The birds and the bees:
pollination of fruit-bearing hedgerow plants and consequences for birds

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Abstract

Hedgerow fruits provide a food resource for several UK farmland bird species from late summer, through winter and into spring. This project aims to develop the understanding of the interactions between fruit-bearing hedgerow flowers, their pollinators, hedgerow fruits and frugivorous birds. Experiments revealed that flowers of blackthorn, hawthorn and ivy all benefited from insect visits in order to develop fruit. The flowers of bramble and dog rose showed little requirement for insect pollination, and produced fruit when insects were excluded. There was evidence that for the hedges under study, the pollination service provided by insects to blackthorn and hawthorn flowers was inadequate since the flowers of these plants were pollen limited. The relative abundance of different insect groups foraging on blackthorn flowers was highly variable between hedges, suggesting that the contribution of a particular insect group to blackthorn pollination may vary according to their local density. Bumblebees, bristly flies and solitary bees were considered to have the greatest value for pollinating blackthorn flowers, based on foraging attributes (bumblebees and solitary bees), and abundance (bristly flies), but their activity did not correlate with the proportion of flowers that set fruit. Solitary bee activity correlated with hawthorn pollination, and there was strong evidence that social wasps were the best pollinators of ivy flowers on the hedges studied. Environmental factors such as hedge aspect did not significantly affect the activity of most pollinators (with the exception of solitary bees) or the proportion of blackthorn flowers that set fruit. Equally, the presence of the mass-flowering, attractive forage source, oilseed rape in fields adjacent to hedgerows, did not significantly influence the activity of most pollinators or the proportion of hawthorn flowers that set fruit. The abundance of some frugivorous birds, in particular the migratory thrushes (redwings and fieldfares) was positively related to the yield of fruits, including sloes and haws in hedges. So the evidence suggests that on these farms, pollinator communities are important for ensuring some hedgerow shrubs provide copious fruit, which may be vital for birds during winter months when invertebrate food is scarce. These links between flowers, pollinators, fruits and birds are discussed, alongside suggestions for safeguarding the fruit supply for farmland birds in the future.

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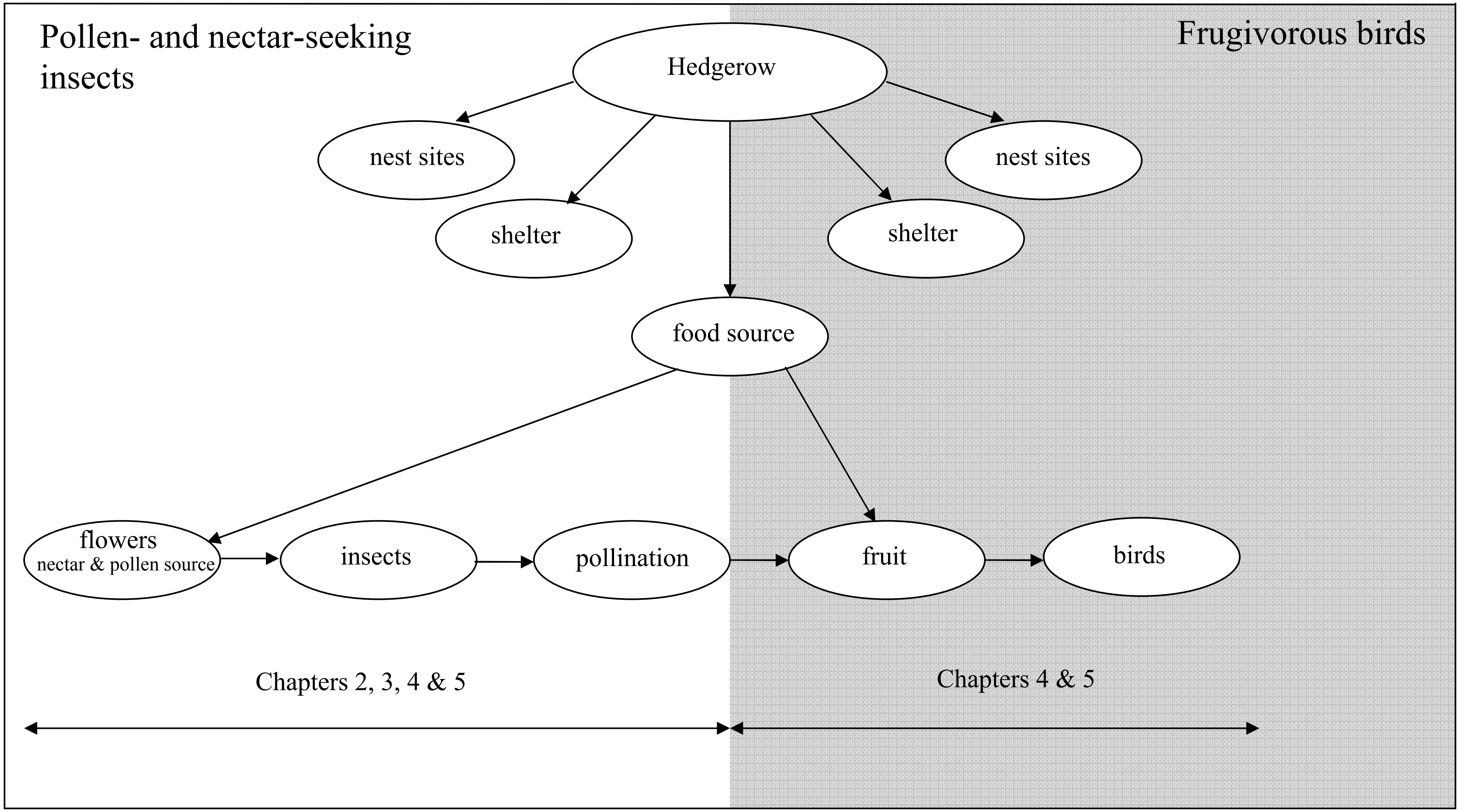
1. Introduction

At present, interactions between hedgerow flowers, their pollinators, hedgerow fruits and birds are poorly understood. These interactions are broadly summarised in Figure 1.1. The extent to which fruit-bearing hedgerow plants rely on entomophilous pollination for the production of fruits is unclear. Whilst much research has focused on the relationship between insects and the pollination and fruit set of commercial crops (e.g. Free, 1993 and references within; Creswell et al., 2002; Klein et al., 2003a; 2003b) and wild herbaceous plants (e.g. Gross and Werner, 1983; Corbet, 1988; Gibson et al., 2006), the services that insects may provide as pollinators of woody and semi-woody fruit-bearing hedgerow plants in the UK has received less attention until now. This project aims to develop a better understanding of these interactions and to establish which groups of flower-visiting insects have the greatest pollination value for ensuring good hedgerow fruit yields.

Figure 1.1. Interactions between hedgerow flowers, flower-visiting insects, fruits and frugivorous birds



1.1. Hedgerows, agricultural change and impacts on farmland biodiversity

Hedgerows are important habitats for wildlife, providing shelter and food for insects (Pollard et al., 1974; Moreby and Southway, 2001; Maudsley, 1999). They hold a huge diversity and abundance of arthropods, for example, Pollard and Holland. (2006) collected 13,390 (51 families in 13 orders) from 181m^3 of hedge. Plants in the hedgerows provide food for the larval stages of some moths and butterflies (Gerrits-Heybroek et al., 1978; Tomlinson and Still, 2002). Whereas the hedges themselves function as movement corridors for adult Lepidoptera (Dover and Sparks, 2000) and provide overwintering sites for beneficial insects such as Carabids (Varchola and Dunn, 2001) and Syrphids (Burgio and Somaggio, 2007). Hedgerows offer prime nest sites for bees (Apoidea) (Osborne et al., 2008b) and a succession of flowers, which is important for a variety of flower-visiting insects with short or long flight periods from early spring to late summer (Osborne et al., 1991; Williams et al., 1991; Proctor et al., 1996). Similarly to insects, birds use hedges for shelter and food (Pollard et al., 1974; Lack, 1992); the fruits of hedgerow plant species such as blackthorn (*Prunus spinosa* L.), hawthorn (*Crataegus monogyna* Jacq.), bramble (*Rubus fruticosus* agg.), dog rose (*Rosa canina* agg.) and ivy (*Hedera helix* L.) provide some birds with a useful winter and spring food resource (Hartley, 1954; Sorensen, 1981; Snow and Snow, 1988), as well as providing food for small mammals (Pollard et al., 1977; Smal and Fairley, 1980; Debussche and Isenmann, 1989).

Hedges have been a feature of the British countryside since the Enclosure movement from 1460 to 1600 (Dowdeswell, 1987; Wilson, 1979), with hedge planting reaching a maximum with the Great Enclosures between 1750 and 1850 (Rackham, 2000). From 1850 up to the present time, farming methods and hence the arable landscape have experienced many changes, which have impacted on farmland wildlife, including birds and pollinators. In the Victorian era, rotational farming to control pests in the crop brought benefits for wildlife such as birds through a diversity of crops, weeds, invertebrates, and seed from winter stubbles (Stoate, 1994). The turn of the 20th Century saw rural to urban migration of farm workers due to higher wages provided by industry and declining wheat prices due to imports from North America, which meant that many arable areas were turned over to grass for meat production or dairy pasture (Stoate, 1995). From 1945, after World War II, government policy secured crop prices and markets, leading to the intensification of agriculture with increased pesticide and fertiliser inputs, draining and ploughing of water meadows, monocultures of grass for silage production, and a change from spring sown cereals in favour of autumn sown cereals (reducing land in winter stubbles). Together these changes reduced the availability of winter food for seed-eating birds, and habitats for wild plants and invertebrates (Stoate, 1996). When Britain joined the European Community in 1973, it adopted The Common Agricultural Policy (CAP), which ensured food production and further encouraged farmland intensification. Although reasons behind declines of farmland birds are complex, winter food availability is thought to be an important factor affecting populations of some birds (Robinson and Sutherland, 2002; Siriwardena et al., 2008), since modern agriculture has reduced the availability of bird food such as invertebrates and seeds (Sotherton and Self, 2000; Benton et al., 2002). Widespread hedgerow removal has increased field sizes in Britain, with approximately 24,000km of hedgerow lost in a six year period in the early 1980s (Barr et al., 1986), rising to approximately 124,000km loss in the late 1980s (Barr et al., 1991). Hedgerow removal has undoubtedly reduced the availability of several flowering and fruiting plant species such as blackthorn, hawthorn, bramble, dog rose and ivy to flower-visiting insects and birds.

1.2. Flower-visiting insects, fruit and birds

1.2.1. Insects and pollination

Visits to flowers for pollen and nectar by insects, are important for the pollination and fruit set of commercial orchard crops, which are related to some fruit-bearing hedgerow plants, such as apple (*Malus domestica* Borkh.), pear (*Pyrus communis* L.), plum (*Prunus domestica* L.) and almond (*Prunus dulcis* (Miller) D.A. Webb) (Corbet et al., 1991; Free, 1993; Williams, 1994). Pollination can be defined as "the transfer of pollen from the anthers of a flower on to the stigma of the same or a different flower, and is a prerequisite for fertilisation, which is usually essential for seed and fruit development" (Corbet et al., 1991). Table 1.2 (pages 24-26) summarises what is already known about the pollination requirements of the hedgerow plants studied in this project, and highlights some contradictory views, especially regarding the extent of self-compatibility. Free (1993) outlined characteristics of an effective insect pollinator: it visits several flowers of the same species in succession (floral constancy); it moves frequently between flowers (high foraging rate); it carries a large amount of pollen on its body; and it brushes against the stigmas of flowers, transferring pollen. Insect pollinators provide an important ecosystem service (Berenbaum et al., 2007; Kremen et al., 2007; Zhang et al., 2007) of enormous economic value to us since 35% of global crops depend on animal pollinators (Klein et al., 2007). Flower-visiting insects vary in their success as pollinators (Primack and Silander, 1975; Schemske and Horvitz, 1984; Herrera, 1987; Kandori, 2002) and of the insects that visit flowers, bees are recognised as important pollinators of crops and wild flowers in agroecosystems (Corbet et al., 1994; Corbet et al., 1991; Osborne and Corbet, 1994; Williams, 1994; 1996; Goulson 2003a; Greenleaf and Kremen, 2006; Winfree et al., 2008; Kremen et al., 2007; Zhang et al., 2007). Their effectiveness as pollinators is largely due to behavioural and morphological adaptations: honeybees, bumblebees and solitary bees all need to collect pollen and nectar to feed their larvae, requiring them to make more flower visits than other insects, increasing their effectiveness as pollinators (Proctor et al., 1996). They show floral constancy i.e. they restrict their visits to flowers of a certain species or colour over other potentially rewarding flowers (Waser, 1986; Heinrich et al., 1977). Honeybees are able to direct members of the colony to a desirable area of forage (von Frisch, 1967), and bumblebees can communicate information about a forage source, if not the location, to their fellow foragers (Dornhaus and Chittka, 1999; 2001), effectively bringing more pollinators to a patch of flowers. Bees also have hairy bodies, which are ideal for transporting pollen grains between flowers (Williams, 1980), and bumblebees and some solitary bees can fly at low temperatures (Heinrich, 1979; Stone and Willmer, 1989), ensuring pollination can occur even under unfavourable conditions for other flower-foraging insects.

Bees have been described as important pollinators of Rosaceous fruit-bearing orchard plants (Corbet et al., 1991; Free, 1993; Kuhn and Ambrose, 1984; Vicens and Bosch, 2000a), and several fruit-bearing hedgerow plants also belong to the Rosaceae family and therefore may have similar requirements for insect pollination in order to bear fruit. In general other pollinators have received less attention, but hoverflies (Syrphidae) and other flies, in particular 'bristly flies' (e.g. Calyptrate Diptera), are also thought to contribute to the pollination of Rosaceous fruit-bearing orchard plants (Brown, 1950; Bohart, 1952; Solomon and Kendall, 1970). They are also recorded as pollinators of a range of other plants, and examples include hoverflies pollinating oilseed rape (*Brassica napus* L.) (Jauker and Wolters, 2008), sweet pepper (*Capsicum annuum* L) (Jarlan et al., 1997) and hogweed (*Heracleum sphondylium* L.) (Zych, 2007), and 'bristly flies' pollinating leek (*Allium ampeloprasum* L.) (Clement et al., 2007), alpenrose (*Rhododendron ferrugineum* L.) (Escaravage and Wagner, 2004) and hogweed (*Heracleum sphodylium* L.) (Zych, 2007). Hoverflies such as *Eristalis* species may be good pollinators of many flowers because they are large, bristly and readily carry pollen on their bodies (Gilbert, 1993), and similarly to bees, hoverflies show constancy in their visits to flowers of plants that they have previously visited (Goulson and Wright, 1998). The importance of identifying ecosystem service providers (such as pollinators) in order to manage and safeguard the services they provide has been highlighted by Kremen (2005) and Berenbaum et al. (2007). This project aims to contribute to this knowledge by identifying the pollination service provided by insects to hedgerow plants and birds. In this project, I will investigate which flower-visiting insects (summarised in Table 1.2) have the greatest pollination value for hedgerow plants.

1.2.2. Birds and fruit

The fruits of plants studied in this project provide a succession of food for several farmland bird species from late summer (bramble), through autumn and winter (bramble, hawthorn, blackthorn, dog rose and ivy) and into late spring (ivy) (see Table 1.2). Snow (1971), Snow and Snow (1988) and McKey (1975) proposed that the coevolution of plants and animals has led to plants investing resources in attracting birds or other animals in return for the dispersal of its seeds (zoochory), and empirical studies show that frugivorous birds do facilitate the dispersal of seeds (e.g. Guevara and Laborde, 1993; Herrera et al., 1994; Jordano and Schupp, 2000). Aside from dispersal away from the parent plant, and the potential for the creation of new plant populations, the consumption of fruits by birds may also assist the establishment of some plant species by improved germination after passage through a bird's gut (Barnea et al., 1991; Clergeau, 1992; Traveset et al., 2001), for example the germination rate of ivy seeds is higher after the pulp has been removed after ingestion by birds (Clergeau, 1992). Whilst frugivorous birds provide a valuable ecosystem service by dispersing seeds, the importance of conserving birds from a societal perspective has been highlighted by their inclusion as a 'quality of life' indicator in the UK Government's Sustainable Development Strategy (HM Government, 2005).

Hedgerow fruits are consumed by partially migrant or resident bird species, but one of the most notable events observed in farmland in autumn is the arrival of large numbers of migratory fieldfares (*Turdus pilaris* L.) and redwings (*T. iliacus* L.). From October onwards, these birds travel from their breeding areas in Fennoscandia and Russia to overwinter in Britain and Ireland (Wernham et al., 2002) and commence feeding on hedgerow fruits. In recent years, blackcaps (*Sylvia atricapilla* L.) have also started to overwinter in the UK in increasing numbers (Bearhop et al., 2005), which in time could result in additional demand for fruits. Birds that forage on hedgerow fruits are generalists (Snow and Snow, 1988) i.e. they are omnivorous bird species that with reduced availability of invertebrate prey supplement their diet with fruits to maintain their energy, or in the case of migratory thrushes such as fieldfares and redwings feed on fruits initially in early winter and switch to soil invertebrates when the fruit supply is exhausted. Sorensen (1981) studied the faeces of blackbirds (*T. merula* L.), fieldfares and redwings throughout a British autumn and winter and observed that they contained a lower proportion of insects as the season progressed. The flesh of hedgerow fruits is nutritious, containing lipids, protein and carbohydrates (Sorensen, 1984; Snow and Snow, 1988), and offer a supplementary food resource for birds when invertebrate food is less available. Fruits, together with a small amount of invertebrate food could help birds build up fat reserves (Berthold, 1976; 1996). Calculations by Boddy (1991) show that 410 elder berries (*Sambucus nigra* L.) can provide 75-90% of the daily energy requirements of the blackcap in less than 10% of daylight hours. Berthold (1976) advocates the planting of fruit-bearing shrubs for migratory birds in staging areas, suggesting that when animal food is scarce fruits enable birds to winter in higher latitudes, successfully rear late broods in their breeding areas, and prepare for migration. Very occasionally fruits are fed to nestlings, e.g. blackbirds and blackcaps have been observed feeding ivy fruits, which are amongst the most nutritious of British fruits (Snow and Snow, 1988), to their young (Hernandez, 2005). Fruits also provide a supply of antioxidants, which assist the immune response of birds (Catoni et al., 2008).

1.2.3. Parallels in the relationships between pollinators and flowers, and birds and fruit

There are interesting similarities between insects and birds in terms of how they locate food, and also between how plants advertise the reward of either nectar and pollen to insects or fruits to birds, which are discussed below. Pollinating insects and birds are mobile organisms and need to locate food within the landscape. Birds use visual cues to find fruits, so the fruits of plants need to be visually attractive to their dispersers. Fruits have evolved bright colours, which attract birds (Murray et al., 1993; Gervais and Noon, 1999), often changing from a cryptic colour when unripe to a colour such as red or black when ripe as a signal to birds (Snow, 1971), both of which colours are favoured by birds (Turček, 1963). The contrast between coloured fruits and the foliage of the rest of the plant (Burns and Dalen, 2002; Schmidt et al., 2004) and the ultra-violet reflectance of waxy blooms on some fruits (Siitari, 1999) also aid the attraction of birds. Colour variation of fruits within and between plant species can be an indicator of quality, for example correlating with antioxidant reward (Schaefer et al., 2007). The size of the fruiting display is also of relevance for bird choice, birds often exhibiting preferences for plants with abundant fruits (Snow, 1971; Sallabanks, 1993). Similarly, plants have evolved flower colours and forms that are attractive to insects, whose visits for pollen and nectar assist the plant's reproduction (Sprengel, 1793). Insects such as bees are able to differentiate between several different colours (Waddington, 1983); colour advertises flowers over a long distance (Waser, 1983) and serves as a visual cue to enable pollinators to locate flowers (von Frisch, 1950; Kevan, 1983 and references therein; Backhaus, 1993). In a similar way to coloured fruits contrasting against leaves of a plant, flowers contrast against background vegetation (Waser, 1983), and ultra-violet reflectance of flowers helps attract pollinators in a similar manner to other wavelengths of reflected light (Kevan, 1978). Some plants have also evolved visible 'nectar guides', directing insects to the nectar reward (Sprengel, 1793; von Frisch, 1950). The size of the fruiting display has a role in attracting frugivorous birds, and equally, the size of the flowering display of a patch of flowers can determine its attractiveness to pollinators, with large flowering displays attracting more visits than smaller displays (Goulson et al., 1998; Grindeland et al., 2005; Feldman, 2006; Makino and Sakai, 2007). Unlike birds, insects are also attracted to flowers by odour originating from flowers and their component parts (von Frisch, 1950; Butler, 1951; Williams, 1983 and references therein; Pernal and Currie, 2002) and bees can easily learn to associate a reward with a particular odour (Pham-Delegue et al., 1993). Characteristics other than colour and the size of the fruiting display also influence the attraction of birds to fruits. These include fruit size (Wheelwright, 1993; Sallabanks, 1993) and a high pulp-to-seed ratio (Howe and Vande Kerchove, 1979; Herrera, 1981; Moermond and Denslow, 1983; Snow and Snow, 1988; Sallabanks, 1993), fruit size in relation to gape width (Wheelwright, 1985), handling costs (Sorensen, 1984; Courtney and Sallabanks, 1992), accessibility (Snow, 1971; Moermond and Denslow, 1983; Whelan and Wilson, 1994) and ripeness (Moermond and Denslow, 1983). With reference to pollinators, floral morphology can affect their foraging preferences, for example the tongue length of insects in relation to corolla length can influence pollinator visitation rates (Inouye, 1980). Additionally, floral characteristics, such as flower size, or the number of flowers open on an inflorescence may be synonymous with nectar reward and pollinators may display a preference for these flowers or inflorescences (e.g. Cresswell and Galen, 1991; Duffield et al., 1993). Floral symmetry is also a selecting factor for some pollinators, for reasons which are unclear, but may be related to nectar reward, an innate preference for symmetrical flowers, or reduced handling costs (Møller and Eriksson, 1995; Neal et al., 1998; West and Laverty, 1998).

The nutritional quality of fruits can also affect the feeding preferences of birds (Stiles, 1993; Snow, 1971; Schaefer et al., 2007; Catoni et al., 2008). Similarly, insects will also respond to nectar reward. For example, bees will avoid flowers that have previously been visited, ensuring they forage on flowers with greater nectar reward

(Heinrich, 1979; Corbet et al., 1984), and are able to shift their foraging patterns according to changes in this reward (Morse, 1980; Cnaani et al., 2006).

1.3. Factors affecting hedgerow fruit availability

1.3.1. Pollinator declines

A heterogeneous landscape with a range of semi-natural habitats providing suitable nest sites and forage is important to support a healthy pollinator community (Banaszak, 1992; Osborne and Corbet, 1994; Williams and Carreck, 1994; Edwards, 1996; Westrich 1996; Svensson et al., 2000; Kremen et al., 2002; Steffan-Dewenter, 2002; Steffan-Dewenter et al., 2002; Kremen et al., 2004; Albrecht et al., 2007; Holzschuh et al., 2007; Williams and Kremen, 2007; Ricketts et al., 2008). In agroecosystems, arable fields often represent dense and ephemeral monocultures, with farmland wildlife largely confined to the non-crop vegetation of semi-natural field margins and hedgerows. Land use changes such as the expansion and intensification of farming has led to a loss of semi-natural habitats such as grasslands, field margin vegetation and hedgerows, and associated nest sites and forage, which has had negative impacts on wild bee populations (Williams, 1982; Osborne and Corbet, 1994; Buchmann, 1996; Williams, 1986; Goulson, 2003b; Carvell et al., 2006a). A species diverse population of pollinators is likely to be best for providing plants with a pollination service and safeguarding against pollinator losses. For example, whilst honeybees may be good pollinators, they should not be relied on to replace wild bees as pollinators (Roubik, 1996; Kremen et al., 2002; Berenbaum et al., 2007). Indeed, some plants achieve better pollination when visited by wild pollinators, for example, bumblebees perform 'buzz-pollination' in crop plants such as tomatoes (Asada and Ono, 1996) and some wild plants (Osborne, 1994; Larson and Barrett, 1999; Kawai and Kudo, 2009). Domesticated honeybees in the UK are also facing challenges, such as declining interest in beekeeping and disease (Williams, Corbet and Osborne, 1991; Budge, G. http://beebase.csl.gov.uk), and if this continues we may be looking to wild bees to compensate for the pollination gap left by honeybees (Kremen et al., 2002; Greenleaf and Kremen, 2006; Berenbaum et al., 2007; Winfree et al., 2007).

There is concern that declines in pollinators due to land-use change will threaten plant-pollinator interactions at a local, landscape and global scale (Buchmann and Nabhan, 1996; Allen-Wardell et al., 1998; Kearns et al., 1998; Kremen et al., 2007; Steffan-Dewenter and Westphal, 2008), potentially threatening the world's food supply since 35% of global crops depend on animal pollinators (Klein et al., 2007; Steffan-Dewenter et al., 2005). However, the notion of a 'global pollination crisis' as a basis for pollinator conservation is still in debate. For example, Ghazoul (2005a; 2005b) raises several points against a worldwide threat to pollination services. He argues that many crops do not require insect pollination (e.g. cereals, lentils, bananas), that it is locally reduced pollinator activity caused by habitat fragmentation, rather than regional losses that limits plant reproductive output, that evidence of pollinator declines is largely from North America and Europe, and that globally, some pollinator communities may be resistant to environmental change. Nevertheless, even if there is not a 'global pollinator crisis', simultaneous declines in pollinators and the wild plants they interact with have recently been identified in Europe (Biesmeijer et al., 2006). The groups of insects identified as declining significantly in diversity by Biesmeijer et al. (2006) in Britain include wild bees (solitary bees and bumblebees). Analysis of aerial insect suction trap biomass between 1973 and 2002 by Shortall et al. (in press) reveals declines over this period in social wasp and large diptera biomass (e.g. Bibionidae and Calliphoridae) at one location representative of Southern Britain. Several of these insect groups may have importance as pollinators of fruit-bearing hedgerow plants, and this will be investigated in this thesis. If insect declines continue, then this could potentially affect fruit availability for farmland birds in the future.

1.3.2. Landscape effects

Having considered which plants need which pollinators, this project also considers factors that could modify pollinator activity and hence the potential for fruit set of hedgerow plants (Chapter 4 and 5). Mass-flowering crops such as oilseed rape (*Brassica napus* L.), field beans (*Vicia faba* L.), clover (*Trifolium* spp.) and field pea (*Pisum sativum* L.), some of which cover an increasing area of the UK arable landscape, have been shown to have positive benefits for one group of pollinators: bumblebee colony size and densities in field margins, or experimental plots of forage, appear to be positively related to the proportion of mass-flowering crops in the landscape (Westphal et al., 2003; Herrmann et al., 2007). Conversely, these large areas of forage may also attract cleptoparasitic *Bombus* species (cuckoo bees) with the result that bumblebee nests are more likely to be invaded by cuckoo bees (Carvell et al., 2008). Although a generally positive effect of a mass-flowering resource on pollinator abundance may occur at a landscape scale, the modification of pollinator activity by a co-flowering plant (e.g. a mass-flowering crop) through competition with an adjacent co-flowering plant (e.g. a hedgerow plant species) for pollinator visits has been observed, sometimes with detrimental effects on the seed set of one of the plants (Chittka and Schürkens, 2001; Brown et al., 2002; Muňoz and Cavieres, 2008; Moragues and Traveset, 2005). Hedge aspect also has the potential to exert an influence on the fruit set of hedgerow plants, since insect activity can increase with temperature, light intensity and solar radiation levels (Wratt, 1968; Beattie, 1971; Szabo and Smith, 1972; Corbet et al., 1993; Vicens and Bosch, 2000b; Klein et al., 2003a, 2003b; Abrol, 2006), which would be expected to be greater on south- and west-facing hedges. Hedge aspect could also potentially affect fruit set directly, regardless of insect activity, for example reduced light levels caused by shading has been shown to reduce the fruit yield of some orchard crops by increasing fruit abscission (Saito et al., 1989; Byers, 1990; George et al., 1993; McArtney et al., 2004). This project aims to test the hypothesis that hedge aspect affects hedgerow fruit set, following up an unpublished study by Sparks (pers.comm.),

Modern agriculture has resulted in a landscape of fragmented habitats, in which hedges could be viewed as refuges for birds and insects after the contraction of woodlands and grasslands (Pollard et al., 1974; Dowdeswell, 1987; Dover and Sparks, 2000). Habitat fragmentation adversely affects plant-pollinator interactions through the isolation of plant and pollinator populations (Rathcke and Jules, 1993), and increasing distance of plants from semi-natural habitats is known to reduce pollinator richness, visitation rate and plant reproductive success (Steffan-Dewenter and Tscharntke, 1999; Klein et al., 2003a, 2003b, Rickets et al., 2008). If fruit-bearing hedgerow plant species are entomophilous, the distance between genetically dissimilar conspecifics could be of importance. For example, although plants within hedges are linked as a corridor, large distances between individuals within the hedge itself or across whole fields may restrict pollen flow and hence fruit set. Geographical isolation of plants is known to affect negatively their reproductive success in terms of pollen deposition, seed set and gene flow (Eriksson and Bremer, 1993; Kunin, 1993; Kwak et al., 1998; Gibbs and Talavera, 2001; Winter et al., 2008). The mechanism behind this is likely to be pollen limitation either through insufficient pollinator visits to the isolated patches affecting pollen delivery (quantity), or pollinator visits may be adequate, but the origin of the pollen that they carry is unsuitable (quality) (Ashman et al., 2004; Knight, T. M. et al., 2005), which may be linked to the propensity of pollinators to move between isolated patches (e.g. Schulke and Waser, 2001). This will also be related to the behaviour of pollinators, for example, whether they can travel large distances between forage patches (Somanathan and Borges, 2004), which will vary between pollinators. Pollinators such as bees are mobile organisms and the distance they travel from their nest varies between the genera, with larger bee species having longer foraging ranges (Greenleaf et al., 2007). Depending on the availability of forage in the landscape, honeybees can travel approximately 1 or 2km (Steffan-Dewenter and Kuhn, 2003) and even up to 9.5km (Beekman and Ratnieks, 2000). Bumblebees' foraging ranges are shorter i.e. within a few hundred metres or a couple of kilometres (Walter-Hellwig and Frankl, 2000; Darvill et al., 2004; Knight, M. E. et al., 2005; Osborne et al., 2008a) and solitary bees are even more restricted in their foraging ranges, to a few hundred metres (Gathman and Tscharntke, 2002; Greenleaf et al., 2007).

