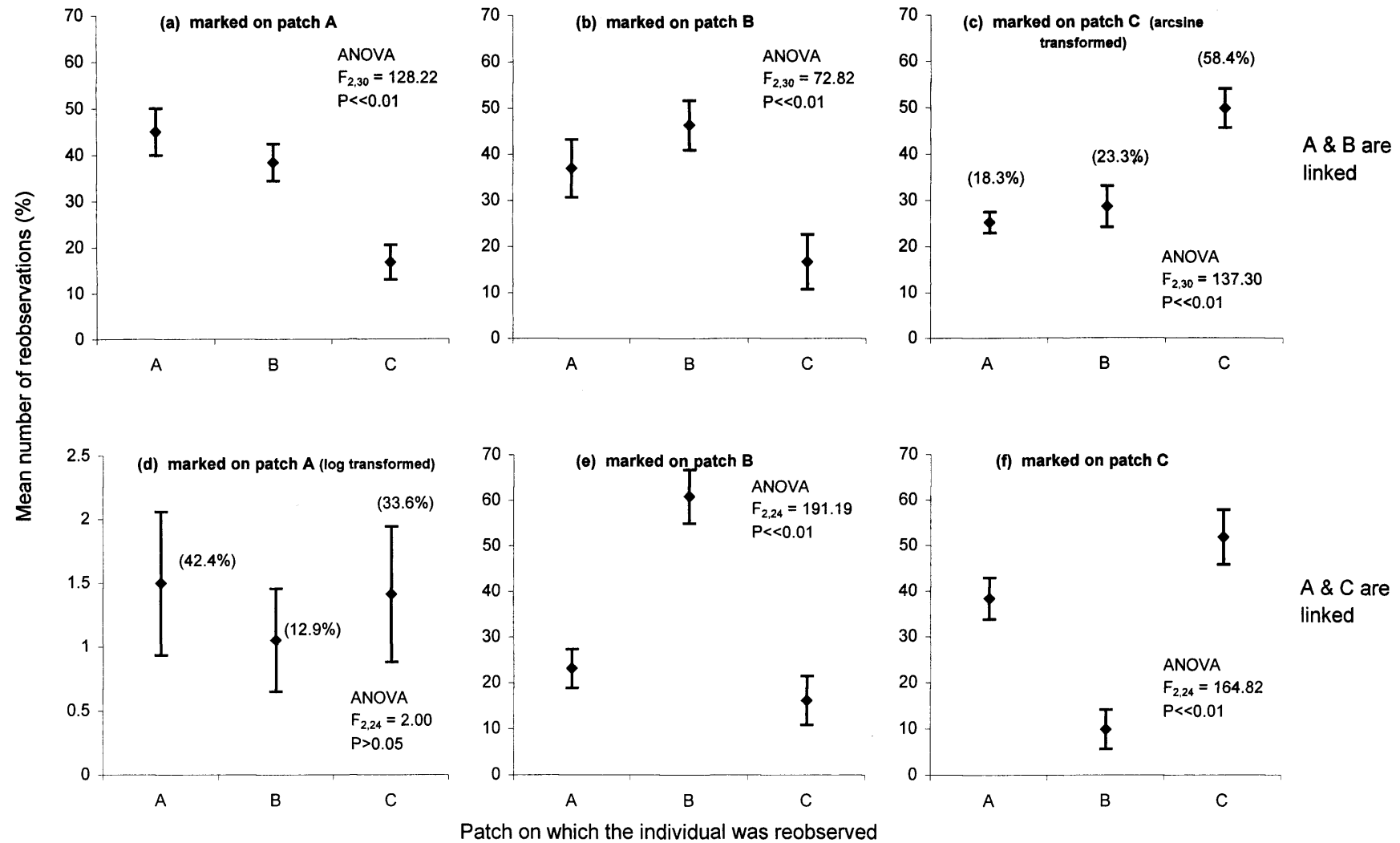


Figure 3.11 Mean percentage reobservations (\pm SD's) and one-way ANOVAs of *Bombus* spp. marked on each patch where a 2D linear feature linked patches A and B (a), (b) and (c), and where the position of the 2D linear feature was changed to connect patches A and C (d), (e) and (f). The scale of the y axis on Figure 3.11(d) has been altered to reflect the data transformation.

Patch B (Figure 3.11b) followed a similar pattern of differences between patches ($F_{2,30} = 72.8$, $p < 0.01$), with the highest number of bees reobserved on the patch on which they were marked (46.3%). Each sample was significantly different from each other with patch C having the smaller mean again (Table 3.4).

There were also significant differences in the mean percentage reobservations between all three patches for bees marked on patch C ($F_{2,30} = 137.3$, $p < 0.01$, Figure 3.11c). The pairwise comparisons summarised in Table 3.4 revealed that only sample C was significantly different from A and B.

Table 3.4 Within-group pairwise comparisons of mean percentage reobservations (one-way ANOVAs) for the 2D artificial feature, before and after changing the position of the linear feature.

	n	Mean	SD	Pair	df	F	P	
A & B linked	Patch A Before							
	A	11	45.0	5.0	A&B	1,20	11.8	0.003
	B	11	38.3	4.0	B&C	1,20	169.6	<0.001
	C	11	16.8	3.8	A&C	1,20	221.5	<0.001
	Patch B Before							
	A	11	37.0	6.2	A&B	1,20	14.2	0.001
	B	11	46.3	5.4	B&C	1,20	149.8	<0.001
	C	11	16.6	5.9	A&C	1,20	60.4	<0.001
	Patch C Before							
A	11	25.2	2.3	A&B	1,20	5.2	0.033	
B	11	28.7	4.5	B&C	1,20	131.2	<0.001	
C	11	49.9	4.2	A&C	1,20	290.2	<0.001	
A & C linked	Patch A After							
	A	9	1.5	0.5	A&B	1,16	3.7	0.072
	B	9	1.1	0.4	B&C	1,16	2.6	0.128
	C	9	1.4	0.5	A&C	1,16	0.1	0.738
	Patch B After							
	A	9	23.1	4.3	A&B	1,16	240.4	<0.001
	B	9	60.7	5.9	B&C	1,16	283.1	<0.001
	C	9	16.2	5.3	A&C	1,16	9.3	0.008
	Patch C After							
	A	9	38.3	4.5	A&B	1,16	188.0	<0.001
	B	9	9.9	4.3	B&C	1,16	291.9	<0.001
	C	9	51.8	6.0	A&C	1,16	28.8	<0.001

After the position of the connection was changed, 38 individuals were reobserved. For patches B and C, individuals marked on their respective patch were significantly more likely to be reobserved visiting that same patch (Figures 3.11e-f). Patch A was the only exception out of all the experiments conducted, where there were no significant differences between the mean percentage reobservations per patch ($F_{2,24} = 2.0$, $p > 0.05$, Figure 3.11d). Pairwise comparisons within patches showed that the unconnected patch

always had the most substantially different mean (Table 3.4). Overall, connected patches shared similar means, with the isolated patch always differing more.

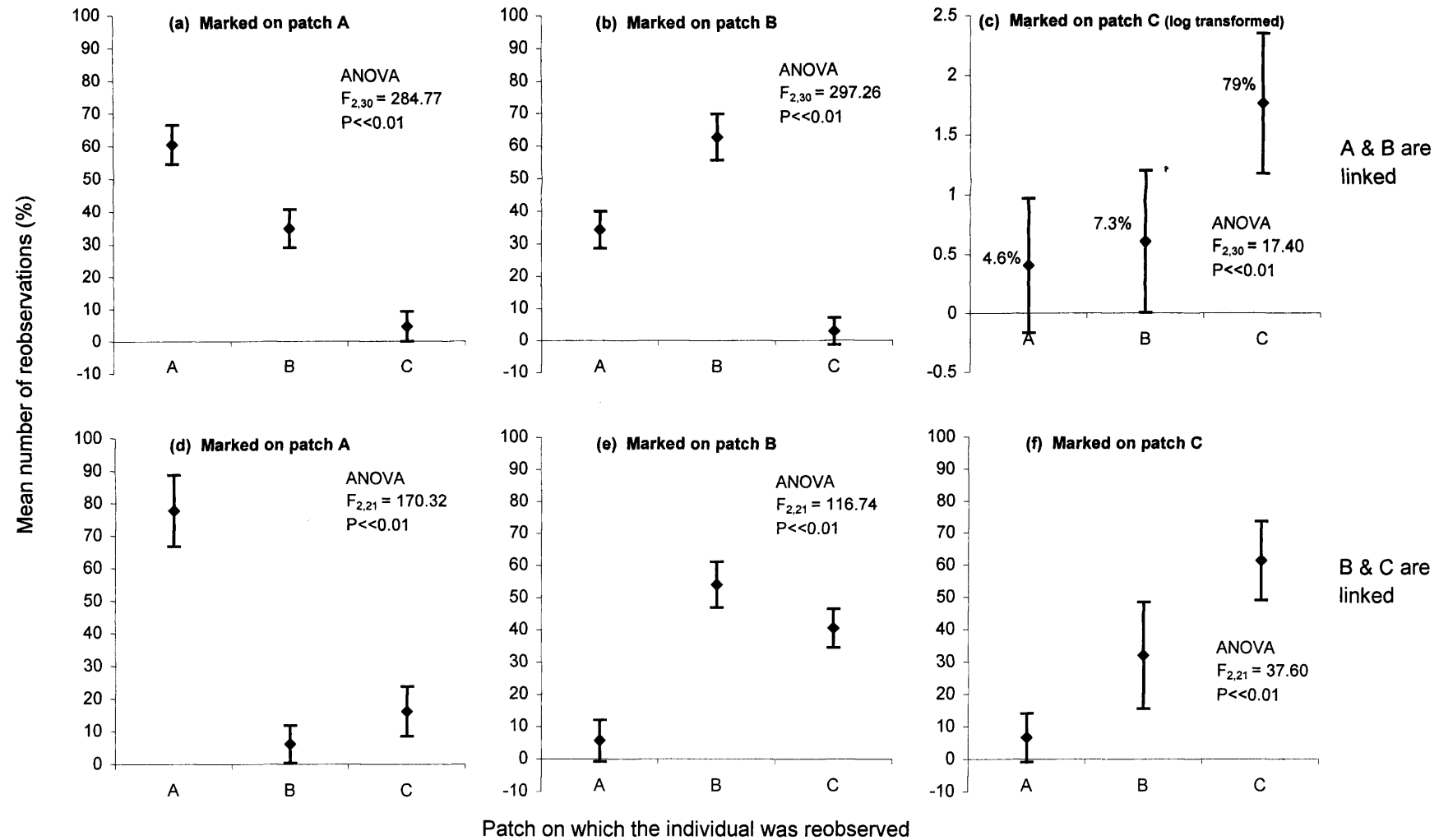


Figure 3.12 Mean percentage reobservations (\pm SD's) and one-way ANOVAs of *Bombus* spp. marked on each patch where a 3D linear feature linked patches A and B (a), (b) and (c), and where the 3D linear feature position was changed to connect patches B and C (d), (e) and (f). The scale of the y axis on Figure 3.12(c) has been altered to reflect the data transformation.

Patches connected by the 3D linear feature

Twenty-six individuals were reobserved over a period of 11 days. All patches had significantly different mean percentage reobservations (Figures 3.12a-c). The hypothesis that individuals marked on a particular patch would be found more frequently on this 'home' patch was accepted. The connected patches always received significantly more visits than the isolated patch (Figures 3.12a-b) except for when the isolated patch was the 'home' patch (Figure 3.12c). Comparisons between paired patches demonstrate that for bees marked on patches A and B, all patches were significantly different from each other (Table 3.5). Pairwise comparisons for bees marked on patch C demonstrated that patches A and B were not significantly different from each other. The unconnected patch always had the most dissimilar mean compared with the linked patches (Table 3.5).

After the connection position was changed, 15 individuals were reobserved, with the unconnected patch once again having a dissimilar mean to the connected patches (Figure 3.12d-f, Table 3.5).

Table 3.5 Within-group pairwise comparisons of mean percentage reobservations (one-way ANOVAs) for the 3D artificial feature, before and after changing the position of the linear feature.

	N	Mean	SD	Pair	df	F	P	
A & B linked	Patch A Before							
	A	11	60.5	6.0	A&B	1,20	104.7	<0.001
	B	11	35.0	5.8	B&C	1,20	183.7	<0.001
	C	11	4.6	4.6	A&C	1,20	600.7	<0.001
	Patch B Before							
	A	11	34.4	5.6	A&B	1,20	108.4	<0.001
	B	11	62.7	7.1	B&C	1,20	579.7	<0.001
	C	11	2.9	4.2	A&C	1,20	220.7	<0.001
	Patch C Before							
A	11	0.4	0.5	A&B	1,20	0.7	0.428	
B	11	0.6	0.6	B&C	1,20	21.1	<0.001	
C	11	1.8	0.5	A&C	1,20	30.5	<0.001	
B & C linked	Patch A After							
	A	8	77.7	11.0	A&B	1,14	265.5	<0.001
	B	8	6.2	5.7	B&C	1,14	8.8	0.010
	C	8	16.1	7.6	A&C	1,14	169.7	<0.001
	Patch B After							
	A	8	5.7	6.4	A&B	1,14	204.6	<0.001
	B	8	54.0	7.1	B&C	1,14	16.8	0.001
	C	8	40.4	6.0	A&C	1,14	125.6	<0.001
	Patch C After							
	A	8	6.7	7.5	A&B	1,14	15.7	0.001
	B	8	32.0	16.5	B&C	1,14	16.3	0.001
	C	8	61.3	12.3	A&C	1,14	115.7	<0.001

Landscape-scale experiment

Fifty-one individuals were reobserved in the landscape experiment. The vast majority of bees marked on a particular patch (between 70 - 80%) were reobserved on the same patch on which they were marked (Figure 3.13a-c). Pairwise comparisons for the connected patches show that there were significantly different numbers of bees reobserved on all patches (Table 3.6). When the mean percentage reobservations of bees marked on patch C were compared, patch C was significantly different from the connected patches (Table 3.6).

Table 3.6. Within-group pairwise comparisons of mean percentage reobservations (one-way ANOVAs) for the patches connected by a hedgerow within the landscape.

	N	Mean	SD	Pair	df	F	P
Patch A							
A	12	71.0	9.4	A&B	1,22	180.7	<0.001
B	12	22.0	8.4	B&C	1,22	28.4	<0.001
C	12	7.1	4.9	A&C	1,22	435.8	<0.001
Patch B							
A	12	22.5	7.1	A&B	1,22	289.2	<0.001
B	12	73.3	7.5	B&C	1,22	740.2	<0.001
C	12	4.2	4.6	A&C	1,22	57.1	<0.001
Patch C							
A	12	7.3	6.0	A&B	1,22	3.4	0.080
B	12	11.9	6.1	B&C	1,22	476.1	<0.001
C	12	80.8	9.1	A&C	1,22	544.8	<0.001

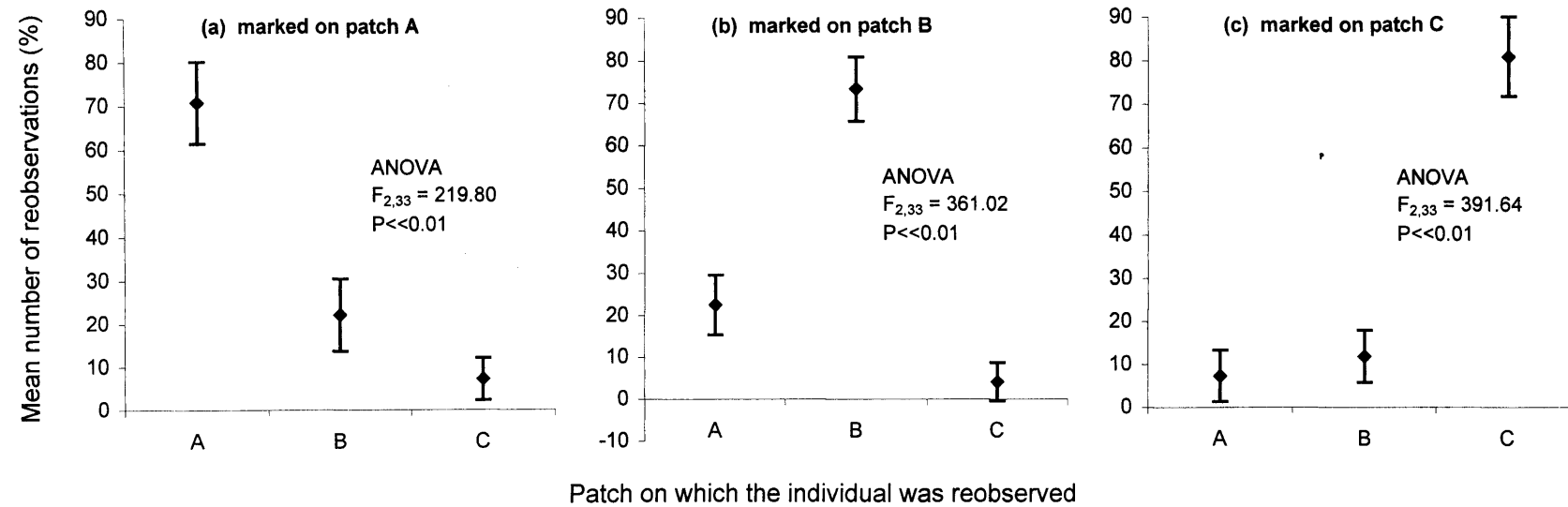


Figure 3.13 Mean percentage reobservations (\pm SD's) and one-way ANOVAs of *Bombus* spp. marked on each patch where an existing hedgerow linked patches A and B (a), (b) and (c).

Hoverflies

Of the nine recorded species of syrphids (Diptera: Syrphidae) observed foraging on *P. tanacetifolia*, six species were found on all patches in all experiments (Table 3.7). *Episyrphus balteatus* was the most numerous hoverfly whilst *Sphaerophoria scripta* and *Syrphus ribesii* were also common. *Baccha* sp., *Ferdinandea cuprea* and *Helophilus* sp. were far less abundant, with the latter species appearing only on the landscape experiment.

Table 3.7 Total hoverfly abundance (all patches combined) recorded at each experiment.

Totals (A+B+C)	Tapes	3D before	3D after	Landscape	2D before	2D after
	6 days	16 days	8 days	12 days	11 days	9 days
	(2000)	(2000)	(2000)	(2001)	(2001)	(2001)
<i>Episyrphus balteatus</i>	68	192	90	131	106	94
<i>Sphaerophoria scripta</i>	18	87	64	193	66	27
<i>Syrphus ribesii</i>	45	162	53	58	46	51
<i>Rhingia campestris</i>	31	70	20	48	25	28
<i>Eristalis tenax</i>	17	57	27	28	23	18
<i>Scaeva pyrastris</i>	21	32	20	19	11	9
<i>Baccha</i> sp.	0	24	10	38	12	8
<i>Ferdinandea cuprea</i>	0	10	6	29	8	0
<i>Helophilus</i> sp.	0	0	0	23	0	0

Mean abundance was remarkably consistent between patches in all experiments and ranged from 1.9 - 3.3 with little variation (Table 3.8). A one-way ANOVA revealed that there were no significant differences in hoverfly abundance between patches within each experiment although there was a statistically weak difference within the tapes experiment ($F_{2,72} = 3.0$, $p=0.06$, Table 3.8).

Table 3.8 Means and one-way ANOVAs of hoverfly visitors to each patch in each experiment.

Tapes	n	Mean	SD	df	F	P
A	20	2.2	2.0	2,72	3.0	0.06
B	27	2.4	1.2			
C	28	3.3	1.9			
2D before						
A	36	1.9	1.6	2,125	1.5	0.22
B	48	2.6	1.9			
C	44	2.3	1.6			
2D after						
A	32	3.0	2.1	2,93	2.6	3.09
B	30	2.2	1.3			
C	34	2.1	1.6			
3D before						
A	68	2.6	1.5	2,217	1.4	0.24
B	81	3.0	1.8			
C	71	3.0	1.8			
3D after						
A	41	3.0	1.9	2,105	1.8	0.16
B	31	2.2	1.4			
C	36	2.7	2.0			
Hedge						
A	71	2.6	1.7	2,197	1.0	0.36
B	70	3.0	2.0			
C	59	3.0	2.2			

Discussion

The results suggest that bumblebees fly along the linear features to visit the connected patches. The number of individuals was comparatively small in relation to the number of flights observed. These data contain repeated observations on the same individual bees. Since bees are known to trap-line (whereby individuals repeatedly follow the same route when visiting flower patches) each observation could not be considered to be independent. It is acknowledged, in hindsight, that these data are essentially pseudoreplicated. In any survey and its subsequent statistical analysis it is crucial to ensure that observations are independent of each other. In most fieldwork it is impossible to know whether the same individual is counted more than once. In this instance, however, the identity of individual bees was known since they were marked with numbered discs. By assuming that all observations were independent, the data are biased and did not satisfy the prerequisites of the G-tests and ANOVAs used.