Although hedges may represent a fragmented habitat, they could also serve as corridors for the movement of wildlife (Dawson, 1994; Dover and Sparks, 2000). Bees have been observed following strips or 'corridors' of flowering plants (Kwak and Vervoort, 2000), behaviour which in theory could assist the pollination of hedgerow flowers along a hedge. Flower visitation and the reproductive success of plants can be increased in patches that are connected by linear features such as hedges, in comparison with unconnected patches (Cranmer, 2004). Conversely, Cant (2006) found that hedges did not serve as guides to gene flow of experimental patches of plants, which she suggests may be due to competition between heterospecific forage in the hedge and the patches.

1.3.3. Hedge management

The management of hedges will also have affected the availability of fruits to frugivorous birds. Croxton and Sparks (2004) found that fruits of hawthorn, blackthorn and dog rose are depleted from hedges between early October and the middle of January. In the past, the practice of hedge cutting between harvest and drilling (July to October) removed the majority of hedgerow fruits (Croxton and Sparks, 2004). Woody shrubs in hedges such as blackthorn and hawthorn also flower and fruit on second year growth (Maudsley et al., 2000; Croxton and Sparks, 2002), and past management regimes have involved the annual trimming of hedges, which has been shown to have a negative effect on the availability of the winter food resources of birds (Maudsley et al., 2000; Croxton and Sparks, 2002). The loss of hedgerows will also have reduced the availability of hedgerow fruits to birds on a large scale, therefore the management of remaining and newly-created hedges is critical to ensure that these hedges produce as many flowers and fruits as possible, and that these are allowed to remain on the hedges until they have been eaten. The UK Government has recently taken steps to protect hedgerow habitats, and these measures and their consequences for hedgerow fruit availability in the future will be discussed in Chapter 6.

1.4. Objectives of current project

This project was designed to improve our understanding of the links between insect pollinators, fruits and frugivorous birds in hedgerows, and the extent to which such habitats need to be preserved or improved (through farmland management) to ensure a strong population of pollinators, and consequently a plentiful supply of fruit for birds over the winter. The specific objectives of this project were as follows:

1. To establish the requirement for insect pollination of common, native, fruit-bearing hedgerow plants.

2. To determine which groups of flower-visiting insects are of the greatest pollination value to fruit-bearing hedgerow plants.

3. To examine the effects of hedge aspect on the activity of insects and the pollination and fruit set of blackthorn.

4. To examine the effects of adjacent crop type on the behaviour activity of insects and the pollination and fruit set of hawthorn.

5. To assess whether the abundance of frugivorous birds is related to the size of the hedgerow fruit crop.

1.5. Thesis overview

The thesis is divided into four chapters of experimental work (Chapters 2 to 5) done to address the objectives listed above. Hypotheses were formulated to help answer each objective:

Chapter 2: Requirements for insect pollination

This chapter describes an investigation of the requirement for insect pollination of the common, native, fruit-bearing hedgerow plant species blackthorn, hawthorn, dog rose, bramble and ivy.

Objective 1

- When insects are excluded from flowers using mesh bags, are hedgerow plants able to set a similar amount of fruit (via self-or wind- pollination) as unbagged flowers?
- Is the fruit set of plants in the study hedgerows pollen limited?

Three plant species (ivy, blackthorn and hawthorn) were then chosen to address Ojectives 2 to 5 and each species is the subject of a chapter.

Chapter 3: Ivy pollination

Objective 2.

- Which insect groups have the greatest pollination value?
    - Which carry the most amount of ivy pollen on their bodies?
    - Which have the fastest flower visitation rate?
    - Which are the most abundant?

  - Does insect abundance correlate with ivy fruit set?

Chapter 4: Blackthorn pollination

Objective 2

- Which insect groups have the greatest pollination value?
  - Which carry the most amount of blackthorn pollen on their bodies?
  - Which have the fastest flower visitation rate?
  - Which make the greatest amount of contact with the reproductive organs of flowers?
  - Which are the most abundant?
  - Does insect abundance correlate with blackthorn fruit set?

Objective 3

- Are insects more abundant on blackthorn flowers on warmer, south- or west-facing sides of hedges compared to cooler north- or east-facing sides?
- Is blackthorn fruit set greater on the warmer side of hedges?

Objective 5

- Are frugivorous birds more abundant in hedges with a large amount of fruits compared to hedges with fewer fruits?

Chapter 5: Hawthorn pollination

Objective 2

- Which insect groups have the greatest pollination value?
  - Does insect abundance correlate with hawthorn fruit set?

Objective 4

- Does the mass-flowering crop *Brassica napus* L., oilseed rape facilitate insect visits to hawthorn flowers, compete with hawthorn flowers for insect visits or have no effect on insect densities on hawthorn flowers?
- Is the proportion of hawthorn flowers that set fruit different in hedges adjacent to oilseed rape, compared to that of hawthorn flowers in hedges adjacent to a non-flowering crop?

Objective 5

- Are frugivorous birds more abundant in hedges with a large amount of fruits compared to hedges with fewer fruits?
-

Appendices A to C contain information relevant to Chapter 2, including more detailed information about the hedges where experiments were done, plus methods and results of supplementary experiments.

1.6. Field sites and plant species

1.6.1. Field sites

Experiments were done at Rothamsted Research’s farm and the local area (Harpenden, Hertfordshire, UK, TL125135) and at The Game and Wildlife Conservation Trust’s ‘Allerton Project’ farm (Loddington, Leicestershire, UK, SK788024) (Figure 1.2 and 1.3). Both operate as commercial farms and represent examples of lowland farming in the UK. Aside from commercial farming they also have areas dedicated to agricultural research: Rothamsted’s research focuses on crop and soil quality, the management of crop pests and pathogens, and farmland biodiversity, and Loddington’s research focuses on the sustainable management of the agricultural landscape for game and other wildlife. At Loddington, where numerous conservation measures are implemented, monitoring of passerine birds has shown that some species have shown significant increases relative to a national trend of long-term declines (Boatman and Stoate, 2000). The land use varies slightly between the two farming areas as illustrated by Table 1.1, which shows the proportion of different land uses for the two years in which experiments were done at both sites simultaneously (Year 1, 2005 and Year 2, 2006).

Table 1.1 Land use characteristics of Rothamsted and Loddington farms: approximate proportions of each land use type

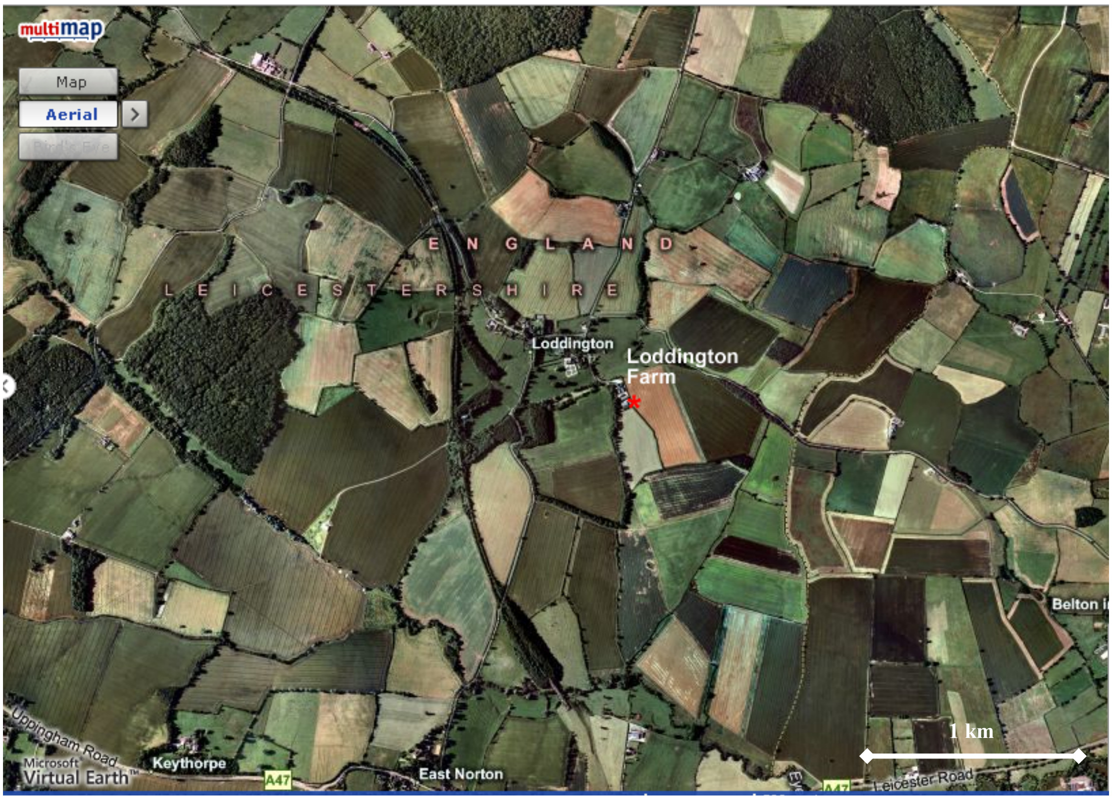
site	year	pasture*	cereal	mass-flowering crop e.g. oilseed rape, turnip rape, field beans, potatoes	semi-natural habitats**	willow	miscellaneous ***	total farm area (hectares)
Rothamsted	winter 2004-autumn 2005	8% (winter only)	44 %	13 %	21 %	3 %	19 %	265.97
	winter 2005-autumn 2006	8% (winter only)	42%	12%	30%	2%	14%	267.77
Loddington	winter 2004-autumn 2005	12 %	43 %	26 %	11 %	N/A	4 %	311.35
	winter 2005-autumn 2006	12 %	47 %	27 %	12 %	N/A	3 %	281.29

*pasture = Rothamsted: sheep grazing (winter only); Loddington: sheep, cattle and horses ** semi-natural habitats = Rothamsted: grasslands; Loddington: conservation headlands, wildlife seed mix, grasslands ***, miscellaneous = e.g. panicum, miscanthus, sugar beet, farmyard

NB: In 2004-2005 and 2005-2006, four hedges at ‘Rothamsted’ were located on farms local to Rothamsted. Land use data were not available for these farms

Figure 1.2 Location map of Rothamsted farm (TL125135) and surrounding area. All hedges were located within 4km of the farm

Figure 1.3 Location map of Loddington farm (SK788024) and surrounding area. All hedges were located within 1.5 km of the farm



Maps reproduced from http://multimap.com

1.6.2. The plant species

Table 1.2 lists the fruit-bearing hedgerow plant species studied in this project and summarises what is already known about their mode of reproduction, the insects that forage on the flowers and the birds that feed on the fruits. Common names of animal and plant species are used throughout the thesis following the inclusion of scientific names at the first mention in each chapter.

Table 1.2 Fruit-bearing hedgerow plant species, their mode of reproduction and requirement for insect pollination, insect flower visitors and frugivorous birds

Plant species	Mode of reproduction and requirement for insect pollination	Insect visitors (from Knuth,1908)	Flowering time	Fruit ripening time	Bird species observed feeding on fruits (from Snow and Snow, 1988)
blackthorn (*Prunus spinosa* L.)	• Self-pollination possible (Knuth, 1908) • Self-incompatible (Guitián, J. et al., 1993, Nunes, 2006) • Vegetative reproduction	Bees (e.g. bumblebees, honeybees and solitary bees), flies, butterflies, beetles	March to May	September to November	Robins, blackbirds, fieldfares, redwings, song thrushes, mistle thrushes, starlings, magpies, crows
hawthorn (*Crataegus monogyna* Jacq.)	• Self-incompatible (Clapham et al., 1987) • Partly self-incompatible (Guitián and Fuentes, 1992; Bradshaw, 1971) • Apomixis may occur in *Crataegus* (Fryxell, 1957; Muniyamma and Phipps, 1979; Richards, 1997) • Self-pollination or apomixis (Yeboah Gyan and Woodell, 1987b)	Bees (e.g. bumblebees, honeybees and solitary bees), flies and beetles (Observed foraging on *C. laevigata,* but morphologically similar to *C. monogyna*)	May to June	September to November	woodpigeons, robins, blackbirds, fieldfares, redwings, song thrushes, mistle thrushes, blue tits starlings, magpies, crows

Table 1.2 Fruit-bearing hedgerow plant species, their mode of reproduction and requirement for insect pollination, insect flower visitors and frugivorous birds

Plant species	Mode of reproduction and requirement for insect pollination	Insect visitors (from Knuth,1908)	Flowering time	Fruit ripening time	Bird species observed feeding on fruits (from Snow and Snow, 1988)
dog rose (*Rosa canina* agg.)	• Self-incompatible (Jones, 1939) • Self-pollination possible (Knuth, 1908) • Apomixis and self-pollination (Wissemann and Hellwig, 1997) • Reduced fruit set in the absence of insects (Yeboah Gyan and Woodell, 1987b)	Bees (e.g. bumblebees, honeybees and solitary bees), flies and beetles	June to July	November to December	Woodpigeons, robins, blackbirds, fieldfares, redwings, song thrushes, mistle thrushes, blackcaps, blue tits, greenfinches
bramble (*Rubus* spp.)	• Pseudogamy and vegetative reproduction (Nybom, 1985, 1988; Proctor et al., 1996; Kollman et al., 2000) • Set fruit in the absence of insects (Yeboah Gyan and Woodell, 1987b)	Bees (e.g. bumblebees, honeybees and solitary bees), flies, butterflies and beetles	May to September	August to October	Moorhens, robins, blackbirds, song thrushes, garden warblers, blackcaps, lesser whitethroat, common whitethroat, blue tits, starlings, greenfinches, bullfinches

Table 1.2 Fruit-bearing hedgerow plant species, their mode of reproduction and requirement for insect pollination, insect flower visitors and frugivorous birds

Plant species	Mode of reproduction and requirement for insect pollination	Insect visitors (from Knuth,1908)	Flowering time	Fruit ripening time	Bird species observed feeding on fruits (from Snow and Snow, 1988)
ivy (*Hedera helix* L.)	• Anecdotal evidence that insect visits are required for fruit set (Wittrock, in Knuth, 1908)	Wasps and flies Observed bees (e.g. bumblebees, honeybees and solitary bees), butterflies and moths foraging on ivy flowers in this study (Chapter 3)	end August to November	end of December to May	Robins, blackbirds, fieldfares, redwings, song thrushes, mistle thrushes, blackcaps, starlings, woodpigeons

1.7. Glossary of terms

Apomixis/Agamospermy

The seeds of flowers mature without any fertilisation from pollen (Proctor et al., 1996).

Geitonogamy

Pollination of a flower by pollen from another flower on the same plant (Proctor et al., 1996)

Microspecies

A set of plants that shows variation within an agamospermous group. Also known as a 'biotype'. (Proctor et al., 1996)

Pseudogamy

Requires pollination to initiate endosperm, and seed development, despite the fact that the ovules require no fertilisation (Proctor et al., 1996). For some plants e.g. brambles, this can be through self-pollination (Nybom, 1985).

2. Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit set

2.1. Introduction

The flowers of fruit-bearing hedgerow plants can provide a succession of forage for insects throughout the year. This chapter investigates whether, for a selection of British hedges, insects provide an adequate pollination service for these plants through their visits to flowers for pollen and nectar. The fruits of plant species found in British hedges form a large part of the winter diet of resident and migratory frugivorous birds on farmland (Hartley, 1954; Sorensen, 1981, 1984; Snow & Snow, 1988). Loss of hedgerows in UK farmland (Barr et al., 1986, 1991; Rackham, 2000) has almost certainly reduced availability of hedgerow fruit. Many farmland birds have declined in recent decades (Mead, 2000; Gregory, 2004; Baillie et al., 2007), but it is not known whether changes in availability of hedgerow fruit have played a contributory role. For granivorous passerines, winter food supply is thought to have contributed to the population declines of some species, and supplementary feeding experiments suggest that breeding abundance is currently influenced by the availability of seed food in winter (Siriwardena et al., 2007).

The flowers of blackthorn (*Prunus spinosa* L.), hawthorn (*Crataegus monogyna* Jacq.), dog rose (*Rosa canina* agg.), bramble (*Rubus fruticosus* agg.) and ivy (*Hedera helix* L.) are visited for pollen or nectar (or both) by several insect species, mainly Aculeate Hymenoptera (bees and wasps), Diptera (true flies), and Lepidoptera (moths and butterflies) (Knuth, 1908; Pollard et al.,1974; Yeboah Gyan and Woodell 1987a; Fussell and Corbet, 1991; Fussell and Corbet, 1992; Guitián & Fuentes, 1992; Porter et al., 1992; Guitián, J. et al., 1993; Proctor et al., 1996; Garcia and Chacoff, 2006;Vezza et al., 2006). It is likely that the flower visits of these insects result in pollination, seed set and fruit set, but the importance of insect visits for hedgerow fruit set will depend on the reproductive system of the plant.

This chapter addressses Objective 1 of the PhD project, and its aims are twofold: to establish the reproductive system and requirements for insect pollination of a range of fruit-bearing hedgerow plants; and for those that are insect pollinated, to establish whether pollination services in the agricultural landscapes studied are limiting fruit set. Pollen limitation is observed as a common phenomenon in plants (Burd, 1994; Ashman et al., 2004; Knight, T. M. et al., 2005) and supplemental pollination experiments have provided evidence of pollen limitation for several plant species (Bierzychudek, 1981; Corbet, 1998; Pflugshaupt et al., 2002; Ward and Johnson, 2005). Factors that could contribute to sub-optimal fruit or seed set are the delivery of incompatible pollen (Campbell and Motten, 1985; Hessing, 1988; de Jong et al., 1993), or low pollinator density (Gross and Werner, 1983; Liu and Koptur, 2003), since pollinator activity can influence seed and fruit set (Waser, 1979; Zimmerman, 1980; Montalvo and Ackerman, 1986; Klein et al., 2003b; Morandin and Winston, 2005). Resource limitation should not be overlooked as this can operate in conjunction with pollen delivery to influence seed set or fruit size (Zimmerman and Pyke, 1988; Zimmerman and Aide, 1989; Campbell and Halama, 1993; Casper and Niesenbaum, 1993). If fruit set is reduced in the absence of insects and pollen limitation is occurring it might be expected that there would be an effect of reducing the time of exposure of flowers to insects. For example

Benedek et al. (1994; 2000; 2006) found that even partial exclusion of pollinators resulted in a decrease in fruit yield for both self-incompatible and self-fertile cultivars of orchard trees.

In this chapter, experiments are presented to establish whether common hedgerow plants require flower visits from insects to set fruit, by excluding flower-visiting insects from flowers using mesh bags. The use of different mesh bags provides some indication of the relative importance of selfing, wind and insects as pollen vectors. The pollination biology of plants that show reduced fruit set in the absence of flower-visiting insects, will be examined further to determine a) whether the fruit set was pollen limited and b) what would happen to fruit set if flowers received reduced exposure to flower-visiting insects. If manual cross-pollination results in greater fruit set than an open-pollinated control then pollen receipt is inadequate, indicating pollen limitation.

2.1.1. The requirement for insect pollination of fruit-bearing hedgerow plants

The plants that will be investigated in this study are listed below, together with their mode of reproduction according to the literature. Plates 2.1 – 2.5 illustrate their flowers and fruits.

2.1.1.1. Blackthorn (*Prunus spinosa* L.), ROSACEAE (Plates 2.1a-c)

Blackthorn is a native, deciduous shrub and is one of the earliest hedgerow plant species to flower (March to May), with the flowers opening before the leaves. As an early forage resource it is of use to insects emerging from hibernation that are looking to establish nests, such as bumblebee queens and solitary bees, and it may help honeybee colony development after the winter. The flowers have an open strucure, are 1.5-2cm in diameter, with five white petals, one stigma, one ovule, and approximately 20 stamens. Knuth (1908) reported that blackthorn can automatically self-pollinate if insect visits are in short supply, although this was not based on empirical evidence, and subsequent research has shown that it is self-incompatible and sets none or very few fruits in the absence of insect visits (Guitián, J. et al., 1993; Nunes, 2006).

2.1.1.2. Hawthorn (*Crataegus monogyna* Jacq.), ROSACEAE (Plates 2.2a-c)

Hawthorn is a native, deciduous shrub, flowering from May to June. The flowers have an open structure, are 1.5-2cm in diameter, with five white petals, one stigma, one ovule, and approximately 20 stamens. According to Clapham et al. (1987), hawthorn is self-incompatible, and it has been shown to set very few fruits through self-pollination (Bradshaw, 1971; Guitián & Fuentes, 1992). Some authors have described *Crataegus* spp. as having apomictic forms, with seeds developing without fertilisation (Fryxell, 1957; Muniyamma and Phipps, 1979; Richards, 1997). In the Rosaceae subfamily Maloideae (of which *Crataegus* is a member), apomixis is usually associated with polyploidy (Campbell et al., 1991) and it is unlikely that apomixis occurs in Britain, since *C. monogyna* is diploid (Dickinson and Campbell, 1991). However, there is one study of a British hawthorn population that found that fruits were set in the absence of insects, indicating self-pollination or apomixis for those plants (Yeboah Gyan and Woodell, 1987b).

2.1.1.3. Dog rose (*Rosa canina* agg.), ROSACEAE (Plates 2.3a-c)

Dog roses are native shrubs, flowering from May to July. The flowers have an open structure, are 7-8cm in diameter, with five white to pink petals, numerous stigmas, and approximately 60 stamens and 30 ovules. In the UK there are three to four types of dog rose and many hybrids between *R. canina* and other *Rosa* species (Graham and Primavesi, 1993). Knuth (1908) proposed that self-pollination was possible, whereas Jones (1939) suggested that flowers were self-incompatible. More recent work has demonstrated that dog roses are able to produce seeds through apomixis and self-pollination (Wissemann and Hellwig, 1997), but a study of a UK population of dog rose showed that fruit set was reduced when insects were prevented from visiting the flowers (Yeboah Gyan and Woodell 1987b).

2.1.1.4. Bramble (*Rubus fruticosus* agg.), ROSACEAE (Plates 2.4a-c)

In the British Isles, *R. fruticosus* is an aggregate of approximately 300 microspecies (Edees and Newton, 1988; Newton and Randall, 2004). It is common in hedgerows and flowers from May to September. The flowers have an open structure, are 3cm in diameter, with five white to pink petals and numerous stigmas, stamens and ovules. Some *Rubus* species are able to set seeds and fruit in the absence of insects, and their breeding system includes pseudogamy, self- and cross-pollination, and vegetative reproduction (Nybom, 1985; 1988; Yeboah Gyan and Woodell 1987b; Proctor et al., 1996; Kollman et al., 2000).

2.1.1.5. Ivy (*Hedera helix* L.), ARALIACEAE (Plates 5a-c)

Ivy is a native climber, flowering from September to November. The flowers have an open structure, are 0.7-1cm in diameter, with five green petals, one stigma, five stamens and five ovules. Because it flowers late in the season it is a useful resource for insects preparing for hibernation, such as bumblebees, butterflies and queen wasps. Little is known of the mode of reproduction of ivy, only anecdotal evidence that insect flower visits are required for pollination and fruit set provided by Wittrock (in Knuth, 1908), who noted that ivy flowering in a greenhouse did not produce fruit.

Whilst some empirical research has been done on the mode of reproduction of some of the fruit-bearing plant species that are found in hedges, this study aims to provide a more comprehensive study of the requirement for insect pollination of blackthorn, hawthorn, dog rose, bramble and ivy in a sample of British hedges. Understanding the links between insect pollinators, fruits and frugivorous birds is important for determining whether habitats for pollinators in agricultural areas need to be maintained or improved (through farmland management) to ensure a strong population of pollinators, and consequently a plentiful winter food resource for birds. This chapter aims to confirm the requirements for insect pollination of blackthorn, hawthorn, dog rose , bramble and ivy in a selection of British hedges; to test for pollen limitation in those plant species that require flower visits from insect pollinators to enhance fruit set; and to investigate the effects of reducing the exposure of flowers to insect visitors (simulating further reductions in pollinator abundance) on the fruit set of those plant species that require flower visits from insect pollinators to enhance fruit set.

Plate 2.1a Blackthorn (*Prunus spinosa* L.) in flower

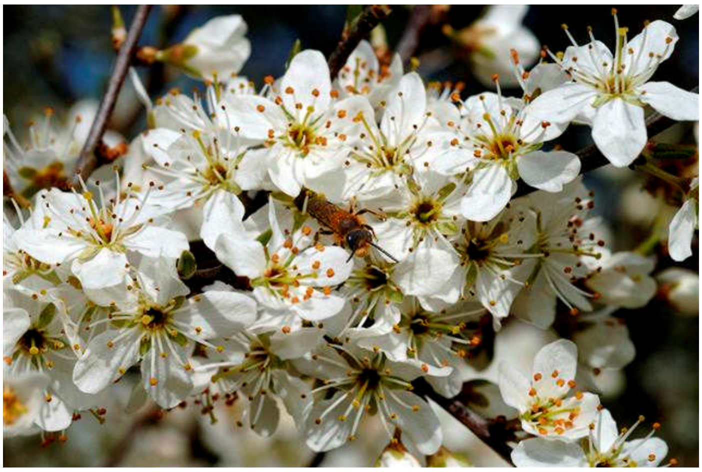


Plate 2.1b Cross-section of blackthorn flower

Plate 2.1c Cross-section of blackthorn fruit (sloe)

Plate 2.2a Hawthorn (*Crataegus monogyna* Jacq.) in flower

Plate 2.2b Cross-section of hawthorn flower

Plate 2.2c Cross-section of hawthorn fruit (haw)

Plate 2.3a Dog rose (*Rosa canina* agg.) in flower

Plate 2.3b Cross-section of dog rose flower

Plate 2.3c Cross-section of dog rose fruit (hip)

Plate 2.4a Bramble (*Rubus fruticosus* agg.) in flower

Plate 2.4b Cross-section of bramble flower

Plate 2.4c Cross-section of bramble fruit (blackberry)

Plate 2.5a Ivy (*Hedera helix* L.) in flower

Plate 2.5b Cross-section of ivy flower

Plate 2.5c Cross-section of ivy fruit

2.2. Methods

2.2.1. Experimental design

Hedges containing blackthorn, hawthorn, dog rose, bramble and ivy were located at Rothamsted Research's farm and neighbouring farms (Hertfordshire, UK, TL1314) and The Game & Wildlife Conservation Trust's 'Allerton Project' farm (Loddington, Leicestershire, UK, SK7902). Experiments were done in 2005 (Year 1) and 2007 (Year 3).

2.2.1.1. Requirements for insect pollination (effects of manipulating the pollination environment) 2005 (Year 1) and 2007 (Year 3)

A preliminary insect exclusion experiment was done in Year 1 (2005) to establish the requirement for insect pollination for fruit set and to identify plant species for studying in more detail. At Rothamsted and Loddington, groups of buds from blackthorn, hawthorn, dog rose, bramble and ivy on one or more hedges were selected before anthesis. Two treatments were applied according to a randomised block design within each hedge:

1. BG: 'bagged' using muslin or nylon (more resilient than muslin to thorns, therefore used for dog rose and bramble) to exclude flower-visiting insects
2. OP: 'open pollination' - flowers were left open to flower-visiting insects.

Plant species that showed reduced fruit set when insects were excluded in Year 1 (2005) were studied in more detail, at Rothamsted in Year 3 (2007), to test for pollen limitation and the effects of restricting exposure to flower-visiting insects on fruit set. In addition, a tulle mesh bag treatment was used alongside the nylon or muslin mesh bag treatment to provide a better assessment of the contribution of wind-pollination. Tulle is sufficiently fine to prevent insects from reaching flowers, but has a coarser weave (1.2mm) than nylon or muslin (0.5-0.7mm), allowing more airborne pollen to pass through, whilst still being insect-proof (see Appendix A). If wind were an important vector of pollen there should be a difference between treatments M100 (muslin) and T100 (tulle).

Groups of buds were selected before anthesis and five treatments (described in more detail in Table 2.1) were applied according to a randomised block design:

1. M100: buds enclosed in muslin bags for the whole duration of flowering
2. T100: buds enclosed in tulle bags for the duration of flowering (allowing a comparison with muslin in terms of wind-pollination)
3. T50: buds enclosed in bridal tulle bags for 50% of the duration of flowering (bags removed for five days and replaced for five days in a continuous cycle);
4. OP: ‘open pollination’ - flowers freely exposed to insect visitors
5. HP: ‘hand cross-pollination’ - flowers supplemented with pollen by hand from a different hedge every two days to test for pollen limitation.

Sample sizes of experiments with results presented in this thesis are listed in Table 2.2.