In all but the tapes experiment, greater direct inter-patch movement was observed between connected patches. Even after the position of the artificial feature was changed, flight directions were concentrated along the artificial feature to reach the connected patches. Preferential use of the linear feature was apparent when bees were approaching and departing the connected patches. Even though the isolated patch was the same distance away, bees did not tend to travel there directly from either of the connected patches. Rather, they would arrive and depart using any other direction. Approximately one third of flight directions were not observed, yet this proportion was consistent in all the experiments and the results are comparable.

In only three of the six experiments did connected patches receive significantly more visits than the isolated patch. It was the direction in which the bees travelled to get to each patch which differed significantly. When the marked bees were analysed separately in the 3D experiment, connected patches received significantly more visits than the isolated patch. Yet, for the first five days, there were no significant differences in mean visits per patch. It was only in the subsequent eleven days that significant differences between visits per patch became apparent. No individual ignored any of the patches but bees marked on a particular patch were far more likely to be reobserved foraging on that

patch than on any other. This observed patch constancy agrees with many other studies illustrating bees' high patch fidelity where even suitable forage nearby might be ignored in favour of the patch on which it is "majoring" at that time (Heinrich, 1976; Saville *et al.*, 1997). Some generalist bees show constancy to a particular plant (Waser, 1986) and they search for that species in time rather than in space. Other suitable flowers are ignored in preference for the plant species that they are concentrating on at that time. If that plant's peak flowering time exceeds the bumblebee's lifetime, she will specialise on that plant for life. However, if resources are low, specialisation or constancy will be abandoned and food is now searched for in a spatial dimension. Such constancy is recorded in 'central place foragers' whereby foragers return to the nest each night (Heinrich, 1975).

Marking of the bees already nectaring on a patch will inevitably reflect their individual foraging preferences at that moment in time. However, this apparent patch fidelity switched almost immediately after the position of the linear feature was changed (Figure 3.9a). The presence of the linear feature might have influenced the number of visits to each patch in this case.

Both the two- and three-dimensional artificial structures using black weed control fabric did appear to affect inter-patch flight movements. Although black has no spectral reflectance, it is unknown whether the contrast between the green background enabled better detection by bees than the white tapes. Black absorbs heat and, on particularly warm days, a heat haze was seen above the fabric structures. It might have been possible that the bumblebees preferred to fly along these artificial features because of the higher temperatures. However, it is well documented that they are not reliant on warm temperatures to operate as they can generate their own metabolic heat and thermoregulate (Goulson, 2003).

The landscape-scale study demonstrated a similar pattern of bumblebees moving between connected patches apparently using the hedgerow. These experiments substantiate earlier observations (Chapter 2) that bumblebees are more likely to be observed making non-foraging flights along hedgerows rather than in adjacent open land. The artificial features within this investigation appeared to influence bumblebee inter-patch flight directions. The artificial features did not contain any foraging resources; therefore it was the presence

of the artificial features, which suggested a visual cue for bumblebee orientation. Horridge (2003) described a visual cue as a constant signal contained within many different types of pattern. Although the overall pattern might change, one parameter remains unchanged and it is this which the insect is able to detect and respond to. Might the linear shape of hedgerow structure provide the visual cue for affecting bumblebee behaviour?

Evidence of the structural arrangement of surrounding vegetation having an effect on pollinator behaviour at the small-scale was reported by Goverde *et al.* (2002) in Switzerland. Areas of calcareous grassland were experimentally fragmented by frequently mowing 5m wide strips to create different sized fragments. The flight and foraging behaviour of *B. veteranus* altered when individuals visited fragmented plots compared with control plots. Bees spent longer periods of time within the fragmented plots and inflorescences were more intensively probed. Fragmented plots were also visited less often. There was also some evidence of flight directionality being altered within the fragmented plots. The turning angles of bees visiting inflorescences within fragments differed significantly from a uniform distribution yet there were no significant differences between the control and experimental plots.

Plowright & Galen (1985) investigated the spatial heterogeneity of bumblebee foraging behaviour between plants at a small-scale. Bees were observed to move more quickly in uniform habitats, compared with those areas containing landmarks such as shrubs projecting above the herb layer. A patch containing such environmental features was thought to be favoured since the landmarks could be used as an orientation feature so that re-visitation of flowers was avoided.

The above two studies demonstrated that foraging behaviour was modified as a result of the spatial arrangements of food plants. Although there is no doubt that hedgerows supply important forage resources for bumblebees, the use of the artificial linear features, devoid of resources, within this investigation demonstrates that the bees do not necessarily use hedgerows as an extension of habitat, but may use them as navigational aids. The overall connectedness of a landscape may therefore be important to the movement of pollinators.

Bees exhibit a great reliance on sight for foraging. A sun compass and the polarisation pattern of the sky (Wehner *et al.*, 1996), as well as landmarks (Chittka *et al.*, 1995a) are used for directional information. Distance estimation relies on the retinal image flow of the landscape structure and specific familiar landmarks as the bee flies along (Esch *et al.*, 2001). Chittka & Tautz (2003) demonstrated that distance estimation could be disrupted in honeybees when their trained flight paths are lined with a chequered pattern.

The relative importance of sight for navigation was investigated by Chittka *et al.* (1999). In complete darkness, *B. impatiens* were observed to walk outside of the nest and locate sucrose solutions. Although odour marks were detected, with the feeder being the primary scent beacon, the marks were not direct and the same trails were never followed twice. Correct directionality was still achieved, albeit to a lesser extent, even after the scent marks were eliminated. The suggested mechanism by which they achieved this was a magnetic compass, also used by honeybees and other arthropods. They were also successful in distance estimation using some sort of internal, non-visual measure of path length. A path integration strategy was not employed indicating that light is required for this. These visual-independent strategies might be used to be able to navigate in the darkness of the nest, although the extent to which tactile cues are also used is unknown. They may also supplement the usual visual cues.

Using an experimental array of artificial landmarks, Chittka *et al.* (1995b) observed that trained honeybees used a combination of artificial landmarks and expected distance from the hive to navigate to a feeding site. The bees clearly exhibited vector learning in that successful location of the feeder was dependent not only by the target landmark itself, but also the preceding landmark. Landmarks, either incorporated in the flight path from the hive to the feeder or marking the location of the feeder, exerted a great influence on bees' choice of goal distance. The expected flight distance was flown first before retrieving memory of the target landmark.

A study of distance estimation in honeybees suggested that they can memorise a sequential landmark array (Chittka & Geiger, 1995). To test whether bees relied on distance rather than landmarks, bees were trained to a feeder located some distance away

from the hive. Artificial landmarks were placed between the hive and the feeder. In different investigations, the number of landmarks was altered. Although the majority of bees still landed on the trained distance feeder, a significant proportion of the bees depended on the number of landmarks encountered (protocounting) to reach a feeder. If there were more landmarks encountered than in training, bees would land at a shorter distance from the feeder, similarly, if some landmarks were removed, the bees would fly a greater distance and overshoot the feeder.

If bumblebees do use familiar landmarks within the landscape for navigation, then it is plausible that the artificial linear features and hedgerow studied in this investigation were used in this way. Bumblebees are capable of remembering the location of forage patches by reference to landmarks (Chittka & Geiger, 1995; Chittka *et al.*, 1995a; Menzel *et al.*, 1998; Goulson & Stout, 2001). However, this does not explain why the isolated patch was not approached directly from either of the other two connected patches, even though it was the same distance away. If the bees were using the linear feature as a landmark to orient toward the connected forage patches, then there would have been the same proportion of flight directions from the other two patches. What was strikingly clear was the direct and linear way in which the bees arrived or left the connected patches. In contrast, the isolated patch was approached from an apparent randomness of directions throughout 360°. The intensive monitoring of patch traffic prohibited prolonged observation of bees after they left. It is not known whether they circled to orientate to the isolated patch. If they had associated flying along the linear feature with a resource patch then no reorientation would be necessary to locate the connected patches. However, the combination of the sun and the linear landmark positions should have made the location of the isolated patch clear. It is unknown just how much of the landscape area is visible to bumblebees, flying at different heights, in just one aerial view (Chittka, pers. comm). The flight heights of bumblebees using the artificial feature were not specifically measured but field notes recorded relatively low heights between the connected patches. These varied from midway up the linear feature to just above it (approximately 0.5m - 1.2m above ground level). Bumblebee arrivals and departures at the isolated patch appeared to be more variable with greater heights being observed. Bees departed with sharp inclines or arrived with steep descents.

Altering the position of the linear feature to connect the otherwise isolated patch did not affect the flight directions of bumblebees between connected patches in this study. Flight directions were significantly more likely to be direct between the connected patches rather than from any other angle. The newly isolated patch was approached and departed using an irregular set of directions. Bumblebees reacted instantly to the new arrangement and changes in their flight directions started from the first day the position was altered. There was no detectable transitional change in the pattern of flight directions which might have indicated the bees were learning a new arrangement. Changing the position of the two dimensional linear feature to connect patches A and C instead of A and B (Figures 3.6a & 3.7a) might have affected the pattern of visitation rates per patch. Before the connection position was changed, the connected patches received significantly greater visits than the isolated patch. After the connection was changed, there were no significant differences in visitation rates between patches. However, the opposite effect was observed using the three-dimensional feature (Figures 3.8a & 3.9a). Connected patches received higher visitation rates *after* the position of the linear feature was changed and not before.

The experiments were performed in separate years and the different environmental conditions together with another year's set of bees make interpretations difficult. The importance of treating pollinators as individuals should not be overlooked since many behavioural differences such as foraging-site and plant preferences as well as level of flower constancy exist between individuals (Chittka & Thomson, 2001). Neurophysiological processes such as flower detection efficiency and learning ability also merge with genetic factors, age and parasite infection. The combined effect of all these variables makes explaining or predicting the behaviour of pollinators incredibly difficult. Results from any study where individual variability is unquantified require cautious interpretation and limited extrapolation to the population as a whole; broad generalisations should be avoided (Chittka & Thomson, 2001). This is particularly pertinent in this study in view of the relatively small number of individuals responsible for making a large number of flights (Table 3.2). However, the majority of individuals responded in the same way in two consecutive years and there was little variation in their response to the experimental array. This replication of the results is an important outcome of the study and demonstrates that different colonies of bees perceived the experimental arrangement in similar ways.

The responses of bees to the position change of the linear feature dispel the possibility that the formerly isolated patch produced less nectar and was therefore less attractive as a resource, independent of its connectedness. Although nectar production was not measured in this study (attempts to measure nectar secretions using micro-capillary tubes were unsuccessful) Williams (1997) found that flowers 4 - 7 hours old yielded the highest secretion rates. Inflorescences contain many simultaneously open flowers and the profusion of flowers over the whole patch appeared to maintain a near constant standing crop for the duration of the study.

There were no significant differences in the pattern of flight directions between patches when the tapes were used as the linear feature. This connecting feature may not have appeared particularly prominent to the bees. Most species of bee have three colour receptor types, most sensitive in the UV, blue and green parts of the spectrum (Spaethe *et al.*, 2001). Spaethe *et al* (2001) also showed that white artificial flowers had poor colour contrast with green backgrounds, which made them difficult to detect for *B. terrestris* even though they had a good brightness contrast. For object recognition and detection over greater distances, bees may not utilise their colour vision, instead they use the signal from their green receptors only (Briscoe & Chittka, 2001; Chittka, 2001).

Hoverflies

The distribution of species over all the experiments reflected their documented habitat preferences (Stubbs & Falk, 2000). *Baccha* sp. and *F. cuprea* prefer more shaded habitats such as woodland margins and hedgerows. In the landscape experiment, patches A and B were considerably more shaded with patch A adjacent to a woodland edge and B close to converging hedgerows and mature trees. Most of the other species prefer more open and sunny areas with the numbers of *E. balteatus*, *S. scripta* known to be boosted by influxes of migrants (Stubbs & Falk, 2000).

Patch connectedness did not affect the abundance of foraging hoverflies at each patch in all the experiments. Although there was a statistically weak difference between patches where tapes were used as the connecting feature (Table 3.8), this result was not repeated

in the other five experiments which were of longer duration. Mean abundance per patch was similar between all patches and all experiments despite differing sample numbers and the data being gathered in different years. The results did not reflect any changes in abundance as a result of seasonal migrants.

A fundamental difference between hoverflies and bumblebees is that the former are non-social insects and do not live in nests. Their only foraging requirements are to improve their own longevity and fecundity (Hickman & Wratten, 1996). Little is known of how hoverflies move across the landscape. Since they do not have to repeatedly return to a nest, it is possible that they do not have to navigate at all. They can follow a nomadic lifestyle and may not be reliant on having to orient themselves to landmarks within the environment. Although hoverflies have excellent vision, the influence of linear features on hoverfly flight paths might have more to do with their physical structure than on providing any orientation function (Colley & Luna, 2000).

Sutherland *et al.* (2001) investigated hoverfly distribution in response to landscape spatial structure. Five single large patches of grass and flower mixtures and four groups of nine smaller patches (with the same area) were created within a barley field. There was little difference in syrphid abundance in both the fragmented and the larger patches. However, *E. balteatus* was more likely to be found at the field margins whilst *Sphaerophoria* spp. had a more uniform distribution. There was a greater diversity and abundance of hoverflies in the hedgerow at the field margin rather than further into the open field, even though the hedge contained fewer floral resources than the within-field patches. It was suggested that the hedgerow supported more *E. balteatus* since it provided shelter from predators and lekking sites. The distribution of hoverflies across the landscape might be dictated by a combination of the density of food plants as well as landscape structure affecting flight paths (Sutherland *et al.*, 2001). Lövei *et al.* (1992) reported that hoverfly mobility is affected by the prevailing winds since greater numbers were found in sticky traps on the windward sides of *P. tanacetifolia* strips.

Because of the difficulty in tracking hoverfly movement, very little information is available on their dispersal abilities across the landscape, although Hickman & Wratten (1996) found evidence of linear features acting as barriers. They examined the

effectiveness of sowing *P. tanacetifolia* strips as a hoverfly attractant to augment the density of aphidophagous hoverflies. The distinctive pollen of the plant enabled identification of those individuals which had fed from the source strip. Gut dissections of *E. balteatus* caught in traps were found to have dispersed 250m away from the source. Hoverfly dispersal may be impeded by the presence of physical structures which disrupt the vegetational ground cover. Fewer hoverflies were caught in traps where a linear feature, such as a tarmac road or a creek and hedge, was located between the pollen source and the traps.

An important consideration on hoverfly movement and response to spatial structure is that it may not just be species-specific (Sutherland *et al.*, 2001), but may differ between individuals, the sexes and stage in the life cycle (Chittka & Thomson, 2001). Adults are highly mobile (Hickman & Wratten, 1996; Sommaggio, 1999; Sutherland *et al.*, 2001) but, in their New Zealand study examining the efficacy of flower strips to enhance aphidophagous hoverflies, White *et al.* (1995) found that gravid *Melanostoma fasciatum* moved away from the flower strips in search of oviposition sites. Immature *M. fasciatum* were more likely to utilise the pollen within the flower strips to aid egg maturation. Such immature females may attract males looking for a mate and therefore disperse less than the gravid females. Some species such as *E. balteatus* are known to frequent lekking places for mate searching (Sutherland *et al.*, 2001). The hoverfly sexes were not distinguished in this study but a higher proportion of immature males and females may have affected their distribution around the experimental patches.

Although *P. tanacetifolia* produces copious amounts of nectar (Williams, 1997), the short labia of most hoverflies prohibits access to it and they probably only feed on the pollen (White *et al.*, 1995). Some species of hoverfly are melliphagous whilst others such as *E. balteatus* feed almost exclusively on pollen (Gilbert, 1993). In this study, all foraging hoverflies were observed to alight on the stamens and feed on pollen. Whilst some species are generalist feeders, many others exhibit a high degree of selectivity in host plant selection (Haslett, 1989). *R. campestris* is known to select blue or purple flowers with deep tubular corollae as it has the longest mouthparts of any British species (>10mm) (Gilbert, 1993). Temporal preferences were observed by Colley & Luna (2000) where hoverflies switched preference from senescing plants to those flowers still in full

flower. When several seed mixtures were compared, Hymenoptera preferred *P. tanacetifolia* whilst syrphids preferred more open flowers (Carreck & Williams, 2002).

Conclusions

Both the two- and three-dimensional black fabric artificial linear features appeared to affect the inter-patch movements of bumblebees. The measuring tapes exerted little or no observable effect. There were more direct flights between patches connected by the artificial feature than to and from the isolated patch, even though it was the same distance away. There were very few direct movements between the isolated patch and the connected patches. Flight was concentrated along the linear features even following a change in its position. This instant change suggested that the bees used the feature as some sort of visual cue or navigational aid. These results were replicated over two years.

In all but the tapes experiment, connected patches received more visits than the isolated patches. However, this was only significant in three out of the six experiments. Bumblebees exhibited patch constancy and were far more likely to be reobserved foraging on the patch on which they were marked. The connected patches in the landscape-scale experiment did receive significantly more bumblebee visits than the isolated patch. Although direct flight paths could not be followed for their duration, the last sighting of individuals leaving the connected patches was always toward the other connected patch rather than toward the isolated patch. Similarly, at the isolated patch, relatively few departures were oriented toward the connected patches. The abundance of visiting hoverflies to each patch was not affected by the presence of any connecting feature.

This chapter has shown that artificial linear features can indeed influence the flight directionality of bumblebees. It supported field observations in Chapter 2 where bumblebees were significantly more likely to be observed flying along hedgerows than in more open habitat. Similar patterns were observed in the landscape-scale experiment, which show that the phenomenon occurs at larger and perhaps more ecologically meaningful scales. Since pollinator movement is so important for gene flow, pollination and seed-set (Waser *et al.*, 1996), the hedgerow network in lowland Britain could serve as a 'transport infrastructure' where bumblebees and perhaps other pollinators are more likely to occur. The presence of plants located close to linear features might receive more visits and therefore be at an advantage compared with those plants situated in relatively insular

patches. This idea is tested in the next chapter where plant fecundity is compared with the plants' apparent connectedness with existing hedgerows in the landscape.

Summary

Previous fieldwork had indicated that non-foraging bumblebees (*Bombus* spp.) were far more likely to be observed flying along hedgerows rather than in adjacent open fields (Chapter 2). This chapter focused primarily on bumblebee movement at a medium-scale, using an experimental array whereby patches of *Phacelia tanacetifolia* (Hydrophyllaceae) were arranged equidistantly at 30m in a triangular arrangement. An artificial linear feature connected two of the patches. Observations of the flight directions (bumblebees) and visitor abundance (bumblebees and hoverflies (Syrphidae)) were recorded. Bumblebees were far more likely to approach and depart the connected patches by flying along the linear feature than by any other direction. The isolated patch, in contrast, was not approached from the other two patches. Bumblebee abundance to the connected patches was not necessarily greater than to the isolated patches. There were no significant differences in hoverfly abundance between patches.

Later, the same experimental array was scaled up to fit within the farm landscape structure, using an existing hedgerow as the connection. A similar pattern of flight directions emerged. Mark, release and reobservation techniques revealed that a relatively small number of individuals made most of the flights in all the experiments. Analysis of mean percentage reobservations showed that individual bumblebees were significantly more likely to be reobserved on the same patch on which they were marked. Linear landscape features might represent navigational aids with which bumblebees orient themselves. The overall connectedness of the landscape may therefore be important to bumblebee movement.

Chapter 4: Pollination of plants in habitat fragments with varying degrees of connectedness: A bioindicator approach

Introduction

Habitat fragmentation has caused many formerly common wild plants to become rare by reducing population size (Fischer & Matthies, 1998; Luijten *et al.*, 2000). Smaller populations are at an increased risk of extinction (Dudash & Fenster, 2000; Eisto *et al.*, 2000; Kéry *et al.*, 2000; Young *et al.*, 1996 & 2000). Human perturbations have degraded and reduced the natural habitats of such plants constraining them to live in small and isolated habitat fragments. This is of particular concern since the evolutionary potential to adapt to the changing environment cannot keep pace with the dramatic reductions in population size. The formerly common plant species are more susceptible to extinction since they are not as resilient as those naturally rare plants, which normally live in small populations with low levels of genetic variation (Charlesworth & Charlesworth, 1987; Huenneke, 1991).