Table 2.1 Experimental treatments and possible routes of pollination

Year	Treatment	Mesh type & gauge	Insects	Wind	Self	Supplemented by hand
1 (2005)	BG	Muslin / nylon 0.7mm	No	Very little	Yes	No
1 (2005	OP	-	Yes	Yes	Yes	No
2 (2007)	M100	Muslin 0.7mm	No	Very little	Yes	No
2 (2007)	T100	Tulle 1.2mm	No	Yes (less)	Yes	No
2 (2007)	T50	Tulle 1.2mm	Yes (50%)	Yes	Yes	No
2 (2007)	OP	-	Yes	Yes	Yes	No
2 (2007)	HP	-	Yes	Yes	Yes	Yes

Table 2.2 Experimental sample sizes in a randomised block design (final n values in graphs may differ since groups were occasionally missing on return to the hedges)

Species	Year	Site	No. of treatments	No. of hedges	No. of buds per treatment (a group)	No. of groups of buds per treatment per hedge
dog rose	1 (2005)	Rothamsted	2	3	~ 3	8 -10
	1 (2005)	Loddington	2	1	~ 3	10
bramble	1 (2005)	Rothamsted	2	3	unknown	10
	1 (2005)	Loddington	2	3	unknown	8 -10
blackthorn	3 (2007)	Rothamsted	5	6	~ 30	5 -10
hawthorn	3 (2007)	Rothamsted	5	6	~ 15	11
ivy	3 (2007)	Rothamsted	5	3	~ 30	6

2.2.2. Experimental methods

For all pollination treatments, groups of flower buds were marked before anthesis using weather-proof enamel paint. Those assigned to the bagged treatments (BG, T50, M100, T100) were covered with a wire frame, and a mesh bag was placed over the frame and secured with a labelled twist tie. The end of the bag was sealed onto the branch using insulating tape to prevent insects from crawling inside. The wire frame avoided the likelihood of contact between the bag and the reproductive organs of the flowers, and prevented stigmas protruding through the bag (Plate 2.6).

Plate 2.6 Tulle (T100) bagged blackthorn flowers, used to investigate the effect on fruit set of excluding flower-visiting insects

Flowers in the HP treatment in 2007 were supplemented with pollen from flowers collected from a different hedge, less than one hour previously, since pollen viability declines over time and can affect the success of hand cross-pollination (Stone et al., 1995). Dehisced anthers from donor flowers were wiped over the stigma of the recipient flower, coating the stigma surface. The timing of pollen presentation was taken into consideration when timing hand pollination. Percival (1955) lists pollen presentation times for some of the plants, and where this information was unavailable it was assessed through experimentation (see Appendix B). Stigma receptivity is also important to consider, and although it was not measured in this experiment, all open flowers in the HP treatment were cross-pollinated by hand every other day to maximise pollen delivery when stigmas were receptive. Each group of treatments (block) was positioned at intervals of at least 3m along the hedge, along a height band of approximately 0.5m to 2m above the ground (determined by ease of access to the buds). More information about the hedges can be found in Tables C.1- C.5 of Appendix C. Each group of treatments was positioned at intervals of at least 3m along the hedge, along a height band of approximately 0.5m to 2m above the ground (determined by ease of access to the buds).

After flowering, bags were removed to avoid shading of the developing fruits. A few days later, the numbers of immature fruits (i.e. small, unripe fruits) were counted in all treatments (see Plates 2.7a-d for images of immature fruits). This provided information on initial levels of pollination, whether through self-pollination or cross-pollination. In fruit-producing plants, abscission of unfertilised immature fruits (which may be due to inadequate pollination) occurs soon after flowering (Jackson, 1999; Tromp and Wertheim, 2005). Mature fruits that had been successfully pollinated, fertilised and retained by the plant were counted later in the season, shortly before ripening, i.e. before birds were attracted to them as a food source (see Plates 2.8a-e for images of mature fruits). In ivy, fruit ripening is highly asynchronous, and inflorescences were covered with netting to prevent bird predation before mature fruits had been counted.

Plates 2.7a-d Immature fruits

2.7a Immature blackthorn fruits

2.7b Immature hawthorn fruits

2.7c Immature dog rose fruits

2.7d Immature ivy fruits

Plates 2.8a-e Mature fruits

2.8a Mature blackthorn fruits

2.8b Mature hawthorn fruits

2.8c Immature and mature bramble fruits

2.8d Mature dog rose fruits

2.8e Mature ivy fruits

2.2.3. Statistical analysis

For the Year 1 (2005) preliminary experiments, the mean proportion (P) of flowers that set a) immature and b) mature fruits was compared for the bagged (BG) and open pollinated (OP) treatments for dog rose using ANOVA in GenStat version 10 (Payne *et al.*, 2007). As some groups of buds set no fruits the original proportion was first adjusted using $P_{adj} = (r + 0.5)/(n + 1)$, where r = number of fruits and n = number of buds. These adjusted proportions were transformed to the logit scale before analysis. Back-transformed means and confidence intervals are presented. Dog rose experiments were done at both Rothamsted and Loddington and so the site main effect and the interaction between site and treatment (i.e. bagged or open pollinated flowers) were included as fixed effects in the model. The nested blocking structure of the ANOVAs according to the notation of Wilkinson and Rogers (1973) was as follows: 'site/hedge/position' or 'positions within hedges within sites' of bud groups within hedges' where the symbol / is the nesting operator (A/B = A+A.B). This analysis could not be applied to data for bramble, which produces flower buds over a long period making it difficult to obtain an accurate count of the number of buds bagged. Bramble fruit set was therefore measured according to the presence/absence of fruit on each treatment group of buds, and these data were analysed using a χ^2-squared test.

For the 2007 (Year 2) experiment, the mean proportion of flowers that set a) immature and b) mature fruits for the bagged (T50, M100, T100), open pollinated (OP) and supplementally pollinated (HP) treatments were also compared for each plant species using ANOVA. As in 2005 (Year 2) experiments, some groups of buds set no fruits so the original proportion was first adjusted using $P_{adj} = (r + 0.5)/(n + 1)$, where r =

number of fruits and *n* = number of buds. These adjusted proportions were transformed to the logit scale before analysis. The overall treatment effect was partitioned into four specific 1 df contrasts:

1. Bagged flowers (M100, T100, T50) vs. open flowers (OP and HP)
2. Open pollination (OP) vs. hand cross-pollination (HP)
3. Continuously bagged flowers (M100, T100) vs. flowers bagged for half of flowering (T50)
4. Flowers bagged with muslin (M100) vs. flowers bagged with tulle (T100)

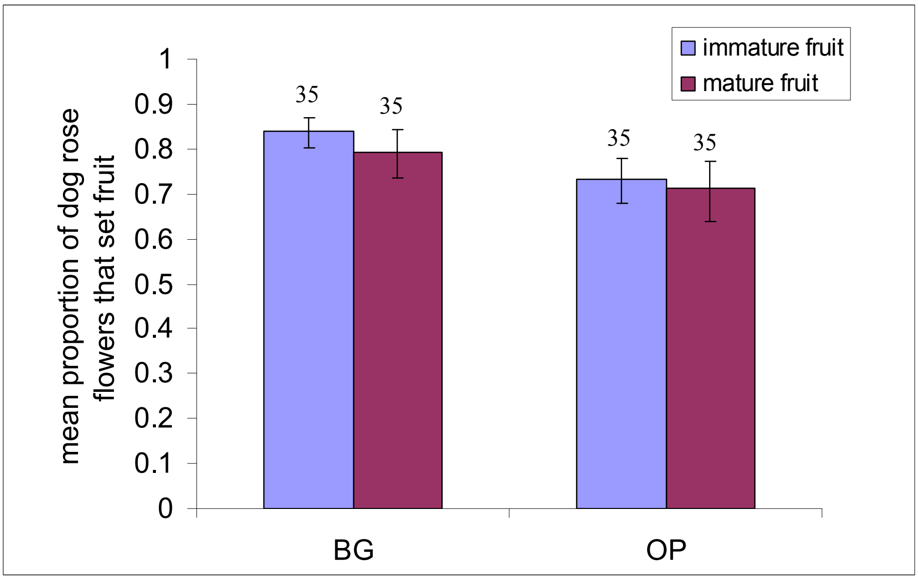
Comparison of confidence intervals was used to examine differences between open pollination (OP) and the bagging treatments (BG, M100, T100, and T50). Back-transformed means and confidence intervals from the models are presented (except for treatments where no fruits were set).

2.3. Results

2.3.1. Dog rose

Initial immature fruit set and final mature fruit set of dog rose flowers was high, with more flowers setting immature fruits within the bags (OP vs BG: $F_{1, 33} = 12.70$, $P = 0.001$, $r^2adj = 0.56$, Figure 2.1). This trend for greater fruit set in the bagged treatment was also found in mature fruit set, although the difference between treatments was not statistically significant at the 5% level (OP vs BG: $F_{1, 33} = 3.62$, $P = 0.066$). Experiments were done at both Rothamsted and Loddington, but there were no significant interactions between site and treatment for immature fruit set (OP vs BG: $F_{1, 33} = 0.15$, $P = 0.697$) and mature fruit set (OP vs BG: $F_{1, 33} = 0.38$, $P = 0.543$). Since it appears that insect pollination is not necessary for fruit set, no further experiments were done on dog rose.

Figure 2.1 Backtransformed mean proportion of dog rose flowers setting fruit for two treatments (± 95% confidence intervals): open pollinated (OP) vs. bagged flowers (BG). Values above columns = no. groups of buds



2.3.2. Bramble

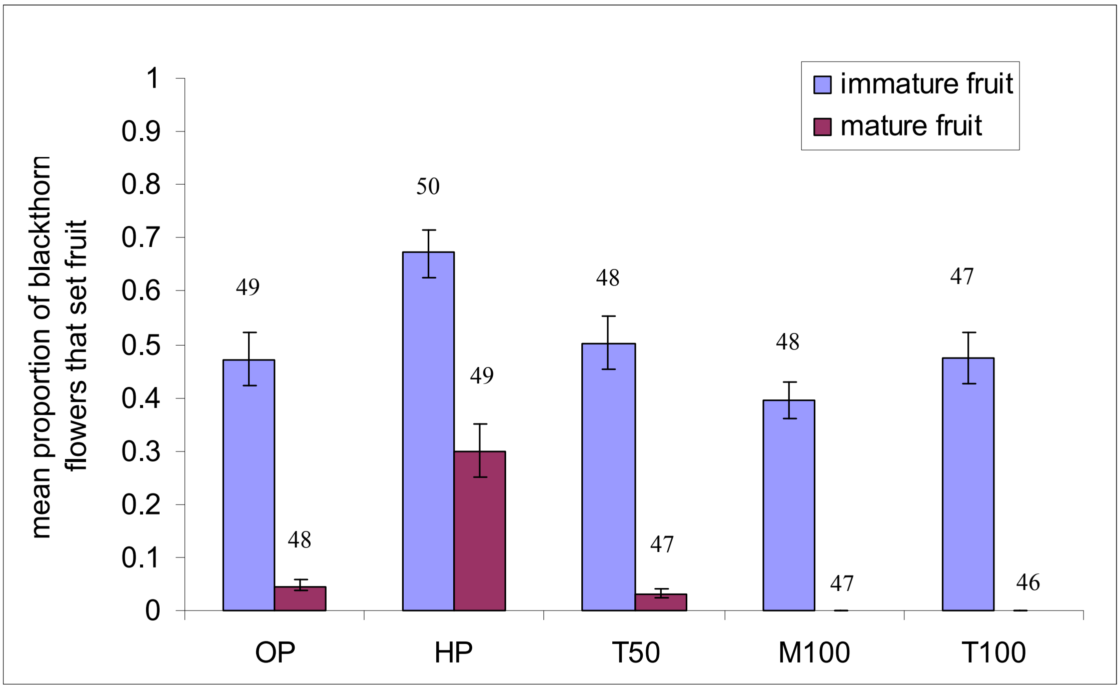
Bramble set mature fruits in 92.31% of inflorescences that had been bagged compared to 77.27% of inflorescences that were left open to insect visitors (χ^2_1, $P = 0.06$). Since there was not a statistically significant effect of excluding flower-visiting insects on bramble fruit set, no further experiments were done.

2.3.3. Blackthorn

Initial fruit set in blackthorn was high in all treatments, but many of these fruits abscised and did not reach maturity (Figure 2.2). Flowers that were supplemented with pollen by hand (HP) initiated more fruits than open pollinated (OP) flowers ($F_{1,\,188} = 32.80$, $P < 0.001$). Overlapping confidence intervals show that there was no difference between the immature fruit set of open pollinated flowers and all three bagging treatments: OP = 0.47 (0.421, 0.521) vs. M100 = 0.39 (0.349, 0.445)**,** T100 = 0.47 (0.423, 0.524) and T50 = 0.50 (0.453, 0.553). Flowers that were bagged for only 50% of the flowering period set more immature fruits than those that were bagged for 100% of the flowering period (M100 + T100 vs. T50**:** $F_{1,\,188} = 4.81$, $P = 0.03$). Immature fruit set was higher in the tulle bags (T100) compared to the muslin bags (M100) ($F_{1,\,188} = 4.70$, $P = 0.031$). The statistical model accounted for 31% of the variation (r^2adj = 0.31).

No mature fruits were set in either of the treatments where flowers were bagged for the whole of the flowering period (M100, T100) (Figure 2.2). The mature fruit set of blackthorn was substantially lower than immature fruit set, but some of the trends were similar: flowers that were supplemented with pollen (HP) set more mature fruits than open pollinated (OP) flowers $F_{1,\,185} = 173.88$, $P < 0.001$) (Figure 2.2). The statistical model accounted for 70% of the variation (r^2adj = 0.70). There was little effect on mature fruit set of reducing the exposure of flowers to insects by half: means with overlapping 95% confidence intervals for each treatment were OP = 0.05 (0.037, 0.057) vs. T50 = 0.03 (0.025, 0.039).

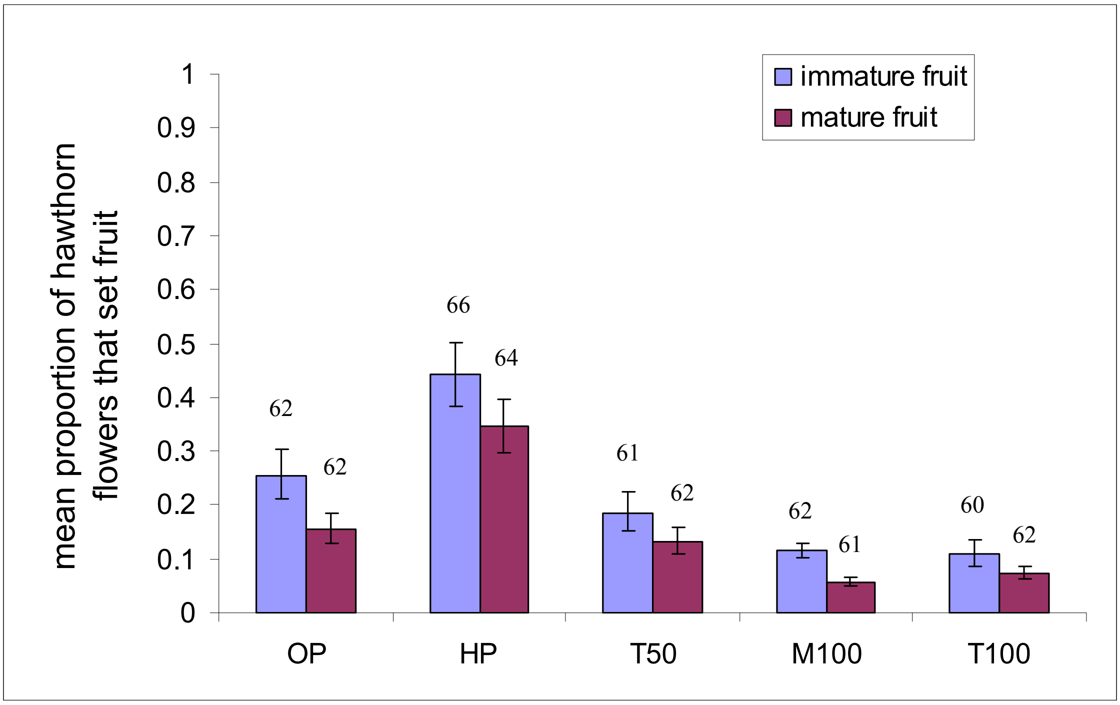
Figure 2.2 Backtransformed mean proportion of blackthorn flowers setting immature fruit and mature fruit (± 95% confidence intervals) for five treatments: open pollinated (OP), supplemental cross-pollination (HP), bagged with muslin for 100% flowering (M100), bagged with tulle for 100% flowering (T100), bagged with tulle for 50% flowering (T50), (Means are taken from the nested ANOVA and are only approximately comparable). Values above columns = no. groups of buds



2.3.4. Hawthorn

Immature fruit set was greater than mature fruit set, but both showed similar trends according to treatment (Figure 2.3). Flowers that were supplemented with pollen (HP) set more fruit than open pollinated (OP) flowers (immature fruit set: $F_{1,\,241} = 22.53$, r^2adj = 0.48, $P < 0.001$, mature fruit set: $F_{1,\,241} = 44.85$, r^2adj = 0.52, $P < 0.001$). Flowers that were open pollinated set more immature and mature fruit than those that were bagged for the entire flowering period: means with distinct 95% confidence intervals for each treatment for immature fruit were OP = 0.26 (0.211, 0.304) vs. M100 = 0.11 (0.092, 0.141) and T100 = 0.11 (0.086, 0.133), and for mature fruit were OP = 0.16 (0.129, 0.186) vs. M100 = 0.06 (0.046, 0.07) and T100 = 0.07 (0.059, 0.088). Of the two meshes, immature fruit set was higher in flowers that were bagged with tulle (M100 vs. T100 immature fruit set: $F_{1,\,241} = 4.85$, r^2adj = 0.48, $P = 0.029$), but mature fruit set was similar irrespective of the mesh used ($F_{1,\,241} = 2.52$, r^2adj = 0.52, $P = 0.114$). Immature and mature fruit set of open pollinated flowers and those that were exposed to insects for 50% of the flowering period was similar as shown by means with overlapping 95% confidence intervals. For immature fruit these were: OP = 0.26 (0.211, 0.304) vs. T50 = 0.19 (0.152, 0.226), and for mature fruit these were: OP = 0.16 (0.129, 0.186) vs. T50 = 0.13 (0.108, 0.158). However, flowers in the T50 treatment set more fruits than those that were bagged for 100% of the flowering period (M100 + T100 vs. T50 immature fruit set: $F_{1,\,241} = 30.09$, r^2adj = 0.48, $P < 0.001$; mature fruit set: $F_{1,\,241} = 33.38$, r^2adj = 0.52, $P < 0.001$).

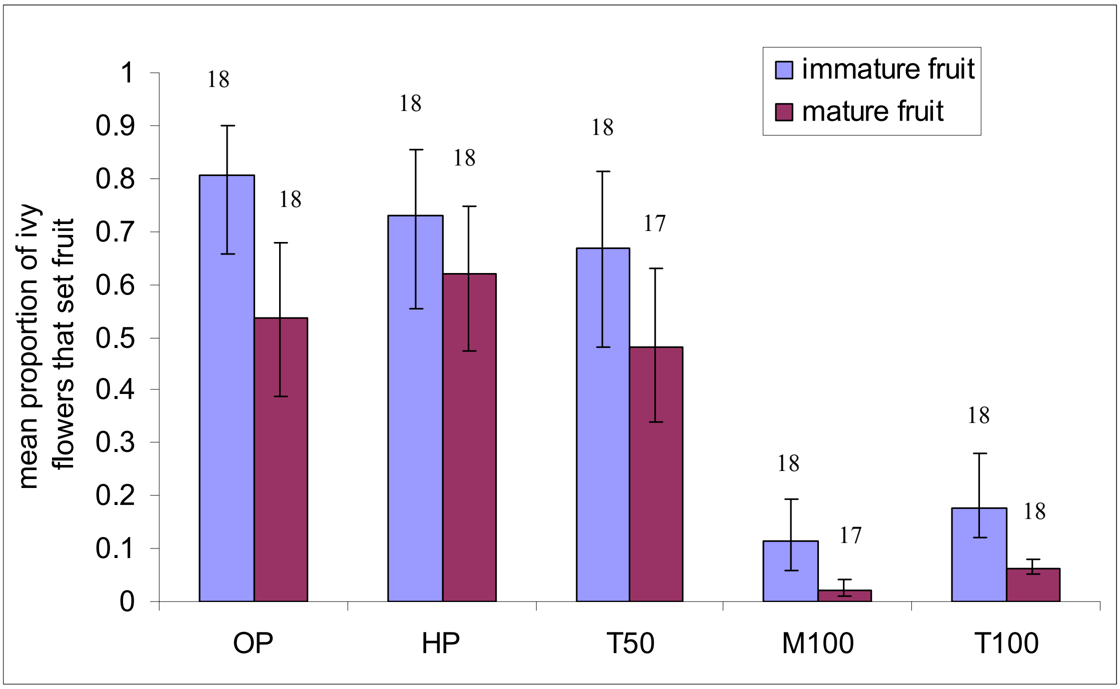
Figure 2.3 Backtransformed mean proportion of hawthorn flowers setting immature fruit and mature fruit (± 95% confidence intervals) for five treatments: open pollinated (OP), supplemental cross-pollination (HP), bagged with muslin for 100% flowering (M100), bagged with tulle for 100% flowering (T100), bagged with tulle for 50% flowering (T50). (Means are taken from the nested ANOVA and are only approximately comparable). Values above columns = no. groups of buds



2.3.5. Ivy

Immature fruit set was greater than mature fruit set, but the trends were fairly similar across treatments (Figure 2.4). There was no difference between flowers that were supplemented with pollen and those that were open pollinated (OP vs. HP immature fruit set: $F_{1,68} = 0.60$, $r^2adj = 0.62$, $P = 0.442$, mature fruit set: $F_{1,66} = 0.67$, $r^2adj = 0.71$, $P = 0.416$). Flowers that were open pollinated set more immature and mature fruit than those that were bagged for the entire flowering period as revealed by distinct means and 95% confidence intervals. For immature fruit these were OP = 0.81 (0.659, 0.900) vs. M100 = 0.11 (0.056, 0.216) and T100 = 0.18 (0.091, 0.319) and for mature fruit these were OP = 0.54 (0.387, 0.677) vs. M100 = 0.02 (0.012, 0.039) and T100 = 0.06. (0.034, 0.105). Initial immature fruit set of flowers bagged with muslin and tulle was similar, but final mature fruit set was higher in flowers that were bagged with tulle (M100 vs. T100 immature fruit set: $F_{1, 68} = 0.91$, $r^2adj = 0.62$, $P = 0.345$, mature fruit set: $F_{1, 66} = 6.01$, $r^2adj = 0.71$, $P = 0.017$). There was no difference in immature and mature fruit set between open pollinated flowers and those that were exposed to insects for 50% of the flowering period: means and overlapping 95% confidence intervals for each treatment for immature fruit were: OP = 0.81 (0.659, 0.900) vs. T50 = 0.67 (0.482, 0.813), and for mature fruit were: OP = 0.54 (0.387, 0.677) vs. T50 = 0.48 (0.339, 0.629). However, flowers in the T50 treatment set more fruit than those bagged for the whole flowering period (M100 + T100 vs. T50 immature fruit set: $F_{1, 68} = 26.79$, $r^2adj = 0.62$, $P < 0.001$, mature fruit set: $F_{1, 66} = 72.68$, $r^2adj = 0.71$, $P < 0.001$).

Figure 2.4 Backtransformed mean proportion of ivy flowers setting immature fruit and mature fruit (± 95% confidence intervals) for five treatments: bagged with muslin for 100% flowering (M100), bagged with tulle for 100% flowering (T100), bagged with tulle for 50% flowering (T50), open pollinated (OP), supplemental cross-pollination (HP). (Means are taken from the nested ANOVA and are only approximately comparable). Values above columns = no. groups of buds



2.4. Discussion

Table 2.3 Overview of results of pollination experiments on mature fruit set

Modes of pollination and environmental factors	Blackthorn	Hawthorn	Ivy
Selfing	No	Maybe	Maybe
Geitonogamy	No	Maybe	Maybe
Outcrossing-wind	No	Maybe	Maybe
Outcrossing-insects	Yes	Yes	Yes
Pollen limitation	Yes	Yes	No
Effect of adjacent crop on pollination	-	Yes, greater fruit set on hedges adjacent to winter oilseed rape	-

Blackthorn, hawthorn and ivy all showed significantly reduced seed set and thus fruit set when insects were excluded from flowers. Flower-visiting insects therefore provide a pollination service for these plant species, and their visits improved fruit set. Dog rose and bramble flowers did not show a significant reduction in fruit set with insect exclusion, which for dog rose is in contrast with the findings of a similar study (Yeboah Gyan & Woodell, 1987b). Since dog rose can set seed through self-pollination or apomixis (Wissemann and Hellwig, 1997), perhaps this offered some buffer for fruit set in the absence of insect visitors. There are three to four forms of dog rose (Graham and Primavesi, 1993) and approximately 300 forms of bramble (Edees and Newton, 1988; Newton and Randall, 2004), presumably with variable modes of reproduction, ranging in self-fertility and the degree to which they require insect pollinators for fruit set. Many *Rubus* species have been documented as self-compatible, but the arrangement of their anthers can determine the extent to which some brambles self- or cross-pollinate (Nybom, 1985). One limitation of my study is that I only measured the effect of different pollination treatments on whole fruit set, and not the number of seeds set by dog rose, bramble or ivy flowers. This would have provided another useful measure of pollination success, and fruit pulp-to-seed ratios could have been calculated. Fruits with a high pulp-to-seed ratio are preferred by some birds (Howe and Vande Kerkhove, 1980; Herrera, 1981; Moermond and Denslow, 1983; Sallabanks, 1993).

Fruit initiation was higher than mature fruit set for blackthorn, hawthorn and ivy. Blackthorn flowers showed the highest fruit initiation, even when insect pollinators were excluded from flowers, but many of these were not retained to maturity. According to Stephenson (1981) immature fruits that are most likely to mature are those that a) set first, b) have the most seeds, or c) result from outcrosses. Self-pollination was the likely cause of abscission of many immature fruits, particularly those that were set from flowers that were bagged.

The absence of mature blackthorn fruits in bags when insects were excluded from flowers supports other evidence for a self-incompatible mode of reproduction (Guitián, J. et al., 1993; Nunes et al., 2006). With little contribution from wind-pollination, insects are likely to be the main pollen vectors and their visits appear to be essential for fruit set. The low mature fruit set of hawthorn and ivy in bagged flowers reflects either a small amount of self-fertility or a little wind cross-pollination. The proportion of fruit set was similar in tulle bags for hawthorn compared to muslin bags, suggesting little additional wind pollination took place. However, the proportion of fruit set was higher in tulle bags for ivy compared to the muslin bags, which may be indicative of wind pollination, but at a very low level. Reduced fruit set of hawthorn in the absence of pollinators supports the evidence of previous studies (Bradshaw 1971; Guitián & Fuentes, 1992) with the exception of one study where fruit set was not reduced in the absence of pollinators (Yeboah Gyan and Woodell, 1987b). My study provides the first empirical evidence of a negative impact on ivy fruit set of excluding flower-visiting insects, which supports the anecdotal evidence of Wittrock (in Knuth, 1908).

Long-lived woody perennials (e.g. blackthorn and hawthorn) are less likely to self-pollinate than herbaceous perennials (Barringer, 2007). Self-incompatibility mechanisms promote outbreeding (Wertheim and Schmidt, 2005), which can be of benefit in terms of plant fitness. In this study, blackthorn and hawthorn flowers that were hand cross-pollinated set more fruits than those that were open pollinated by insects, providing evidence of pollen limitation in plants at the study sites. In contrast, there was no difference in fruit set between open pollinated flowers and hand cross-pollinated flowers in ivy suggesting that this plant species was not pollen limited at the study sites. Pollen limitation occurs more frequently in woody plant species than in herbaceous species, which Larson and Barrett (2000) propose may be due to larger floral displays reducing the number of pollinator visits that each flower receives. Despite a large floral display, and contrary to the results of my study, blackthorn was not pollen limited in a Spanish blackthorn community (Guitián, J. et al., 1993). This could reflect differences in insect abundance between my study sites and the Spanish study site. The majority of flower visitors in the Spanish study were bees (predominantly honeybees, but also bumblebees), which are known to be excellent pollinators of plants (Corbet et al., 1991; Free, 1993). Observations of insect activity on blackthorn in my study revealed that flies were most abundant and bees formed a lower proportion of the flower-visiting population (see Chapter 4), which may explain why fruit set was pollen limited at these locations. Guitián and Fuentes (1992) also studied the pollination biology of a Spanish hawthorn community and found no evidence of pollen limitation, which again may reflect differences in insect abundance between my study sites and theirs. Yeboah Gyan and Woodell (1987b) examined a British population of hawthorn and in contrast to the results of my study found no evidence of pollen limitation. This could suggest that insect declines since the last 20 years (e.g. Benton et al., 2002; Biesmeijer et al., 2006; Shortall et al., in press) have resulted in hawthorn now being pollen limited. But, hawthorn flowers in their study also set fruits in the absence of flower-visiting insects (in contrast to my findings). Additionally, hawthorn fruit set was very high, irrespective of pollination treatment (~80-90%), which implies that the differences in our findings may simply be a consequence of variation in the reproductive system of hawthorn.

Despite ivy showing reduced fruit set in the absence of pollinators, it was not pollen limited in this experiment, and pollinator activity was sufficient for maximal fruit set at these study sites in these years. However, other experiments on the same hedges revealed a relationship between ivy fruit set and pollinator visits (Chapter 3), which is surprising if pollen limitation is not occurring on these hedges. This part of the study (Year 3 experiments) was done using terminal inflorescences and since these flowers open first they are likely to receive frequent pollinator visits, resulting in high fruit set. In Year 1 experiments determining whether excluding flower-visiting insects reduces ivy fruit set, both terminal and lateral inflorescences were included in the experiments and the difference in fruit set between open pollinated flowers in Year 1 and Year 3 was marked. The possibility that insect pollinators may be more important in determining the fruit set of later flowering lateral inflorescences and the amount of pollen limitation may differ temporally and spatially within a plant, merits further investigation.

Pollen limitation in blackthorn and hawthorn may be a result of inadequate pollen delivery to flowers, but it is not only pollen quantity that could influence fruit set, but pollen quality too (Aizen and Harder, 2007). If pollinator activity is too localised within a patch of flowers it may restrict the delivery of outcrossed pollen and increase geitonogamy (pollination between flowers on the same plant), which can compromise seed set (Hessing, 1988; de Jong et al., 1993). In the case of blackthorn, which readily reproduces vegetatively, a hedge could feasibly contain areas dominated by genetically identical clones. Yeboah Gyan and Woodell (1987b) studied the pollination requirements of a British blackthorn population, and found that fruit set on open pollinated branches was extremely low, which they suggest was due to the population being clonal, thus restricting fruiting. Although they did not test this further, other researchers have demonstrated that fruiting or seed production can be restricted by the population structure of clonal plants (Eriksson and Bremer, 1993; references within Charpentier, 2002; Aigner, 2004; Honnay et al., 2006). For plants that have a degree of self-incompatibility, the distances to an outcrossed pollen source could also be of relevance for fruit set, especially if plants are isolated in hedges. Large distances between plants can reduce outcross pollen deposition (Duncan et al., 2004) and seed and fruit set (Eriksson and Bremer, 1993; Kunin, 1993; Gibbs and Talavera, 2001). The number of individual plants within a hedge could also affect fruit set, since and seed and fruit set can be lower in small populations (i.e. with low numbers of individual plants) compared to large populations (Kéry et al., 2000; Jacquemyn, 2002; Waites and Ågren, 2004; Zorn-Arnold and Howe, 2007). For these hand cross-pollination experiments I brought pollen in from outside the immediate area, which may have highlighted the pollen limitation effect.

Concern has been raised by some researchers (Zimmerman and Pyke, 1988; Burd, 1994; Knight et al., 2006) that differences in fruit set between open pollinated flowers and those that have been supplemented with pollen is a result of diversion of resources away from open pollinated branches. To overcome this they recommend having a second open pollinated control on a different plant. With the difficulty of separating individual plants within the hedge it was impossible to do this, but the pattern of fruit set for the pollen limited hawthorn and blackthorn in open pollinated treatments in Year 1 experiments was as low as those of Year 3. This supports the interpretation that absence of pollen limitation, as opposed to resource reallocation, accounts for higher fruit set in supplementally pollinated flowers.

Excluding flower-visiting insects for half the duration of flowering to partially reduce the amount of exposure of flowers to pollinators had no detrimental effect on the fruit set of blackthorn, hawthorn or ivy. This result is surprising, since supplementing flowers with outcrossed pollen increased fruit set for all three species (providing evidence of pollen limitation), and excluding pollinators for the duration of flowering significantly reduced fruit set for blackthorn, hawthorn and ivy. The fruit of flowers that were bagged for half the flowering period was reduced, but not significantly when compared with open pollinated flowers. Insect visits were infrequent (e.g. an approximate estimate using insect abundance and foraging rate data shows that flowers in the hedges received on average 0.37 insect visits per hour, (see Chapter 4), and fruit set was low, which may explain why this difference was difficult to detect. Other researchers have tested the effects on seed and fruit set of selective exposure of flowers to pollinators by bagging flowers and exposing them to pollinator visits for a cumulative number of days (Pellmyr, 1989; Tepedino et al., 1999), or bagging for the first or second half of flowering (Benedek et al., 1994; 2000; 2006). In some of these studies even partial exclusion of pollinators resulted in a decrease in fruit or seed set. Due to time constraints it was not possible to expose flowers for a cumulative number of days, and bags were opened and closed in five day cycles across the whole flowering period. It is possible that all the flowers in several of the bags were open at some point when the bags were off, receiving sufficient pollen to set a similar amount of fruit to that of open pollinated flowers. The purpose of this experiment was to determine whether flower-visiting insects have the potential to influence hedgerow fruit yield. Other studies have looked at the effects of increasing the opportunity for pollination on the seed and fruit set of plants by introducing insects such as honeybees (Fries and Stark, 1983; Stern, 2001). Such experiments are conditional upon the insects foraging on the chosen plant species. An alternative method is to measure insect visitation and fruit set parameters directly to evaluate whether pollinator activity is related to hedgerow fruit yield, and I did this for blackthorn (Chapter 4), hawthorn (Chapter 5) and ivy (Chapter 3).

This study demonstrates a requirement for flower visits from insect pollinators to provide fruits of blackthorn, hawthorn and ivy in British hedges, and provides evidence that for two of these plants, blackthorn and hawthorn, pollinator abundance may limit fruit set. If this is so, then improved management of farmland for pollinators (for example provision of ‘pollen and nectar’ flower strips along field margins (Carvell et al., 2007) could be investigated as means of increasing fruit set for farmland birds. Of course other factors such as hedgerow management also greatly affect the availability of some fruits (Sparks & Martin, 1999; Maudsley et al., 2000; Croxton & Sparks, 2002), but sensitive hedge management and the provision of habitats for pollinators on farmland should help ensure a winter fruit supply for birds.

3. Pollinator effectiveness and fruit set in ivy, *Hedera helix* L. (ARALIACEAE)

3.1. Introduction

Ivy (*Hedera helix* L.) is a native climber, common in UK hedges, flowering late in the year between September and November, and provides a useful forage resource for insects preparing for hibernation. The open flowers, accessible to a range of insect visitors, are clustered together usually in one terminal and several lateral spherical umbels, and freely secrete nectar from easily accessible, exposed nectaries (Vezza et al., 2006). The flowers attract a range of insects seeking nectar and pollen such as Aculeates (bees and wasps), Diptera (true flies), and Lepidoptera (moths and butterflies) (Knuth, 1908; Free, 1970; Howes, 1979; Ferrazzi, 1988; Dirlbeck, 1990; Proctor et al., 1996; Cross, 2002; Metcalfe, 2005; Vezza et al., 2006). The dark purple fruits contain up to five seeds and are a nutritious food resource for farmland and garden birds in the UK due to the high energy content of the pulp (Sorensen, 1984; Snow and Snow, 1988). Birds observed feeding on ivy fruits, mainly from December to May, include blackbirds (*Turdus merula* L.), song thrushes (*T. philomelos* Brehm.), mistle thrushes (*T. viscivorus* L.), fieldfares (*T. pilaris* L.), redwings (*T. iliacus* L.), robins (*Erithacus rubecula* L.), blackcaps (*Sylvia atricapilla* L.), starlings (*Sturnus vulgaris* L.) and woodpigeons (*Columba palumbus* L.) (Hartley, 1954; Sorensen, 1981, 1984; Guitián, 1987; Snow and Snow, 1988; Hernandez, 2005; Metcalfe, 2005).

Ivy has a requirement for insect pollination to produce fruit, since the proportion of flowers that set fruit is significantly reduced in the absence of flower-visiting insects (Chapter 2). Ivy flowers attract several insect taxa, and flower-visiting insects are known to vary in their pollinating abilities (Primack and Silander, 1975; Schemske and Horvitz, 1984; Herrera, 1987; Kandori, 2002). The aim of this study is to investigate the relationship between insects that visit ivy flowers, pollination and fruit set. This was done indirectly by measuring insect abundance, visitation rates and the amount of pollen carried on the bodies of insects, and directly by examining whether insect activity was related to fruit set. The success of a group of insects as pollinators can be related to their abundance and common visitors are sometimes the most important pollinators of a plant (Jennersten and Morse, 1991; Utelli and Roy, 2000; Aizen, 2001). Insects also carry different amounts of pollen on their bodies (Jennersten, 1984; Yeboah Gyan and Woodell, 1987a; Carthew, 1993; Fishbein and Venable, 1996; Tepedino et al., 1999; Ivey et al., 2003; Adler and Irwin, 2006), differ in their flower visitation rates when foraging (Primack and Silander, 1975; Yeboah Gyan and Woodell, 1987a; Herrera, 1989; Vicens and Bosch, 2000a; Monzón et al., 2004) and vary in the amount of contact they make with the stigma of a flower (Vicens and Bosch, 2000a; Monzón et al., 2004; Stout, 2007). These parameters have been used to investigate the value of flower visitors as pollinators in several studies, but there are caveats: abundant visitors are not always the best pollinators and infrequent visitors can be good pollinators (Schemske and Horvitz, 1984), large pollen loads do not always equate with high pollen delivery (Fishbein and Venable, 1996), insect taxa with slow foraging rates can be more effective at pollen transfer than those with high foraging rates (Ivey et al., 2003), and insects vary in the amount of pollen they deposit on stigmas (Primack and Silander, 1975; Herrera, 1987; Yeboah Gyan and Woodell, 1987a; Thomson and Goodell, 2001).

Nevertheless, indirect measures of the pollination value of flower visitors can be coupled with direct measures such as the relationship between pollinator visitation and fruit set (which has been demonstrated in some plants, e.g. Waser, 1979; Zimmerman, 1980; Montalvo and Ackerman, 1986; Klein et al., 2003b; Morandin and Winston, 2005), to provide an overall assessment of their contribution to ivy fruit production.

This chapter addresses Objective 2, and describes work to establish which flower-visiting insects are of greatest value in pollinating ivy flowers and whose visits are therefore important for determining the availability of ivy fruit to birds.

3.2. Methods

Experiments were done in 2005 (Year 1/2) and 2007 (Year 3/4) on ivy in hedges on Rothamsted Research farm and in the local area of Hertfordshire, UK. Flower-visiting insects were assigned to the following morphological and functional groups:

- bumblebees
- honeybees
- wasps
- bristly flies (mainly calyptrate diptera)
- hoverflies: large, thick bodied >1cm; small, thin bodied <1cm

Further details of these flower-visiting insects can be found in Table 3.1, which lists examples of some of the species, genera or families of insects that were observed.

Table 3.1 Insects observed foraging on ivy flowers

Insect group	Examples of species, genera or families
honeybees	*Apis mellifera* (L.)
bumblebees	*Bombus terrestris* (L.) /*lucorum* (L.) (difficult to separate reliably in the field) *Bombus hypnorum* (L.) *Bombus pascuorum* (Scopoli)
wasps	*Vespula vulgaris* (L.) *Vespula germanica* (Fabr.)
bristly flies	Muscidae Tachinidae Sarcophagidae Calliphoridae
hoverflies	
large >1cm or thick bodied	*Episyrphus balteatus* (de Geer) *Eristalis tenax* (L.) and other *Eristalis* spp. *Helophilus* spp. *Myathropa florea* (L.) *Syrphus ribesii* (L.) *Syrphus vitripennis* (Meigen) *Volucella inanis* (L.)
small <1cm or thin bodied	*Melanostoma* spp. *Sphaerophoria scripta* (L.) *Syritta pipiens* (L.)

3.2.1. Relative abundance of insect groups foraging on ivy flowers

Observations of insect activity in 0.5m^2 quadrats on flowering ivy in six hedges were made in 2005 and 2007 to examine relationships between insect visits and fruit set (see section 3.2.4; Table 3.2). Pooled data from these observations were used to calculate the proportion of visits attributable to each insect group.

3.2.2. Flower and umbel visitation rates

Flower and umbel visitation rate data were collected for up to 21 individuals from the insect groups most frequently found foraging on ivy. This was to assess the ability of insects to transfer pollen between flowers and umbels in a unit of time, which is of relevance to pollination. Observations of insects visiting patches of ivy in full flower were made at Rothamsted farm (grid references: TL104132, TL124139 and TL134139), between 13th September 2007 and 5th October 2007 under the following weather conditions: temperature 13.1-22.2ºC, relative humidity 41-92%, wind speed 1 – 3 (Beaufort scale), cloud cover 10-80%. Where possible a similar number of individuals from each insect group were observed on each ivy patch to control for any differences between patches that might influence foraging activity. Each insect was followed for up to 20 visits, and the number of flowers and umbels that it visited was recorded. If a visitor foraged slowly, observations were stopped after two minutes. It was also noted whether their bodies touched the reproductive organs of the flower during foraging, although it was not possible to quantify this because their bodies often obscured the stigma.

3.2.3. Pollen carried on the bodies of insects

Twelve individuals from the main groups of flower-visiting insects were collected from patches of ivy in full flower at Rothamsted farm (grid references of patches TL134131, TL123137, TL124133). Bumblebees were fairly infrequent visitors to ivy on Rothamsted farm, but were found in abundance on ivy in a local residential area (TL148131) and some insect samples were caught for pollen analysis from this location.

It was important to catch insects from different patches of ivy to those where correlations between insect visits and fruit set were being explored (see section 3.2.4) to avoid affecting the experiment by depleting the local pollinator population. As with observations on insect visitation rates, a similar number of individuals from each insect group were caught from each patch to control for differences in pollen presentation between patches. Each insect was caught in an individual glass tube or polythene bag to avoid cross-contamination of pollen loads. A catching device was used when insects were out of reach, or were flighty and difficult to approach without disturbing (design by R. Holdgate, pers. comm.). This comprised a long pole with a loop of cable at one end over which a polythene bag was placed. As with a net, the bag could be placed over the foraging insect. When the insect flew away from the flower it usually flew into the bag; the cable was pulled, closing the bag and trapping the insect. The insects were killed immediately (before they could groom pollen from their bodies) by inserting a piece of filter paper, which had been dipped in ethyl acetate, into the bag or tube. The insect samples were stored in a freezer at -18ºC until the pollen grains could be removed and counted.

Insects were placed in 50ml Apex tubes for washing. The hind legs of bees were removed first to exclude corbicular loads from the pollen counts, since this pollen was not available for pollination. Any residual pollen grains in the bag or glass tube were rinsed out into the Apex tube using approximately 30ml of 0.05% Triton X detergent solution (250µl of Triton X in 500ml distilled water). This was usually a sufficient amount of detergent to remove pollen grains, whilst still allowing the pollen to be centrifuged into a pellet rather than dispersing. The Apex tubes were placed on a shaker and shaken at 250rpm for 10 minutes to dislodge pollen grains from the body of the insect. Insects were removed from the tubes, washed with distilled water to remove any residual grains and checked under a stereo microscope for remaining pollen. If there were many residual pollen grains the insect was returned to the tube of detergent solution, additional Triton X was added to the tube and the sample shaken again. There was often some pollen left in the joints of the body of the insect, but this was unlikely to be available for pollination.

The resulting pollen suspension was centrifuged at 14,000rpm for 15 minutes. A double cavity slide was placed onto a hotplate and the pollen load was pipetted into one well of the slide (100µl was sufficient volume of pipetted liquid to remove the whole pollen load from the tube). The pollen rapidly sedimented onto the bottom of the well and the hotplate assisted the evaporation of the Triton X solution. To ensure that the total pollen load had been extracted, the remaining liquid in the Apex tube was re-centrifuged and any residual pollen was pipetted into the second well. Once the Triton X solution had evaporated the sample in each well was fixed with 3 drops of gelvatol and a coverslip.

A counting graticule was made by drawing 1.5mm width lines on a piece of acetate to fit under the wells of the cavity slide. The number of ivy pollen grains (identified using Hodges, 1974 and a reference collection) in each line traverse was counted using a microscope objective magnification of x 40 and an eyepiece magnification of x 10. The grid lines fitted the field of the microscope and allowed the majority of the total pollen load to be counted.

3.2.4. Pollination Potential (PP) Index

Several researchers have developed ‘pollinator effectiveness’ indices to assess the value of different groups of insects as pollinators (e.g. Herrera, 1987, 1989; Lindsey, 1984; Potts et al., 2001). Herrera (1989) used abundance x visitation rate to measure pollination ‘quantity’, and pollen deposition on stigmas as one measure of pollination ‘quality’(Herrera, 1987). Data collected on the pollinator effectiveness of ivy flower visitors were adapted to components of these indices to construct an approximate Pollination Potential (PP) index score out of 1 for each insect group observed on blackthorn hedges in the study, relative to each other (Table 3.2). The closer the score is to 1 the greater the contribution of that insect group to ivy pollination.

Table 3.2 Pollination Potential (PP) index

PP index score = (PQN x PQL)/ ∑(PQN x PQL for all insect groups)

Where:

PQN (pollination quantity) = A x FVR
(A = total abundance in all quadrats over total sampling period,
FVR = mean flower visitation rate per minute)

PQL (pollination quality) = PG i.e. mean number of pollen grains carried by a single insect on their body (instead of pollen grain deposition on stigmas since this was not recorded)

3.2.5. Do pollinator visits relate to fruit set?

In 2005 and 2007, the number and diversity of foraging insects visiting 0.5m^2 quadrats of flowering ivy in hedges were monitored. The number and location of the quadrats, hedge attributes, and the range of dates and weather conditions under which the observations were done are shown in Table 3.3. Quadrats on the same hedges were spaced at least 5m apart. Insect activity on each quadrat was monitored in two ten minute periods (morning and afternoon) twice weekly. Recording continued until over 90% of the flowers were without petals because although nectar is still secreted by the disc and attracts insects, the stigma is not receptive at this stage (Vezza et al., 2006). Insect activity was measured in terms of 'patch arrivals', defined as an insect entering the quadrat, landing on a flower and commencing foraging.

Before flowering, the average number of buds on 20-30 randomly picked umbels was calculated. This average was multiplied by the total number of umbels in the quadrat to provide an estimate of buds at the start of flowering. Flower density was recorded twice weekly during flowering. The number of mature fruits in each quadrat was assessed in December before birds ate the fruits. According to bird feeding records of Snow and Snow (1988) ivy fruit ripens from December to January, and birds do not start feeding in good numbers until January. Fruit set was estimated by calculating the average number of fruits on 30 randomly picked umbels within the quadrat and multiplying by the total number of umbels with ripe fruit. Since ivy fruit often ripens asynchronously, fruits that were large and green and had yet to darken in colour were included in the count as these would be available to birds later in the season. Some quadrats contained recently finished flowers or very immature fruits (which were usually yellow in colour) and a sample of these were marked and quadrats revisited in March; very few of these produced mature fruits and consequently were not included in the final quadrat fruit set.

Hedges were selected according to the presence of flowering ivy, so hedge aspect could not be controlled for. To account for any effects of solar radiation on insect activity and fruit set, solar radiation was measured using tube solarimeters at each hedge on a sunny day in October, for incorporation into the statistical analysis. The solarimeters, which were placed on stands close to the hedge at a height of 1m, and readings were taken between sunrise (~0645h) and sunset (~1920h). They were calibrated against data provided by the meteorological station at Rothamsted Research and the solar radiation in MJm^{-2} for each hedge was calculated.

Table 3.3 Location of 0.5m^2 quadrats of flowering ivy on hedges, attributes, and weather conditions during insect activity observations

Year	Hedge id.	Hedge grid reference	Hedge aspect	Solar radiation (MJm^{-2})	Number of quadrats on hedge	Date range of observations	Temperature range (ºC)	Relative humidity range (%)	Cloud cover range (%)	Wind speed range (Beaufort scale)
2005	1. Osier	TL109129	N	7.895	4	21.09.05 - 16.11.05	9.3 -23.3	42-98	10-100	0-3
	2. Great Knott I	TL118135	WNW	4.536	2					
	3. Little Hoos I	TL123137	WNW	4.185	3					
2007	4. Great Knott II	TL116139	ESE	10.463	3	15.09.07 – 01.11.07	8.9-20.4	43-98	5-100	0-4
	5. Little Hoos II	TL124139	NW	2.261	3					
	6. Black Horse	TL104132	SE	10.370	3					

3.2.6. Diurnal vs. nocturnal pollinators

This study primarily investigated the role of diurnal flower-visiting insects in ivy pollination, but ivy flowers also receive nocturnal visits from moths (Knuth, 1906). To assess the value of nocturnal flower visitors to ivy pollination, insect activity in a 0.5 m^2 quadrat of ivy flowers at Rothamsted Research (TL134131) was observed throughout one night. A video camera with an infrared filter was set up approximately 1.5m in front of the patch, which was illuminated with a red light for filming during the night. The red light was used to provide a light source for the camera and was assumed to be out of the visual wavelength of most nocturnal flower visitors, as all but a few moth species do not have red receptors (Briscoe and Chittka, 2001). The video was set on time lapse to record three frames per second and filming commenced before sunset and finished at sunrise (1850h-0630h). Filming was done under favourable conditions for moth activity: the temperature was fairly warm at 14.2-17.2 ºC, the wind speed was low at 1-2 on the Beaufort scale and the sky was cloudy. To compare the number of nocturnal flower visitors with the number of diurnal flower visitors, two ten minute observations of insect activity were made in the morning and afternoon of the next day under the following weather conditions: temperature 16.5-18.0ºC, wind speed 2 (Beaufort scale), cloud cover 60-100%.

3.2.7. Statistical analysis

Differences between insect groups in terms of the number of pollen grains carried, flower visitation rates and umbel visitation rates were analysed using ANOVA in GenStat version 10, with $\log_e$ transformations where the data did not conform to usual normality assumptions. There was no blocking in the analyses since each experiment represented a complete randomised design (CRD), and data from all patches of ivy were assumed to be homogeneous. The overall treatment effect was partitioned into four independent one degree of freedom contrasts, representing differences between:

1. Hymenoptera (bumblebees, honeybees and wasps) vs. Diptera (hoverflies and bristly flies)
2. hoverflies vs. bristly flies
3. bumblebees and honeybees vs. wasps
4. bumblebees vs. honeybees

Linear relationships between the proportion of flowers that set fruit and the activity of different flower-visiting groups on ivy flowers in 2005 (Year 1/2) and 2007 (Year 3/4) were fitted using stepwise multiple regression (Payne et al., 2007). For each quadrat, a variable for 'patch arrivals' per flower was calculated to represent the pollination service received by flowers, i.e. the total number of 'patch arrivals' from each insect group was divided by the number of flowers in the quadrat. Other variables that might influence fruit set were also included in the model, such as the amount of solar radiation received by hedges and the last date of flowering (to account for any effects of the time of flowering on fruit set). The analysis used forward selection to include new variables, with an F_{in} ratio of 2 (a significance level of entry into the model of $P = 0.15$), and backward selection using an F_{out} ratio of 4 (a significance level to stay in the model of $P = 0.05$) to eliminate variables.

3.3. Results

3.3.1. Relative abundance of insect groups foraging on ivy flowers

The greatest proportion of visits to patches of flowering ivy was from wasps and bristly flies (Table 3.4).

Table 3.4 Relative abundance of insect groups visiting 18 x $0.5m^2$ patches of flowering ivy (pooled data from all counts)

Insect group	Number of visits	Proportion of visits (%)
wasps	1435	54.67
bristly flies	881	33.56
large hoverflies >1cm	140	5.33
small hoverflies <1cm	68	2.59
honeybees	57	2.17
bumblebees	42	1.60
small solitary bees <1cm	2	0.08
Total insects	2625	100

3.3.2. Flower and umbel visitation rates

In general, flower and umbel visitation rates were recorded for the most frequent visitors to quadrats of ivy in farmland hedgerows, e.g. of the hoverflies, only the large hoverflies were recorded because small hoverflies were relatively uncommon and from casual observation had low foraging rates and rarely touched the stigma of the flower. Honeybees and bumblebees were infrequent visitors to the quadrats, but data on their pollination effectiveness were collected because they were found to be locally abundant on ivy outside of farmland hedgerows e.g. honeybees were common on ivy at Rothamsted Apiary (TL134131) and bumblebees were common on ivy in a nearby residential area (TL148131).

On a per insect basis, Hymenoptera (bumblebees, honeybees and wasps) had a faster visitation rate to both flowers and umbels than Diptera (large hoverflies and bristly flies) (flowers per minute: $F_{1,86} = 48.32$, $P < 0.001$, Figure 3.1; umbels per minute: $F_{1,86} = 10.58$, $P = 0.002$, Figure 3.2). Large hoverflies and bristly flies visited a similar number of flowers per minute ($F_{1,86} = 0$, $P = 0.992$) but large hoverflies visited more umbels per minute ($F_{1,86} = 6.81$, $P = 0.011$, Figure 3.2). Bees (bumblebees and honeybees) visited more flowers and umbels per minute than wasps (flowers per minute: $F_{1,86} = 31.38$, $P < 0.001$, Figure 3.1; umbels per minute: $F_{1,86} = 7.45$, $P = 0.008$, Figure 3.2). Of the bees, bumblebees had a faster visitation rate to flowers than honeybees ($F_{1,86} = 7.28$, $P = 0.008$, Figure 3.1), but their umbel visitation rate was similar ($F_{1,86} = 3.46$, $P = 0.066$, Figure 3.2). The statistical models accounted for 48% of the variation in the flower visitation rate data (r^2adj = 0.48) and 21% of the variation in the umbel visitation rate data (r^2adj = 0.21).

Figure 3.1 Mean flower visitation rates of groups of insects visiting ivy flowers (± 95% confidence intervals). Values above columns = no. insects observed

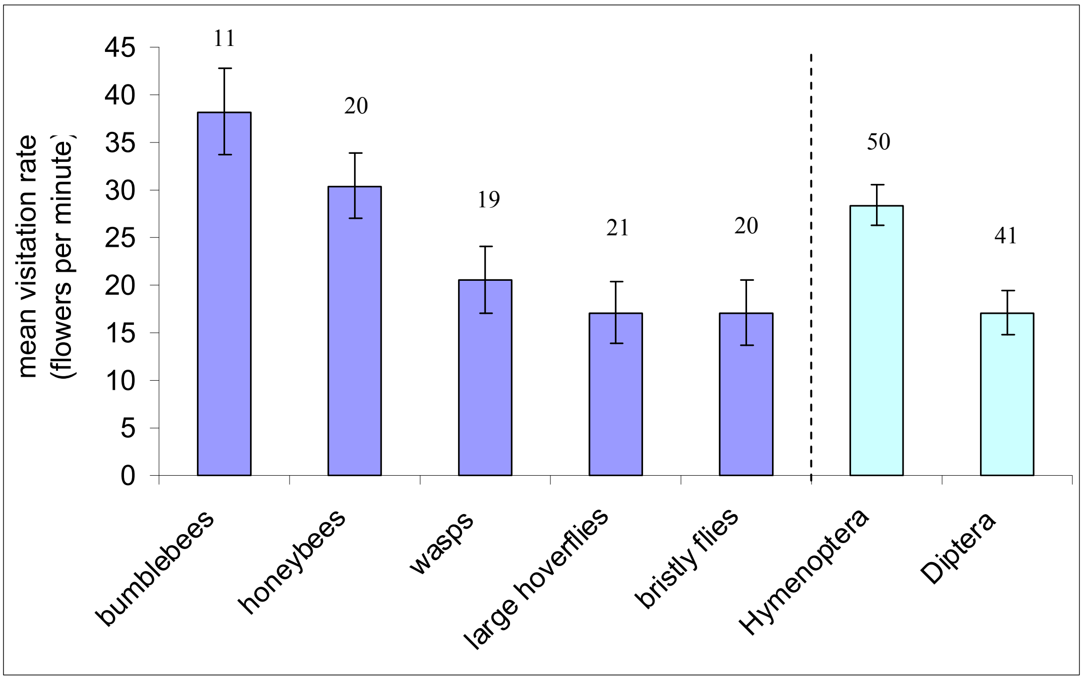
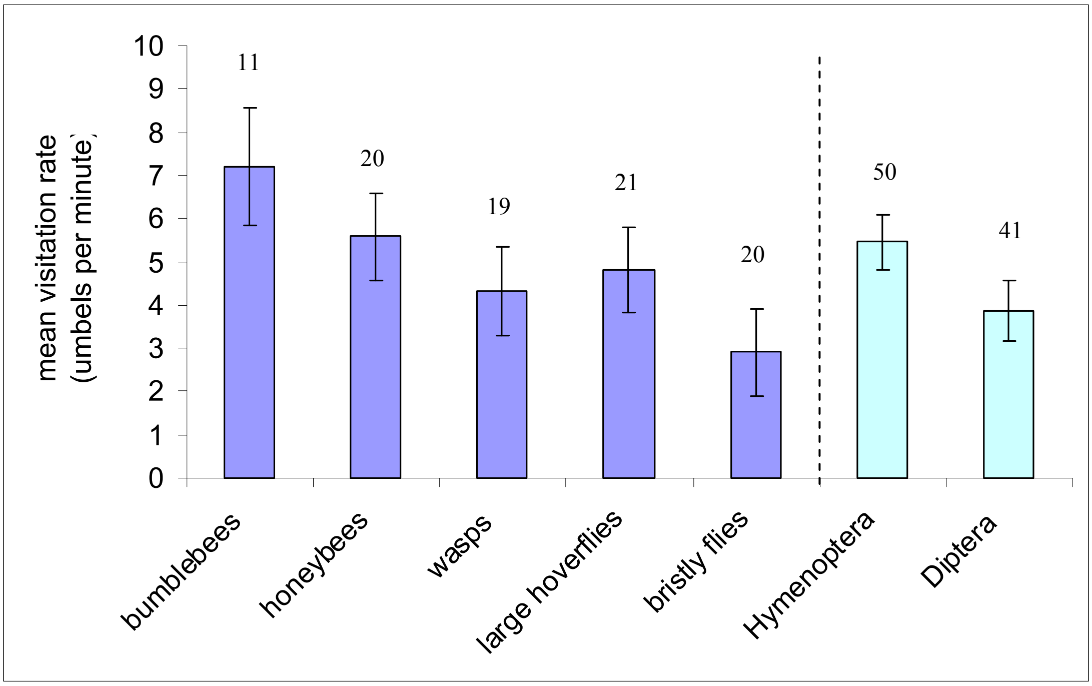


Figure 3.2 Mean umbel visitation rate for groups of insects visiting ivy flowers (± 95% confidence intervals). Values above columns = no. insects observed



Further observations of insect foraging behaviour revealed that bristly flies, hoverflies and bees made less contact with the stigma than wasps when foraging (not quantified as noted in method). Bristly flies, hoverflies and bees possess long proboscices and were able to forage with their bodies held away from the stigma (Plate 3.1). The exception was bumblebees, which occasionally contacted the stigmas of flowers with their tails when foraging over the umbel. In contrast, wasps possess short mouthparts and foraged low down in the flower, making frequent contact with the stigma with their pollen-covered heads (Plate 3.2).