When a population is reduced in size, the number of individuals and therefore genetic variation between those individuals decreases. Small populations tend to be more homozygous whilst larger populations exhibit greater variation. Genetic drift therefore exerts a more prominent role within the gene pool. Genetic drift is a normal process and occurs in all populations. Random fluctuations in the fitness of different alleles and therefore gene frequencies occur and are expressed in the offspring resulting in a non-representative sample of the parental genes (Young *et al.*, 1996).

However, the stochastic effects of genetic drift become more influential when the population is small. The frequency of certain alleles can alter significantly even though natural selection has not occurred. There are relatively few alleles with intermediate frequencies therefore chance alone dictates whether alleles are more likely to become extinct or to become fixed as the only allele present (Ouborg & van Treuren, 1994; Dudash & Fenster, 2000; Eisto *et al.*, 2000; Luijten *et al.*, 2000). The variation originally present within the ancestral population diminishes in the absence of immigration or mutation, as even adaptively superior alleles are permanently lost from the gene pool.

Such small populations undergo indeterminate evolution, which is little influenced by the relative adaptiveness of the various alleles (Keeton & Gould, 1993; Young *et al.*, 1996).

Significant reductions in reproduction were directly related to the small population sizes of the declining perennials *Primula veris* and *Gentiana lutea*. It was suggested that the lower seed-set per fruit and per plant were attributable to inbreeding depression or pollen limitation (Kéry *et al.*, 2000). Fischer & Matthies (1998) also found that fecundity was reduced in small populations of the rare *Gentianella germanica* and concurred that genetic effects were the cause, although pollen limitation may also have contributed to fitness reductions in the field. Significant reductions in the fitness of small populations of *Arnica montana* were reported by Luijten *et al.* (2000). However, there was no evidence that inbreeding was responsible since selfing rates were assumed to have been reduced by the self-incompatibility of the plant. Pollen limitation or the absence of cross-compatible mates were probable causal factors since the probability of asynchronous flowering is higher in smaller, sparser populations.

Depressed reproduction may also be attributable to habitat quality as reproduction is often influenced by resource availability (Oostermeijer *et al.*, 1998). Of the few studies that have investigated the relationship between population size and fitness, discernible evidence of reproduction being resource limited varies depending on the measure of fitness being investigated (Fischer & Matthies, 1998). More detailed knowledge of the inbreeding histories of small populations is required before generalisations that genetic effects are the sole cause of reduced reproduction can be made (Ouborg & van Treuren, 1994).

Another consequence of fragmentation is the loss of fitness within the plant population. As the percentage of homozygosity for deleterious traits increases, there is an increased likelihood of inbreeding with closely related neighbours which leads to inbreeding depression (Silvertown & Charlesworth, 2001).

Plant-pollinator interactions within fragmented habitats

Allele immigration, via pollen and seed dispersal, can also be impeded by habitat fragmentation. The population viability of plants is strongly influenced by pollinators as they determine both the quantity and quality of offspring through pollen limitation and the

extent of self-fertilisation (Waser *et al.*, 1996). Pollinators require a regular and reliable supply of nectar both spatially and temporally (Corbet, 1995). The geographical distance between plant populations should not exceed natural pollinator foraging distances if they are to receive sufficient pollinator service and gene flow (Kwak *et al.*, 1998).

An unrewarding mosaic of non-entomophilous monocultures, often surrounds plant populations growing in habitats fragmented by agricultural land (Jennersten *et al.*, 1992). The network of hedgerows which intersect arable land can therefore provide valuable floral resources which can enhance the foraging distances of pollinators (Saville *et al.*, 1997; Walther-Hellwig & Frankl, 2000).

Pollinator diversity is reduced by habitat fragmentation and plant-pollinator interactions are disrupted. Smaller, isolated plant populations are more likely to suffer from reduced reproductive success and inbreeding depression (Lamont *et al.*, 1993; Ågren, 1996). Pollinator behaviour may also be affected with individuals spending less time on each plant (Ågren, 1996) yet this may be species-specific (Kwak *et al.*, 1998; Goverde *et al.*, 2002). Plant-pollinator interactions are more sensitive to change in smaller plant populations as the plants receive fewer visits and pollen transfer is reduced as the comparatively low densities are less attractive to pollinators as an energy source (Ågren, 1996; Jennersten *et al.*, 1992; Kwak *et al.*, 1991). Outcrossing is reduced and selfing more frequent, resulting in a reduced fitness of the population to enable it to withstand stochastic events (Kearns *et al.*, 1998).

In contrast, Kwak *et al.* (1998) found that large populations of *Salvia pratensis* (Labiatae) produced lower seed-set than those in smaller populations. This relates to the fact that the legitimate pollinators were more frequent at lower *S. pratensis* densities than in those patches with high pollinator species richness, where there were a larger number of nectar robbers. High plant species richness has been correlated with higher visitor numbers. It was not worth the effort expended for nectar robbers to visit these sparser populations. Since different species respond in differing ways to the spatio-temporal heterogeneity of floral resources, those bumblebees (*Bombus* spp.) with greater foraging ranges are able to utilise more patches within their larger range (Walther-Hellwig & Frankl, 2000).

Mustajärvi *et al.* (2001) suggested that the size and spatial arrangement of plant populations influences plant-pollinator interactions. By examining the density of plant populations, they showed that sparse populations of *Lychnis viscaria* (Caryophyllaceae) had higher reproductive success than those plants in larger populations. The greater visibility and larger sized inflorescences within sparse populations received higher visitation rates by bumblebees, the principal pollinators, and more flowers were probed. As long as individual plants growing in sparse populations were vigorous, self-compatible and had few interspecific competitors, reproductive success need not be compromised. Bumblebee foraging behaviour appears to remain relatively constant in habitats where one plant species dominates over a more diverse mix of species (Brittain & Newton, 1933; Brian, 1954). Plant density is generally considered to be a more important factor than population size (Kwak *et al.*, 1998). However, pollinator visitation was the most important limiting factor in the outcrossing rate of self-incompatible plants (Rathcke & Jules, 1993; Mustajärvi *et al.*, 2001).

Nectar production is a heritable, costly trait and volumes vary between individuals of the same species and between flowers on the same plant. Pollinators are able to discriminate between high and low rewarding flowers of different species, with nectar-rich flowers receiving greater pollination service. However, Klinkhamer *et al.* (2001) reported that it becomes increasingly difficult for pollinators to remember the exact location of high rewarding flowers within a population of the same species. The small-scale spatial arrangement of *Echium vulgare* was important in affecting the relationship between nectar production rates and pollination service. Nectar poor plants are able to benefit from the pollination services enjoyed by neighbouring nectar rich plants. Pollinators exhibited increased discrimination when plants were separated by distances of more than 6m.

Facilitation by other co-flowering plants can assist in gene flow as pollinators are attracted to these areas. Oostermeijer *et al.* (1998) reported increased pollinator service by bumblebees and higher seed-set in *Gentiana pneumonanthe* where heathers such as *Erica tetralix* and *Calluna vulgaris* were flowering nearby. When adaptively superior alleles are lost, the plant population is less likely to adapt to be able to withstand stochastic events and extinction becomes more probable. However, the negative effects of genetic erosion can be ameliorated by increased gene flow within the landscape.

Pollen from other populations can augment the genetic diversity of small isolated populations. Increasing pollinator movement between habitat remnants to increase pollen flow is therefore an important factor in maintaining plant population viability (Kwak & Vervoort, 2000).

The results of fieldwork conducted in 2000 suggested that pollinating insects did appear to fly along hedgerows more frequently than in adjacent, more open habitats (Chapter 2). Landscape scale studies of pollinator flight are inherently difficult to conduct owing to the large distances that must be covered and the unfeasibility of manipulating landscape structure for experimental purposes. To isolate whether linear features did influence pollinator flight, a small-scale experiment using three *Phacelia tanacetifolia* (Hydrophyllaceae) patches and an artificial linear feature linking two of the patches demonstrated bumblebee preferences for the linear feature (Chapter 3). Bumblebee flight directions were strongly influenced by the artificial features with the vast majority of flights concentrated along the linear structures. It was then necessary to investigate whether this same pattern occurred at the landscape scale. Using the same experimental design, three *P. tanacetifolia* patches were planted within the landscape. Two of the patches were connected via an existing hedgerow with the third patch located midfield with no connections (Chapter 3). Once again, at the point of last sighting, bumblebees were more likely to use the hedge when arriving at or departing from patches. Individual bees marked at the connected patches were significantly more likely to be re-observed visiting one of the connected patches rather than the isolated patch.

These studies were based on field observations, which provided insights into pollinator abundance, flight direction and visits to particular locations. Whilst investigating pollinator behaviour within the landscape is quintessential to addressing the aims of this study, their functional role as pollinators required some quantification. Measuring the fecundity of plants that require bumblebee visitation to set seed could provide a useful bioindication of pollination success, which complement the previous studies of pollinator flight at the landscape-scale.

Having established the predisposition of bumblebees to fly along hedgerows, it followed that plants growing within patches where these hedgerows converge may receive greater

pollinator visitation, ultimately leading to higher seed-set, than those plants in patches with fewer or no connections (Figure 4.1).

In order to test this hypothesis, the reproductive success of *Salvia pratensis* (Labiatae), planted in 15 differently connected patches, was compared and used as a bioindicator of pollinator visitation.



Figure 4.1 Location and connectedness of *S. pratensis* patches. Scale: 1:10,000. Photograph taken: May 1990, reproduced with permission from NRSC Ltd.

Patch no.	No. connections
1	5
2	4
3	4
4	4
5	3
6	3
7	3
8	3
9	2
10	2
11	2
12	2
13	0
14	0
15	0

Methods

All observations and experiments were conducted at the same farm location as described in the 'study site' section in Chapter 2.

Plant selection

S. pratensis was chosen for this experiment because it fulfilled a number of prerequisites necessary to demonstrate that seed-set was limited by pollinator activity. *S. pratensis* is a rare and threatened herbaceous perennial (Figure 4.2), found on calcareous grasslands and is native to southern England. It prefers well-drained soil and reaches 30 - 100cm in height (Rose, 1981). Flowering in June and July, the purple/blue flowers are zygomorphic, with a hood-forming sickle shaped upper lip (Figure 4.3).



Figure 4.2 *S. pratensis* flowering from successive whorls



Figure 4.3 Typical flower

The protandrous, nectar-rich flowers possess a see-saw pollination mechanism in which pollen transfer is triggered by way of an insect-mediated design. The tissue between the two anther-lobes (connective) is elongated and at its lower end forms an enlarged blade which partly obstructs the entrance to the flower. The connective is joined to the corolla by a spring-loaded torsion joint made up of compressed short anther-filaments. To obtain nectar, a bee must push its head into the flower. As it does so, it drives the anther blade

backwards and upwards, thereby causing the anther lobes to swing downwards, transferring pollen to the bee's abdomen. The stigmas mature later and protrude from the front of the flower ready to receive pollen from visiting insects (Proctor *et al.*, 1996). The plant is self compatible but requires bumblebee visitation to set seed (van Treuren *et al.*, 1993; Kwak *et al.*, 1996). The superior ovary has four lobes which ripen to four separate one-seeded nutlets (Rose, 1981).

The species is recorded as extinct within Northamptonshire (Gent & Wilson, 1995; McCollin *et al.*, 2000). Species records at Northamptonshire Wildlife Trust reported only unconfirmed sightings of the plant within the county in 1978 (Allen Smith, pers. comm.). *S. pratensis* is a suitable species because its absence within the study area meant that no other populations could act as a pollen source, providing a "closed" system. Secondly, seed production was only possible via insect-mediated pollen transfer. Consequently, all seeds produced within the experiment were directly attributable to insect vectors within the system.

Although *S. pratensis* flowers are protandrous, geitonogamy is still possible. This restricts the amount of genetic variation within small populations and is no different from autogamy. The greater the distance between populations of *S. pratensis*, the less likely they are to be visited by bumblebees carrying pollen from other *S. pratensis* populations, creating genetic isolation. Such effects may be ameliorated by the presence of connecting hedgerows, which can augment the gene flow of this species. Even large patches of isolated super abundant resources such as entomophilous crops may only be accessed by bumblebee species with large mean foraging distances. Species such as the rare, long-tongued *Bombus muscorum*, which does tend to forage locally, appear reliant on connections to nearby foraging patches. Habitat fragmentation within the arable landscape may be particularly damaging to their continued existence (Walther-Hellwig & Frankl, 2000).

Although this research recorded non-foraging flight along hedgerows (Chapter 2), there is no doubt that the numerous flowering hedgerow plants were an important food resource, providing nectar which was otherwise absent in the surrounding cropped areas (Clements & Tofts, 1992a). The presence of simultaneously flowering species in fragmented habitats can act as stepping stones for pollinators, allowing them to reach more distant

plant populations. Without such resources, gene flow may seriously be inhibited even over relatively short distances (Kwak *et al.*, 1998).

S. pratensis is particularly vulnerable to the effects of habitat fragmentation since it is specialised on long and medium tongued bumblebees for its pollination. Continual selfing of *S. pratensis* in small populations with already high levels of homozygosity results in gradual yet persistent reductions in plant fitness (Hegland *et al.*, 2001). Field experiments demonstrated that survival of outcrossed progeny was 16 - 63% higher than selfed progeny. Such genetic erosion is particularly apparent in those populations with a long history of inbreeding. A positive correlation between population size and genetic variation was demonstrated both in the field and glasshouse (Ouborg & van Treuren, 1994).

Site Selection

Semi-natural habitat patches were selected for their varying degrees of connectedness, suitability for plant growth and accessibility. The patches were all non-cropped areas of land principally field corners and their locations are shown in Figure 4.1. Patch descriptions, planting and observation dates are summarised in Table 4.1. An effort was made to replicate connection numbers, which ranged from 0 - 5, in an attempt to represent different patch attributes. However, landscape scale experiments are difficult to rigorously standardise since each area will be inherently different in terms of its species composition and surrounding land use (see discussion in Chapter 1).

Table 4.1 Patch descriptions, adjacent land use, planting and observation dates in 2001.

Patch no. & name	No. of connections	Date planted	Observation dates and times	Approx. area (m ²)	No. of other experimental patches within 300m radius	Land type	Adjacent field use
New spinney (1)	5	24 May	17 July 1245-1355 23 July 1510-1620 30 July 0900-1010	5300	1	newly planted spinney	barley; pasture
Cherry spinney (2)	4	24 May	19 July 1645-1755 21 July 1340-1450 25 July 1525-1635	2025	2	mature cherry tree spinney	pasture; wheat
Cattle crush (3)	4	24 May	17 July 1555-1705 24 July 1705-1815 26 July 1630-1740	18	4	gateway/field intersection	pasture; fallow
B (4)	4	22 May	17 July 1725-1835 21 July 1510-1620 26 July 1000-1110	23	2	field corner	barley; pasture; oilseed rape
Christmas tree (5)	3	24 May	19 July 1220-1330 22 July 1025-1135 26 July 0830-0940	1069	3	Christmas tree plantation	wheat; pasture
Snowdrop (6)	3	18 May	19 July 1345-1455 24 July 1000-1110 25 July 1655-1805	1466	3	scrub/carr	pasture
A (7)	3	18 May	20 July 0830-0940 23 July 1345-1455 26 July 1120-1230	1227	3	woodland edge	barley; <i>Vicia</i> sp.; pasture
Stream (8)	3	22 May	18 July 0900-1010 22 July 1150-1300 27 July 1645-1755	12	4	stream-side	pasture
Oak tree (9)	2	25 May	18 July 1025-1135 22 July 0900-1010 27 July 1520-1630	2468	2	mature oak wood	pasture; wheat
Stables (10)	2	24 May	18 July 1155-1305 21 July 1205-1315 27 July 1340-1450	305	0	newly planted spinney	pasture
Thistle (11)	2	25 May	20 July 1125-1235 23 July 1215-1325 30 July 1215-1325	689	4	field corner	wheat; pasture
Big sheep (12)	2	22 May	20 July 1645-1755 21 July 1640-1750 25 July 1400-1510	10	4	field corner	pasture; wheat
C (13)	0	18 May	19 July 1510-1620 24 July 0830-0940 27 July 1210-1320	825	2	disused barn with enclosure *	barley
Reservoir (14)	0	25 May	20 July 0955-1105 23 July 1635-1745 25 July 1225-1335	278	1	covered reservoir	pasture
Blackpool (15)	0	22 May	17 July 1425-1535 24 July 1140-1250 30 July 1035-1145	5ha	0	fallow field	wheat; pasture

Notes:

Pasture contained occasional weeds such as *Cirsium* spp., *Urtica* spp. and *Trifolium* spp.

Fallow fields had recently been treated with a herbicide application.

The fields of *Vicia* spp. and oilseed rape had finished flowering by the time *S. pratensis* was in flower.

* Contained 12 x 25cm diameter of *P. tanacetifolia* from a concurrent study within this PhD (Chapter 3).

The majority of hedgerows used in this study were centuries rather than decades old and well established field boundaries. The principal woody species comprised *Crataegus* spp. and *Prunus spinosa*, with *Urtica dioica*, *Cirsium* spp. and *Rumex* spp. dominating the herb layer. Parallel drainage ditches were frequently present, sometimes with additional fencing. All hedgerows were mechanically trimmed approximately every other year.

The number of hedgerows converging on a patch was counted. If a patch was situated in the middle of a hedgerow, it was considered to have two connections since insects could reach the patch from both directions. Although this is still true for those patches with, for example, three and above converging hedgerows, the numbering system reflected number of hedgerows and not flight directions.

***S. pratensis* planting**

Forty five *S. pratensis* plants were purchased from English Cottage Garden Nurseries, Aldington, Kent. Sown on 3 March 2001, the plants were in their first season of growth and had not previously flowered. All plants were at approximately the same stage of growth with circa six basal leaves and five emerging leaves.

Three plants were used per patch to allow for possible plant failure. Each plant was assigned a random number generated on an MS Excel 97 spreadsheet (Microsoft Corp., 1997). The numbers were then sorted into ascending order. The first set of three plants was allocated to the first patch and the next three to the next patch, and so on. The location of the plants within each habitat patch was determined by ensuring that the area was as central and as open as possible to allow sufficient light to satisfy the species' natural growth requirements.

S. pratensis were planted directly into the ground in each of the 15 patches and surrounded by open-topped wire cages to prevent mammal browsing. The cages were constructed using 1.0 - 1.5m high chicken wire, mesh size 25mm, and secured with three hazel poles approximately 1m high, hammered into the ground (Figure 4.4). Existing vegetation was cleared and the soil lightly dug over. The plants were planted in a triangular formation, approximately 30cm apart and watered. Slug mini-pellets containing metaldehyde were applied within the wire cage so that pellets fell 10 - 15cm apart. Every plant within each set was labelled with an identification number.



Figure 4.4 Recently planted *S. pratensis* in the Stream patch.

Seed production

Flower production

The sets of plants were monitored every week for general plant health and developing inflorescences. The inflorescences were numbered and labelled with string tags for future identification. The progress of individual flowers was followed every day for 25 days.

numbers were recorded in situ

Whorls of flowers were counted from the inflorescence base. Each whorl was examined and flower production and longevity was recorded. The number of buds, open flowers and shrivelled flowers was counted to ensure that reproduction was occurring normally. The resulting seed numbers were then a true reflection of pollination; any deficit in seed numbers would most likely be attributable to pollination failure and not to other factors such as predation or bud abortion.

Variation in plant vigour between sets

The plants were still flowering at the end of the investigation and continued to flower, albeit less intensely, until October. However, time restrictions prevented further monitoring. The relatively short time period from bud to seed-set provided sufficient data for the purposes of this study.

Pollinator abundance

Visiting insects were observed for one hour at each patch on three non-consecutive days between 17 - 30 July 2001 (Table 4.1). The order in which each patch was observed was

randomised and the total time expended to observe pollinators in 15 patches was considerable (45 hours). It was therefore not feasible, within the fieldwork period, to record temporal patterns of insect visitation. The aim of the exercise was to record visiting insect diversity, identify legitimate pollinators and quantify visitor abundance. Legitimate pollinators were those which came into contact with the fertile anthers which swung downwards as the insect pushed its head into the flower, or were observed to contact the mature stigmas of older flowers (Proctor *et al.*, 1996).