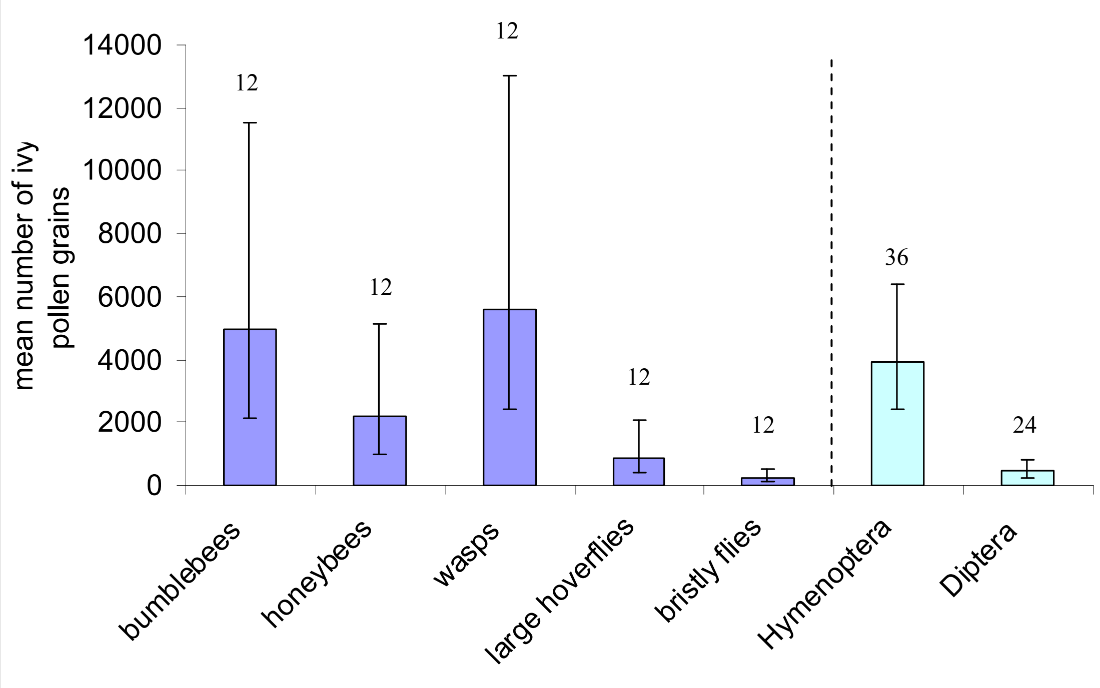
Plate 3.1 Honeybee foraging on ivy flowers. Its body is held clear of the stigma due to its long proboscis.

Plate 3.2 Wasp foraging on ivy flowers. Its face makes frequent contact with the stigma due to its short, flat mouthparts.

3.3.3. Pollen carried on the bodies of insects

Hymenoptera (bumblebees, honeybees and wasps) carried more pollen grains on their bodies than Diptera (large hoverflies and bristly flies) ($F_{1,55} = 30.55$, $P < 0.001$, Figure 3.3). Large hoverflies carried more pollen grains on their bodies than bristly flies ($F_{1,55} = 5.03$, $P = 0.029$, Figure 3.3). There was no difference in pollen grain load between wasps and bees (bumblebees and honeybees) ($F_{1,55} = 1.00$, $P = 0.321$, Figure 3.3), or between bumblebees and honeybees ($F_{1,55} = 1.79$, $P = 0.187$, Figure 3.3). The statistical model accounted for 58% of the variation in the data ($r^2adj = 0.58$)

Figure 3.3 Mean number of ivy pollen grains carried on the bodies of insects visiting ivy flowers backtransformed from the $\log_e$ scale (± 95% confidence intervals). Values above columns = no. insects sampled



3.2.4. Pollination Potential (PP) Index

The overall scores for each insect group are shown in Table 3.5, alongside a breakdown of components of the index. The means and ranges of scores for each insect group across the hedges are shown in Table 3.6. Wasps have a high score, whereas all other flower visitors have much lower scores.

Table 3.5 Pollination Potential (PP) index scores for each group of ivy flower visitors

Insect group	PQN (pollination quantity)		PQL (pollination quality)	PP (Pollination Potential) index score
	A (abundance)	FVR (flower visitation rate)	PG (number of pollen grains on body)	
honeybees	57	30.42	2208	0.02
bumblebees	42	38.24	4964	0.04
wasps	1435	20.59	5597	0.90
large hoverflies > 1cm	140	17.11	889	0.01
bristly flies	881	17.08	228	0.02

Table 3.6 Means and ranges of Pollination Potential (PP) index scores for six hedges

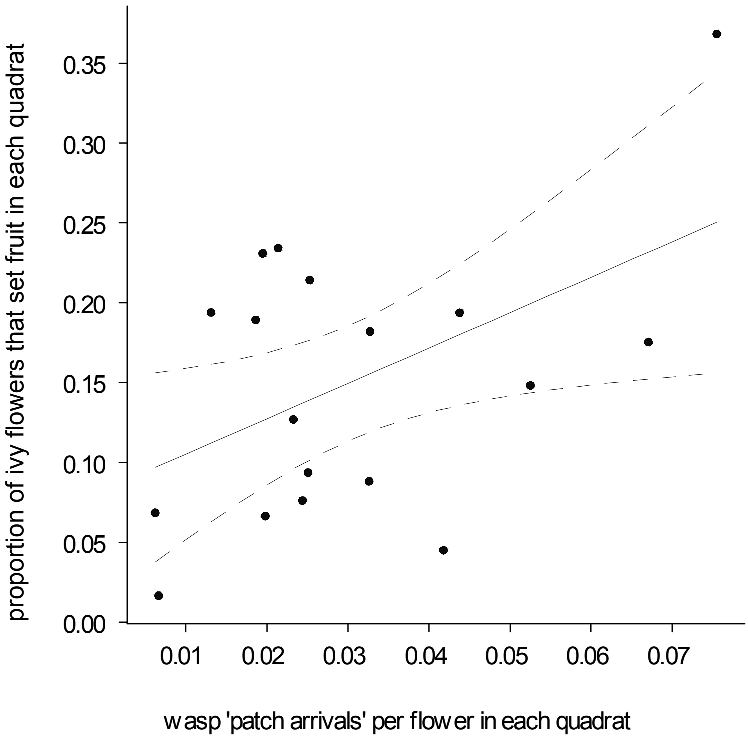
Insect group	Mean hedge PP index score	Range of scores
honeybees	0.02	0.01-0.04
bumblebees	0.06	0-0.13
wasps	0.89	0.78-0.95
large hoverflies > 1cm	0.01	<0.01-0.03
bristly flies	0.02	<0.01-0.06

3.3.5. Do pollinator visits relate to fruit set?

For the statistical analysis, honeybee and bumblebee data were pooled to give the number of visits for bees as a group due to their low proportion of visits to the quadrats (2.17% and 1.6% of visits, respectively) and their broad similarities in terms of pollination value. Two visits from small solitary bees were not included in this group as they were unlikely to be of similar pollination value. Small hoverflies were also infrequent visitors (2.59% of visits), but were not pooled with large hoverflies since they are unlikely to be comparable in terms of their value as pollinators (see 3.3.2 and 3.3.3). Although small hoverflies and total bees represented <5% of the visiting population, they were included in the model since it cannot be ruled out that infrequent visitors could be responsible for a reasonable proportion of fruit set (Schemske and Horvitz, 1984).

Stepwise multiple regression revealed a positive relationship between the number of wasp 'patch arrivals' per flower and the proportion of flowers setting fruit ($\hat{y} = 0.083 + 2.216x$, $F_{1, 16} = 5.03$, $P = 0.039$, $r^2adj = 0.192$, Figure 3.4). No other variables (bees, small hoverflies, large hoverflies, bristly flies, solar radiation, last day of flowering) were selected by the model as relating to fruit set.

Figure 3.4 Relationship between the proportion of ivy flowers that set mature fruit in 18 x 0.5m^2 quadrats and the number of wasp ‘patch arrivals’ per flower. Dotted lines represent 95% upper and lower confidence limits for the mean response



3.3.6. Diurnal vs. nocturnal pollinators

Table 3.7 shows the results of observations of nocturnal and diurnal insect activity. Visits from nocturnal flower visitors were infrequent throughout the night, especially when compared with the number of diurnal insects observed visiting the same patch in only twenty minutes. Only three moths were observed in the patch and they spent little time foraging on flowers: one moth remained still for 2 hours 10 minutes from 2120h to 2330h.

Table 3.7 Observations of nocturnal and diurnal insect activity on a 0.5m^2 patch of flowering ivy

Date	Time of observation	Duration of observation	Insect visits to ivy flowers (number of 'patch arrivals' in brackets)
12/10/07	1850h-0630h	11 hours, 40 minutes	moths (3)
13/10/07	1100h-1110h	10 minutes	honeybees (9), small hoverflies (3)
	1410h-1420h	10 minutes	honeybees (4), wasps (4), small hoverflies (1) large hoverflies (2) bristly diptera (4)

3.4. Discussion

Ollerton et al. (2007) measured the abundance of insects visiting ivy flowers and the amount of pollen carried on their bodies and hypothesised that although ivy flowers appear to be generalised and attract a range of insect foragers, they exhibit "functional specialization" and are primarily pollinated by wasps. The results presented in this chapter provide evidence in support of this hypothesis, since wasp activity on the hedges in the study was positively correlated with the proportion of ivy flowers that set fruit. My indirect assessments of the pollination value of groups of flower visitors are broadly in agreement with the observations of Ollerton et al. (2007), who found that wasps were abundant on ivy and carried more pollen on their bodies than Calliphorid flies and hoverflies. In the current study, Hymenoptera (honeybees, bumblebees and wasps) carried more pollen on their bodies than Diptera, and had faster visitation rates. Bumblebees, honeybees and wasps carried a similar amount of pollen on their bodies, but bees had faster flower and umbel visitation rates. Despite the faster visitation rates of bees compared to wasps, it is probably the abundance of wasps, the large number of pollen grains carried on their bodies, their relatively fast visitation rates, and the frequent contact with stigmas during foraging (J. Jacobs, pers. obs.) that gives them the greatest value as pollinators for determining the availability of ivy fruit for birds. Pollination Potential (PP) index scores support this, since wasps had a markedly high scores (overall score = 0.90, mean score per hedge = 0.89) compared to all other insect visitors (overall score range = 0.01-0.04, mean score per hedge range = 0.01-0.06). Whilst bees are known to be important pollinators of a variety of plants, wasps have also been documented by other authors as pollinators of species such as orchids, blueberries and bilberries (e.g. Nazarov, 1995; Nousiainen et al., 1978).

Foraging wasps collect nectar from flowers such as ivy, presumably as a carbohydrate source for their own energy requirements, but it is also intended for other colony members, which they feed through trophallaxis on their return to the nest (Jandt and Jeanne, 2005). The availability of carbohydrate sources may be important for supporting social wasp colonies and determining wasp population sizes (Raveret-Richter, 2000). Local enhancement processes such as the sight and odour of conspecifics at a food source assist the recruitment of wasps to a particular location (D'Adamo et al. 2000, 2001, 2003, 2004; D'Adamo and Lozada, 2005). They are also able to locate food from its odour (Moreyra et al. 2006) and will search for a food source after experiencing the odour on foragers returning to the nest (Overmyer and Jeanne 1998; Jandt and Jeanne 2005). In addition to olfactory cues, wasps use local visual cues, or landmarks for navigation to a food resource (Collet 1995, D'Adamo and Lozada 2007; Jandt et al. 2005). These foraging attributes, which are similar to those of other Hymenopteran pollinators such as bumblebees and honeybees, ensure that wasps can readily learn and return to food sources. *Vespula* wasps have also been shown to compete for forage sources with other insects, for example by attacking flower-foraging bumblebees (Thomson 1988). The ability to remember where to find food and recruit colony members, and their competitive foraging behaviour could ensure their success as pollinators: through increased local abundance in patches of flowering ivy and hence increased pollination and fruit set.

Whilst wasps are likely to be the most valuable pollinators of ivy, the relative abundance and hence effectiveness of pollinators can vary temporally and spatially (Fishbein and Venable, 1996; Kandori, 2002; Ivey at al., 2003; Kudo and Kasagi, 2004). Limits may be set on wasp visits according to the proximity of ivy flowers to a nest and the foraging range of wasps. For one species, *Vespula pensylvanica,* foraging range has been recorded as within 2,000ft (610m) of the nest to a carbohydrate source for the majority of workers, but up to 3,293ft (1.04km) for some individuals (Akre et al., 1973). Translocation experiments showed workers could return to the nest from at least 1.4 miles (2.25km) (Akre et al., 1973) and if wasps are able to forage this far, they could be capable of long distance pollen transfer. In this study I observed variation in pollinator communities between patches of ivy on farmland and patches of ivy near gardens: wasps were frequent visitors to ivy on the Rothamsted farm but bumblebees were infrequent visitors. The reverse was true for a patch of ivy flowering in a residential area with bumblebees making frequent visits to ivy relative to wasps. I did observe some bumblebees making stigmatic contact with the end of their tail and I propose that they may function as secondary pollinators in the absence of wasps. Secondary pollinators may buffer any discrepancies in seed and fruit set when the primary pollinator is absent (Suzuki and Akazome, 2000). To illustrate further how ivy pollinator communities vary, a study by Vezza et al. (2006) of insects visiting ivy flowers in Italy found that the most frequent visitors were honeybees, with few visits from bumblebees, wasps and butterflies. Ivy flowers along the south coast of England have experienced a recent change to their pollinator communities with the arrival of *Colletes hederae* Schmidt & Westrich, a solitary bee species new to the UK, which forages almost exclusively on ivy flowers (monolecty). This species has been recorded in good numbers along the South coast since 2001 (Cross, 2002). In some locations there may be thousands of nests of *C. hederae* close to patches of ivy (S. Roberts, pers. comm.), which may have implications for pollination and fruit availability in these areas. Further research could focus on determining the relative contributions of different insect groups to the pollination of ivy when wasps are not the dominant flower visitor, by concentrating on direct measures of pollinator effectiveness, such as the number of pollen grains deposited on stigmas (e.g. Primack and Silander, 1975; Herrera, 1987; Yeboah Gyan and Woodell, 1987a), or the amount of seed or fruit set after single flower visits from insects (e.g. Motten et al., 1981; Spears, 1983; Dieringer, 1992; Keys et al., 1995; Vicens and Bosch, 2000a; Monzón et al., 2004). All of which could be incorporated into the Pollination Potential (PP) index described earlier.

The importance of diurnal flower visitors as pollinators of ivy has been highlighted in this chapter. Nocturnal visitors were also considered in this study, although only for one night and for one quadrat. I conclude that they probably contribute little to ivy pollination and fruit set at the location studied, but due to the small sample size, further experimentation may be needed for confirmation. Visits from butterflies and moths were infrequently observed and nocturnal filming revealed that moths were fairly inactive foragers, especially in relation to diurnal insects. Whereas Lepidoptera may be good pollinators of some plants (Pettersson, 1991; Willmott and Búrquez 1996), on generalist shaped flowers such as ivy, they may be limited in their contribution to pollination and fruit set due to their body morphology since they have been shown to rarely touch the reproductive organs of some flowers and carry few pollen grains (Wiklund et al., 1979; Jennersten, 1984; Carthew, 1993). Therefore, diurnal flower visitors are likely to be of greater importance for ensuring ivy fruits for birds than nocturnal flower visitors. In future studies, this could be assessed quantitatively through bagging experiments: exposing ivy flowers to either nocturnal visitors at night or diurnal visitors during the day and comparing fruit set (e.g. Jennersten, 1988; Guitián, P. et al., 1993; Keys et al., 1995).

Results described in Chapter 2 for ivy flowers on the same hedges as those used in this chapter showed that although the flowers required insect visitors for pollination and fruit set, they were not pollen limited i.e. flowers receiving supplemental pollen set a similar amount of fruits to those that did not receive supplemental pollen. This suggests that flowers received adequate pollen through visits from the local pollinator population, yet counter-intuitively, the results from this chapter revealed differences in fruit set that were related to differences in insect activity. An explanation for this could be that experiments testing for pollen limitation (Chapter 2) were done using terminal umbels, whereas experiments investigating relationships between insect activity and fruit set (this Chapter) included lateral inflorescences too. In general, the proportion of flowers that set fruit on terminal umbels was much higher than the proportion of flowers that set fruit in $0.5m^2$ quadrats. This difference may be a reflection of high levels of insect activity and pollination since the terminal umbels are the first to flower, are more prominent and insects may be more likely to visit them, although this was not measured. There is also scope for further investigation of whether pollinator activity affects not only the amount of fruit available to birds, but the quality of fruits. Differences in pollination can affect seed number, fruit shape and size in a variety of plants e.g. tomatoes (Palma et al., 2008), blueberries (Brewer and Dobson, 1969) and apples (Wei et al., 2002). Snow and Snow (1988) proposed that fruits with a small seed burden and therefore a high pulp to seed ratio would be more profitable to birds; they took the example of ivy, that smaller fruits containing fewer seeds would be the optimal food resource. As far as I am aware, no research has been done on whether this preference exists for birds feeding on ivy fruits, but other studies have shown that a high pulp to seed ratio can be of importance for the selection of fruit by frugivorous birds (Howe and Vande Kerkhove, 1980; Herrera, 1981; Moermond and Denslow, 1983; Sallabanks, 1993).

This chapter has highlighted the value of wasps in particular as pollinators of ivy, and their visits may be important for ensuring a supply of fruits for birds. One example of a bird that includes ivy fruits as a relatively large proportion of its fruit diet is the blackcap (Snow and Snow, 1988). There have been changes in the migratory behaviour of this species over the last 50 years, with more individuals overwintering in the UK (Leach, 1981; Berthold et al., 1992; Bearhop et al., 2005) and appearing more frequently in gardens (Glue, 2004; Toms, 2005). If this trend continues, the provision of food resources such as ivy fruits on farmland and in gardens, alongside food provided at garden bird tables, may help these birds survive the winter. Since ivy is an important food resource for blackcaps, wildlife friendly gardeners may wish to allow ivy to flower and fruit, and wasps to visit the flowers; in terms of providing fruit for birds, wasps should be viewed as beneficial insects rather than pests. Gardens also provide favourable habitats for bumblebees as demonstrated by the high number of nests found in gardens (Osborne et al., 2008b); where wasps are eradicated as pests, bumblebees may function as secondary pollinators of ivy, although this warrants further investigation. Ivy flowers late in the year and may have evolved to favour wasp pollination since this is when the number of bees are diminishing, but it is the time when wasp colonies are producing males and queens (Spradbery, 1973) and become very nectar-hungry.

4. The effect of hedge aspect and insect activity on fruit set in blackthorn, *Prunus spinosa* L. (ROSACEAE) and the consequences for frugivorous birds

4.1. Introduction

Blackthorn (*Prunus spinosa* L.) is a native, deciduous shrub, commonly found in UK hedges and is one of the earliest hedgerow plant species to flower (March to May), with the flowers opening before the leaves. The white flowers have an open structure and are attractive to a wide variety of insects seeking pollen and nectar such as Apoidea (bees), Diptera (true flies), and Lepidoptera (butterflies) (Knuth, 1908; Yeboah Gyan, 1984; Yeboah Gyan and Woodell, 1987a; Guitián, J. et al., 1993). Blackthorn fruits (or sloes as they are hereafter referred to) are dark purple drupes containing one seed, and the flesh provides a food source for a range of birds over the winter (Hartley, 1954; Simms, 1978; Sorensen, 1981, 1984; Snow & Snow, 1988). These include include resident or partially migratory birds such as blackbirds (*T. merula* L.), song thrushes (*T. philomelos* Brehm.), mistle thrushes (*T. viscivorus* L.) and robins (*Erithacus rubecula* L.), and migratory fieldfares (*Turdus pilaris* L.) and redwings (*T. iliacus* L.), which breed in Fennoscandia and Russia, but overwinter in Britain and Ireland (Wernham et al., 2002). Hedgerow loss has occurred on a large scale over the last few decades (Barr et al., 1986, 1991; Rackham, 2000), which has reduced the availability of fruits to birds, but it is not known whether the availability of hedgerow fruits in winter has contributed to the declines of frugivorous farmland birds. Large fruit crops should attract more frugivores than small fruit crops (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977), and the abundance of some birds is tied to the spatial and/or temporal availability of fruit resources (Levey, 1988; Loiselle and Blake, 1991,1993; Rey, 1995; Kinnaird et al., 1996; Moegenburg and Levey, 2003; Kwit et al., 2004; Saracco et al., 2004; Telleria and Pérez-Tris, 2007; Telleria et al., 2008) with a few exceptions when this relationship is not as clear (e.g. Guitián and Bermejo, 2006; Galetti and Aleixo, 1998; Herrera, 1998).

The proportion of blackthorn flowers that set fruit was significantly reduced in the absence of flower-visiting insects (Guitián, J. et al., 1993; Chapter 2), and evidence of pollen limitation was found in a sample of plants in UK hedges (Chapter 2). These results suggest the activity of pollinating insects could potentially influence the yield of sloes in hedges. Their activity could be modified by factors such as hedge aspect, since insect pollinators such as bees require heat for the activation of flight muscles and have various temperature thresholds for flight (Burrill, 1981; Corbet, et. al. 1995; Stone and Wilmer, 1989), indicating they may show a preference for foraging on the sunny sides of hedges. If this is so, there may be implications for hedgerow fruit set, for example, an unpublished study showed more fruits on the west side of a hedge, which was not due to differences in flower numbers, but possibly to greater pollinator activity on the west side (receiving warmer afternoon sun) than the east side (receiving cooler morning sun), although this was not examined (T. Sparks pers.comm.). Certainly, pollinator foraging activity has been found to increase with increasing temperature, light intensity and solar radiation (Wratt, 1968; Beattie, 1971; Szabo and Smith, 1972; Corbet et al., 1993; Vicens and Bosch, 2000b; Klein et al., 2003a, 2003b; Abrol, 2006). Insect activity can also be influenced by floral nectar reward (Heinrich and Raven, 1972; Corbet et al., 1979; Abrol, 2006), which itself is related to environmental variables such as temperature and relative humidity (Corbet et al., 1979; Willmer, 1983). Aside from potential differences in insect activity between shady and sunny sides of hedges affecting pollination and fruit set of blackthorn flowers, plant physiology may also be influenced by solar radiation. Growing fruits require carbohydrate, which is primarily produced by photosynthesis in the adjacent spur and shoot leaves (Grapadelli, 1994; Tromp and Wertheim, 2005). Photosynthesis is dependent on light and radiation, and shading has been shown to reduce the fruit yield of some orchard crops by increasing fruit abscission (Saito et al., 1989; Byers, 1990; George et al., 1993; McArtney et al., 2004).

This chapter addresses Objective 4 by using a hedgerow scale experiment to test for effects of hedge aspect on insect activity and the proportion of flowers that set fruit. It also addresses Objective 2 by aiming to establish which flower-visiting insects are likely to be of greatest value in pollinating blackthorn flowers, and whether their activity determines the availability of sloes to birds. This was assessed a) indirectly, from measurements of relative insect abundance, the amount of pollen carried on their bodies, and flower visitation rates and b) directly, by exploring relationships between insect activity and the proportion of blackthorn flowers that set fruit. Finally, it addresses Objective 5 by aiming to assess if birds are using these hedges, by examining whether the abundance of frugivorous birds in hedges is linked to the size of the sloe crop.

4.2. Methods

Experiments were done between 2005 (Year 1) and 2007 (Year 3) on hedges containing blackthorn on Rothamsted Research's farm and the surrounding area (Hertfordshire, UK) and at The Game & Wildlife Conservation Trust's 'Allerton Project' farm (Loddington, Leicestershire, UK). The majority of experiments were done on 16 hedges in 2005 (Year 1), which contained flowering blackthorn and were selected to include ones that faced:

1. south or west (assigned 'warm' hedges).
2. north or east (assigned 'cool' hedges)

The hedges and their aspects are listed in Table 4.1. It was difficult to find hedges that contained blackthorn and faced the desired aspects exactly, so hedges were assigned to 'warm' if their aspect was on the south and west side of a northwest-southeast axis, and 'cool' if on the opposite side of this axis. Assuming that the ambient temperature next to a hedge is correlated with solar radiation, the division of hedges into 'warm' and 'cool' was checked by measuring the amount of solar radiation reaching hedges using tube solarimeters on 17th April 2008 at Rothamsted, and 25th April 2008 at Loddington. The tube solarimeters were placed on stands close to the hedge at a height of 1m, and readings were taken between 0700h and 1900h. They were calibrated against data provided by the meteorological station at Rothamsted Research and the solar radiation in MJm^{-2} for each hedge was calculated (see Table 4.1.). A second factor of interest originally incorporated into the experimental design was the effect of adjacent crop type on insect activity and whether a mass-flowering crop such as oilseed rape had a competitive or facilitative effect on blackthorn pollination and fruit set. Hedges were selected that were adjacent to a) winter oilseed rape or b) cereal/pasture (see Table 4.1). Unfortunately the winter oilseed rape crop at Loddington did not flower until much later in the year due to pigeon damage and poor establishment, and at Rothamsted the winter oilseed rape reached full flowering as blackthorn flowering was declining. For these reasons it was thought inappropriate to include crop type in the analysis; but the positioning of the hedges ensured they were next to a spread of different crops. The effect of crop was examined more comprehensively in 2006 (Year 2) using hedges containing hawthorn (Chapter 5). Because characteristics such as hedge dimensions can influence bird abundance (Osborne, 1984; Sparks et al., 1996; Parish et al., 1994) this was the final criterion for selecting hedges, and they were standardised by choosing ones of similar height and width where possible (see Table 4.1 for hedge dimensions, locations and attributes).

Table 4.1 Location and attributes of blackthorn hedges where pollinator activity, fruit set and bird activity were studied

Site	Hedge id.	Grid reference	Aspect	Warm /cool	Solar radiation MJm^{-2}	Adjacent crop type	WOSR[1] growth stage[2] at start of blackthorn flowering	WOSR[1] growth stage[2] at end of blackthorn flowering	Approximate hedge height (m)	Approximate hedge width (m)	No. of groups of marked buds (approx. 30 buds per group)
Rothamsted	1. Thrales End A	TL124158	SW/SSW	warm	17.247	WOSR	59-60	64-65	3	3	10
	2. Little Hoos	TL123137	WNW	warm	15.121	WOSR	59-64	65	3	3	10
	3. Thrales End C	TL123168	WNW	warm	13.588	cereal	n/a	n/a	3	3	10
	4. Great Knott	TL118135	WNW	warm	18.890	cereal	n/a	n/a	3	3	10
	5. Butlers E	TL118093	NE	cool	7.955	WOSR	53	65	2.5	2.5	20**
	6. Osier	TL109129	N	cool	10.439	WOSR	53	65	2.5	3	0*
	7. Thrales End B	TL124169	ESE	cool	11.212	cereal	n/a	n/a	3	3	20**
	8. Summerdells	TL119127	N	cool	12.430	cereal	n/a	n/a	3-5	3	0 *
Loddington	1. Bottom Collie W	SK805026	SSW	warm	9.010	WOSR	no flowers[3]	no flowers[3]	3.5	3.5	10
	2. Paradise	SK799019	WNW	warm	8.180	WOSR	no flowers[3]	no flowers[3]	3	3.5	10
	3. 44 Acre	SK798016	SSW	warm	9.671	cereal	n/a	n/a	3.5	3.5	10
	4. Buildings	SK795019	SW	warm	10.290	pasture	n/a	n/a	4	4	10
	5. Bottom Collie C	SK801023	N	cool	6.499	WOSR	no flowers[3]	no flowers[3]	3.5	4	10
	6. 31 Acre	SK791014	ESE	cool	9.229	WOSR	no flowers[3]	no flowers[3]	2.5	3	10
	7. Holloways	SK788014	ESE	cool	8.677	cereal	n/a	n/a	3	3	10
	8. Barrow Hill	SK798022	NNE	cool	7.351	cereal	n/a	n/a	3	3	10

1. WOSR = winter oilseed rape. 2. BBCH growth stages (Lancashire et al., 1991): **53 - 59** = flower buds still closed **60** = first flowers open **64** = 40% of flowers on main raceme open **65** = full flowering, 50% of flowers on main raceme open 3. WOSR crop flowered late (June) at Loddington due to poor establishment and pigeon damage
* = little flowering blackthorn ** = 10 additional groups of buds marked on these hedges to compensate for no blackthorn on hedges 6 and 8 at Rothamsted

4.2.1. Hedge aspect and blackthorn fruit set

Along the hedges in the study, groups of approximately 30 blackthorn flower buds were marked before anthesis using weather-proof enamel paint, and were labelled using white insulation tape and a marker pen (see Table 4.1 for number of groups per hedge). These were returned to in mid-August, when fruits were almost mature, but before they became ripe and attractive to birds (which occurs in September according to Snow and Snow, 1988). The number of maturing fruits was counted, and the proportion of flowers that set fruit was calculated to look for evidence of a difference in fruit set between ‘warm’ and ‘cool’ hedges.

4.2.2. Insect activity, hedge aspect and blackthorn fruit set

Before the blackthorn flowering period, four line transects each of 25m in length were marked out using flexicanes along each hedge, spaced according to the presence of blackthorn. Insects foraging on blackthorn flowers along these transects were surveyed on three sampling dates between 2nd April 2005 and 26th April 2005 at Rothamsted under the following weather conditions: temperature 8.6-18.2ºC, relative humidity 27-89%, wind speed 1 – 3 (Beaufort scale) and cloud cover 30-100%. Insects were surveyed between 4th April 2005 to 21st April 2005 at Loddington under the following weather conditions: temperature 10.0-17.3ºC, relative humidity 48-95%, wind speed 1 – 3 (Beaufort scale), cloud cover 5-100%. On each sampling day insects were surveyed in the morning and afternoon using the line transect method (Banaszak, 1980): each 25m transect was walked slowly at a rate of 20m/min^{-1} and all insects observed foraging on blackthorn flowers up to a height of 2.2m were recorded.