Pollen deposition

Fallen flowers were collected from each set on 24 August and 3 September 2001 and preserved in 70% alcohol. In the laboratory, the stigmas were removed from the flowers and the number of pollen grains adhering to each stigma was counted with the aid of a binocular dissecting microscope.

Seed production

Following fertilisation, the four-lobed ovary developed into 4 separate one-seeded nutlets. Fertilised ovules were easily distinguishable from non-fertilised ones by their greatly expanded size and their black colouration following ripening. The black seeds within each whorl were clearly visible. All whorls were examined on each visit and their seed numbers were recorded in situ.

Data analysis

All statistical analyses were conducted using SPSS for Windows, Version 9.0 (SPSS Inc., 1998). All data were checked for normality using a Kolmogorov-Smirnov test prior to analyses.

Variation in plant vigour between sets

Variation in mean inflorescence and flower number of each set of plants was compared between patches using one-way ANOVA. An F_{\max} test confirmed that the variances were homogenous and all observations were obtained randomly. This would indicate whether plants were distributed randomly between patches with respect to their general vigour, thus minimising potential bias in reproductive success.

Seed-set

Percentage seed-set was calculated to allow comparison between the different patches, taking into account the natural variation in inflorescence number between discrete patches. Using existing knowledge of *S. pratensis* reproductive biology, each whorl normally produces six flowers, with each flower usually producing four seeds (Scott, 1989).

$$\text{Seed success} = \left(\frac{\text{observed seed set}}{\text{potential seed set}} \right) \times 100$$

Pearson correlations were used to indicate possible relationships between the number of connections and:

1. Total insect visitor number per patch
2. Pollen grain number per stigma, per patch
3. Mean per cent seed-set per patch

These observations were on a ratio scale and all sample units were obtained randomly.

In hindsight, a proximity matrix of Pearson correlations was conducted to include a measurement of the nearness of patches to each other. For the distances between patches, measurements were taken using a ruler on a 1:5,000 scale map, then converted into metres and entered into a proximity matrix. Taking Patch 1 for example, the distance between this patch and all the other patches was tabulated and the mean calculated. This process was repeated for all other patches and then entered into a Pearson correlation matrix (Table 4.9).

Results

Plant vigour between and within sets

All plants within the experimental assay developed normally compared with other documented studies (Scott, 1989; Hegland *et al.*, 2001) and reproduced successfully, yielding means of between 8 - 12 inflorescences per patch (Table 4.2). The largest variation in plant vigour between patches was in the number of whorls and flowers produced from the inflorescences (24.8 and 88.3, respectively). Patch A and the New Spinney patch produced the highest number of flowers (>700). Twelve out of the 15 patches produced between 500 - 700 flowers each. The vast majority of flowers lasted 2.4 days before the lower lobe withered and the stigma began to brown, with very little variation between patches (SD=0.1). Homogeneity of variance was confirmed using the F_{\max} test.

Table 4.2 Summary of mean reproductive potential of *S. pratensis* between patches (sorted by flower number)

Patch no.	Patch name	No. connections	Infl-plant		Whrls-infl		Flwrs-plant		Flwr longevity (days)	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
7	A	3	12.0	2.6	20.6	1.1	770.7	163.1	2.5	0.6
1	New spinney	5	12.0	2.0	17.1	3.8	749.7	167.5	2.4	0.6
12	Big sheep	2	11.3	4.9	19.6	1.4	680.0	353.3	2.5	0.7
11	Thistle	2	10.7	2.1	20.1	3.3	661.7	130.5	2.4	0.7
10	Stables	2	11.0	1.7	19.8	0.8	661.0	110.8	2.4	0.7
4	B	4	10.3	3.5	20.3	1.4	648.0	272.1	2.5	0.7
14	Reservoir	0	9.7	1.2	20.8	2.2	629.7	175.3	2.4	0.7
13	C	0	9.7	2.1	20.0	1.5	594.3	173.8	2.4	0.6
3	Cattle crush	4	9.3	2.5	20.3	0.8	579.7	156.6	2.6	0.6
6	Snowdrop	3	9.7	1.5	19.3	1.5	564.3	98.3	2.5	0.7
8	Stream	3	9.7	2.1	19.2	1.7	563.0	169.7	2.4	0.7
5	Christmas tree	3	8.7	1.2	20.1	1.2	531.0	114.1	2.4	0.7
9	Oak tree	2	8.7	1.5	19.8	1.5	527.3	109.6	2.5	0.8
2	Cherry spinney	4	8.0	1.0	20.8	1.1	512.0	90.6	2.5	0.7
15	Blackpool	0	8.3	2.5	18.2	1.2	456.0	135.6	2.4	0.7

ANOVA Tables 4.3 and 4.4 demonstrate there were no significant differences in inflorescence or flower number between or within all plants in the 15 different patches. The plants' general vigour was therefore randomly distributed, thus minimising potential bias in reproductive success.

Table 4.3 ANOVA summary table: Inflorescences between patches

Source of variation	SS	df	S ²	F	P
Between	67.8	14	4.84	0.860	0.61
Within	169.0	30	5.63		
Total	236.8	44			

Table 4.4 ANOVA summary table: Flowers between patches

Source of variation	SS	df	S ²	F	P
Between	327436.0	14	23388.29	0.765	0.70
Within	916871.0	30	30562.37		
Total	1244307.0	44			

Pollinators

A total of three bumblebee and two hoverfly (Syrphidae) species were recorded in most *S. pratensis* patches (Table 4.5). Only *B. pascuorum* and *B. hortorum* were observed to trip the see-saw pollination mechanism. The patch with five connecting hedgerows had the highest number of individual insects (50) overall, and the greatest abundance of species, except for the hoverfly *Episyrphus balteatus*. The Blackpool patch had the lowest abundance of visiting insects with just six individuals of two different species being recorded over the three sample dates. *B. pascuorum* was the most numerous and ubiquitous species, and was observed in all patches. *B. hortorum* was the least recorded species, observed in only eight patches around the farm. The other hoverfly species, *Rhingia campestris* was recorded in all but one of the experimental patches. Patch C had no connections, but was still the third most visited set of plants, particularly by *B. pascuorum*.

Table 4.5 Total number of insects and mean insect visitors per hour, per patch. Ranked by insect abundance

No. connections	Patch	Total no. insects	Mean visitors/hour				
			<i>B. pascuorum</i>	<i>B. hortorum</i>	<i>B. pratorum</i>	<i>E. balteatus</i>	<i>R. campestris</i>
5	New spinney	50	5.7	4.3	2.7	1.3	2.7
4	Cattle crush	34	4.0	2.0	1.7	2.0	1.7
0	C	27	4.3		1.7	1.7	2.0
4	B	24	4.0	2.3	1.0	1.0	1.0
3	Xmas tree	23	2.3	1.0	2.3	1.3	2.0
4	Cherry spinney	19	3.3		1.0	2.0	1.7
3	Stream	19	1.7	1.0	1.0	2.3	2.0
3	Snowdrop	18	3.3			2.3	1.0
3	A	18	2.3	1.0	1.3	1.0	1.5
2	Oak tree	18	1.7		2.0	1.7	2.0
2	Stables	18	1.0	2.0		2.3	1.0
2	Thistle	17	2.3		1.0	2.0	2.0
2	Big sheep	17	2.0	1.7		2.0	
0	Reservoir	10	2.7				1.0
0	Blackpool	6	1.7				1.0

With the exception of Patch C, Figure 4.5 suggests that there was a general trend of increased insect visitor abundance as the number of connections per patch increased. There was a significant correlation between the total numbers of legitimate pollinators (*B. pascuorum* and *B. hortorum*) and patch connectedness (Pearson correlation: $r = 0.68$, $df = 13$, $p < 0.01$). When species were analysed individually, there was no correlation between discrete species and connectedness (Table 4.6).

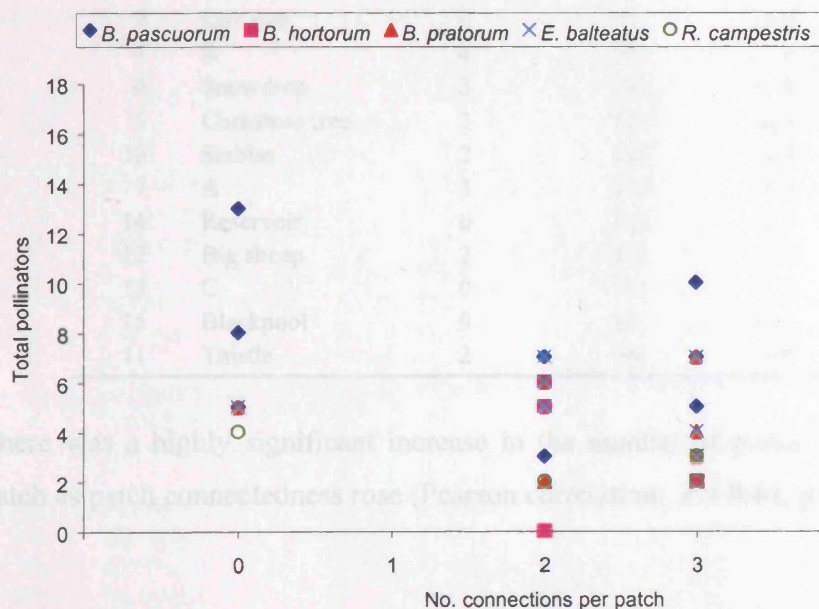


Figure 4.5 Total number of individual visitors per patch over three days. Pearson correlation: $r = 0.63$, $df = 13$, $p < 0.05$

Table 4.6 Pearson correlation results of the relationship between individual species abundance and number of connections per patch (* = $p < 0.05$, ** = $p < 0.01$)

Species	r	df	n
<i>B. pascuorum</i>	0.45	13	15
<i>B. hortorum</i>	0.68	4	6
<i>B. pratorum</i>	0.03	8	10
<i>E. balteatus</i>	-0.18	9	11
<i>R. campestris</i>	0.49	7	9
<i>B. pascuorum</i> + <i>B. hortorum</i>	0.68**	13	15
Total visitors	0.63*	13	15

Pollen deposition

There was large variation in the number of pollen grains deposited per stigma (Table 4.7). The Cherry Spinney patch had the highest mean number of pollen grains (32.2). Thirteen patches contained means of between 10 and 29 pollen grains per stigma. The largest difference between the highest and lowest scoring patches was just under 200 pollen grains.

Table 4.7 Summary of the number of pollen grains per patch (sorted by mean pollen grains per stigma)

Patch no.	Patch name	No. connections	Pollen grains per patch	Pollen grains per stigma		
			Total	Mean	SD	N
2	Cherry spinney	4	290	32.2	8.2	9
1	New spinney	5	290	29.0	19.0	10
8	Stream	3	282	28.2	11.5	10
3	Cattle crush	4	232	25.8	8.9	9
9	Oak tree	2	250	25.0	5.8	10
4	B	4	202	22.4	7.3	9
6	Snowdrop	3	197	21.9	13.6	9
5	Christmas tree	3	147	16.3	12.6	9
10	Stables	2	128	16.0	10.9	8
7	A	3	152	15.2	10.8	10
14	Reservoir	0	118	13.1	5.4	9
12	Big sheep	2	112	12.4	8.6	9
13	C	0	111	12.3	8.5	9
15	Blackpool	0	101	10.1	7.6	10
11	Thistle	2	99	9.9	11.4	10

There was a highly significant increase in the number of pollen grains per stigma per patch as patch connectedness rose (Pearson correlation: $r = 0.44$, $p < 0.01$, Figure 4.6).

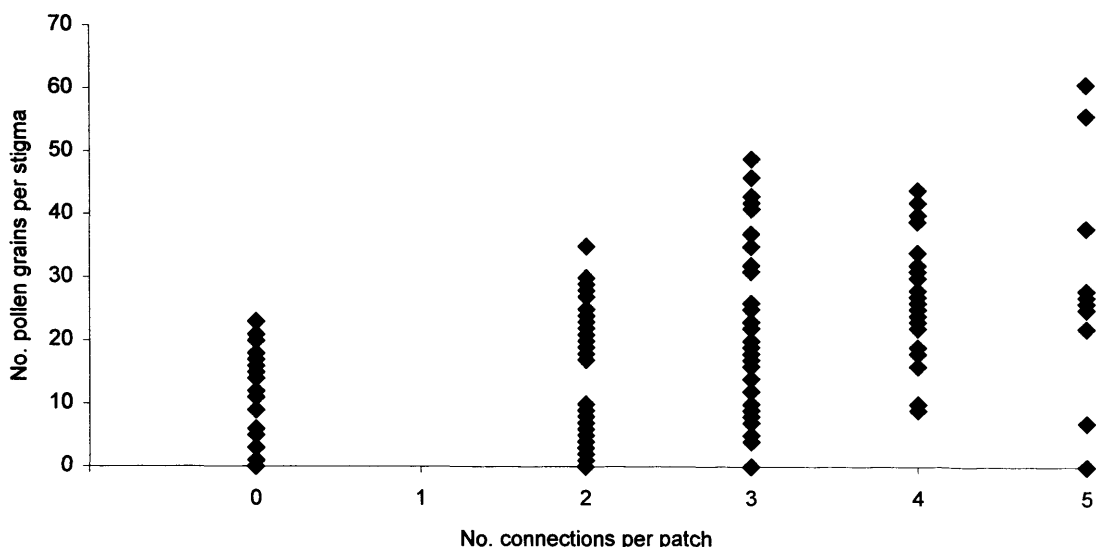


Figure 4.6 Number of pollen grains per stigma per patch. Pearson correlation: $r = 0.44$, $df = 138$, $p < 0.01$

Seed-set

Higher seed-set was recorded for patches with a greater number of connections (Table 4.8). Patches 1, 2 and 3 all yielded over 70% seed-set compared with Patches 14 and 15, which had less than 55%. A highly significant relationship was apparent when percentage seed success was plotted against patch connectedness (Figure 4.7). Plants with four or five connections produced between 7 - 23% more seeds than those plants within unconnected patches.

Table 4.8 Mean and total seed-set per patch and per cent seed success

Patch no.	Patch name	No. connections	Seed-set per patch		Potential seed-set	Total per patch	
			Mean	SD		Observed seed-set	Per cent seed-set (obs/pot)*100
1	New spinney	5	2186.7	519.1	8996	6560	72.9
3	Cattle crush	4	1669.3	414.5	6956	5008	72.0
2	Cherry spinney	4	1435.7	256.0	6144	4307	70.1
4	B	4	1789.0	749.5	7776	5367	69.0
8	Stream	3	1514.7	454.0	6756	4544	67.3
9	Oak tree	2	1391.7	317.3	6328	4175	66.0
7	A	3	1994.7	380.2	9248	5984	64.7
5	Christmas tree	3	1356.3	280.3	6372	4069	63.9
6	Snowdrop	3	1403.7	278.8	6772	4211	62.2
11	Thistle	2	1638.7	341.6	7940	4916	61.9
13	C	0	1422.0	448.1	7132	4266	59.8
10	Stables	2	1540.0	275.1	7932	4620	58.2
12	Big sheep	2	1559.7	894.1	8160	4679	57.3
14	Reservoir	0	1382.0	491.8	7556	4146	54.9
15	Blackpool	0	937.0	287.4	5472	2811	51.4

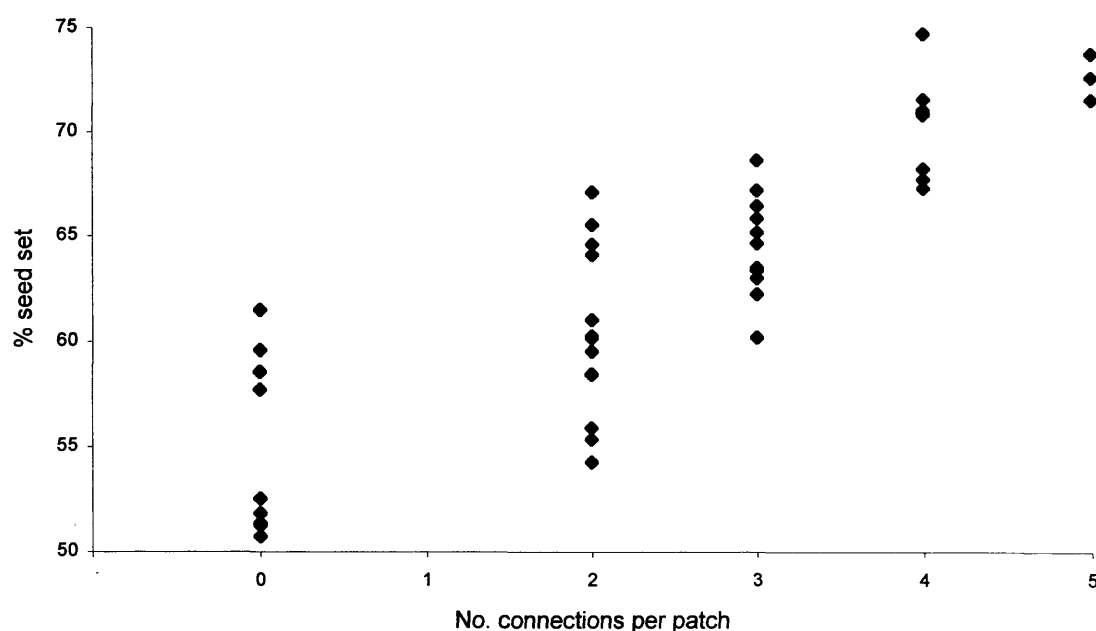


Figure 4.7 The relationship between percentage seed-set per patch and patch connectedness. Pearson correlation: $r = 0.89$, $df = 13$, $p < 0.01$

Table 4.9 Proximity matrix (Pearson correlations) ** = significant at 0.01 (2-tailed).

	No. connections	Mean flwrs	Mean % seed-set	Total pollinators	Mean pollinators	Mean pollen grains	Mean distance between patches
No. connections	.280	.890**	.660**	.415	.761**	-.305	
Mean flwrs	.280		-.003	.407	.239	-.170	-.165
Mean % seed-set	.890**	-.003		.578**	.357	.834**	-.055
Total pollinators	.660**	.407	.578**		.791**	.659**	-.101
Mean pollinators	.415	.239	.357	.791**		.361	.140
Mean pollen grains	.761**	-.170	.834**	.659**	.361		-.165
Mean distance between patches	-.305	-.165	-.055	-.101	.140	-.165	

As well as the previously mentioned correlations with the number of connections, there were significant correlations between mean pollen grains, total pollinators and mean per cent seed-set. Mean distances between patches and flower number per patch had no significant relationships with the other variables (Table 4.9).

Discussion

Flowers

No systematic bias was evident in the general vigour of plants since there were no significant differences in inflorescence or flower number between patches (Tables 4.3 & 4.4). Although the majority of *S. pratensis* flowers are hermaphrodite, male-sterile and intermediate flowers are known to occur (Scott, 1989). Flower type was not measured in this study and it is possible that this factor may have accounted for some of the observed variation in seed production between patches. However, Scott (1989) reported that the incidence of hermaphrodite flowers was approximately 88 - 95% and that even male-sterile plants achieved good seed-set. Flower type should have been evenly distributed around the different patches since all plants were randomly allocated to patches. In this study, flower and inflorescence number were used as a measure of plant vigour and therefore potential fecundity. However, genetic variation between plants may still determine the extent to which the process between pollen deposition, fertilisation and the production of viable seeds is successful. Plant clones could have been used to ensure genetic homogeneity between plants and patches to mitigate against any genetic disparities. Apart from the practical limitations of successfully rearing the required plant quantities within time constraints, genetic variation between plants is a natural phenomenon and the experiment represented the genetic heterogeneity in naturally occurring populations.

Pollinators

A general trend of increasing visitor abundance with greater patch connectedness was apparent when all insects were totalled. When the total numbers of *B. pascuorum* and *B. hortorum* were summed, there was a highly significant relationship between these legitimate pollinators and patch connectedness. No correlation between individual species and patch connectedness was evident. However, plants located in patches with high connectedness, appeared to benefit from an increased pollinator service. This is particularly important for plants that depend upon specific pollinators to set seed.

Although 45 hours of observations were conducted for 15 patches, this equated to only three hours per patch. The time of day at which each patch was sampled was randomised but only snapshots of insect visitation could therefore be recorded. It could not quantify

diurnal variation in pollinator visitation rates. The recording of plant-pollinator interactions often requires many hours of observations in return for relatively little data.

However, the increased pollinator abundance in the highly connected patches does agree with the results from Chapters 2 and 3 that pollinators, particularly bumblebees, were more likely to be observed flying along hedgerows. The increased connectedness of these patches might have increased the permeability of the landscape and made movement across it easier (Baudry & Merriam, 1988).

Although Patch C had no connections, it still received a relatively high visitation rate compared with the other isolated patches. This patch also contained 12 x 25cm diameter pots of *P. tanacetifolia* which were part of another investigation within this project (Chapter 3). It is certainly possible that the nectar rich *P. tanacetifolia* was a contributory factor for the comparatively high visitation rate as many individuals were observed to move between the two plants and forage on both species. However, the mean pollen grains per stigma (Table 4.7) and mean percentage seed-set (Figure 4.7) were relatively low for this patch indicating that pollination was not as successful as the visitation rate might suggest. This was a surprising finding as in all other cases a high visitation rate resulted in high pollen deposition and greater seed-set. Nectar robbing from holes bitten in the base of the corolla tubes could have explained this phenomenon. Scott (1989) reported *B. pascuorum* was a secondary robber using existing holes probably bitten by *B. terrestris* and *B. lucorum*. In this study, although no nectar robbing was directly observed, it might still have occurred as flowers were not systematically examined for holes.

The presence of the *P. tanacetifolia* could have caused a reduction in pollen deposition due to a dilution effect; yet this is unlikely as it was also present in patches A and B and no similar effect was observed there. In all other cases, patches with a high number of connecting hedgerows received higher visitation rates. That the presence of *P. tanacetifolia* possibly influenced a greater visitation rate in this isolated patch suggests that it is not necessarily only the patch's isolation which may affect the plant's attractiveness to pollinators and therefore its reproductive success, but the quality of the surrounding matrix even at relatively small scales. Patch C was an open and sunny site

and contained many plants attractive to pollinators such as *Cirsium* spp., compared with many of the other experimental patches.

Only six individuals were recorded at the isolated 'Blackpool' patch. The plants here also yielded the fewest seeds. This patch was the most isolated in terms of distance to the nearest linear feature (Figure 4.1). The field in which the plants were located had also received a herbicide application a few weeks prior to their planting resulting in very little living vegetation within the whole field. It is unknown if the patch's poor performance might have been a result of its isolated location within the landscape or because there was a lack of vegetation in the vicinity but was probably a combination of these two factors.

It is acknowledged that it is difficult to establish conclusively that the increased bumblebee visitation rates in the highly connected patches were due solely to more connecting hedgerows converging on these patches. Alternative explanations such as the suitability of the surrounding matrix and presence of attractive forage could have provided other reasons to explain the greater pollinator abundance in the highly connected patches (Mustajärvi *et al.*, 2001).

B. pascuorum and *B. hortorum* are the only previously recorded pollinators of *S. pratensis*, (Kwak *et al.*, 1996) having tongue lengths long enough to reach the nectar (8.6mm and 13.5mm, respectively). *B. pratorum* has a much shorter tongue length (7.1mm) (Prÿs-Jones & Corbet, 1991), but was observed visiting the flowers. The individuals observed might have been newly emerged bees merely attempting to feed. Although this can result in pollen transfer, their pollinating ability would depend upon the number of attempts made and the abundance of individuals. *R. campestris* has the longest mouthparts of all the hoverflies (>10mm) and is known to prefer deep throated blue flowers (Gilbert, 1993). The hoverfly was not observed to trip the pollination mechanism but was most often observed alighting on and probing the exposed style in the more mature flowers. Occasionally it would probe on the bottom lip of the flower, possibly drinking from tiny droplets of nectar spilt from a previous visit from a bumblebee. *E. balteatus*, which is known to feed almost exclusively on pollen, was rarely observed feeding. These two hoverfly species may cause some indirect pollen transfer between flowers of *S. pratensis*, but are unlikely to be important pollinators and have not been recorded previously in the literature.

Pollen deposition

There were significantly more pollen grains deposited on the stigmas on flowers within the highly connected patches (Figure 4.6). The high variation in the number of pollen grains attached to each stigma between patches reflects the natural variation of successful pollen transfer (Robertson, 1992) and is probably attributable to the low sample size of fallen flowers collected and examined under the microscope ($n=8 - 10$, Table 4.7). The total mean number of flowers recorded from all patches ranged from 456 - 771 but inspected flowers constituted only 2.2% and 1.3%, respectively, of the total flowers present. However, the higher pollinator visitation rates and greater seed-set recorded in the highly connected patches provide another measure of pollen transfer.

Successful pollination of protandrous, self-compatible flowers depends upon the number of flowers open simultaneously on the same plant, pollinator behaviour and the quantity of pollen transmission (Proctor *et al.*, 1996). Frequently, less than 20% of the insect's pollen load is transferred to each flower it visits (Robertson, 1992). Pollen deposition reduces concomitantly with distance travelled from the source flower (Levin & Kerster, 1974). Yet pollination may still be extensive, albeit highly variable, depending on the amount of pollen carried, the length of visit, pollinator behaviour and flower condition (Pettersson, 1991). Pollen delivery is often the most important limiting factor on flowering plant fecundity due to the wide variation and unpredictability of spatial and temporal abundance of pollinators (Jennersten, 1988; Larson & Barrett, 1999).

Seed-set

Since *S. pratensis* depends upon insect pollination to set seed, it is likely, with the exception of Patch C, that the higher seed yields in the highly connected patches were influenced by the greater abundance of legitimate pollinators (Figure 4.5, Table 4.6) and the increased pollen deposition (Figure 4.6). Although the species can suffer from bud abortion, flower and seed predation, for populations not suffering from inbreeding depression, the most important factor affecting seed-set is pollen limitation (Scott, 1989; Kwak *et al.*, 1996).

The results suggest that these pollinators appear to be concentrated alongside hedgerows. Therefore, where these hedgerows converge, the increased 'pollinator traffic' can have a

beneficial effect on plant reproductive success. In a similar study, *Centaurea jacea* was grown in 15 landscapes around Göttingen, Germany, differing in the proportion of semi-natural habitats. Seed predation and number of flower-visiting bees increased with landscape complexity. There was a positive relationship between flower visitation rate and seed number per undamaged flower heads. However, seed-set did not increase with increasing landscape complexity, possibly due to a concomitant rise in seed predation (Steffan-Dewenter *et al.*, 2001).

In a separate study, further evidence that plant-pollinator interactions are sensitive to habitat fragmentation was recorded by Steffan-Dewenter & Tscharnke (1997) in *Sinapis arvensis* and *Raphanus sativus*. Forty small patches of these self-incompatible species were planted at increasing distances away from eight species-rich chalk grasslands. For both species, the diversity and abundance of flower visiting bees declined at increasing distances away from the established grasslands, whereas other insect groups did not change. Seed-set followed a similar trend with *R. sativus* evidently more vulnerable to habitat fragmentation with a 50% reduction in seed-set at just 260m (Steffan-Dewenter & Tscharnke, 1997).

In a three-year study, Murren (2002) reported conflicting results of the effects of habitat fragmentation on the epiphytic orchid *Catasetum viridiflavum* in the tropical biome of Central America. The orchid depends upon the endemic, euglossine bee *Eulaema cingulata* for reproductive success. The study examined the orchids' pollinators, pollinia viability and reproductive success on ten island fragments created during the construction of the Panama Canal, compared with those on five mainland sites. Although there was no difference in the frequency of bees on both the islands and the mainland sites, all trapped bees were visitors from the mainland sites. Island plants suffered significantly lower fruit set for two out of three years compared with those from mainland sites. However, for one year (an El Niño year) there were no significant differences in the reproductive success between each habitat type suggesting a degree of connectedness between sites. The dramatic variations between sites and years demonstrate the need for longitudinal studies in such situations to allow for temporal variations in environmental conditions before more reliable summations about the effects of habitat fragmentation on pollinators and plant reproductive success may be drawn.

Rocha & Aguilar (2001) demonstrated that pollinator visitation and pollen deposition were reduced in discontinuous habitat. They reported that the reproductive biology of the dry forest tree *Enterolobium cyclocarpum* was disrupted by habitat fragmentation. Trees in continuous forest habitats had more pollen deposited on their flowers, produced greater fruit and seed-set and the vigour of seedlings was greater than in those trees existing in pasture habitat.

It is highly unlikely that the positive correlation of seed-set and connectedness could have occurred merely as a result of greater densities of legitimate pollinators naturally present in the locality. Patches with both high and low connectedness were located relatively close to each other (Figure 4.1, Table 4.9), but still yielded dissimilar seed-set results. Observation walks revealed no evidence of bumblebee nests located within any of the patches, providing more support that it was the greater number of converging hedgerows which was the most important factor explaining the higher seed-set. However, recent evidence suggests that bees do not forage close to their nests anyway (Osborne *et al.*, 1999; Saville *et al.*, 1997).

Plant reproductive success was measured in this investigation by quantifying seed production. However, the quality of seed production was not assessed. The plant was used as a convenient tool to indicate pollinator visitation. Seed viability and germination success would be more appropriate in studies measuring the reproduction of *S. pratensis* populations within the landscape. It is acknowledged that seed production only accounts for female reproduction and that this experiment has not considered the male component of pollen production and dispersal. However, the fertility of *S. pratensis per se* was not being examined in this study. The plants were used as bioindicators of pollinator visitation within the landscape. Even if pollen dispersal was poor, sufficient pollen was distributed by pollinators to produce a significant correlation between seed-set and highly connected patches.

Implications for the conservation of plant-pollinator interactions

The results from this investigation have implications for both plant and insect conservation. The mutual relationship between *S. pratensis* and bumblebees exemplifies many plant-pollinator interactions and reflects the problems involved in their conservation (Fisher, 1998). The rare *S. pratensis* depends upon relatively few species of

insect, principally long-tongued bumblebee species for its reproductive success. The nectar-rich flowers provide an energy source to sustain colonies of bumblebees. These important pollinators are themselves becoming rarer, partly as a result of reduced availability of nectar-rich flowers throughout their life-cycle (Williams, 1982; Prŷs-Jones & Corbet, 1991; Osborne *et al.*, 1991; Benton, 2000; Corbet, 2000). An inevitable cycle of decline compounds the problem of rarity in both guilds (Kearns & Inouye, 1997).

Only two bumblebees (*B. hortorum* and *B. pascuorum*) were observed to pollinate the specialised *S. pratensis*. These findings agree with Kwak *et al.* (1996) who studied the relationship between the pollination of rare plant species and insect diversity in the Netherlands. *B. hortorum* is declining in the Netherlands and is predicted to disappear soon leaving *B. pascuorum* as the only remaining legitimate pollinator. However, the existence of the species is not enough to ensure survival of *S. pratensis* since the presence of *B. pascuorum* workers must coincide with the flowering phenology the plant. Very few workers were observed during their study and no other insect groups are known to pollinate the plant (Kwak *et al.*, 1996).

The well documented national declines in bumblebee abundance and localised species' extinctions have been attributed to a reduction in food and nest sites as a consequence of agricultural intensification and changes in land use (Osborne *et al.*, 1991; Banaszak, 1996; Westrich, 1996). Pollination of both wild flowers and entomophilous crops are being compromised (Free, 1993). Sowing nectar and pollen-rich plants in non-cultivated land can ameliorate the adverse effects of an impoverished farmland. For example, Banaszak (1983) and Kwak *et al.* (1996) identified a positive relationship between food plant diversity and insect diversity. Wildflower mixtures sown in set-aside or conservation headlands produce a profusion of flowers and attract a wide variety of pollinators and other beneficial insects (Hickman & Wratten, 1996; Carreck, *et al.*, 1999; Frank, 1999; Ullrich & Edwards, 1999). Whilst such flowers have obvious benefits for the target insects, Kevan & Baker (1984) suggested that the more invasive plant species incorporated within the wildflower mixtures may outcompete those rarer plants requiring conservation by attracting more pollinators to the detriment of the rarer plants. Keller *et al.* (2000) warned that native plant populations may also be at increased risk of genetic introgression of foreign genes from wildflower mixtures. Only plants of relatively local origin should be used within such seed mixtures.

The successful implementation of these conservation strategies demands that they be agronomically practical and inexpensive (Carreck *et al.*, 1999). The results from this study indicate that the siting of wildflower mixtures might be more beneficial in areas of land with high connectivity.

Habitat fragmentation and destruction can cause dramatic changes in the size and spatial structure of plant populations (Elstrand & Elam, 1993; Oostermeijer *et al.*, 2000) affecting complex ecological interactions (Rathcke & Jules, 1993; Fisher, 1998). Small, more isolated populations are more vulnerable to chance events and local extinction (Young *et al.*, 1996). The results from this study suggest that an examination of the landscape context in which the threatened plant species grows would contribute to an understanding of how it persists, allowing more appropriate conservation strategies to be applied.

The importance of landscape scale research in plant-pollinator interactions has only recently started to be addressed (Steffan-Dewenter & Tschardtke, 1997; Steffan-Dewenter *et al.*, 2001). Too often, investigations have focused upon small-scale interactions, or species in isolation. A multi-disciplinary research approach is required if the application of conservation management strategies is to be optimised (Bronstein, 1995; Dramstad & Fry, 1995; Corbet, 1997; Allen-Wardell *et al.*, 1998). This investigation has monitored plant-pollinator interactions over the landscape-scale and demonstrated that the spatial arrangement of linear features can influence bumblebee visits and plant fecundity.

Conclusions

This chapter has shown that total insect visitor abundance was greater in the more highly connected patches. In the majority of cases, as a result of the greater number of legitimate pollinators, more pollen was transferred to flower stigmas, which in turn led to greater seed-set. There was no correlation between individual insect species abundance and increasing patch connectedness. Yet when the abundance of the two legitimate pollinators (*B. pascuorum* and *B. hortorum*) was totalled, there was a highly significant positive relationship between pollinator abundance and patch connectedness.

There was great variation in the number of pollen grains adhering to the stigmas both within and between patches. Although this reflected the natural variation in pollen deposition, the observed variation was probably more likely to be attributable to the small sample size of flowers analysed. The plants chosen for this study required bumblebee visitation to set seed. The recorded seed-set was therefore directly attributable to the activity of bumblebees. The connectedness of the landscape may therefore have important implications for the movement of insects across the landscape and the maintenance of plant and pollinator populations, especially where the plant is dependent upon a particular pollinator to set seed.

Although it was not the aim of this study to assess outcrossing rates and gene flow between the plants located in the different habitat patches, it would have provided an insight into the scale of bumblebee movements and how much pollen was being transferred between patches. Without genetic markers, this is impossible to ascertain since the species is self-compatible. The more extensive the spatial scale of pollen transfer in this landscape then the more likely populations of this rare plant could maintain genetic heterozygosity (Ouborg & van Treuren, 1994).

The next chapter summarises the conclusions from this project. It consolidates the results and conclusions from each of the experimental chapters and discusses some of the implications, limitations and improvements for developing fruitful areas for further research.

Summary

The typical arable landscape of lowland Britain is characterised by numerous linear features such as hedgerows, roadside verges and drainage ditches, which are important habitats for wildlife (Clements & Tofts, 1992a; Kirby, 1995). Previous fieldwork had suggested that artificial linear features did influence pollinator flight behaviour and that hedgerows appeared to facilitate pollinator movement across the landscape (Chapters 2 and 3). Therefore, plants in semi-natural habitat patches possessing numerous connections, might receive greater pollinator visitation than those patches with few or no connecting hedgerows. A bioindicator experiment was designed to elucidate the relationship between the reproductive successes of *Salvia pratensis* (Labiatae) growing in patches with a high number of connections compared with plants growing within poorly connected patches. The results suggested that pollinator abundance, pollen grains per stigma and seed-set were greater in highly connected patches compared with patches with fewer connections. The overall connectedness of a landscape may therefore be important to both pollinators and those plants which depend on them for reproduction.

Chapter 5: Conclusions

This thesis has examined the way in which linear landscape features influence pollinator flight behaviour, concentrating on hedgerows. Although bees and butterflies have been the subject of intensive study by researchers, there was a dearth of information on how these insects interacted with linear landscape elements and how this may affect their movement through the landscape. By using a combination of direct observation and experimental manipulation, this study has provided further insight into the way in which linear features can modify pollinator flight directionality.

One of the dominant landscape features within lowland agricultural Britain is the hedgerow network. Their widespread distribution permeates the farmland matrix increasing the structural and biotic heterogeneity in an otherwise unsuitable agricultural environment (Forman & Baudry, 1984; Clements & Tofts, 1992a; Baudry & Bunce, 2001). The results from Chapter 2 showed that linear flight of non-foraging bumblebees (*Bombus* spp.) and butterflies was far more likely to occur adjacent to the hedgerow than in the open fields, which they bordered. Since these insects were not searching for food, it was postulated that pollinators may have been using the hedgerows as landmarks in which to orient their movement through the landscape. It was therefore suggested that landscapes rich in hedgerow networks are likely to exert a greater effect on insect flight directionality, than in less well connected landscapes that contain sparser hedgerow complexes. Fruitful areas for further research might involve a ‘before and after’ scenario where observations recorded along the length of an artificial linear feature are then compared with observations in the same location, following removal of the linear feature. This would indicate whether the presence of the linear feature was a factor explaining the observed pollinator flight activity. Another variation on the observations of pollinator flight along hedgerows in this investigation could have involved selecting a hedgerow with another hedgerow parallel to the first, in the same field. Observations could have continued, perpendicular to the first hedgerow, across the field to the other hedgerow. Not only would this have given more information about flight directionality in relation to hedgerows in the same locality but it might also have revealed patterns of possible attenuation of linear flight directions and abundance between the two parallel hedgerows.

The results from this first investigation generated many questions such as: Is the structure of the linear feature important? Does it have to be two or three dimensional? Would stone walls, roads, ditches or canals etc. exert the same effect? Can linear features facilitate or enhance movement of pollinators across the landscape? What are the implications for both insects and plants? In a heavily fragmented landscape, can linear features connect otherwise isolated patches and augment pollination, seed set and gene flow?

The investigation in Chapter 3 sought to answer some of these questions, using a medium-scale experimental array with artificial linear features thus connecting two patches of potted *Phacelia tanacetifolia* (Hydrophyllaceae) leaving one patch isolated. This attempted to produce a more controlled environment in which to address insect flight behavioural responses to linear features. Would the observed linear flight directions along hedgerows recorded in the field observations in Chapter 2 be replicated in an artificial arena?

The results demonstrated that most of the artificial linear features were used by bumblebees, both to approach and depart the connected patches. These findings confirmed the field observations from Chapter 2 that linear features appeared to influence flight behaviour. The black weed control fabric used in the two and three dimensional artificial linear features influenced bumblebee flight directionality, whilst the measuring tapes had no observable effect. Even though the isolated patch was the same distance away, arriving bumblebees did not appear to approach it directly from the other two connected patches. The same pattern also applied to departing bumblebees. The artificial features had a profound influence on bumblebee flight directionality when foraging on these three patches. Altering the position of the linear feature to link two different patches confirmed that it was the linkage component between the patches that affected flight behaviour rather than any inherent differences in the attractiveness of the patches themselves, or their location within the landscape. The number of individuals observed making the flights was relatively small compared with the number of actual flights made. However, the experiment was repeated several times using different artificial features and in two separate years with consistent results.

The results from the present study clearly indicated that a linear feature could strongly influence flight directionality at the medium-scale. It was then necessary to conduct the investigation at the landscape scale using an existing hedgerow as the connecting structure (Chapter 3). The outcome of this experiment accorded with those at the medium-scale. The presence of the hedgerow appeared to affect bumblebee approaches and departures to the connected patches. Because of the distances involved, it was not possible to observe direct bumblebee movement between the connected patches. However, until out of sight, bumblebees were significantly more likely to arrive and depart the connected patches, using the hedgerow, than in any other direction. Furthermore, it was more probable that bumblebees marked on each of the connected patches would be reobserved on each of the connected patches than on the isolated patch.