Flower-visiting insects were assigned to the following morphological and functional groups for all experiments:

- bumblebees
- honeybees
- solitary bees
- bristly flies (mainly calyptrate diptera)
- hoverflies

Further details of these flower-visiting insects can be found in Table 4.2, which lists examples of some of the species, genera or families of insects that were observed.

Table 4.2 Insects observed foraging on blackthorn flowers

Insect group	Examples of species, genera or families
honeybees	*Apis mellifera* (L.)
bumblebees	*Bombus terrestris* (L.) /*lucorum* (L.) (difficult to separate workers reliably in the field) *Bombus lapidarius* (L.) *Bombus vestalis* (Geoffroy)
solitary bees	Andrena spp. Anthophora sp. Osmia sp. Nomada sp.
hoverflies	*Eristalis tenax* (L.) and other *Eristalis* spp. *Syrphus ribesii* (L.) *Syrphus vitripennis* (Meigen) *Volucella bombylans* (L.) *Helophilus* sp. *Melanostoma* sp.
bristly flies	Bibionidae Muscidae Sarcophagidae Scathophagidae Calliphoridae

Blackthorn flower density records were made within one to two days of insect observations to take account of the effect of the number of flowers on insect activity. A tape measure was used to mark 1m sections along each 25m transect. The cover of blackthorn flowers was assessed as a percentage of every 1m x 2.2.m (height) section. The number of flowers within a 1% section (in full flower) of one of the 1m x 2.2m sections was counted. This was then multiplied by the percentage cover value in each section, with results totalled to provide an estimate of the number of flowers in each 25m transect. Although this was a crude measure, it was a time efficient method for hedges where flower density was high. Fruit set was assessed for each hedge using the same buds that were marked according to the method in the previous section (4.2.1) and relationships between fruit set and insect activity were explored. Pooled data from observations of insect activity on transects of flowering blackthorn made in 2005 (Year 1) were used to calculate the proportion of visits attributable to each insect group.

4.2.3. Pollination value of blackthorn flower visitors

4.2.3.1. Flower visitation rates

Data on flower and visitation rates were collected for between 15 and 29 individuals from each insect group foraging on blackthorn in full flower at Rothamsted farm and the local area (TL124169, TL170125, TL124138, TL124139, and TL105134) and Loddington farm (SK805026). This was to assess the likely ability of insects to transfer pollen between flowers in a unit of time, which is of relevance to pollination. Observations were made from 27th April 2006 to 3rd May 2006 and 27th March 2007 to 2nd May 2007 under the following weather conditions: temperature 14.1-21.0ºC, relative humidity 53-77%, wind speed 1-2 (Beaufort scale), cloud cover 20-70%. Where possible a similar number of individuals from each insect group were observed on each patch of blackthorn to control for any differences between patches that might influence foraging activity. This was not always possible because the pollinator community varied between sites e.g. honeybees were abundant on blackthorn at TL105134, but not at other sites. Each insect was followed for up to 20 visits, and the number of flowers that it visited was recorded. If a visitor foraged slowly, observations were stopped after two minutes.

4.2.3.2. Contact with the anthers and stigmas of flowers

Each flower that was visited during a foraging bout was recorded using a code to assess whether the body of the insect touched the reproductive organs: A = insect touched anthers only, B = insect touched both stigmas and anthers, O = insect foraged without touching the reproductive organs. (No insect was observed solely touching the stigma). The proportion of visits where an insect touched both reproductive organs (B) was calculated, since it was assumed that an insect had more value as a pollinator if it touched the stigma.

4.2.3.3. Pollen carried on the bodies of insects

Approximately ten individuals from the main groups of flower-visiting insects were collected from patches of blackthorn in full flower at Rothamsted farm and the local area (TL154153, TL105134, TL051095, and TL170125). Insects were caught from different patches of blackthorn to those where relationships between insect visits and fruit set were being explored (see section 4.2.2) to avoid affecting the experiment by depleting the local pollinator population. As with observations of insect visitation rates, a similar number of individuals from each insect group were caught from each blackthorn patch to control for differences in pollen presentation between patches. Each insect was caught in an individual glass tube or polythene bag to avoid cross-contamination of pollen loads. A catching device was used when insects were out of reach, or were flighty and difficult to approach without disturbing (design by R. Holdgate, pers. comm.). This comprised a long pole with a loop of cable at one end over which a polythene bag was placed. As with a net, the bag could be placed over the foraging insect. When the insect flew away from the flower it usually flew into the bag; the cable was pulled, closing the bag and trapping the insect. The insects were killed immediately (before they could groom pollen from their bodies) by inserting a piece of filter paper, which had been dipped in ethyl acetate, into the bag or tube. The insect samples were stored in a freezer at -18ºC until the pollen grains could be removed and counted.

Insects were placed in 50ml Apex tubes for washing. The hind legs of bees were removed first to exclude corbicular loads from the pollen counts, since this pollen was not available for pollination. Any residual pollen grains in the bag or glass tube were rinsed out into the Apex tube using approximately 30ml of 0.05% Triton X detergent solution (250µl of Triton X in 500ml distilled water). This was usually a sufficient amount of detergent to remove pollen grains, whilst still allowing the pollen to be centrifuged into a pellet rather than dispersing. The Apex tubes were placed on a shaker and shaken at 250rpm for 10 minutes to dislodge pollen grains from the body of the insect. Insects were removed from the tubes, washed with distilled water to remove any residual grains and checked under a stereo microscope for remaining pollen. If there were many residual pollen grains the insect was returned to the tube of detergent solution, additional Triton X was added to the tube and the sample shaken again. There was often some pollen left in the joints of the body of the insect, but this was unlikely to be available for pollination.

The resulting pollen suspension was centrifuged at 14,000rpm for 15 minutes. A double cavity slide was placed onto a hotplate and the pollen load was pipetted into one well of the slide (100µl was sufficient volume of pipetted liquid to remove the whole pollen load from the tube). The pollen rapidly sedimented onto the bottom of the well and the hotplate assisted the evaporation of the Triton X solution. To ensure that the total pollen load had been extracted, the remaining liquid in the Apex tube was re-centrifuged and any residual pollen was pipetted into the second well. Once the Triton X solution had evaporated the sample in each well was fixed with three drops of gelvatol and a coverslip.

A counting graticule was made by drawing 1.5mm width lines on a piece of acetate to fit under the wells of the cavity slide. The number of blackthorn pollen grains (identified using Hodges, 1974 and a reference collection) in each line traverse was counted using a microscope objective magnification of x 40 and an eyepiece magnification of x 10. The grid lines fitted the field of the microscope and allowed the majority of the total pollen load to be counted.

4.2.3.4. Pollination Potential (PP) Index

The value of different groups of insects as pollinators has been assessed by several researchers using ‘pollinator effectiveness’ indices (e.g. Herrera, 1987, 1989; Lindsey, 1984; Potts et al., 2001). Herrera (1989) used abundance x visitation rate to measure pollination ‘quantity’, and pollen deposition on stigmas as one measure of pollination ‘quality’(Herrera, 1987). Data collected on the pollinator effectiveness of blackthorn flower visitors were adapted to components of these indices to construct an approximate Pollination Potential (PP) index score out of 1 for each insect group observed on blackthorn hedges in the study, relative to each other (Table 4.3).

Table 4.3 Pollination Potential (PP) index

PP index score = (PQN x PQL)/ ∑(PQN x PQL for all insect groups)

Where:

PQN (pollination quantity) = A x FVR
(A = total abundance across all hedges over total sampling period, FVR = mean flower visitation rate per minute)

PQL (pollination quality) = PG x ROT
(PG = mean number of pollen grains carried by a single insect on their body, instead of pollen grain deposition on stigmas since this was not recorded, ROT = mean proportion of flower visits in a foraging bout where contact with both reproductive organs was made)

4.2.4. Hedgerow fruit crop and the abundance of frugivorous birds

The number of fruits of all plant species, including sloes, and the abundance of frugivorous birds in hedges were recorded over the autumn and winter of 2005-2006 (Year 1-2). Fruits were counted and birds were surveyed every two weeks at Rothamsted between 22nd September 2005 and 13th January 2006, and at Loddington between 28th September 2005 and 17th January 2006. The number of all fruits in each 1m x 2.2m section of the 25m transects was counted or estimated. Fruits were counted individually up to 100, after which the number was estimated to the nearest 25 fruits. Counting fruits on only one side of the hedge is equivalent to subsampling the fruit yield of the whole hedge unless there are large differences in the number of fruits between sides. Time did not allow for comprehensive fruit counts on the other side, or the ‘back’, of the hedge, but a rough assessment of the fruit crop on the back of the hedge was made by noting whether the species composition and size of the fruit crop was similar or different. Birds were surveyed in the morning between approximately 0730h and 1000h using the line transect method (see Bibby et al., 2000). This involved walking the length of each hedge at a rate of $20 m/min^{-1}$ counting all birds seen, heard, or flushed out of the hedge, and assigning them to areas either within or outside the transects.

4.2.5. Statistical analysis

All data were analysed using GenStat Version 11 (Payne et al., 2008).

4.2.5.1. Hedge aspect and blackthorn fruit set

To validate the classification of hedges according to their aspect, a General Linear Model with binomial errors and logit link function was used to examine differences in solar radiation between hedges defined as ‘warm’ and ‘cool’. Solarimeter radiation measurements were the dependent variable in the model, with ‘warm’/’cool’ as two factors.

To examine the effects of hedge aspect on fruit set, the proportion of blackthorn flowers (that were marked as buds) that set mature fruits (sloes) on ‘warm’ versus ‘cool’ hedges were calculated, and the data were analysed using ANOVA, with a test for interactions between ‘site’ (Rothamsted or Loddington) and ‘aspect’. The structure of the ANOVA according to the notation of Wilkinson and Rogers (1973) was as follows: ‘blocks’ = sites/hedges/position of the group of buds within each hedge and ‘treatments’ = site*aspect. The term / is a nesting operator (A/B = A+A.B) and the term * is a crossing operator (A*B = A+B+A.B). Since the data did not fit the assumption of normality, they were transformed. An adjusted proportion (P_{adj}) was calculated due to zeros in the data: $P_{adj} = (r + 0.5)/(n + 1)$, where r = number of fruits and n = number of buds. The adjusted proportion (P_{adj}) was transformed using the logit function: logit (P_{adj}) = ln (P_{adj} /1- P_{adj}). The residual plots from analyses with the adjusted and transformed data were satisfactory. Backtransformed means and confidence intervals are presented in the figures, although it is not possible to backtransform the offset and the means are therefore approximate.

4.2.5.2. Insect activity, flower density, hedge aspect and blackthorn fruit set

Using regression analysis, linear relationships between the activity of the different insect groups and flower density were investigated, with ‘site’(Rothamsted or Loddington) and ‘aspect’ (‘warm’ or ‘cool’) included as factors with two levels. Data were transformed (using $\log_{10}$ or square root transformations) to normalise residuals when appropriate. Regression analysis was also used to investigate linear relationships between the proportion of blackthorn flowers that set fruit and insect activity. Fruit set data were transformed to normalise residuals, and it was necessary to calculate an adjusted proportion of flowers setting fruit (P_{adj}) due to zeros in the data: $P_{adj} = (r + 0.5)/(n + 1)$, where r = number of fruits and n = number of buds. The adjusted proportion (P_{adj}) was transformed using the logit function: logit (P_{adj}) = ln (P_{adj} /1- P_{adj}). Log_{10} transformations were used for insect counts. The effect of flower density on fruit set was taken into account first by adding an estimate of flower cover into the model. The estimate of flower cover was calculated by totalling the number of flowers on hedges from all three sampling dates, and is not an accurate count of the total number of flowers over the season. Visitation data for an insect group was then added to the model to see if this improved the relationship. Separate models were created for each insect group. Unfortunately, two hedges had to be omitted from the study (Osier 'cool' and Summerdells 'cool', both at Rothamsted) since they did not contain sufficient flowering blackthorn for fruit set to be measured. This had the effect of reducing the available degrees of freedom and for this reason the factors 'site' and 'aspect' were not included in models exploring relationships between the proportion of blackthorn flowers that set fruit and insect activity.

4.2.5.3. Pollination value of blackthorn flower visitors

Differences in pollen grain counts and flower visitation rates between insect groups were analysed using ANOVA with $\log_{10}$ transformations where the data did not conform to usual normality assumptions. Proportional data from measures of contact with the reproductive organs of the flower by insect visitors were analysed using a General Linear Model with binomial errors and logit link function. Deviance ratios were estimated to correct for overdispersion when necessary. The overall treatment effect was partitioned into four independent one degrees of freedom contrasts, representing differences between:

1. Apoidea (bumblebees, honeybees and solitary bees) vs. Diptera (hoverflies and bristly flies)
2. hoverflies vs. bristly flies
3. social bees (bumblebees and honeybees) vs. solitary bees
4. bumblebees vs. honeybees

Backtransformed means and confidence intervals are presented in the figures.

4.2.5.4. Hedgerow fruit crop and the abundance of frugivorous birds

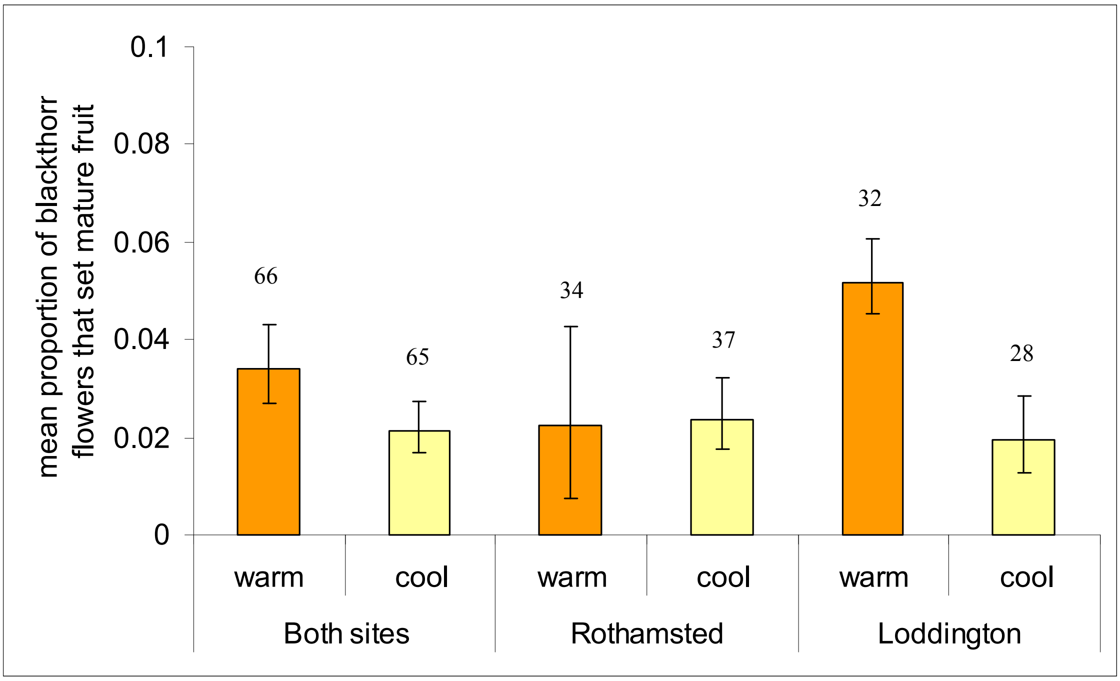
Regression analysis was used to investigate linear relationships between the total abundance of potential sloe consuming birds (pooled for all transects over the season) and the mean number of sloes in the hedge over the season. Data were transformed (using $\log_{10}$ transformations) to normalise residuals where appropriate. Unfortunately, two hedges were lost from the study since they were accidentally cut (31 Acre at Loddington, and Butlers E at Rothamsted), so once again factors of ‘site’ and ‘aspect’ could not be investigated in the regression model due to the reduction in the available degrees of freedom.

4.3. Results

4.3.1. Hedge aspect and blackthorn fruit set

The hedges were classified as ‘warm’ and ‘cool’ according to hedge aspect. Solarimeters were used to verify these groups by measuring the total amount of solar radiation received by each hedge for one day. Differences in solar radiation between ‘warm’ and ‘cool’ hedges were significant ($F_{1, 13} = 12.18$, $P = 0.004$, $r^2adj = 0.68$) and justified the grouping of hedges by aspect. More fruits were set from flowers on ‘warm’ hedges versus ‘cool’ hedges ($F_{1, 10} = 8.72$, $P = 0.014$, Figure 4.1). There was an interaction between site and aspect, due to the differences in the effect of aspect on fruit set at Loddington compared to Rothamsted ($F_{1, 10} = 11.22$, $P = 0.007$, Figure 4.1). However, the measure of fit of the model ($r^2adj = 0$) suggests there was inherently a lot of variability amongst hedges, which was greater than could be explained by aspect and site. The aspect treatments were also pseudoreplicated, which is not ideal, but is within the constraints of the experiment.

Figure 4.1 Backtransformed mean proportion (including offset) of blackthorn flowers setting mature fruit (±95% confidence intervals) on warm vs. cool hedges (defined using hedge aspect). Values above columns = no. groups of buds



4.3.2. Insect activity, flower density, hedge aspect and blackthorn fruit set

The greatest proportion of visits to patches of flowering blackthorn was from bristly flies (Table 4.4).

Table 4.4 Relative abundance of insect groups visiting 15 hedges of flowering blackthorn (pooled data from all counts)

Insect group	Number of insects	Percentage of visits (%)
bristly flies	350	71.43
solitary bees	59	12.04
hoverflies	47	9.59
bumblebees	32	6.53
honeybees	2	0.41
Total insects	490	100

The abundance of insects on hedges was positively related to blackthorn flower density for bumblebees, hoverflies and bristly flies ($P < 0.05$, see Table 4.5) but was of borderline significance for solitary bees. For nearly all insect groups there was no evidence that their abundance varied between hedge aspects ($P > 0.05$, see Table 4.5), with the exception of solitary bees, with more bees observed on warm hedges ($F_{1, 37} = 4.20$, $P = 0.048$, Table 4.5, Figure 4.2). The relationship between flower density and bumblebee abundance was the same at both sites, but there were more bumblebees on blackthorn flowers at Rothamsted ($P < 0.05$, see Table 4.5, r^2adj = 0.30, Figure 4.3). Similarly, the relationship between flower density and solitary bee abundance was the same at both sites, but there were more solitary bees on blackthorn flowers at Rothamsted ($P < 0.05$, see Table 4.5, r^2adj = 0.16, Figure 4.4). There was evidence of more bristly flies on blackthorn flowers at Loddington, but the relationship between flower density and bristly fly abundance was similar ($P < 0.05$, see Table 4.5, r^2adj = 0.30, Figure 4.5).

Table 4.5 Results of regression analyses testing the effects of flower density, aspect and site on the abundance of different insect groups visiting blackthorn flowers (when terms are included in the models in that order). F. probability highlighted when *P*<0.005.

		Insect abundance (total insects observed over blackthorn flowering period)							
		bumblebees		solitary bees		hoverflies		bristly flies	
	d.f.	v.r.	F. pr	v.r.	F. pr	v.r.	F. pr	v.r.	F. pr
flower density	1	12.97	**<0.001**	3.64	0.064	22.85	**<0.001**	18.39	**<0.001**
+ aspect	1	0.2	0.895	4.51	**0.041**	0.13	0.717	0.04	0.833
+ site	1	8.45	**0.006**	5.96	**0.02**	0.08	0.777	4.55	**0.04**
Residual	37								

Figure 4.2 Relationship between solitary bee abundance (log 10) and blackthorn flower density (square root), in relation to hedge aspect (warm vs. cool). Observations from 15 hedges on three separate dates. (From the fitted model excluding non-significant terms.)

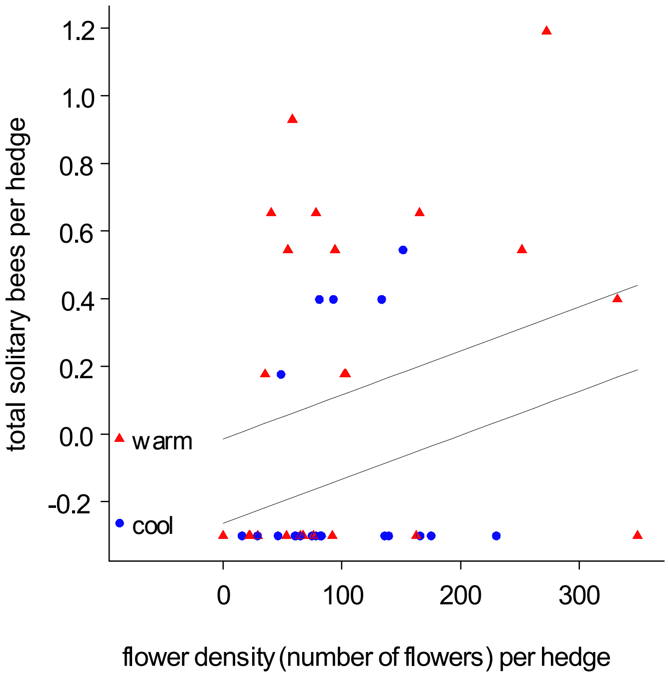


Figure 4.3 Relationship between bumblebee abundance (log 10) and blackthorn flower density (square root), in relation to site (Roth = Rothamsted, Lodd = Loddington). Observations from 15 hedges on three separate dates. (From the fitted model excluding non-significant terms.)

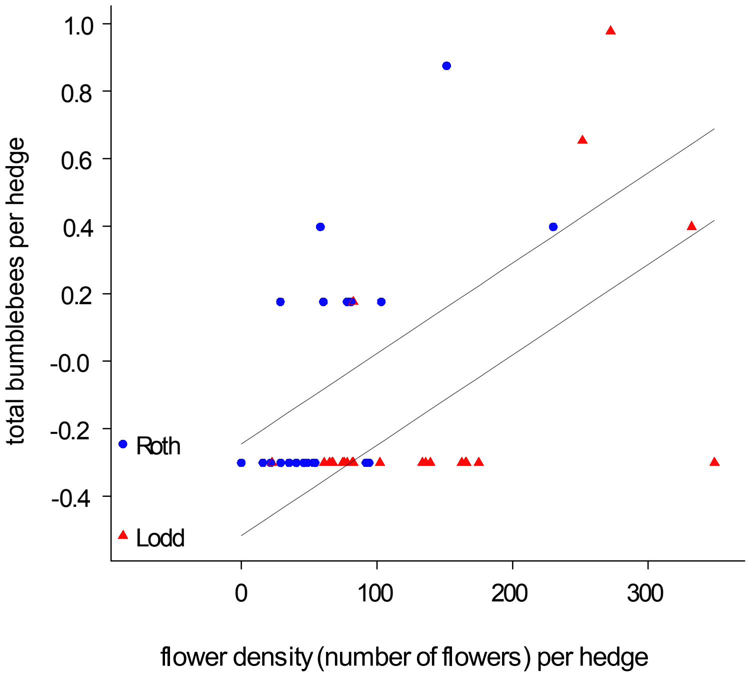


Figure 4.4 Relationship between solitary bee abundance (log 10) and blackthorn flower density (square root), in relation to site (Roth = Rothamsted, Lodd = Loddington). Observations from 15 hedges on three separate dates. (From the fitted model excluding non-significant terms.)

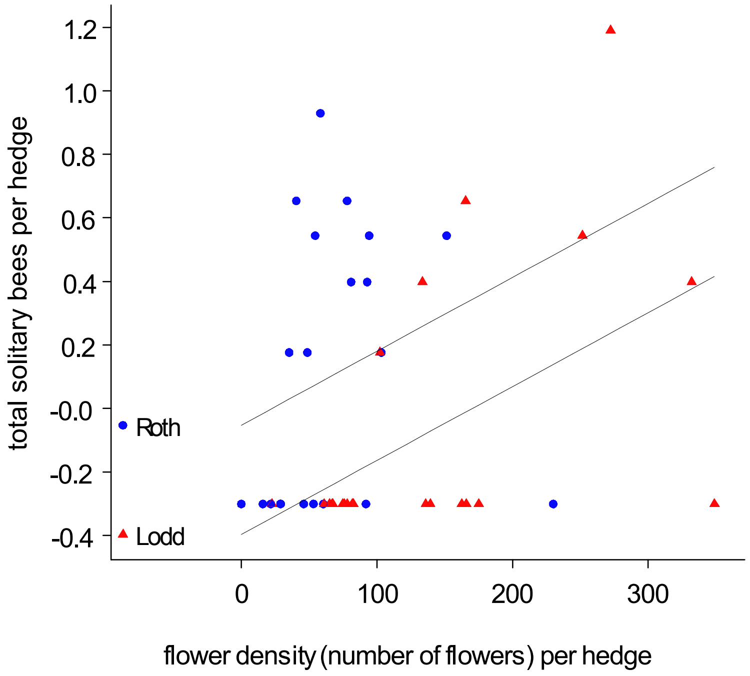
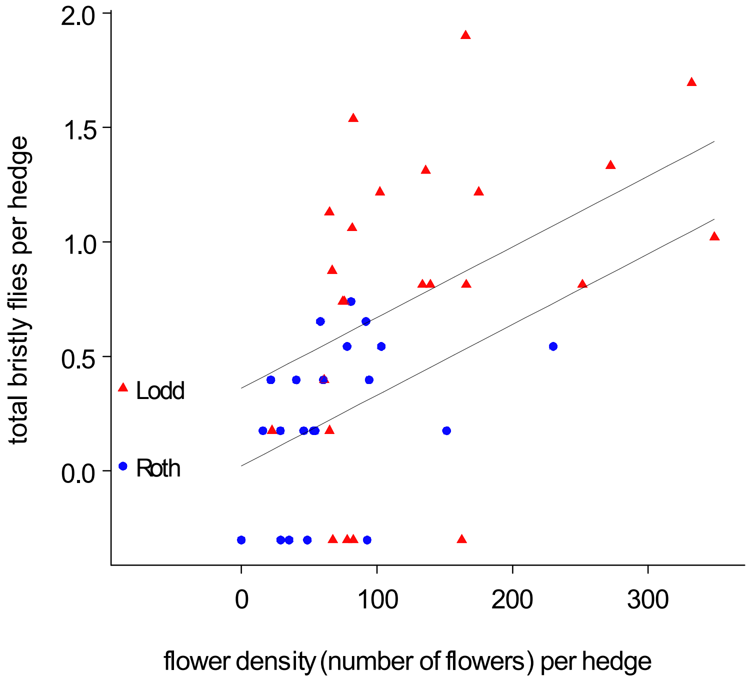


Figure 4.5 Relationship between bristly fly abundance (log10) and blackthorn flower density (square root), in relation to site (Roth = Rothamsted, Lodd = Loddington). Observations from 15 hedges on three separate dates. (From the fitted model excluding non-significant terms.)



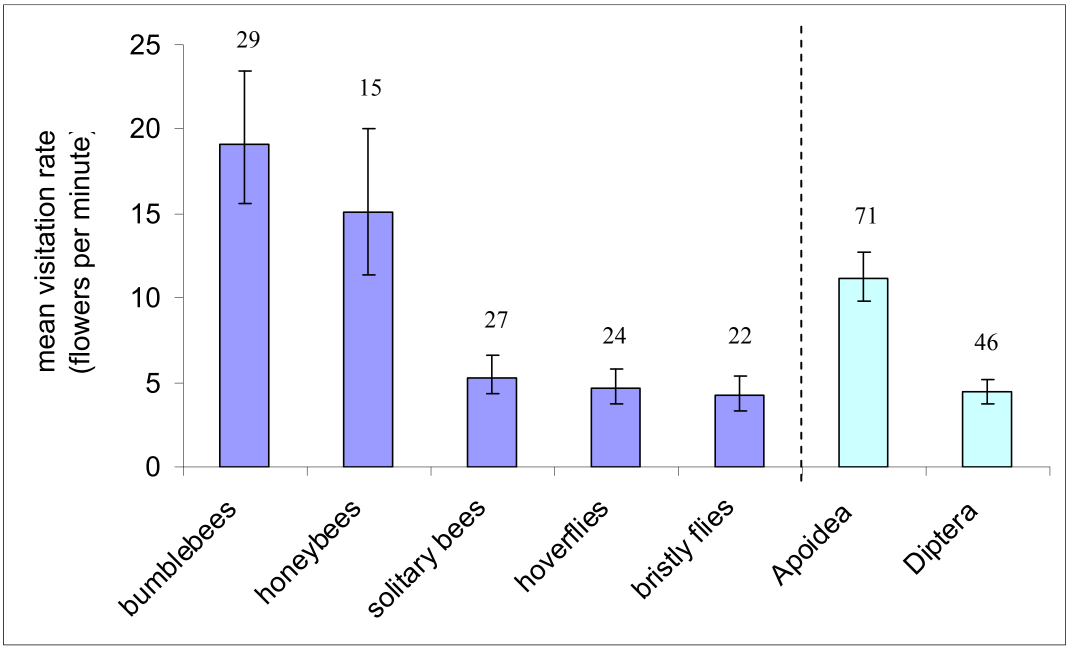
There was no evidence that the proportion of blackthorn flowers that set fruit was positively related to flower density (*P* >0.05 for all models) or the abundance of bumblebees ($F_{1, 11} = 0.22$, *P* = 0.647), solitary bees ($F_{1, 11} = 0.04$, *P* = 0.837), total bees ($F_{1, 11} = 0.02$, *P* = 0.882), hoverflies ($F_{1, 11} = 2.76$, *P* = 0.125), bristly flies ($F_{1, 11} = 0.58$, *P* = 0.462), or all insects combined ($F_{1, 11} = 0.50$, *P* = 0.496).