One very important finding from the medium-scale experiments was that visitation rates to the isolated patches were not necessarily lower than those to the connected patches. This illustrates that approximately the same numbers of bumblebees were visiting all three patches but it was the direction of inter-patch movements which was influenced by the linear feature. In three of out five of the medium-scale experiments, there were no significant differences between visitation rates to the connected and unconnected patches. Yet when the data for the marked bees only were analysed separately, the connected patches were visited more than the isolated one. There was no explicit evidence that the insular patches were disadvantaged in terms of bumblebee visitation due to their lack of connection to the other patches at thirty metres. However, in the landscape scale study, it was interesting to note that visitation rates to the isolated patch were significantly smaller than those to the two connected patches. Furthermore, the marked bees observed visiting the isolated patch were largely comprised of a different set of bees from the ones visiting the connected patches. Approximately 90 - 95% of bees marked on patches A and B were reobserved on the connected patches with the few remaining, visiting the isolated patch. The reciprocal pattern of patch visitation was also recorded for patch C. In each of the six experiments, individual bees displayed high forage patch fidelity, which is consistent with other studies (Dramstad, 1996; Saville *et al.*, 1997). Bees marked on a particular patch were far more likely to be reobserved foraging on that patch than on any other. One major drawback of assessing differences in visitation rates between the patches is that the bees were marked whilst they were foraging, rather than at the nest. Since it is well documented that bumblebees exhibit high rates of patch constancy whilst foraging,

marking of nectaring bees will inevitably reflect their favoured patches (Goulson, 2003). However, the viability of this technique was valuable in showing the flight directions of individual bees.

A number of different designs could have been incorporated into the medium-scale experimental arrays, one of which could have included four flower patches, two of which were connected and two left isolated. In the present study, there was only one isolated patch. Having another isolated patch would have made the experiment more balanced and allowed some broader comparisons of flight directionality and visitation rates between the isolated patches. Secondly, an array involving an artificial linear feature terminating with only one patch might have revealed whether bumblebees might have associated the linear feature with a food source. Any number of differing combinations of patches and linear features might have been used to test different hypotheses. However, within the limited fieldwork time available, the design used in this experiment did demonstrate directional movement along the linear feature's length.

In all six experiments in Chapter 3, hoverfly (Syrphidae) abundance on all three patches was not significantly different and numbers did not appear to be affected by the presence of the connecting linear feature. Because of time constraints only one 'snapshot' count of individuals was taken on each day. More frequent counts would have generated a bigger data set, which would have allowed comparisons to be made within, as well as between, each day. Flight directions of these flies are extremely difficult to follow by eye due to their small size and rapid, darting movements. It would have been very interesting to gain information on their flight directions in response to the artificial linear features. New technology such as harmonic radar currently used to track bees and butterflies (Osborne *et al.*, 1999) may well be adapted to follow hoverfly flights in the future. Information on hoverfly movement through the landscape would be invaluable as they are known to be highly mobile and potentially good environmental bioindicators at large scales (Sommaggio, 1999). Although their distribution across a range of habitats has been studied, their assemblages are likely to reflect their particular habitat requirements (Gilbert, 1993; Morris, 1998). Some species are strong fliers and highly territorial but little is known of the distances they fly on a daily basis. Hoverfly movements are likely to differ greatly from that of social insects, where foraging is solely for individual survival rather than for the benefit of a colony.

In some of the medium-scale experiments, the isolated patches received significantly fewer bumblebee visits than the connected patches. These, together with the findings of the landscape scale study, might have important implications for plant fecundity in those populations existing in fragmented landscapes. Habitat fragmentation has frequently been cited as being a significant detrimental factor in the decline of many specialist plant populations (Rathcke & Jules, 1993; Young *et al.*, 1996; 1999; Kearns *et al.*, 1998). If linear features do facilitate pollinator movement across the landscape then some quantification of bumblebee-mediated pollen transfer may give some indication as to the functional role of these landscape elements in improving connectivity of plant populations within fragmented landscapes. Seed set as a measure of fecundity might provide some tangible evidence of a landscape's connectivity having an effect on a plant's reproductive success. This was assessed in a bioindicator experiment in Chapter 4 where *Salvia pratensis* (Labiatae) was planted in 15 different patches around the farm study area, all varying in their connectedness to existing hedgerows. Pollinator visits, pollen deposition and seed-set were all significantly greater on plants in those patches with high connectedness to hedgerows. Confidence in these results was particularly strong since the plant is dependent on bumblebee visitation to set seed and so the higher reproductive success found in the highly connected patches was directly attributable to the higher bumblebee visitation rates recorded. Secondly, the plant had previously been recorded as an extinct species from the county in which the investigation took place, there were consequently no other populations which might have 'donated' pollinators.

The maintenance of genetic heterogeneity is a fundamental factor determining the existence of plant populations within the landscape (Kwak *et al.*, 1996; Young *et al.*, 1996). Interesting areas of further research involving the measurement of gene flow between habitat patches would provide further insights into the effects of landscape connectivity on plant-pollinator interactions. Studies of pollinator and gene movement across the landscape, using genetic markers in *Trifolium repens* and *Cirsium arvense*, are currently under investigation by Elizabeth Cant at Rothamsted Research (unpublished). The measurement of gene flow in Chapter 4 would have helped to elucidate the larger spatial scale of successful pollen transfer between the 15 different patches of *S. pratensis*. The experiment focused solely on the relationship between a patch's connectedness and the reproductive success of the plants within it. Since the plants were self-compatible, it

was not known whether the plants were fertilised by pollen originating from within the patch or from other patches. Genetic markers would have been invaluable in assessing the effects of distance and connectedness on inter-patch pollinator movements and gene flow.

The inherent difficulties of making direct observations of insect movements within the landscape have no doubt been a contributory factor to the lack of research in this area. However, advancements in new technology may offer more opportunities to address these questions.

When all the fieldwork investigations conducted within this project are combined, a more complete picture of pollinator flight within the landscape has emerged. The project has examined a wide variety of issues pertaining to the influence of linear landscape features on pollinator behaviour. This holistic approach is a theme which is increasingly being recognised by researchers who stress the importance of the use of appropriate spatial scales in relation to the plant-pollinator landscape (Lima & Zollner, 1996; Steffan-Dewenter, 2003).

Fieldwork has focused on pollinator behaviour and responses to both artificial experimental arrays and natural hedgerows. Such a complex issue necessarily encompasses discussion on a multitude of disciplines such as insect vision, their cognitive and navigational skills and animal movement at the landscape scale. The genetic consequences of this pollinator service within the context of landscape connectivity, have been addressed, as population stability within fragmented habitats is a recurrent theme within landscape ecology. The overall results of this project concur with many studies which have found evidence that insects are influenced by structures and patterns both at the small-scale (Plowright & Galen, 1985; Dafni *et al.*, 1997; Horridge, 1996; 2003) and at the landscape scale (Chittka & Geiger, 1995; Chittka *et al.*, 1995b; Wehner *et al.*, 1996; Dover & Fry, 2001; Westphal *et al.*, 2003).

In the light of the documented declines of pollinator diversity (Williams, 1986; O'Toole, 1993; Westrich, 1996) and widespread habitat fragmentation in lowland Britain, the effects of linear features on pollinator movement within a fragmented landscape have never been more important. The results gained from this study contribute to an expanding

knowledge base of animal movements within the landscape. The conservation of pollination systems is far more likely to be effective at habitat or landscape levels where a wider view of the influences on plant-pollinator interactions can be taken (Corbet, 1997). At a time when the complexity of ecological interactions is only just being understood, it is becoming increasingly clear that landscape level processes can play a role in affecting plant-pollinator relationships.

Context of this study

This study encompasses the disciplines of landscape ecology, conservation biology, behavioural and pollination ecology. It is evident from the literature that large knowledge gaps exist when these specialities are combined (Lima & Zollner, 1996). Until relatively recently, pollinator research has mainly focused upon small-scale studies of foraging behaviour but with little information on the way in which this relates to the landscape. The landscape ecology literature has increasingly addressed connectivity, but studies on direct measurement of movement corridors lack clarity or suffer from poor experimental design, and in any case, insect studies within the landscape are poorly represented (Beier & Noss, 1998). Bronstein (1995) emphasised the importance of pollinator movement within the landscape, which is particularly pertinent in view of continuing declines in pollinator diversity and abundance and of continuing fragmentation in lowland Britain.

The results of this study contribute knowledge to the way in which particular linear landscape features influence the flight behaviour of pollinators. The findings have implications for the conservation management of plant and pollinator populations. It also provides a greater understanding of the way in which crop and wild flower pollination is influenced by landscape structure, and potential extent of pollen transfer. It attempts to consolidate knowledge from previously disparate ecological specialisms to provide a realistic picture of the way in which insects travel through the landscape and investigate which factors influence such movements.

References

Ågren, J (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology*, **77**, 1779-1790.

Alerstam, T (1990). *Bird Migration*. Cambridge: Cambridge University Press.

Allen-Wardell, G; Bernhardt, P; Bitner, R; Burquez, A; Buchmann, S; Cane, J; Cox, PA; Dalton, V; Feinsinger, P; Ingram, M; Inouye, D; Jones, EJ; Kennedy, K; Kevan, P; Koopowitz, H; Medellin, R; Medellin-Morales, S; Nabhan, GP; Pavlik, B; Tepedino, V; Torchio, P & Walker, S (1998) The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology*, **12** (1), 8-17.

Andreassen, HP; Halle, S & Ims, RA (1996) Optimal width of movement corridors for root voles: not too narrow and not too wide. *Journal of Applied Ecology*, **33**, 63-70.

Andrews, J (1993) The reality and management of wildlife corridors. *British Wildlife*, **5** (1), 1-7.

Appelqvist, T; Gimdal, R & Bengtson, O (2001) Insects and mosaic landscapes. *Naconex*, 14-24, [online] URL: http://www.pro-natura.net/naconex/news5/E1_2.pdf

Auestad, A; Norderhaug, A & Austad, I (1999) Road verges – species-rich habitats. *Aspects of Applied Biology*, **54**, 269-274.

Baillie, SR; Gregory, RD & Siriwardena, GM (1997) Farmland bird declines: patterns, processes and prospects. In: Kirkwood, RD (Ed). *Biodiversity and Conservation in Agriculture*. BCPC Symposium Proceedings No. 69. Farnham: British Crop Protection Council, 65-87.

Banaszak, J (1983) Ecology of bees (Apoidea) of agricultural landscape, *Polish Ecological Studies*, **9** (4), 421-505.

- Banaszak, J (1996) Ecological bases of conservation of wild bees. *In*: Matheson, A; Buchmann, SL; O'Toole, C; Westrich, P & Williams, IH (Eds). *The Conservation of Bees*. London: Academic Press for The Linnean Society of London and The International Bee Research Association, 55-62.
- Bankowska, R (1980) Fly communities of the family Syrphidae in natural and anthropogenic habitats of Poland. *Memorabilia Zoologica*, **33**, 3-93.
- Barr, CJ & Gillespie, MK (2000) Estimating hedgerow length and pattern characteristics in Great Britain using Countryside Survey data. *Journal of Environmental Management*, **60** (1), 23-32.
- Barr, CJ; Bunce, RGH; Clarke, RT; Fuller, RM; Furse, MT; Gillespie, MK; Groom GB; Hallam, CJ; Hornung, M; Howard, DC; Ness, MJ (1993) *Countryside Survey 1990: Main Report*. Volume 2. London: Department of the Environment.
- Barr, CJ; Howard, DC; Bunce, RGH; Gillespie, MK & Hallam, CJ (1991) *Changes in hedgerows between 1984 and 1990*. ITE Contact Report to the Department of the Environment. Grange-over-Sands: Institute of Terrestrial Ecology.
- Bascompte, J; Jordano, P; Melián, CJ & Olesen, JM (2003) The nested assembly of plant-animal mutualistic networks. *PNAS*, **100** (16) 9383-9387.
- Baudry, J & Bunce, RGH (2001) An overview of the landscape ecology of hedgerows. *Hedgerows of the World, IALE (UK) 2001*, 3-16.
- Baudry, J & Merriam, G (1988) Connectivity and connectedness: functional versus structural patterns in landscapes. *In*: Schreiber, KF (Ed). *Connectivity in Landscape Ecology*. Proceedings of the 2nd International Seminar of the International Association for Landscape Ecology. Munster: Münstersche Geographische Arbeiten **29**, 23-28.
- Begon, M; Harper, JL & Townsend, CR (1990) *Ecology: Individuals, Populations and Communities*. (2nd ed.) Oxford: Blackwell Scientific Publications.

- Beier, P & Noss, RF (1998) Do habitat corridors provide connectivity? *Conservation Biology*, **12** (6) 1241-1252.
- Bellamy, PE; Shore, RF; Ardesir, D; Treweek, JR and Sparks, TH (2000) Road verges as habitat for small mammals in Britain. *Mammal Review*, **30** (2), 131-139.
- Benton, T (2000) *The Bumblebees of Essex*. Wimbish: Lopinga Books.
- Berthold, P (1993) *Bird Migration: A General Survey*. Oxford: Oxford University Press.
- Bhattacharya, M; Primack, RB & Gerwein, J (2003) Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biological Conservation*, **109**, 37-45.
- Bissonette, JA & Storch, I (2002) Fragmentation: is the message clear? *Conservation Ecology*, **6** (2):14. [online] URL: <http://www.consecol.org/vol6/iss2/art14>
- Bond, DA & Pope, M (1974) Factors affecting the proportions of cross-bred and self-bred seed obtained from field bean (*Vicia faba* L.) crops. *Journal of Agricultural Science*, **83**, 343-351.
- Boots, AJ (2001) The effect of connection to woodlands on the woody species composition of hedgerows: a case study on the Mendip Hills plateau, North Somerset. *Hedgerows of the World, IALE (UK) 2001*, 157-162.
- Bowers, MA (1985) Bumblebee colonisation, extinction and reproduction in subalpine meadows in northeastern Utah. *Ecology*, **66** (3), 914-927.
- Bowie, MH; Gurr, GM; Hossain, Z; Baggen, LR & Frampton, CM (1999) Effects of distance from field edge on aphidophagous insects in a wheat crop and observations on trap design and placement. *International Journal of Pest Management*, **45** (1), 69-73.

- Brandt, J (1998) Key concepts and inter-disciplinarity in landscape ecology: a summing-up and outlook. *In: Dover, JW & Bunce, RGH (Eds). Key Concepts in Landscape Ecology*. IALE (UK), 421-434.
- Brian, AD (1954) The foraging of bumble bees. Part 1: Foraging behaviour. *Bee World*, **35** (4) 61-67.
- Bright, PW (1998) Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. *Animal Behaviour*, **56**, 1485-1490.
- Briscoe, AD & Chittka, L (2001) The evolution of colour vision in insects. *Annual Review of Entomology*, **46**, 471-510.
- Brittain, WH & Newton, DE (1933) A study in the relative constancy of hive bees and wild bees in pollen gathering. *Canadian Journal of Research*, **9**, 334-349.
- Bronstein, JL (1994) Our current understanding of mutualism. *Quarterly Review of Biology*, **69**, 31-51.
- Bronstein, JL (1995) The plant-pollinator landscape. *In: Hansson, L; Fahrig, L & Merriam, G (Eds). Mosaic Landscapes and Ecological Processes*. London: Chapman & Hall, 256-288.
- Buchmann, SL & Nabhan, GP (1996) *The Forgotten Pollinators*. Washington: Island Press/Shearwater Books, 274.
- Bunce, RGH; Howard, DC; Barr, CJ; Cummins, RC & French, D (1994) Botanical diversity in British hedgerows. *In: Boatman, N (Ed). Field Margins: Integrating Agriculture and Conservation*. British Crop Protection Monograph No. 58. Farnham: British Crop Protection Council, 43-52.
- Burel, F (1989) Landscape structure effects on carabid beetles spatial patterns in western France. *Landscape Ecology*, **2** (4), 215-226.

- Burel, F (1996) Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences*, **15** (2), 169-190.
- Calabuig, I (2000) Solitary bees and bumblebees in a Danish agricultural landscape. PhD-Thesis, University of Copenhagen, Department of Population Ecology.
- Cant, L (unpublished) *Do linear features within the landscape influence pollinator movement and consequent plant gene flow?* Rothamsted Research, Harpenden, UK.
- Carreck, NL & Williams, IH (1997) Observations on two commercial flower mixtures as food sources for beneficial insects in the UK. *Journal of Agricultural Science*, **128**, 397-403.
- Carreck, NL & Williams, IH (2002) Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation*, **6**, 13-23.
- Carreck, NL; Williams, IH & Oakley, JN (1999) Enhancing farmland for insect pollinators using flower mixtures. *Aspects of Applied Biology*, **54**, 101-108.
- Chapman, J & Sheail, J (1994) Field margins - An historical perspective. In: Boatman, N (Ed). *Field Margins: Integrating Agriculture and Conservation*. British Crop Protection Monograph No. 58. Farnham: British Crop Protection Council, 3-12.
- Charlesworth, D & Charlesworth, B (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics*, **18**, 237-268.
- Charrier, S; Petit, S & Burel, F (1997) Movements of *Abax parallelepipedus* in woody habitats of a hedgerow network landscape: a radio-tracing study. *Agriculture, Ecosystems & Environment*, **61**, 133-144.
- Chittka, L & Geiger, K (1995) Can honey bees count landmarks? *Animal Behaviour*, **49**, 159-164.

- Chittka, L & Tautz, J (2003) The spectral input to honeybee visual odometry. *The Journal of Experimental Biology*, **206**, 2393-2397.
- Chittka, L & Thomson, JD (2001) Pollinator individuality: when does it matter? *In*: Chittka, L & Thomson, JD (Eds). *Cognitive Ecology of Pollination*. Cambridge: Cambridge University Press, 191-213.
- Chittka, L (2001) Camouflage of predatory crab spiders on flowers and the colour perception of bees (Aranida: Thomisidae/Hymenoptera: Apidae). *Entomologia Generalis*, **3**, 181-187.
- Chittka, L; Geiger, K & Kunze, J (1995b) The influences of landmarks on distance estimation of honeybees. *Animal Behaviour*, **50**, 23-31.
- Chittka, L; Kunze, J; Shipman, C & Buchmann, SL (1995a) The significance of landmarks for path integration in homing honeybee foragers. *Naturwissenschaften*, **82**, 341-343.
- Chittka, L; Williams, NM; Rasmussen, H & Thomson, JD (1999) Navigation without vision: bumblebee orientation in complete darkness. *Proceedings of the Royal Society of London*, **266**, 45-50.
- Clements, DK & Tofts, RJ (1992a) Hedges make the grade - a look at the wildlife value of hedges. *British Wildlife*, **4** (2), 87-95.
- Clements, DK & Tofts, RJ (1992b) *Hedgerow Evaluation and Grading System (HEGS): A Methodology for the Ecological Survey, Evaluation and Grading of Hedgerows*. Cirencester: Countryside Planning and Management.
- Colley, MR & Luna, JM (2000) Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environmental Entomology*, **29** (5), 1054-1059.

- Congreve, AR (2001) The future for hedgerow protection in England and Wales. *Hedgerows of the World, IALE (UK) 2001*, 355-360.
- Corbet, SA (1995) Insects, plants and succession: advantages of long-term set-aside. *Agriculture, Ecosystems & Environment*, **53**, 201-217.
- Corbet, SA (1997) Role of pollinators in species preservation, conservation, ecosystem stability and genetic diversity. *Acta Horticulturae (ISHS)*, **437**, 219-230.
- Corbet, SA (2000) Conserving compartments in pollination webs. *Conservation Biology*, **14** (5), 1229-1231.
- Corbet, SA; Fussell, M; Ake, R; Fraser, A; Gunson, C; Savage, A; Smith, K (1993) Temperature and the pollinating activity of social bees. *Ecological Entomology*, **18**, 17-30.
- Corbet, SA; Williams, IH & Osborne, JL (1991) Bees and the pollination of crops and wild flowers in the European Community. *Bee World*, **72** (2), 47-59.
- Corbit, M; Marks, PL & Gardescu, S (1999) Hedgerows as habitat corridors for forest herbs in central New York, USA. *Journal of Ecology*, **87**, 220-232.
- Corke, D (1997) *The butterflies of Essex*. Wimbish: Lopinga Books.
- Countryside Survey (2000) Linear boundary feature table L3.2 - Summary groups, stock in 1998. [online] URL: http://www.cs2000.org.uk/M01_tables/reports/linlev1nov0198.html
- Cowgill, SE; Wratten, SD & Sotherton, NW (1993) The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. *Annals of Applied Biology*, **122** (2), 223-231.
- Cranmer, L (unpublished) *Pollinator diversity along hedgerows*. University College Northampton, UK.

- Crawley, MJ (Ed.) (1986) *Plant Ecology*. Oxford: Blackwell Scientific Publications.
- Cresswell, JE (2000) A comparison of bumblebees' movements in uniform and aggregated distributions of their forage plant. *Ecological Entomology*, **25**, 19-25.
- Croxton, PJ; Carvell, C; Mountford, JO & Sparks, TH (2002) A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. *Biological Conservation*, **107**, 365-374.
- Cushman, JH & Beattie, AJ (1991) Mutualisms: assessing the benefits to hosts and visitors. *Trends in Ecology & Evolution*, **6**, 193-195.
- Dafni, A; Lehrer, M & Kevan, PG (1997) Spatial flower parameters and insect spatial vision, *Biological Review*, **72**, 239-282.
- Davidson, C (1998) Issues in measuring landscape fragmentation. *Wildlife Society Bulletin*, **26**, 32-37.
- DEFRA (2003) Table 3.1: Agricultural land use. [online] URL: <http://www.defra.gov.uk/esg>
- Denys, C & Tscharntke, T (2002) Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, **130**, 315-324.
- D'Eon; RG; Glenn, SM; Parfitt, I & Fortin, MJ (2002) Landscape connectivity as a function of scale and organism vagility in a real forested landscape. *Conservation Ecology*, **6** (2), [online] URL: <http://www.consecol.org/vol6/iss2/art10>.
- Department for Transport (2001) Transport statistics bulletin, Statistics Report SB (02) 23. *Road traffic statistics: 2001*, 23.
- Dicks, LV; Corbet, SA & Pywell, RF (2002) Compartmentalisation in plant-insect flower visitor webs. *Journal of Animal Ecology*, **71**, 32-43.

- Doubleday, OP; Clark, A & McLaughlin, B (1994) Hedges - A farmer's view. *In*: Boatman, N (Ed). *Field Margins: Integrating Agriculture and Conservation*. British Crop Protection Monograph No. 58. Farnham: British Crop Protection Council, 377-384.
- Dover, JW & Fry, GLA (2001) Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape. *Entomologia Experimentalis et Applicata*, **100**, 221-233.
- Dover, JW & Sparks, TH (2000) A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management*, **60**, 51-63.
- Dover, JW & Sparks, TH (2001) Green lanes: biodiversity reservoirs in farmland? *Hedgerows of the World, IALE (UK) 2001*, 241-250.
- Dover, JW (1990) Butterflies and wildlife corridors. *The Game Conservancy Review*, 21-64 (Fordingbridge, The Game Conservancy Trust).
- Dover, JW (1996) Factors affecting the distribution of Satyrid butterflies on arable farmland. *Journal of Applied Ecology*, **33**, 723-734.
- Dover, JW; Clarke, SA & Rew, L (1992) Habitats and movement patterns of satyrid butterflies (Lepidoptera: Satyridae) on arable farmland. *Entomologist's Gazette*, **43**, 29-44.
- Dover, JW; Sotherton, N & Gobbett, K (1990) Reduced pesticide inputs on cereal field margins: the effects on butterfly abundance. *Ecological Entomology*, **15**, 17-24.
- Dover, JW; Sparks, TH; Clarke, S; Gobbett, K & Glossop, S (2000) Linear features and butterflies: the importance of green lanes. *Agriculture, Ecosystems & Environment*, **80**, 227-242.

- Dramstad, WE & Fry, G (1995) Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agriculture Ecosystems & Environment*, **53** (2), 123-135.
- Dramstad, WE (1996) Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behaviour*, **9** (2), 163-182.
- Dramstad, WE; Fry, GLA & Schaffer, MJ (2003) Bumblebee foraging - is closer really better? *Agriculture, Ecosystems & Environment*, **95** (1), 349-357.
- Dudash, MR & Fenster, CB (2000) Inbreeding and outbreeding depression in fragmented populations. In: Young, AG & Clarke, GM (Eds). *Genetics, Demography and Viability of Fragmented populations*. Cambridge: Cambridge University Press, 35-53.
- Dukas, R & Morse, DH (2003) Crab spiders affect flower visitation by bees. *Oikos*, **101**, 157-163.
- Dunning, JB, Jr; Borgella, R, Jr; Clements, K & Meffe, GK (1995) Patch isolation, corridor effects, and colonisation by a resident sparrow in a managed pine woodland. *Conservation Biology*, **9** (3), 542-550.
- Dunning, JB; Danielson, BJ & Pulliam, HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65** (1), 169-175.
- Edwards, M (1996) Optimising habitats for bees in the United Kingdom - a review of recent conservation action. In: Matheson, A; Buchmann, SL; O'Toole, C; Westrich, P & Williams, IH (Eds). *The Conservation of Bees*. London: Academic Press for The Linnean Society of London and The International Bee Research Association, 35-45.
- Egelhaaf, M & Kern, R (2002) Vision in flying insects. *Current Opinion in Neurobiology*, **12**, 699-706.
- Eisto, A; Kuitunen, M; Lammi, A; Saari, V; Suhonen, J; Syrjäso, S & Tikka, PM (2000) Population persistence and offspring fitness in the rare bellflower *Campanula cervicaria*

in relation to population size and habitat quality. *Conservation Biology*, **14** (5), 1413-1421.

Ellstrand, NC & Elam, DR (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics*, **24**, 217-242.

Esch, HE; Zhang, S; Srinivasan, MV & Tautz, J (2001) Honeybee dances communicate distances measured by optic flow. *Nature*, **411**, 581-583.

Fahrig, L & Merriam, G (1994) Conservation of fragmented populations. *Conservation Biology*, **8** (1), 50-59.

Fahrig, L & Paloheimo, JE (1988a) Determinants of local population size in patchy habitats. *Theoretical Population Biology*, **34**, 194-213.

Fahrig, L & Paloheimo, JE (1988b) Effect of spatial arrangement of habitat patches on local population size. *Ecology*, **69** (2) 468-475.

Fahrig, L & Paloheimo, JE (1987) Interpatch dispersal of the cabbage butterfly. *Canadian Journal of Zoology*, **65**, 616-622.

Farina, A (1998) *Principles and methods in landscape ecology*. London: Chapman & Hall.

Feber, RE; Smith, H & Macdonald, DW (1999) The importance of spatially variable field margins management for two butterfly species. *Aspects of Applied Biology*, **54**, 155-162.

Fischer, M & Matthies, D (1998) Effects of population size on performance in the rare plant *Gentianella germanica*. *Journal of Ecology*, **86**, 195-204.

Fisher, BL (1998) Insect behaviour and ecology in conservation: preserving functional species interactions. *Annals of the Entomological Society of America*, **91** (2), 155-158.

- Forman, RTT & Baudry, J (1984) Hedgerows and hedgerow networks in landscape ecology. *Environmental Management*, **8** (6), 495-510.
- Frank, T (1999) Density of adult hoverflies (Diptera: Syrphidae) in sown weed strips and adjacent fields. *Journal of Applied Entomology*, **123** (6), 351-355.
- Free, JB & Williams, IH (1976) Pollination as a factor limiting the yield of field beans (*Vicia faba* L.). *Journal of Agricultural Science*, **87**, 395-399.
- Free, JB (1993) (2nd ed.) *Insect Pollination of Crops*. London: Academic Press.
- Fry, GLA (1994) The role of field margins in the landscape. In: Boatman, N (Ed). *Field Margins: Integrating Agriculture and Conservation*. British Crop Protection Monograph No. 58. Farnham: British Crop Protection Council, 31-40.
- Fuller, RJ; Chamberlain, DE; Burton, NHK & Gough, SJ (2001) Distributions of birds in lowland agricultural landscapes of England and Wales: how distinctive are bird communities of hedgerows and woodland? *Agriculture, Ecosystems & Environment*, **84**, 79-92.
- Fussell, M & Corbet, SA (1992) Flower usage by bumblebees: a basis for forage plant management. *Journal of Applied Ecology*, **29**, 451-465.
- Galen, C & Plowright, RC (1985) Contrasting movement patterns of nectar-collecting and pollen-collecting bumblebees (*Bombus terrestris*) on fireweed (*Chamaenerion angustifolium*) inflorescences. *Ecological Entomology*, **10**, 9-17.
- Gent, G & Wilson, R (1995) *The Flora of Northamptonshire and the Soke of Peterborough*. Rothwell: Robert Wilson Designs.
- Gilbert, F; Gonzalez, A & Evans-Freke, I (1998) Corridors maintain species richness in the fragmented landscapes of a microecosystem. *Proceedings of the Royal Society, London*, **265**, 577-582.

- Gilbert, FS (1993) (2nd ed.) *Hoverflies*. Slough: Richmond Publishing Co. Ltd.
- Goulson, D & Stout, JC (2001) Homing ability of the bumblebee *Bombus terrestris* (Hymenoptera: Apidae). *Apidologie*, **32**, 105-111.
- Goulson, D & Wright, NP (1998) Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). *Behavioural Ecology*, **9** (3), 213-219.
- Goulson, D (2003) *Bumblebees, Their Behaviour and Ecology*. Oxford: Oxford University Press.
- Goulson, D; Ollerton, J & Sluman, C (1997) Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch? *Animal Behaviour*, **53**, 1009-1016.
- Goverde, M; Schweizer, K; Baur, B & Erhardt, A (2002) Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands. *Biological Conservation*, **104**, 293-299.
- Haas, CA (1995) Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology*, **9** (4), 845-854.
- Haddad, NM & Baum, KA (1999) An experimental test of corridor effects on butterfly densities. *Ecological Applications*, **9** (2), 623-633.
- Haddad, NM (1999) Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications*, **9** (2), 612-622.
- Haddad, NM (2000) Corridor length and patch colonisation by a butterfly, *Junonia coenia*. *Conservation Biology*, **14** (3), 738-745.
- Haddad, NM; Bowne, DR; Cunningham, A; Danielson, BJ; Levey, DJ; Sargent, S & Spira T (2003) Corridor use by diverse taxa. *Ecology*, **84** (3), 609-615.

- Hanski, I (1998) Metapopulation dynamics. *Nature*, **396**, 5 November, 41-49.
- Harrison, S (1989) Long-distance dispersal and colonisation in the Bay Checkerspot butterfly, *Euphdryas Editha Bayensis*. *Ecology*, **70** (5), 1236-1243.
- Harwood, RWJ; Hickman, JM; MaCleod, A; Sherratt, TN & Wratten, SD (1994) Managing field margins for hoverflies. In: Boatman, N (Ed). *Field Margins: Integrating Agriculture and Conservation*. British Crop Protection Monograph No. 58. Farnham: British Crop Protection Council, 147-152.
- Haslett, JR (1989) Interpreting patterns of resource utilisation: randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia*, **78**, 433-432.
- Hegland, SJ; van Leeuwen, M & Oostermeijer, JGB (2001) Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *Journal of Applied Ecology*, **38**, 1277-1289.
- Heinrich, B (1975) Energetics of pollination. *Annual Review of Ecology & Systematics*, **6**, 139-170.
- Heinrich, B (1976) The foraging specialisations of individual bumblebees. *Ecological Monograph*, **46**, 105-128.
- Helps, MB (1994) Field margins - An agricultural perspective. In: Boatman, N (Ed). *Field Margins: Integrating Agriculture and Conservation*. British Crop Protection Monograph No. 58. Farnham: British Crop Protection Council, 21-30.
- Hickman, JM & Wratten, SD (1996) Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *Journal of Economic Entomology*, **89** (4), 832-840.

- Hill, JK; Collingham, YC; Thomas, CD; Blakeley, DS; Fox, R; Moss, D & Huntley, B (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters*, **4**, 313-321.
- Hinsley, SA & Bellamy, PE (2000) The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management*, **60**, 33-49.
- Hobbs, RJ (1992) The role of corridors in conservation: solution or bandwagon? *Trends in Ecology and Evolution*, **7** (11), 389-392.
- Hogbin, PM; Ayre, DJ & Whelan, RJ (1998) Genetic variation and reproductive success of road verge populations of the rare shrub *Grevillea barklyana* (Proteaceae). *Heredity*, **80**, 180-186.
- Horridge, GA (1996) The relation between pattern and landmark vision of the honeybee (*Apis mellifera*). *Journal of Insect Physiology*, **42** (4), 373-383.
- Horridge, GA (2003) Discrimination of single bars by the honeybee (*Apis mellifera*). *Vision Research*, **43**, 1257-1271.
- Huenneke, LF (1991) Ecological implications of genetic variation in plant populations. In: Falk, DA & Holsinger, KE (Eds). *Genetics and Conservation of Rare Plants*. Oxford: Oxford University Press, 31-44.
- Ims, RA & Andreassen, HP (1999) Effects of experimental habitat fragmentation and connectivity on root vole demography. *Journal of Animal Ecology*, **68**, 839-852.
- Jennersten, O (1988) Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conservation Biology*, **2**, 359-366.
- Jonsen, ID & Fahrig, L (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology*, **12**, 185-197.

- Joyce, DA & Pullin, AS (2003) Conservation implications of the distribution of genetic diversity at different scales: a case study using the marsh fritillary butterfly (*Euphydryas aurinia*). *Biological Conservation*, **114**, 453-461.
- Kearns, CA & Inouye, DW (1993) *Techniques for Pollination Biologists*. Niwot: University Press of Colorado.
- Kearns, CA & Inouye, DW (1997) Pollinators, flowering plants and conservation biology. *Bioscience*, **47** (5), 297-306.
- Kearns, CA (2001) North American Dipteran pollinators: assessing their value and conservation status. *Conservation Ecology*, **5** (1). [online] URL: <http://www.consecol.org/vol5/iss1/art5>
- Kearns, CA; Inouye, DW & Waser, NM (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecological Systematics*, **29**, 83-112.
- Keeton, WT & Gould, JL (1993) *Biological Science* (5th ed.) London: WW Norton & Company, 426-429.
- Keller, M; Kollmann, J & Edwards, PJ (2000) Genetic introgression from distant provenances reduces fitness in local weed populations. *Journal of Applied Ecology*, **37**, 647-659.
- Kerr, JT (2001) Butterfly species richness patterns in Canada: energy, heterogeneity and the potential consequences of climate change. *Conservation Ecology*, **5**, 1:10. [online] URL: <http://www.consecol.org/vol5/iss1/art10>.
- Kéry, M; Matthies, D & Spillman, H (2000) Reduced fecundity and offspring performance in small populations of the declining grassland plants *Primula veris* and *Gentiana lutea*. *Journal of Ecology*, **88**, 17-30.

- Kevan, P & Baker, H (1984) Insects on flowers. *In*: Huffaker, CB & Rabb, RL (Eds). *Ecological Entomology*. New York: John Wiley & Sons, 607-632.
- Kevan, PG & Phillips, TP (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. *Conservation Ecology*, **5** (1) [online] URL: <http://www.consecol.org/vol5/iss1/art8>.
- Kevan, PG (1999) Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems & Environment*, **74**, 373-393.
- Keyghobadi, N; Roland, J & Strobeck, C (1999) Influence of landscape on the population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). *Molecular Ecology*, **8**, 1481-1495.
- Kirby, K (1995) *Rebuilding the English countryside: habitat fragmentation and wildlife corridors as issues in practical conservation*. English Nature Science Report, No 10, Peterborough: English Nature.
- Klinkhamer, PGL; de Jong, TJ & Linnebank, LA (2001) Small-scale spatial patterns determine ecological relationships: an experimental example using nectar production rates. *Ecology Letters*, **4**, 599-567.
- Krauss, J; Steffan-Dewenter, I & Tschamtkke, T (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, **30**, 889-900.
- Kremen, C & Ricketts, T (2000) Global perspectives on pollination disruptions. *Conservation Biology*, **14** (5), 1226-1228.
- Kremen, C; Williams, NM & Thorp, RW (2002) Crop pollination from native bees at risk from agricultural intensification. *PNAS*, **99** (26), 16812-16816.
- Kwak, MM & Vervoort, N (2000) Bumblebee visitation and dispersal of fluorescent dye powder between bridged and isolated experimental patches of *Phyteuma nigrum*

- (Campanulaceae). *Det Norske Videnskaps-Akademi. I. Matematisk Naturvidenskapelige klasse, Skrifter, Ny Serie*, **39**, 1-11.
- Kwak, MM (1987) Marking a bumblebee without anaesthesia. *Bee World*, **68**, 180-181.
- Kwak, MM; Velterop, O & Boerrigter, EJM (1996) Insect diversity and the pollination of rare plant species. *In: Matheson, A; Buchmann, SL; O'Toole, C; Westrich, P & Williams, IH (Eds). The Conservation of Bees.* London: Academic Press for The Linnean Society of London and The International Bee Research Association, 115-124.
- Kwak, MM; Velterop, O & van Andel., J (1998) Pollen and gene flow in fragmented habitats. *Applied Vegetation Science*, **1**, 37-54.
- La Polla, VN & Barrett, GW (1993) Effects of corridor width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecology*, **8**, 25-37.
- Lamont, BB; Klinkhamer, PGL & Witkowski, ETF (1993) Population fragmentation may reduce fertility to zero in *Banksia goodii* – a demonstration of the Allee effect. *Oecologia*, **94**, 446-450.
- Larson, BMH & Barrett, SCH (1999) The ecology of pollen limitation in buzz-pollinated *Rhexia virginica* (Melastomataceae). *Journal of Ecology*, **87**, 371-381.
- Lehrer, M (1990) How bees use peripheral eye regions to localise a frontally positioned target. *Journal of Comparative Physiology A*, **167**, 173-185.
- Lehrer, M; Wehner, R & Srinivasan, MV (1985) Visual scanning behaviour in honeybees. *Journal of Comparative Physiology A*, **157**, 405-415.
- Leimar, O; Norberg, U & Wiklund, C (2003) Habitat preference and habitat exploration in two species of satyrine butterflies. *Ecography*, **26**, 474-480.

- León-Cortés, JL; Cowley, MJR & Thomas, CD (2000) The distribution and decline of a widespread butterfly *Lycaena phlaeas* in a pastoral landscape. *Ecological Entomology*, **25**, 285-294.
- Levin, DA & Kerster, HW (1974) Gene flow in seed plants. *Evolutionary Biology*, **7**, 139-220.
- Lima, SL & Zollner, PA (1996) Towards a behavioural ecology of ecological landscapes. *Trends in Ecology & Evolution*, **11** (3), 131-135.
- Lövei, GL; McDougall, D; Bramley, G; Hodgson, DJ & Wratten, SD (1992) Floral resources for natural enemies: the effect of *Phacelia tanacetifolia* (Hydrophyllaceae) on within-field distribution of hoverflies (Diptera: Syrphidae). *Proceedings of the 45th New Zealand Plant Protection Conference*, 60-61.
- Luijten, SH; Dierick, A; Oostermeijer, JGB; Raijmann, LEL & Den Nijs, HCM (2000) Population size, genetic variation, and reproductive success in a rapidly declining, self-incompatible perennial (*Arnica montana*) in the Netherlands. *Conservation Biology*, **14** (6), 1776-1787.
- Mabberley, DJ (1987) *The plant-book: a portable dictionary of the higher plants*. Cambridge: Cambridge University Press, 285-286.
- Malanson, GP & Cramer, BE (1999) Landscape heterogeneity, connectivity, and critical landscapes for conservation. *Diversity and Distributions*, **5**, 27-39.
- Mann, CC & Plummer, ML (1995) Are wildlife corridors the right path? *Science*, **270**, 1428-1430.
- Marshall, EJP; West, TM & Maudsley, MJ (2001) Treatments to restore the diversity of herbaceous flora of hedgerows. *Hedgerows of the World, IALE (UK) 2001*, 319-328.

- Mauremooto, JR; Wratten, SD; Worner, SP & Fry, GLA (1995) Permeability of hedgerows to predatory carabid beetles. *Agriculture, Ecosystems & Environment*, **52**, 141-148.
- McCollin, D; Jackson, JI; Bunce, RGH; Barr, CJ & Stuart, R (2000) Hedgerows as habitat for woodland plants. *Journal of Environmental Management*, **60**, 77-90.
- Meek, B; Loxton, D; Sparks, T; Pywell, R; Pickett, H & Nowakowski, M (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, **106**, 259-271.
- Memmott, J (1999) The structure of a plant-pollinator food web. *Ecology Letters*, **2**, 276-280.
- Menzel, R; Geiger, K; Joerges, J; Muller, U & Chittka, L (1998) Bees travel novel homeward routes by integrating separately acquired vector memories. *Animal Behaviour*, **55**, 139-152.
- Merriam, G (1991) Corridors and connectivity: animal populations in heterogeneous environments. *In: Saunders, DA & Hobbs, RJ (Eds). Nature Conservation 2: The Role of Corridors*. Chipping Norton, New South Wales: Surrey Beatty & Sons, 133-142.
- Micheli, F & Peterson, CH (1999) Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology*, **13** (4), 869-881.
- Microsoft Corporation (1997) *Excel 97 SR-2*. Microsoft Corporation (Corporate HQ), 1 Microsoft Way, Redmond, Washington 98052, USA.
- Morris, RKA & Ball, SG (2002) An introduction to British hoverflies and the Hoverfly Recording Scheme. *British Wildlife*, **October**, 38-45.
- Morris, RKA (1998) *Hoverflies of Surrey*. Woking: Surrey Wildlife Trust.