4.3.4. Pollination value of blackthorn flower visitors

4.3.4.1. Flower visitation rates

Honeybees were infrequent visitors to the hedgerow transects (a total of two were seen: Table 4.4), but data on their pollination effectiveness were collected because they were found to be locally abundant on a hedge of blackthorn in a subsequent year. They have also been recorded as frequent visitors to blackthorn flowers in other studies (Yeboah Gyan, 1984; Yeboah Gyan and Woodell, 1987a; Guitián, J. et al., 1993) and may have a role in pollination and fruit set where present. On a per insect basis, Apoidea (bumblebees, honeybees and solitary bees) had a faster visitation rate to flowers than Diptera (large hoverflies and bristly flies) ($F_{1, 112} = 75.38$, $P < 0.001$, Figure 4.6). Large hoverflies and bristly flies visited a similar number of flowers per minute ($F_{1, 112} = 0.28$, $P = 0.596$, Figure 4.6), but bees as a group differed in the number of flowers they visited per minute ($F_{1, 112} = 38.89$, $P < 0.001$, Figure 4.6). Social bees (bumblebees and honeybees) had similar visitation rates ($F_{1, 112} = 1.73$, $P = 0.191$, Figure 4.6), which was faster than that of solitary bees ($F_{1, 112} = 76.05$, $P < 0.001$, Figure 4.6). The statistical model accounted for 56% of the variation in the flower visitation rate data (r^2adj = 0.56). Confidence intervals show that solitary bee visitation rate appeared to be more similar to that of hoverflies and bristly flies.

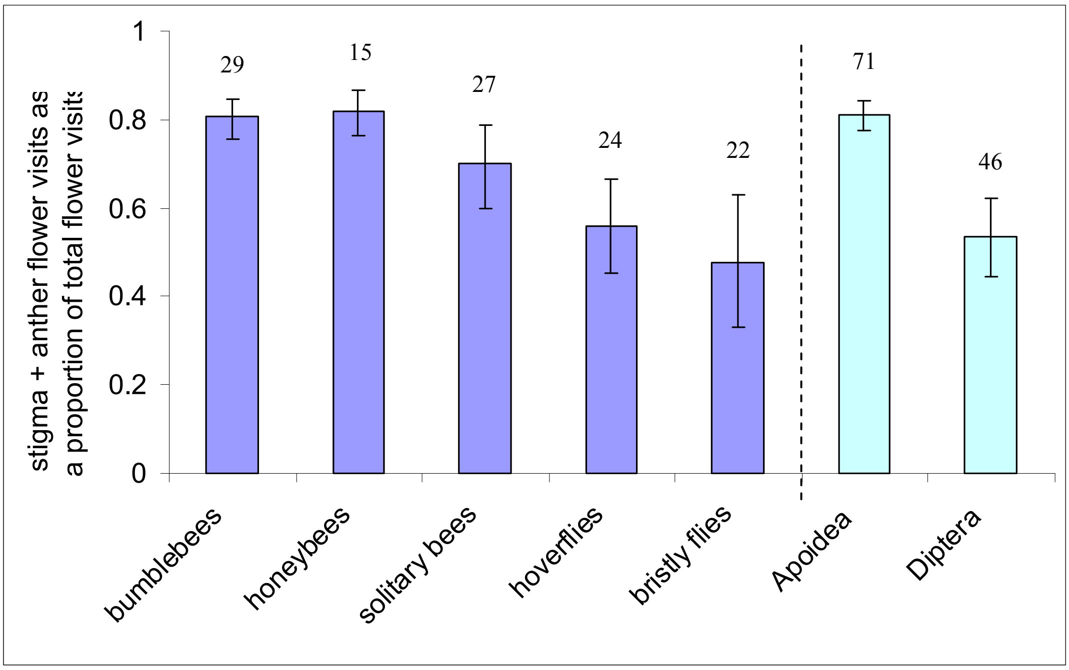
Figure 4.6 Mean flower visitation rates of groups of insects visiting blackthorn flowers, backtransformed from the $\log_{10}$ scale (± 95% confidence intervals). Values above columns = no. insects observed



4.3.4.2. Contact with the anthers and stigmas of flowers

Of the visits made by Apoidea, a greater proportion made contact with the stigma and anthers in each foraging bout when compared to Diptera ($F_{1,\,112} = 33.37$, $P < 0.001$, Figure 4.7), which the confidence intervals show can probably be attributed to the behaviour of social bees (bumblebees and honeybees) rather than solitary bees, since the data from bumblebees and honeybees do not overlap with those of data from the two Dipteran groups. The proportion of visits where contact was made with both reproductive organs was similar between hoverflies and bristly flies ($F_{1,\,112} = 0.72$, $P = 0.399$, Figure 4.7). Within bees as a group, the social bees (bumblebees and honeybees) made more contact with both reproductive organs than solitary bees ($F_{1,\,112} = 5.37$, $P = 0.022$, Figure 4.7), but bumblebees and honeybees made equal contact with the reproductive organs ($F_{1,\,112} = 0.15$, $P = 0.696$, Figure 4.7). The statistical model accounted for 23% of the variation in the data (r^2adj = 0.23).

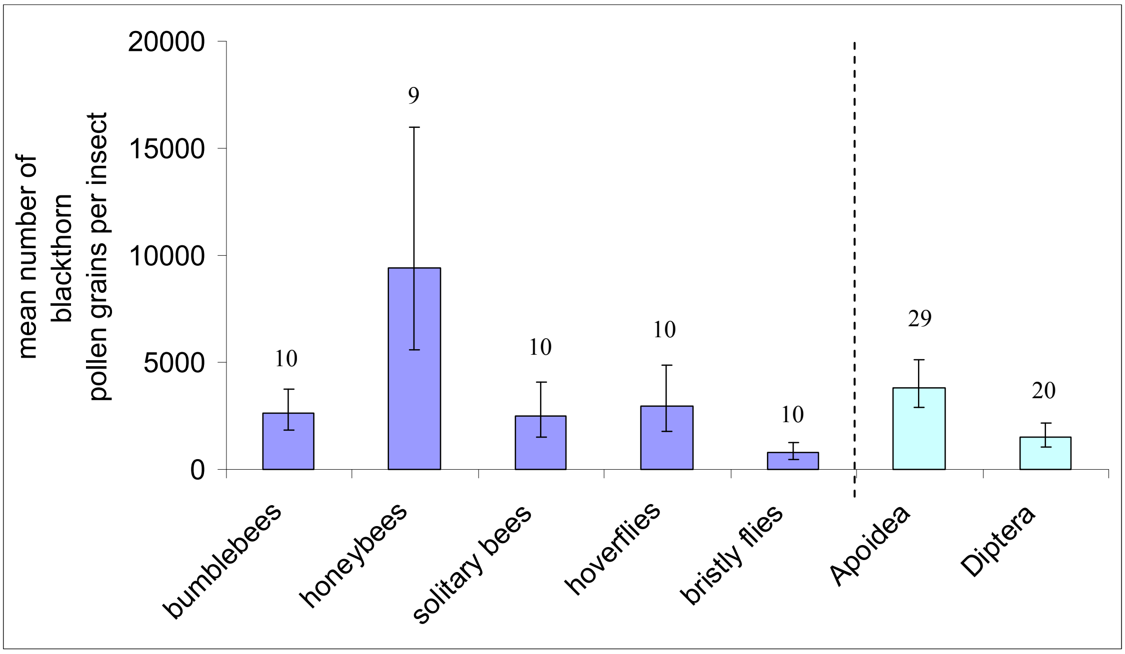
Figure 4.7 Mean proportion of flower visits in a foraging bout where simultaneous contact was made with the stigma and anthers of the blackthorn flower, backtransformed from the logit scale (± 95% confidence intervals). Values above columns = no. insects observed



4.3.4.3. Pollen carried on the bodies of insects

Apoidea carried more blackthorn pollen grains on their bodies than Diptera ($F_{1, 44}$ = 16.03, $P < 0.001$, Figure 4.8). Of the Diptera, large hoverflies carried more pollen grains on their bodies than bristly flies ($F_{1, 44}$ = 13.89, $P < 0.001$, Figure 4.8). All the bees carried different amounts of pollen ($F_{1, 44}$ = 8.14, $P < 0.001$), with social bees (bumblebees and honeybees) carrying more than solitary bees ($F_{1, 44}$ = 4.55, $P = 0.038$, Figure 4.8) and honeybees carrying more than bumblebees ($F_{1, 44}$ = 11.73, $P = 0.001$, Figure 4.8). The statistical model explained 47% of the variation in the pollen grain counts (r^2adj = 0.47). Distinct confidence interval ranges in the number of pollen grains per insect group show that honeybees carried significantly more pollen than any other insect group, and bristly flies significantly less than any other insect group. The range of pollen grain numbers was similar between bumblebees, solitary bees and hoverflies.

Figure 4.8 Mean number of blackthorn pollen grains carried on the bodies of insects visiting blackthorn flowers, backtransformed from the $\log_{10}$ scale (± 95% confidence intervals). Values above columns = no. insects sampled



4.3.3.4. Pollination Potential (PP) Index

Insect groups with the highest values are likely to have contributed the most to blackthorn pollination. The PP index scores of each insect group are shown in Table 4.6, alongside a breakdown of components of the index. Bumblebees have the highest score (0.44). The score for honeybees was very low (0.08), but solitary bees (0.18), bristly flies (0.18) and hoverflies (0.12) had similar scores. The PP index scores of each insect group was highly variable amongst the individual hedges, and on a mean hedge basis, bristly flies had the highest score (0.37) (Table 4.7).

Table 4.6 Pollination Potential (PP) index scores for each group of blackthorn flower visitors

Insect group	PQN (pollination quantity)		PQL (pollination quality)		PP (Pollination Potential) index score
	A (abundance)	FVR (flower visitation rate)	PG (number of pollen grains on body	ROT (proportion of visits with contact with stigma)	
honeybees	2	15.10	9940.61	0.82	0.08
bumblebees	32	19.14	2654.61	0.81	0.44
solitary bees	59	5.31	2471.72	0.70	0.18
hoverflies	47	4.62	2944.42	0.56	0.12
bristly flies	350	4.23	769.13	0.48	0.18

Table 4.7 Means and ranges of Pollination Potential (PP) index scores for 15 hedges

Insect group	Mean hedge PP index score	Range of scores
honeybees	0.09	0-0.64
bumblebees	0.27	0-0.90
solitary bees	0.19	0-0.89
hoverflies	0.08	0-0.36
bristly flies	0.37	0.01-1.00

4.3.4. Hedgerow fruit crop and the abundance of frugivorous birds

Sloes comprised only 26% of fruits in the hedges; the remainder were hawthorn (*Crataegus monogyna* Jacq.) (43%), *Rosa* spp (17%), bramble (*Rubus fruticosus* agg.) (8%), and white bryony (*Bryonia dioica* Jacq.), elder (*Sambucus nigra* L.), woody nightshade (*Solanum dulcamara* L.) and black bryony (*Tamus communis* L.) (6% combined). Statistical analyses were done to look for evidence of a relationship between the mean number of sloes in hedges over the season and the total number of birds observed that were known to include sloes in their winter diet (according to Snow and Snow, 1988) – these are described as 'potential sloe consumers'. Birds fitting this description seen on the transects were blackbirds (49 % of potential sloe consumers observed), fieldfare (32%), robin (17%), and song thrush (2%). Since other fruits were present in the hedge, the relationship between the remaining fruits and the abundance of potential sloe consumers was also explored. The majority of the hedges appeared to have fairly similar plant species composition and fruit yield on the back of the hedge at the commencement of fruit and bird counts (Table 4.8).

Table 4.8 Assessment of the abundance of fruits (sloes) on the back of hedges

Site	Hedge	Grid reference	Similar no. berries on back of hedge at start of counts?	Reason for difference
Rothamsted	1. Thrales End A	TL124158	fewer	Hedge on slope, therefore lower on back
	2. Little Hoos	TL123137	similar	
	3. Thrales End C	TL123168	fewer	Back of hedge cut
	4. Great Knott	TL118135	fewer	Less bramble
	6. Osier	TL109129	similar	
	7. Thrales End B	TL124169	similar	
	8. Summerdells	TL119127	similar	
Loddington	1. Bottom Collie W	SK805026	fewer	Similar amount of blackthorn, but ~75% fewer sloes
	2. Paradise	SK799019	similar	
	3. 44 Acre	SK798016	similar	
	4. Buildings	SK795019	similar	
	5. Bottom Collie C	SK801023	similar	
	7. Holloways	SK788014	similar	
	8. Barrow Hill	SK798022	similar	

There was not a significant relationship between the mean number of sloes in a hedge over the season and the total number of blackbirds ($F_{1,12} = 3.31$, $P = 0.094$) or robins ($F_{1,12} = 3.48$, $P = 0.087$). Fieldfares were present in the hedges as a relatively high proportion of the potential sloe eaters seen (32%), but their distribution was confined to only two hedges. For this reason, data for fieldfares and song thrushes (which were few in number) and blackbirds were pooled to form a ‘thrush’ group. There was a positive relationship between ‘thrushes’ and the average number of sloes in the hedge ($\hat{y} = 0.2652x + 0.344$, $r^2adj = 0.532$, $F_{1,12} = 15.80$, $P = 0.002$, Figure 4.9). Since other fruits comprised 74% of the fruit crop the relationship between these birds and the remaining fruit crop was tested, but no relationship was found for blackbirds ($F_{1, 12} = 0.01$, $P = 0.915$) robins ($F_{1, 12} = 0.05$, $P = 0.832$) or 'thrushes' ($F_{1, 12} = 0.25$, $P = 0.625$). However, when all fruits were pooled, a positive relationship was found between 'thrushes' and the mean number of all fruits of in the hedges ($\hat{y} = 0.0.813x - 1.89$, r^2adj = 0.26, $F_{1, 12} = 5.57$, $P = 0.036$, Figure 4.10). No relationship was found between the mean number of all fruits in the hedges and blackbirds ($F_{1, 12} = 0.59$, $P = 0.459$) or robins ($F_{1, 12} = 0.19$, $P = 0.672$).

Figure 4.9 Relationship between the abundance of 'thrushes' seen over 14 transects and the number of sloes in hedges over the winter (x and y axis on log scale). Dotted lines represent 95% upper and lower confidence limits for the mean response.

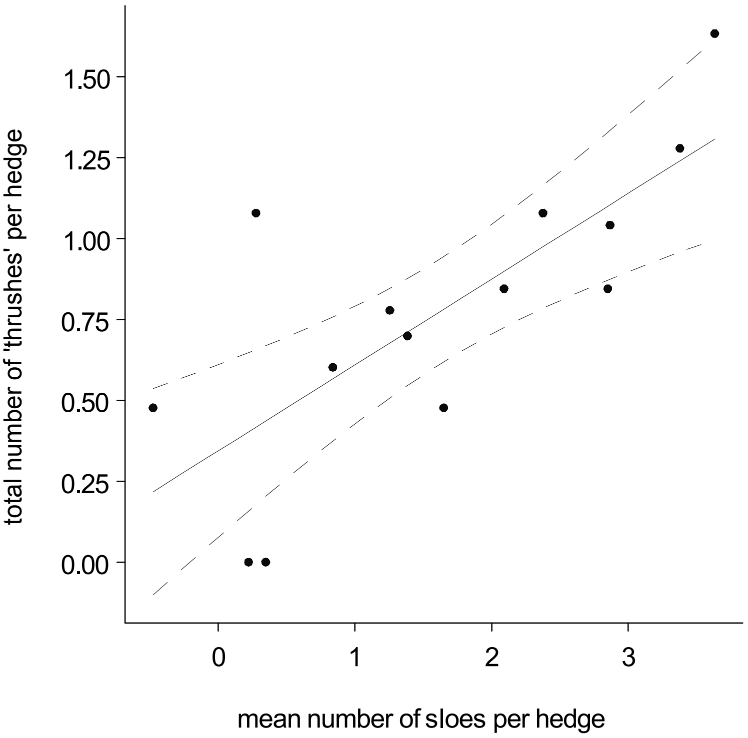
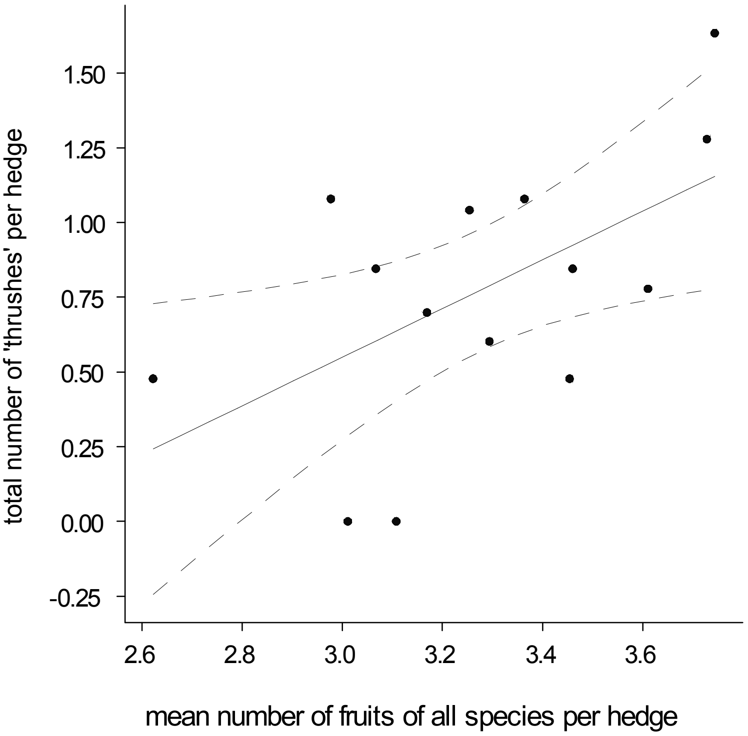


Figure 4.10 Relationship between the abundance of ‘thrushes’ seen over 14 transects and the mean number of fruits in hedges over the winter (x and y axis on log scale). Dotted lines represent 95% upper and lower confidence limits for the mean response.



4.4. Discussion

A greater proportion of flowers set fruit on ‘warm’ hedges, although this could largely be attributed to hedges at Loddington, since fruit set was similar between hedges at Rothamsted. The classification of hedges into ‘warm’ and ‘cool’ was validated using solarimeters, and if time had allowed they could also have been supplemented with ‘black globe’ temperature measurements when recording insect activity on the hedges (see Corbet et al., 1993), since it provides a measure of microclimatic temperature that is closer to that experienced by an insect.

Evidence of an effect of hedge aspect on the abundance of foraging insects was only found for solitary bees. Insect activity can be influenced by temperature, light intensity and solar radiation (Wratt, 1968; Beattie, 1971; Szabo and Smith, 1972; Corbet et al., 1993; Vicens and Bosch, 2000b; Klein et al., 2003a, 2003b; Abrol, 2006). The increased abundance of solitary bees on blackthorn flowers on warm hedges may reflect a preference amongst some solitary bees to nest in warm sites (Potts and Willmer, 1997; O'Toole and Raw, 1991) and forage close to their nest (Gathmann and Tscharntke, 2002). Other insects that are found foraging on blackthorn flowers may be adapted to forage in cool, spring temperatures and may not require warm conditions for flight e.g. pollinators such as bumblebees can generate heat for the activation of flight muscles and fly at low temperatures (Heinrich, 1979). Willmer (1983) found that the foraging activity of dark insects (e.g. *Eristalis,* some other flies, *Apis* and *Bombus*) was poorly correlated with radiation (in agreement with my study), which she suggests is to avoid overheating when radiation is high, whereas metallic-coloured insects e.g. Calliphoridae, Lucilia and some Syrphidae did correlate with radiation, in contrast to my findings. Blackthorn flowers appear before the leaves, and the hedge structure is fairly open to light penetration, which could reduce differences in insect activity between the 'warm' and 'cool' sides of hedges. Indeed, the differences in solar radiation (MJm^{-2}) between 'warm' and 'cool' hedges were not particularly large, e.g. at Rothamsted solar radiation ranged from 13.588 MJm^{-2} to18.890 MJm^{-2} for 'warm' hedges and 7.955 MJm^{-2} to 12.430 MJm^{-2} for 'cool' hedges; at Loddington solar radiation ranged from 9.010 MJm^{-2} to 10.290 MJm^{-2} for 'warm' hedges and 6.499 MJm^{-2} to 8.667 MJm^{-2} for 'cool' hedges.

There were significant effects of 'site', with more bumblebees and solitary bees on hedges at Rothamsted and more bristly flies on hedges at Loddington. The greater abundance of bees on blackthorn hedges at Rothamsted warrants further investigation. Around Rothamsted and nearby farms there is a high density of gardens, in contrast to Loddington, which is predominantly rural. These may provide bees with a good supply of forage, with potentially positive effects on their life cycles and abundance. Gardens are recognised as popular habitats for nesting bumblebees (Osborne et al., 2008b) and it is possible that gardens surrounding Rothamsted and local farms provided a pool of bumblebees, contributing to the difference in abundance between sites. There was also a slightly higher proportion of land in semi-natural habitats at Rothamsted, where 4 out of 8 'Rothamsted' hedges were located (21% in Year 1, 2004-2005), compared to Loddington (11% in Year 1, 2004-2005), which may provide more habitats for bees. Bumblebee populations are also known to be positively affected by the proportion of mass-flowering crops in a landscape (Westphal et al., 2003; Herrmann et al., 2007), and there may have been a greater proportion at Rothamsted in the previous year compared to Loddington. At Loddington there were more areas in pasture (12% in Year 1, 2004-2005), in contrast to Rothamsted and local farms, which are predominantly arable. Some families of the bristly flies observed on blackthorn (e.g. Calliphoridae, Muscidae, Sarcophagidae and Scathophagidae) are known to be associated with dung (Skidmore, 1978), which could account for the greater abundance of bristly flies on blackthorn flowers at Loddington. Unfortunately it was not possible to explore any of these hypotheses further.

The activity of most insects responded positively to flower density, as has been found in studies of other plants (Goulson et al., 1998; Grindeland et al., 2005; Feldman, 2006;

Makino and Sakai, 2007), but neither flower density nor insect activity was positively related to the proportion of flowers that set fruit. It is perhaps surprising that insect activity was not related to fruit set, since in Chapter 2 blackthorn flowers were shown to set more fruits when exposed to pollinators than when insects were excluded from flowers, and there was also evidence that flowers were pollen limited. For these reasons it might be expected that insect visits should relate to fruit set, but the fruit set was very low (3% of flowers setting fruits on average) and could simply be too low to detect a relationship. This is highlighted by experiments from Chapter 2 where flowers were exposed to insect visitors for only half of the flowering period. Although the fruit set of these flowers was slightly lower than those that were open for the entire flowering period, there was no statistically significant difference between the two treatments, possibly because insect visits were already infrequent and fruit set was so low.

As mentioned earlier, there was greater fruit set on ‘warm’ hedges, although this pattern was clear in hedges at Loddington, but not at Rothamsted. Hedge aspect could be influencing blackthorn fruit set, but factors other than insect activity must be operating, such as the effects of aspect on plant physiology. Growing fruits require carbohydrate, which is primarily produced by photosythesis in the adjacent spur and shoot leaves (Grapadelli, 1994; Tromp and Wertheim, 2005). Photosynthesis is dependent on radiation, and the fruit yield of some orchard crops has shown reductions through increased fruit abscission in association with low light levels from shading (Saito et al., 1989; Byers, 1990; George et al., 1993; McArtney et al., 2004), or cloudy weather (Byers et al., 1991). This could explain the lower fruit set on ‘cool’ hedges. Plants in hedges are likely to only be partially shaded, with some branches in the sun on the other side of the hedge, which may buffer against fruit abscission from photosynthesis in these branches, as experiments shading individual limbs of fruit trees showed fruits were still abscised but the proportion was slightly reduced (Berüter and Droz, 1991; Byers et al., 1991). From these experiments, the effect of hedge aspect on resource availability remains unclear since there was not strong evidence of consistently greater fruit set on 'warm' hedges at both sites. As mentioned earlier, blackthorn fruit set was extremely low generally (zero for marked buds on some hedges) as were the number of insects seen on hedges, which makes obtaining conclusions about the reproduction of blackthorn in these hedges difficult. Future studies should aim to estimate fruit set for the whole transect and measure insect activity more frequently to explore direct links between insect visitation and fruit set (see Chapter 5).

Blackthorn fruit set is probably influenced by a combination of factors, including insect activity (Chapter 2), pollen origin, solar radiation and possibly hedge age, since in younger fruit trees compared to mature fruit trees, assimilates are diverted to growing parts of the plant over fruits (Chalmers and Van den Ende, 1975). Of these factors, I propose that the amount (quantity) and origin (quality) of pollen reaching stigmas is of high importance for determining the fruit set of blackthorn flowers. This is supported by work done in Chapter 2 (with hedge aspect controlled for), which showed that a sample of blackthorn flowers in hedges was strongly pollen limited, with significantly more fruits being set on flowers that had been supplemented with cross-pollen than open pollinated control flowers. Blackthorn often produces a large display of flowers, and whilst this study and others have shown that pollinator abundance increases with flower density (Goulson et al., 1998; Grindeland et al., 2005; Feldman, 2006; Makino and Sakai, 2007), the numbers of insects visiting blackthorn flowers are generally low. An approximate estimate using insect abundance and foraging rate data shows that flowers in the hedges received on average 0.37 insect visits per hour, which could affect the ‘quantity’ component of pollen delivery. Although high flower densities may attract more insect visitors than low flower densities there is the disadvantage that individual flowers in large floral displays can receive fewer visits than flowers in smaller floral displays (Goulson, 2000; Grindeland et al., 2005; Benitez-Vieyra et al., 2006; Feldman, 2006), which will also reduce the ‘quantity’ of pollen reaching stigmas. Blackthorn fruit set could also be affected by pollen ‘quality’, since it readily reproduces vegetatively and it is feasible that hedge populations could consist of large areas of single clones. Large floral displays on the same plant, promote geitonogamy (pollination between flowers on the same plant) (Hessing, 1988; Harder and Barrett, 1995), which can result in lower seed set (Hessing, 1988; de Jong et al., 1993) because self-pollen is of poor ‘quality’ compared to outcrossed pollen. Fruit set in blackthorn could also be inherently low because it has been proposed that plants with large floral displays produce more flowers than fruits to ensure a reserve supply of ovaries in case of high mortality, whilst allowing the plant to abort poor quality fruits (Stephenson, 1979; Ehrlén, 1991; Guitián, 1993). To ensure that as many flowers as possible set quality fruits, providing blackthorn flowers with a strong pollinator community and ensuring hedges are planted with varied genetic stock may improve the size of the sloe crop for birds.

A positive relationship was found between ‘thrushes’ (fieldfares, blackbirds and song thrushes) and the size of the sloe crop, which could suggest that these birds were more attracted to hedges with more sloes. However, a positive relationship was also found between ‘thrushes’ and the size of the overall hedgerow fruit crop, meaning it is not possible to exclusively attribute bird abundance to sloe abundance. The relationships between bird and fruit abundance in hedges were found in this study, supports the theory that plants with an abundant display of fruits attract more birds (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977; Pyke et al., 1977), since birds can reduce time and energy expenditure searching for fruits. Other studies have also found a relationship between the abundance of some bird species and fruits (Levey, 1988; Loiselle and Blake, 1991, 1993; Kinnaird et al., 1996; Moegenburg and Levey, 2003; Saracco et al., 2004; Telleria and Pérez-Tris, 2007; Telleria et al., 2008), and in particular, thrushes (Rey, 1995; Kwit et al., 2004; Jordano, 1993). But some studies have shown that there are interspecific differences in the relationship between bird and fruit abundance (Rey, 1995; Telleria et al., 2008), and similarly, no relationship between blackbirds or robins and sloe abundance was found in this study.

Birds in the ‘thrushes’ group appeared to conform to the ‘ideal free distribution’, which predicts that frugivores will forage optimally and distribute themselves among a food patch so that there are more indviduals in profitable patches (i.e. hedges with lots of fruits) and fewer in unprofitable patches (i.e. hedges with few fruits) (Fretwell and Lucas, 1970). This could explain why they were often found in hedges with the largest fruit yields. The majority of birds in the ‘thrushes’ group were fieldfares, which are gregarious and travel and feed in flocks. Blackbirds and song thrushes are less gregarious (Simms, 1978) but blackbirds were sometimes present in the same hedges as fieldfares (J. Jacobs pers. obs.). It is advantageous for birds to flock together, because it is easier for them to locate new areas of food as a result of social learning and an increased chance of encountering food when they are in large numbers (Krebs et al., 1972; Krebs, 1973; Giraldeau, 1984), Birds that feed as flocks also roost together, and these communal roosts are thought to benefit birds through the dissemination of information about the location of food according to the 'information-centre hypothesis' (Ward and Zahavi, 1973). Individuals that were unsuccessful in locating good feeding sites tend to follow birds that were successful, perhaps indicated by behaviour such as chattering before depature from the roost site. Not all birds achieved an 'ideal free distribution' among the hedges. Indeed, the absence of a correlation between robin and fruit abundance could be due to their territorial behaviour (Lack, 1947) fixing their distribution, irrespective of fruit abundance.

The relationship between sloe/fruit and bird abundance does not imply that birds were consuming the fruits, nevertheless, there is evidence that large fruit crops sometimes have more fruits removed from than small fruit crops (Davidar and Morton, 1986; Sallabanks, 1993; Garcia et al., 2001; Ortiz-Pulido and Rico-Gray, 2000, Ortiz-Pulido et al., 2007). The size of the fruit crop from other plant species did not relate to the abundance of the birds, although only relationships between potential sloe consumers and the plant species combined as a whole were examined. Fruit abundance was variable enough between hedges to detect a positive increase in 'thrushes' as the size of the fruit crop increased, but other researchers have investigated the extent of bird-fruit relationships by artificially manipulating the number of fruits available to birds (e.g. Moegenburg and Levey, 2003). In the future, it could be interesting to investigate the temporal aspect of frugivory and whether competition for fruits exists between resident and migratory birds on British farmland.