- Muir, R & Muir, N (1987) *Hedgerows: Their History and Wildlife*. London: Michael Joseph Ltd.
- Müller, M & Wehner, R (1988) Path integration in desert ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences, USA*, **85**, 5287-5290.
- Munguira, ML & Thomas, JA (1992) Use of road verges by butterfly and burnet populations, and the effect of roads on adult dispersal and mortality. *Journal of Applied Ecology*, **29**, 316-329.
- Murren, CJ (2002) Effects of habitat fragmentation on pollination: pollinators, pollinia viability and reproductive success. *Journal of Ecology*, **90**, 100-107.
- Mustajärvi, K; Siikamäki, P; Rytönen, S & Lammi, A (2001) Consequences of plant population size and density of plant-pollinator interactions and plant performance. *Journal of Ecology*, **89** (1), 80-87.
- Nicholls, AO & Margules (1991) The design of studies to demonstrate the biological importance of corridors. In: Saunders, DA & Hobbs, RJ (Eds). *The Role of Corridors*. Chipping Norton, New South Wales: Surrey Beatty & Sons, 49-61.
- Olesen, JM & Jain, SK (1994) Fragmented plant populations and their lost interactions. In: Loeschcke, V; Tomiuk, J & Jain, SK (Eds). *Conservation Genetics*. Basel: Birkhäuser, 417-426.
- Ollerton, J & Cranmer, L (2002) Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? *Oikos*, **98**, 340-350.
- Ollerton, J; Johnson, SD; Cranmer, L & Kellie, S (2003) The pollination ecology of an assemblage of grassland Asclepiads in South Africa. *Annals of Botany*, **92**, 807-834.
- Oostermeijer, JGB; Luijten, SH; Křenová, ZV & Den Nijs, HCM (1998) Relationships between population and habitat characteristics and reproduction of the rare *Gentiana pneumonanthe* L. *Conservation Biology*, **12** (5), 1042-1053.

- Oostermeijer, JGB; Luijten, SH; Petanidou, T; Kos, M; Ellis-Adam, AC & Den Nijs, HCM (2000) Pollination in rare plants: is population size important? *Det Norske Videnskaps-Akademi. I. Matematisk Naturvidenskapelige klasse, Skrifter, Ny Serie*, **39**, 201-213.
- Osborne, JL & Williams, IH (1996) Bumblebees as pollinators of crops and wild flowers. *In: Matheson, A (Ed). Bumblebees for Pleasure and Profit*. Cardiff: International Bee Research Association, 24-32.
- Osborne, JL; Clark, SJ; Morris, RJ; Williams, IH; Riley, JR; Smith, AD; Reynolds, DR & Edwards, AS (1999) A landscape-scale study of bumblebee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology*, **36**, 519-533.
- Osborne, JL; Williams, IH & Corbet, SA (1991) Bees, pollination and habitat change in the European Community. *Bee World*, **72** (3), 99-116.
- O'Toole, C (1993) Diversity of native bees and agroecosystems. *In: LaSalle, J & Gauld, ID (Eds). Hymenoptera and Biodiversity*. Wallingford: CAB International, 169-196.
- Ouborg NJ, & van Treuren R (1994) The significance of genetic erosion in the process of extinction IV. Inbreeding load and heterosis in relation to population size in the mint *Salvia pratensis*. *Evolution*, **48**, 996-1008.
- Paton, DC (2000) Disruption of bird-plant pollination systems in southern Australia. *Conservation Biology*, **14** (5), 1232-1234.
- Pettersson, MW (1991) Pollination by a guild of fluctuating moth populations: option for unspecialisation in *Silene vulgaris*. *Journal of Ecology*, **79**, 591-604.
- Pither, J & Taylor, PD (1998) An experimental assessment of landscape connectivity. *Oikos*, **83**, 166-174.
- Plowright, RC & Galen, C (1985) Landmarks or obstacles: the effects of spatial heterogeneity on bumble bee foraging behaviour. *Oikos*, **44**, 459-464.

- Pollard, E & Yates, TJ (1993) *Monitoring butterflies for ecology and conservation*. London: Chapman & Hall.
- Pollard, E; Hooper, MD & Moore, NW (1974) *Hedges*. London: William Collins Sons & Co Ltd.
- Potts, GR (1991) The environmental and ecological importance of cereal fields. In: Firbank, LG; Carter, N; Darbyshire, JF & Potts, GR (Eds). *The Ecology of Temperate Cereal Fields*. 32nd Symposium of The British Ecological Society. Oxford: Blackwell Scientific Publications, 3-21.
- Proctor, M; Yeo, P & Lack, A (1996) *The Natural History of Pollination*. London: HarperCollins Publishers.
- Prÿs-Jones, OE & Corbet, SA (1991) *Bumblebees*. Slough: Richmond Publishing Co Ltd.
- Pulliam, HR; Dunning, JB Jr & Liu, J (1992) Population dynamics in complex landscapes: a case study. *Ecological Applications*, **2** (2), 165-177.
- Ratcliffe, DA (1977) *A Nature Conservation Review: the Selection of Sites of Biological National Importance to Nature Conservation in Britain*. Cambridge: Cambridge University Press.
- Rathcke, BJ & Jules, ES (1993) Habitat fragmentation and plant-pollinator interactions. *Current Science*, **65** (3), 273-277.
- Riley, JR; Reynolds, DR; Smith, AD; Edwards, AS; Osborne, JL & McCartney, HA (1999) Compensation for wind drift by bumblebees. *Nature*, **400**, 8 July, 126.
- Robertson, AW (1992) The relationship between floral display size, pollen carryover and geitonogamy in *Myosotis colensoi* (Kirk) Macbride (Boraginaceae). *Biological Journal of the Linnean Society*, **46**, 333-349.

- Robinson, RA & Sutherland, WJ (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, **39**, 157-176.
- Rocha, OJ & Aguilar, G (2001) Reproductive biology of the dry forest tree *Enterolobium cyclocarpum* (Guanacaste) in Costa Rica: A comparison between trees left in pastures and trees in continuous forest. *American Journal of Botany*, **88** (9), 1607-1614.
- Rose, F (1981) *The wild flower key*. London: Penguin Books Ltd.
- Rosenberg, DK; Noon, BR & Meslow, EC (1997) Biological corridors: form, function and efficacy. *Bioscience*, **47** (10), 677-687.
- Roubik, DW (2000) Pollination system stability in tropical America. *Conservation Biology*, **14** (5), 1235-1236.
- Roubik, DW (2001) Ups and downs in pollinator populations: when is there a decline? *Conservation Ecology*, **5** (1), [online] URL: <http://www.consecol.org/vol5/iss1/art2>.
- Ruefenacht, B & Knight, RL (1995) Influences of corridor continuity and width on survival and movement of deermice. *Biological Conservation*, **71**, 269-274.
- Rüegg, WT; Richner, W; Stamp, P & Feil, B (1998) Accumulation of dry matter and nitrogen by minimum-tillage silage maize planted into winter cover crop residues. *European Journal of Agronomy*, **8**, 59-69.
- Saunders, DA & Hobbs, RJ (Eds) (1991) *The Role of Corridors*. Chipping Norton, New South Wales: Surrey Beatty & Sons.
- Saunders, DA & Ingram, JA (1987) Factors affecting survival of breeding populations of Carnaby's cockatoo *Calyptorhynchus funereus latirostris* in remnants of native vegetation. In: Saunders, DA, Arnold, GW, Burbidge, AA & Hopkins, AJM (Eds). *Nature Conservation: The Role of Remnants of Native Vegetation*. Chipping Norton, New South Wales: Surrey Beatty & Sons, 249-258.

- Saville, NM; Dramstad, WE; Fry, GLA & Corbet, SA (1997) Bumblebee movement in a fragmented agricultural landscape. *Agriculture, Ecosystems & Environment*, **61** (2-3), 145-154.
- Schmid-Hempel, P (1985) How do bees choose flight direction while foraging? *Physiological Entomology*, **10**, 439-442.
- Schtickzelle, N & Baguette, M (2003) Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration - patch area relationships in fragmented landscapes. *Journal of Animal Ecology*, **72**, 533-545.
- Scott, A (1989). *The ecology and conservation of Meadow Clary (Salvia pratensis L.)*. MSc Dissertation in Conservation, University College London.
- Scott-Dupree, CD & Winston, ML (1987) Wild bee pollinator diversity and abundance in orchard and uncultivated habitats in the Okanagan Valley, British Columbia. *Canadian Entomologist*, **119**, 735-745.
- Sih, A & Baltus, MS (1987) Patch size, pollinator behaviour and pollinator limitation in catnip. *Ecology*, **68**, 1679-90.
- Silvertown, JW & Charlesworth, D (2001) *Introduction to Plant Population Biology*. (4rd ed.) Oxford: Blackwell Scientific Publications.
- Simberloff, D & Cox, J (1987) Consequences and costs of conservation corridors. *Conservation Biology*, **1**, 63-71.
- Simberloff, D; Farr, JA; Cox, J & Mehlman, DW (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology*, **6** (4), 493-504.
- Sjögren-Gulvö, P (1994) Distribution and extinction patterns within a northern metapopulation of the pool frog (*Rana lessonae*). *Ecology*, **75**, 1357-1367.

- Smart, SM; Firbank, LG; Bunce, RGH & Watkins, JW (2001) Quantifying changes in abundance of food plants for butterfly larvae and farmland birds. *Journal of Applied Ecology*, **37** (3), 398-414.
- Sommaggio, D (1999) Syrphidae: can they be used as environmental indicators? *Agriculture, Ecosystems & Environment*, **74** (1-3), 343-356.
- Sotherton, NW; Boatman, ND & Rands, MRW (1989) The 'Conservation Headland' experiment in cereal ecosystems. *The Entomologist*, **108** (1&2), 135-143.
- Sowig, P (1989) Effects of flowering plant's size on species composition of pollinator communities, foraging strategies and resource partitioning in bumblebees (Hymenoptera: Apidae). *Oecologia*, **78**, 550-558.
- Spackman, SC & Hughes, JW (1995) Assessment of minimum stream corridor width for biological conservation: species richness and distribution along mid-order streams in Vermont, USA. *Biological Conservation*, **71**, 325-332.
- Sparkes, DL; Ramsden, SJ; Jaggard, KW & Scott, RK (1998) The case for headland set-aside: consideration of whole-farm gross margins and grain production on two farms with contrasting rotations. *Annals of Applied Biology*, **133**, 245-256.
- Sparks, TH & Parish, T (1995) Factors affecting the abundance of butterflies in field boundaries in Swavesey Fens, Cambridgeshire, UK. *Biological Conservation*, **73**, 221-227.
- Sparks, TH; Hann, JP & Greated-Davies, JN (1999) The influence of field boundary structure on butterflies. *Aspects of Applied Biology*, **54**, 235-240.
- Sparks, TH; Meek, W; Pywell, RF & Nowakowski, M (2000) The influence of field margin management on the butterfly fauna of a Yorkshire arable farm. *Aspects of Applied Biology*, **58**, 407-410.

- SPSS Inc., (1998) *SPSS for Windows, Version 9.0*. SPSS Inc. Headquarters, 233 S. Wacker Drive, 11th floor, Chicago, Illinois 60606, USA.
- Srinivasan, MV; Poteser, M & Kral, K (1999) Motion detection in insect orientation and navigation. *Vision Research*, **39**, 2749-2766.
- Srygley, RB (2001) Compensation for fluctuations in crosswind drift without stationary landmarks in butterflies migrating over seas. *Animal Behaviour*, **61**, 191-203.
- Steffan-Dewenter, I & Tschardtke, T (1997) Bee diversity and seed set in fragmented habitats. *Proceedings of the International Symposium on Pollination, Acta Horticulturae, (ISHS)*, **437**, 231-234.
- Steffan-Dewenter, I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, **17** (4), 1036-1044.
- Steffan-Dewenter, I; Münzenberg, U & Tschardtke, T (2001) Pollination, seed set and seed predation on a landscape scale. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268** (1477), 1685-1690.
- Steffan-Dewenter, I; Münzenberg, U; Bürger, C; Thies, C & Tschardtke, T (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, **83** (5), 1421-1432.
- Stout, JC; Allen, JA & Goulson, D (1998) The influence of relative plant density and floral morphological complexity on the behaviour of bumblebees. *Oecologia*, **117**, 543-550.
- Stubbs, AE & Falk, SJ (2000) (3rd ed.) *British Hoverflies*. Reading: The British Entomological and Natural History Society.

- Sutcliffe, OL & Thomas, CD (1996) Open corridors appear to facilitate dispersal by Ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conservation Biology*, **10** (5), 1359-1365.
- Sutherland, JP; Sullivan, MS & Poppy, GM (2001) Distribution and abundance of aphidophagous hoverflies (Diptera: Syrphidae) in wildflower patches and field margin habitats. *Agricultural and Forest Entomology*, **3**, 57-64.
- Svensson, B; Lagerlöf, J & Svensson, BG (2000) Habitat preferences of nest-seeking bumblebees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems & Environment*, **77**, 247-255.
- Taylor, P; Fahrig, L; Henein, K & Merriam, G (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68** (3), 571-573.
- Taylor, PD & Merriam, G (1995) Wing morphology of a forest damselfly is related to landscape structure. *Oikos*, **73**, 43-48.
- Tewksbury, JJ; Levey, DL; Haddad, NM; Sargent, S; Orrock, JL; Weldon, A; Danielson, BJ; Brinkerhoff, J; Damschen, EI & Townsend, P (2002) Corridors affect plants, animals and their interactions in fragmented landscapes. *PNAS*, **99** (20), 12923-12926.
- Thies, C; Steffan-Dewenter, I & Tschardtke, T (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18-25.
- Thomas, CD & Kunin, WE (1999) The spatial structure of populations. *Journal of Animal Ecology*, **68**, 647-657.
- Thomas, CFG & Marshall, EJP (1999) Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems and Environment*, **72**, 131-144.
- Thomas, JA & Lewington, R (1991) *The Butterflies of Britain and Ireland*. London: Dorling Kindersley.

- Torchio, PF (1990) Diversification of pollination strategies for US crops. *Environmental Entomology*, **19**, 1649-1656.
- Tscharntke, T; Gathmann, A & Steffan-Dewenter, I (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, **35**, 708-719.
- Turchin, P (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology*, **72** (4), 1253-1266.
- Turner, MG (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, **20**, 171-197.
- Ullrich, KS & Edwards, PJ (1999) The colonisation of wild flower-strips by insects (Heteroptera). *Heterogeneity in Landscape Ecology*, IALE (UK), 131-138.
- Van Dyck, H & Matthysen, E (1999) Habitat fragmentation and insect flight: a changing 'design' in a changing landscape? *Trends in Ecology & Evolution*, **14** (5) 172-174.
- Van Treuren, R; Bijlsma, R; Ouborg, NJ and van Delden, W (1993) The significance of genetic erosion in the process of extinction. IV. Inbreeding depression and heterosis effects caused by selfing and outcrossing in *Scabiosa columbaria*. *Evolution*, **47**, 1669-1680.
- Vermeulen, HJW (1994) Corridor function of a road verge for dispersal of stenotopic heathland ground beetles: Carabidae. *Biological Conservation*, **69**, 339-349.
- Visser, AJ (2000) Prototyping on farm nature management, a synthesis of landscape ecology, development policies and farm specific possibilities. *Aspects of Applied Biology*, **58**, 299-304.
- Walther-Hellwig, K & Frankl, R (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, **124**, 299-306.

- Waser, NM (1986) Flower constancy: definition, cause and measurement. *American Naturalist*, **127**, 593-603.
- Waser, NM; Chittka, L; Price, MV; Williams, NM & Ollerton, J (1996) Generalisation in pollination systems, and why it matters. *Ecology*, **77** (4) 1043-1060.
- Watt, WB; Hoch, PC & Mills, SG (1974) Nectar resource use by *Colias* butterflies: chemical and visual aspects. *Oecologia*, **14**, 353-374.
- Wehner, R; Michel, B & Antonsen, P (1996) Visual navigation in insects: coupling of egocentric and geocentric information. *Journal of Experimental Biology*, **199**, 129-140.
- Westphal, C; Steffan-Dewenter, I & Tschardtke, T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, **6**, 961-965.
- Westrich, P (1996) Bees and the problems of partial habitats. In: Matheson, A; Buchmann, SL; O'Toole, C; Westrich, P & Williams, IH (Eds). *The Conservation of Bees*. London: Academic Press for The Linnean Society of London and The International Bee Research Association, 1-16.
- White, AJ; Wratten, SD; Berry, NA & Weigmann, U (1995) Habitat manipulation to enhance biological control of *Brassica* pests by hoverflies (Diptera: Syrphidae). *Journal of Economic Entomology*, **88** (5) 1171-1176.
- Williams, C (1997) Nectar secretion rates, standing crops and flower choice by bees on *Phacelia tanacetifolia*. *Journal of Apicultural Research*, **36** (1) 23-32.
- Williams, CS (1995) Conserving Europe's bees: why all the buzz? *Trends in Ecology & Evolution*, **10** (8), 309-310.
- Williams, IH & Carreck, NL (1994) Land use changes and honeybee forage plants. In: Matheson, A (Ed). *Forage for Bees in an Agricultural Landscape*. Cardiff: International Bee Research Association, 7-20.

- Williams, IH & Christian, DG (1991) Observations on *Phacelia tanacetifolia* Benth (Hydrophyllaceae) as a food plant for honey bees and bumble bees. *Journal of Apicultural Research*, **30** (1), 3-12.
- Williams, IH (1994) The dependence of crop production within the European Union on pollination by honeybees. *Agricultural Zoology Reviews*, **6**, 229-257.
- Williams, IH (1996) Aspects of bee diversity and crop pollination in the European Union. In: Matheson, A; Buchmann, SL; O'Toole, C; Westrich, P & Williams, IH (Eds). *The Conservation of Bees*. London: Academic Press for The Linnean Society of London and The International Bee Research Association, 63-80.
- Williams, IH; Corbet, SA & Osborne, JL (1991) Beekeeping, wild bees and pollination in the European Community. *Bee World*, **72** (4), 170-180.
- Williams, PH (1982) The distribution and decline of British bumblebees (*Bombus* Latr.). *Journal of Apicultural Research*, **21**, 236-245.
- Williams, PH (1986) Environmental change and the distribution of British bumblebees (*Bombus* Latr.). *Bee World*, **67**, 50-61.
- Wyland, LJ; Jackson, LE; Chaney, WE; Klonsky, K; Koike, ST & Kimple, B (1996) Winter cover crops in a vegetable cropping system: impacts on nitrate leaching, soil water, crop yield, pests and management costs. *Agriculture, Ecosystems & Environment*, **59**, 1-17.
- Young, AG & Clarke, GM (2000) Conclusions and future directions: what do we know about the genetic and demographic effects of habitat fragmentation and where do we go from here? In: Young, AG & Clarke, GM (Eds). *Genetics, Demography and Viability of Fragmented Populations*. Cambridge: Cambridge University Press, 361-266.
- Young, AG; Boyle, T & Brown, AHD (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, **11** (10), 413-418.

- Young, AG; Brown, ADH; Murray, BG & Miller, CH (2000) Genetic erosion, restricted mating and reduced viability in fragmented populations of the endangered grassland herb *Rutidosia leptorrhynchoidea*. In: Young, AJ & Clark, GM (Eds). *Genetics, Demography and Viability of Fragmented Populations*. Cambridge: Cambridge University Press, 335-359.
- Zhang, SW; Lehrer, M & Srinivasan, MV (1999) Honeybee memory: navigation by associative grouping and recall of visual stimuli. *Neurobiology of Learning and Memory*, **72**, 180-201.
- Zollner, PA & Lima, SL (1997) Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos*, **80**, 51-60.
- Zollner, PA & Lima, SL (1999) Illumination and the perception of remote habitat patches by white-footed mice. *Animal Behaviour*, **58**, 489-500.