Hedge aspect affects the activity of only one group of insects that visit blackthorn flowers: solitary bees. However, it has been difficult to conclusively establish whether hedge aspect influences blackthorn fruit set, and also whether there is a direct relationship between pollinator activity and blackthorn fruit set. In Chapter 2, blackthorn flowers were found to require visits from insects in order to set fruit, but the local pollinator community was not providing an adequate pollination service because pollen limitation was evident. In the present study, it appears that pollinator activity and fruit set may have been too low to detect a relationship between insects and fruit set. Alternatively, pollen ‘quality’ may have been restricting fruit set, either through a paucity of cross-pollen in the landscape, which is necessary for blackthorn fruit set (see Chapter 2), or through localised insect activity resulting in geitonogamy. Experiments assessing the pollination value of insect flower visitors suggest that bees should be excellent pollinators of blackthorn, but more research is required to determine whether it is important to improve habitats for pollinators, to genetically diversify the blackthorn hedge populations, or to do both in order to ensure an abundant sloe crop for birds. To do this, future studies could examine whether the proportion of flowers setting fruit is increased when the abundance of insect flower visitors increases, for example, by introducing colonies of honeybees to hedges in flower (e.g. Fries and Stark, 1983; Stern 2001), or use molecular techniques to establish whether blackthorn fruit set is limited by clonal growth and poor pollen ‘quality’ (e.g. Eriksson and Bremer, 1993; Honnay et al., 2006; Araki et al., 2007; Llaurens et al., 2008).

5. The effect of adjacent crop type and insect activity on fruit set in hawthorn, *Crataegus monogyna* Jacq. (ROSACEAE) and the consequences for frugivorous birds

5.1. Introduction

Hawthorn (*Crataegus monogyna* L.) is a native, deciduous shrub, commonly found in UK hedges, flowering from May to June. The white flowers have an open structure and are attractive to a wide variety of insects seeking pollen and nectar such as bees (Apoidea), true flies (Diptera), and butterflies (Lepidoptera) (Knuth, 1908; Yeboah Gyan, 1984; Yeboah Gyan and Woodell, 1987a; Guitián and Fuentes, 1992). Hawthorn fruits (or haws) are red drupes containing one seed, and the flesh provides a food source for a range of birds over the winter (Hartley, 1954; Simms, 1978; Snow & Snow, 1988; Sorensen, 1981, 1984; Courtney and Manzur, 1985). These include migratory fieldfares (*Turdus pilaris* L.) and redwings (*T. iliacus* L.), which from October onwards travel from their breeding areas in Fennoscandia and Russia to overwinter in Britain and Ireland (Wernham et al., 2002). Haw consumers also include partially migratory or resident birds such as blackbirds (*T. merula* L.), song thrushes (*T. philomelos* Brehm.), mistle thrushes (*T. viscivorus* L.), robins (*Erithacus rubecula* L.), woodpigeons (*Columba palumbus* L.), starlings (*Sturnus vulgaris* L.) and blue tits (*Cyanistes caeruleus* L.). Several farmland bird species have declined in recent decades, and some frugivores such as song thrushes and mistle thrushes are of conservation concern (Mead, 2000; Gregory, 2004; Baillie et al., 2007). Although the reasons for population declines in farmland birds are complex, the availability of seed food in winter has been shown to influence the breeding abundance of granivorous passerines (Siriwardena et al., 2007). It is not known whether the availability of hedgerow fruits in winter has contributed to the decline of frugivorous farmland birds or is limiting populations, but widespread hedgerow loss has occurred over the last few decades (Barr et al., 1991; Rackham, 2000), reducing the availability of fruits to birds. It has been hypothesised that large fruit crops should attract more frugivores than small fruit crops (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977). Some frugivorous birds preferentially choose shrubs with more fruit (Sallabanks, 1993) and bird abundance has often been found to be positively related to the spatial and/or temporal availability of fruit resources (Levey, 1988; Loiselle and Blake, 1991,1993; Rey, 1995; Kinnaird et al., 1996; Moegenburg and Levey, 2003; Kwit et al., 2004; Saracco et al., 2004; Telleria and Pérez-Tris, 2007; Telleria et al., 2008) although there are some exceptions when this relationship was not as apparent (e.g. Guitián and Bermejo, 2006; Galetti and Aleixo, 1998; Herrera, 1998).

The availability of haws to birds is presumably influenced by the pollinating activities of insects, since the proportion of hawthorn flowers that set fruit is reduced in the absence of flower visiting insects (Guitián and Fuentes, 1992; Chapter 2), and evidence of pollen limitation was found in a sample of plants in UK hedges (Chapter 2). Flower-visiting insects vary in their pollinating abilities (Primack and Silander, 1975; Schemske and Horvitz, 1984; Herrera, 1987; Kandori, 2002) and at present it is unclear which groups are the most important for ensuring pollination and the development of haws. In theory, the activity of pollinating insects and hence fruit set could also be modified by factors such as adjacent crop type. Oilseed rape (*Brassica napus* L.) is a common feature of the modern UK agricultural landscape, since production in the UK has increased since the 1970s (Defra, 2003). Winter oilseed rape flowers from May to June, coinciding with hawthorn flowering, and the oilseed rape flowers are visited for nectar and pollen by insects such as Apoidea (bees) and Diptera (true flies) (Kirk, 1992). Since the flowers of both plant species attract similar insect groups, it is possible that hawthorn is in competition for pollinators with this mass-flowering crop. Alternatively the presence of a large floral resource could facilitate the pollination of hawthorn flowers by attracting pollinators into the area. Plant-pollinator interactions are thought to range along a continuum from facilitation to competition according to plant abundance (Rathcke, 1983). Studies on the effects of co-flowering plant species have ranged from documenting seed set reduction due to competition for pollinator visits i.e. an influence on pollen quantity (Chittka and Schürkens, 2001; Brown et al., 2002; Muňoz and Cavieres, 2008; Moragues and Traveset, 2005), the loss of pollen to competing flowers (Campbell and Motten, 1985; Bell et al., 2005), or the deposition of heterospecific pollen on stigmas i.e. an influence on pollen quality (Waser and Fugate, 1985; Jackobsson et al., 2008; Brown and Mitchell, 2001) to facilitative effects on pollination and seed set (e.g. Moragues and Traveset, 2005; Laverty, 1992; Johnson et al., 2003; Muňoz and Cavieres, 2008; Ghazoul, 2006). Neutral effects on seed set have also been documented (Moragues and Traveset, 2005; Muňoz and Cavieres, 2008; Totland, 2006; Rathcke, 1988, Caruso, 1999; Jones, 2004; Aigner, 2004). This study takes a new perspective by examining the effects of a mass-flowering crop (winter oilseed rape) on the pollination and seed set of a hedgerow plant species native to the UK. An incidental finding by Roy et al. (2003) who studied the effect of the management of genetically modified herbicide tolerant crops on farmland biodiversity, was that there was a higher density of bees on flowers in field margins next to spring oilseed rape when compared to margins next to beet and maize. Provided that the field margins did not differ inherently, this suggested oilseed rape had the potential to facilitate the pollination of field margin flora in those fields.

This chapter describes the use of a hedgerow/field scale experiment to address Objective 4 by testing the effects of adjacent crop type on insect activity and the proportion of hawthorn flowers that set fruit. It aims to investigate whether a mass-flowering crop like oilseed rape has a competitive, facilitative or neutral effect on hawthorn pollination and fruit set. It addresses Objective 2 by aiming to suggest which flower-visiting insects are likely to be of greatest value in pollinating hawthorn flowers by exploring the relationships between insect activity and the proportion of hawthorn flowers that set fruit. Finally, it addresses Objective 5, by aiming to determine whether the abundance of frugivorous birds in hedges is linked to the size of the haw crop.

5.2. Methods

Experiments were done in 2006 (Year 2) and 2007 (Year 3) on hedges containing hawthorn on Rothamsted Research farm and the local area (Hertfordshire, UK) and at The Game & Wildlife Conservation Trust's 'Allerton Project' farm (Loddington, Leicestershire, UK). Experiments were done on 16 hedges, which contained flowering hawthorn and were selected to include eight hedges adjacent to 'WOSR' (winter oilseed rape – the mass flowering treatment) and eight hedges adjacent to fields of crops providing virtually no floral resources, grouped as 'grass' (cereal/pasture/set aside). Ideally, all hedges adjacent to 'grass' would have been adjacent to cereal fields, but it was not possible to satisfy these requirements, so set aside and pasture had to be included.

The hedges were orientated across a spread of aspects to control for any effects of hedge aspect on insect activity, pollination and fruit set. Because characteristics such as hedge dimensions can influence bird abundance (Osborne, 1984; Sparks et al., 1996; Parish et al., 1994), this was the final criteria for selecting hedges, and they were standardised by choosing ones of similar height and width where possible. The hedges and their adjacent crop types, aspects and dimensions are listed in Table 5.1.

Table 5.1 Location and attributes of hawthorn hedges where pollinator activity, fruit set and bird activity was studied

Site	Hedge id.	Grid reference	Aspect	Adjacent crop type	WOSR[1]growth stage[2] at start of hawthorn flowering	WOSR[1]growth stage[2] at end of hawthorn flowering	Approximate hedge height (m)	Approximate hedge width (m)
Rothamsted	1. Black Horse	TL103132	NE	Cereal	n/a	n/a	3	2.5
	2. Summerdells	TL119127	NW	Cereal	n/a	n/a	3-5	3.5
	3. Barnfield	TL118143	SE	Cereal	n/a	n/a	3-5	3
	4. Little Hoos	TL124140	SW	Cereal + setaside grassland (few flowers)	n/a	n/a	3.5	3
	5. Annables	TL103145	NE	WOSR	67	69-70	3	3
	7. Fiddlers Hill	TL114165	NW	WOSR	67	69-70	3.5	3
	6. Thrales End	TL117168	SE	WOSR	67	69-70	3	4
	8. Dodds Lane	TL053095	SW	WOSR	64	68	3.5	3
Loddington	1. Greengates	SK794025	E	Cereal	n/a	n/a	3	3
	2. Churchills	SK791027	E	Pasture	n/a	n/a	3	3
	3. Barrow Hill	SK798025	SW	Cereal	n/a	n/a	3	3
	4. Upper Pond	SK798016	WNW	Cereal	n/a	n/a	3	3
	5. Top Collie	SK799025	NE	WOSR	67	69	3.5	3.5
	6. Pond Field	SK793011	E	WOSR	67	69-70	3.5	3
	7. Collie's Hump	SK799026	NW	WOSR	67	69	3.5	3.5
	8. Cabins	SK797011	WNW	WOSR	67	69-70	2.5	3

1. WOSR = winter oilseed rape. 2. BBCH growth stages (Lancashire et al., 1991): **65** = full flowering, 50% of flowers on main raceme open **69** = end of flowering **70** = pod development

5.2.1. Adjacent crop type and hawthorn fruit set

Before the hawthorn flowering period, four line transects each of 25m in length were marked out using flexicanes along each hedge, spaced according to the presence of hawthorn. Regular counts of the number of hawthorn flowers in the hedge were made throughout the flowering period (see section 5.2.2. below for timings). A tape measure was used to mark 1m sections along each 25m transect, and the cover of hawthorn flowers was assessed by counting the first 100 flowers and estimating the final number to the nearest 25 flowers in each segment. A simulation model based on these flower counts and the average number of days that a hawthorn flower is open for was used to obtain an estimate of the total number of hawthorn flowers on each hedge (see section 5.2.4.1. for model details). Counts of all mature fruits in the hedges (including haws) were done as described in section 5.2.3. Using the flower number estimate from the simulation model and the first count of the number of fruits in the hedges (8th September 2006 at Rothamsted farm and the surrounding area; 11th September 2006 at Loddington), the proportion of hawthorn flowers that set fruit per hedge was calculated to look for evidence of a difference in fruit set between hawthorn adjacent to 'WOSR' and 'grass'.

5.2.2. Insect activity, adjacent crop type and hawthorn fruit set

Insects foraging on hawthorn flowers along the hedge transects and on the winter oilseed rape (WOSR) were surveyed on four sampling dates between 17th May 2006 and 4th June 2006 at Rothamsted under the following weather conditions: temperature 10.6-24.4ºC, relative humidity 32-98%, wind speed 1-5 (Beaufort scale) and cloud cover 5-

100%. Insects were surveyed between 18th May 2006 to 7th June 2006 at Loddington under the following weather conditions: temperature 11.3-23.5ºC, relative humidity 56-98%, wind speed 1-6 (Beaufort scale) and cloud cover 5-100%. The weather in May to June 2006 was showery, but sampling continued on regular dates regardless. On each sampling day insects foraging on hawthorn flowers and winter oilseed rape flowers were surveyed in the morning and afternoon using the line transect method (Banaszak, 1980). For the hedge transects each 25m transect was walked slowly at a rate of 20m/min^{-1} and all insects observed foraging on hawthorn flowers up to a height of 2.2m were recorded. Insects foraging on winter oilseed rape along the edge of the crop adjacent to each 25m hedge transect were sampled by walking along each 25m transect slowly at a rate of 20m/min^{-1} and recording all insects foraging on oilseed rape flowers along a 2.2m belt. The crop stage of the winter oilseed rape was noted according to Lancashire et al. (1991). Flower-visiting insects were assigned to the following morphological and functional groups for all experiments:

- bumblebees
- honeybees
- solitary bees: large >1cm long, small <1cm long
- bristly flies (mainly from sub-order Cyclorrhapa, series Schizophora, section Calyptrata, but also some from sub-orders Nematocera e.g. Bibionidae, and Brachycera e.g. Empididae)
- hoverflies: large, thick-bodied >1cm long; small, thin-bodied <1cm long

Further details of these flower-visiting insects can be found in Table 5.2, which lists examples of some of the species, genera or families of insects that were observed.

Table 5.2 Insects observed foraging on hawthorn flowers

Insect group	Examples of species, genera or families
honeybees	*Apis mellifera* (L.)
bumblebees	*Bombus terrestris* (L.) /*lucorum* (L.) (difficult to separate workers reliably in the field) *Bombus lapidarius* (L.) *Bombus pascuorum* (Scopoli) *Bombus pratorum* (L.) *Bombus hortorum* (L.) *Bombus vestalis* (Geoffroy)
solitary bees	
large >1cm	*Andrena* spp. *Nomada* spp. *Osmia rufa* (L.)
small >1cm	*Andrena* spp. *Nomada* spp.
hoverflies	
large >1cm or thick bodied	*Eristalis* spp. *Syrphus* sp. *Myathropa florea* (L.) *Episyrphus balteatus* (de Geer) *Volucella bombylans* (L.) *Leucozona lucorum* (L.) *Rhingia campestris* (Meigen).
small <1cm or thin bodied	*Sphaerophoria scripta* (L.) *Syritta pipiens* (L.)
bristly flies	Bibionidae Empididae Scathophagidae Calliphoridae Tachinidae

Hawthorn flower density records were made within one to two days of insect observations and also at the end of flowering, using the method described in section 5.2.1. This was to provide information for the simulation model and to allow the effects of flower density on insect activity to be considered in subsequent data analysis.

5.2.3. Hawthorn fruit crop and the abundance of frugivorous birds

The number of fruits of all plant species, including haws, and the abundance of frugivorous birds in hedges were recorded over the autumn and winter of 2006-2007 (Year 2-3). Fruits were counted and birds were surveyed every two weeks at Rothamsted between 8th September 2006 and 28th January 2007, and at Loddington between 11th September 2006 and 31st January 2007. For the first count, the numbers of fruits in each 1m segment of the 25m transects were counted. Due to the high number of fruits and time constraints, on following occasions the fruit yield of the hedges was subsampled by counting fruits in every other 1m x 2.2m section of the 25m transects i.e. fruits were counted in 13 segments in each transect. Fruits were counted individually up to 100, after which the number was estimated to the nearest 25 fruits. Counting fruits on only one side of the hedge is equivalent to subsampling the fruit yield of the whole hedge unless there are large differences in the number of fruits between sides. Time did not allow for comprehensive fruit counts on the other side, or the 'back' of the hedge, but a rough assessment of the fruit crop on the back of the hedge was made by noting whether the species composition and size of the fruit crop was similar or different. Birds were surveyed on two consecutive mornings between approximately 0730h and 1000h using the line transect method (see Bibby et al., 2000). This involved walking the length of each hedge at a rate of 20m/min^{-1} counting all birds seen, heard, or flushed out of the hedge, and assigning them to areas either within or outside the transects. Any birds observed within 2m of the transect were assigned 'within' the transect.

5.2.4. Statistical analysis

All data were analysed using GenStat version 11.

5.2.4.1. Adjacent crop type and hawthorn fruit set

In previous experiments, fruit set proportions were calculated by subsampling buds along hedges (see Chapters 2 and 4) and counting the number of buds which set mature fruit. Out of concern that subsampling may not be truly representative of fruit set of the whole hedge, the aim was to calculate an overall fruit set value for each hedge. This would then allow for closer comparison when investigating the relationship between fruit set and insect activity. To calculate a fruit set value for each hedge, it was first necessary to determine the number of flowers present on each hedge. It was impractical to count each bud so a simulation model (MATLAB Version 7. http://www.mathworks.com/access/helpdesk/help/techdoc/matlab.html developed by S. Gezan at Rothamsted Research) was used to estimate the number of flowers (m) present on each hedge, from five flower counts that were made approximately every two weeks (see text box below for model details).

It was assumed that the distribution of the start of flowering for all the hedges followed a normal distribution N (p, sd^2), where p = the estimated start date of flowering. This distribution was termed Z. Initial values for three parameters: m, p and sd_I were specified e.g. $m_I = 55{,}000$ flowers, $p_I = 11$ days, $sd_I = 3.4$ days. For each of m_I flowers a (rounded) start date s_i, $i = 1 \ldots m_I$ ($1 \quad si < 50$) was randomly selected from Z. Flowering period values, ℓ_i, were selected at random from the empirical distribution L and the end date, e_i, computed as (rounded) $e_i = s_i + \ell_i$ ($1 < e_i < 50$). After a series of flowering profiles were created and an ‘expected’ distribution of buds in flower for each of 50 days of flowering was achieved. Observed values (O_j) were compared with (E_j) using a standard chi-square test: $\sum (O_j - E_j)^2 / E_j$. An iterative algorithm was then employed to minimise the chi-squared statistic, i.e. the values of m, p and sd were varied, and the simulation procedure repeated to find the parameter combination which achieves the minimum chi-square value. The entire procedure was repeated for each hedge separately.

First, a small experiment was designed to determine the average number of days that a hawthorn flower was open. This was done on one hedge containing hawthorn at Rothamsted's farm (TL132132) between 10th May and 26th May 2008. Twenty buds were marked on each of six hawthorn shrubs (three shrubs were on the front of the hedge and three were on the back of the hedge to allow for effects of aspect on flower longevity, should there be any). The flowers were checked every day and it was noted when all the petals had dropped. On average, flowers lasted for 10.47 days.

The proportion of flowers on each hedge that set fruit (P) was calculated as follows: P = r/n, where r = number of fruits and n = the estimated number of flowers on each hedge. Differences in fruit set between hedges was tested for using ANOVA (Payne et al., 2008), to look for effects of adjacent crop type on fruit set and to explore whether these effects differed between the two sites (Rothamsted and Loddington). The structure of the ANOVA according to the notation of Wilkinson and Rogers (1973) was as follows: 'blocks' = hedge and 'treatments' = crop*site where / is a nesting operator (A/B = A+A.B) and * is a crossing operator (A*B = A+B+A.B). The residual plots were checked and no transformations were necessary since the large sample sizes meant that the data approximated to a reasonably good normal distribution rather than a binomial distribution.

5.2.4.2. Insect activity, flower density, adjacent crop type and hawthorn fruit set

Linear relationships between the activity of the different insect groups and flower density were fitted using regression analysis (Payne et al., 2008), with 'crop' ('WOSR' or ‘grass’) included as a factor with two levels. Data were transformed (using $\log_{10}$ transformations) to normalise residuals where appropriate. Regression analysis was also used to investigate relationships between the proportion of hawthorn flowers that set fruit and insect activity, to determine if the activity of a particular insect group related to fruit set. The effect of flower density on fruit set was taken into account first by adding the estimated total number of flowers for each hedge into the model. Visitation data for an insect group was then added to the model to see if this improved the relationship. Separate models were created for each insect group. Adjacent crop type was also added to the model as a factor to test whether it affected the relationship between insect abundance and fruit set. For example is it possible that the insect visitors to hawthorn, next to an oilseed rape field, would deposit oilseed rape pollen on the hawthorn stigmas, causing clogging and this might adversely affect fruit set.

5.2.4.3. Hawthorn fruit crop and the abundance of frugivorous birds

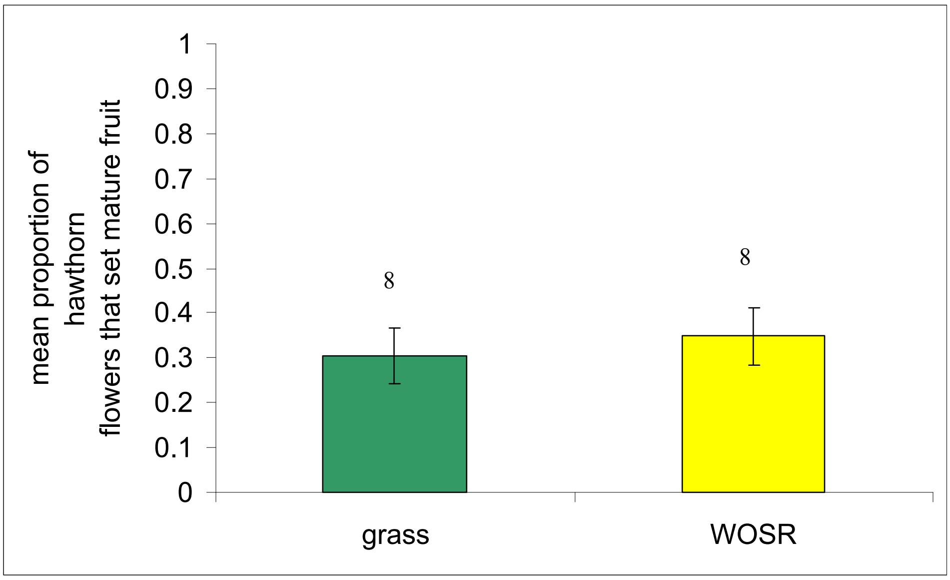
Regression analysis (Payne et al., 2008), was used to investigate the relationship between the mean number of haws in the hedge over the season and the total abundance of potential frugivorous birds (pooled for all transects over the season). Data were transformed (using $\log_{10}$ transformations) to normalise residuals when appropriate.

5.3. Results

5.3.1. Adjacent crop type and hawthorn fruit set

The proportion of hawthorn flowers that set fruit was similar irrespective of adjacent crop type ($F_{1, 12} = 0.86$, $P = 0.371$, Figure 5.1) and this trend was similar at both sites (Rothamsted and Loddington) ($F_{1, 12} = 0.10$, $P = 0.755$). There was also no difference in overall fruit set between sites ($F_{1, 12} = 0.01$, $P = 0.922$).

Figure 5.1 Mean proportion of hawthorn flowers setting mature fruit (±95% confidence intervals) on hedges adjacent to grass vs. hedges adjacent to winter oilseed rape (WOSR). Values above columns = no. of hedges



5.3.2. Insect activity, flower density, adjacent crop type and hawthorn fruit set

Hawthorn flowers were visited by a range of insects, and the relative abundances of each insect group observed foraging on flowers in the hedge transects for each crop type are listed in Table 5.3, together with the abundance of insects observed foraging on winter oilseed rape (WOSR).

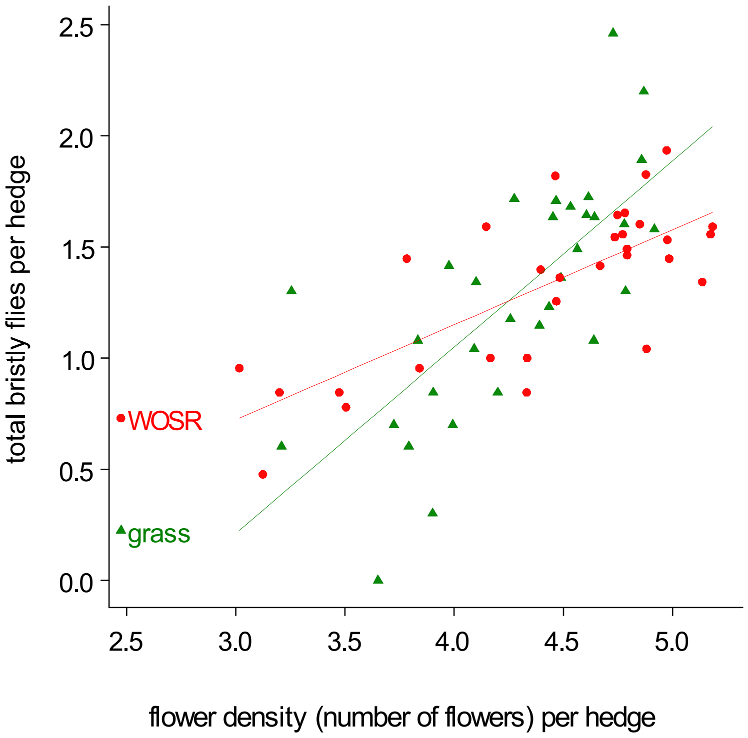
Table 5.3 Relative abundance of insect groups visiting all hedge transects of hawthorn and all 2m winter oilseed rape (WOSR) transects, over the hawthorn flowering period

	All hawthorn transects combined (‘WOSR’ &’grass’) (4 transects x 16 hedges)		Hawthorn transects next to ‘grass’ (4 transects x 8 hedges)		Hawthorn transects next to ‘WOSR’ (4 transects x 8 hedges)		‘WOSR’ transects (4 transects x 8 hedges)	
Insect group	Number of visitors	Percentage of visits (%)	Number of visitors	Percentage of visits (%)	Number of visitors	Percentage of visits (%)	Number of visitors	Percentage of visits (%)
honeybees	2	0.08	1	0.09	1	0.07	13	1.10
bumblebees	24	0.96	14	1.28	10	0.72	20	1.69
solitary bees								
large >1cm	204	8.20	121	11.10	83	5.94	49	4.15
small >1cm	22	0.88	4	0.37	18	1.29	8	0.68
Total bees	252	10.13	140	12.84	112	8.02	90	7.62
hoverflies								
large >1cm or thick bodied	80	3.22	52	4.77	28	2.00	23	1.95
small <1cm or thick bodied	85	3.42	22	2.02	63	4.51	25	2.12
Total hoverflies	165	6.63	74	6.79	91	6.51	48	4.06
bristly flies	2071	83.24	876	80.37	1195	85.54	1043	88.31
Total insects	2488	100	1090	100	1398	100	1286	100

The relationship between insect activity and flower density was investigated for the most abundant insect groups (generally those that comprised >5% of the flower-visiting population). The effect of adjacent crop type on this relationship was also considered as the main factor of interest. Because the relationship between hawthorn fruit set and adjacent crop type was similar at both Rothamsted and Loddington (section 5.3.1), 'site' was not included in the analysis. Bristly flies were the most abundant flower visitors (83.24% of observations). Honeybees and bumblebees were relatively infrequent visitors (0.08% and 0.96% respectively) and were combined with all solitary bees to form total bees (10.13%). Due to their abundance (8.20%) large solitary bees were also considered separately. Although large hoverflies were low in abundance (3.22%) they were included in analyses since research suggests they may contribute to the pollination of rosaceous plants (Yeboah Gyan and Woodell, 1984; 1987a).

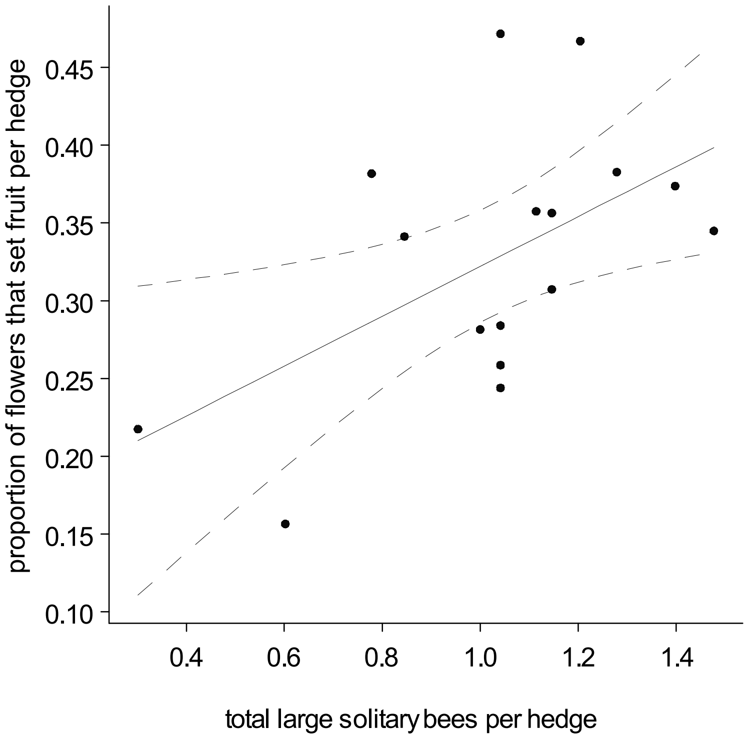
Positive linear relationships were found between hawthorn flower density and the number of large solitary bees ($F_{1, 60} = 20.49$, $P < 0.001$), total bees ($F_{1, 60} = 18.42$, $P < 0.001$), large hoverflies ($F_{1, 60} = 7.64$, $P = 0.008$) and bristly flies ($F_{1, 59} = 59.44$, $P < 0.001$) on each hedge. There was no effect of crop type on insect density for large solitary bees ($F_{1, 60} = 0.10$, $P = 0.751$), total bees ($F_{1, 60} = 0.58$, $P = 0.449$), large hoverflies ($F_{1, 60 =}$ 0.74, $P = 0.394$) and bristly flies ($F_{1, 59 =}$ 0.18, $P = 0.674$) and there were also no interaction effects (flower density x crop type) for these insect groups ($P > 0.05$). However, the relationship between bristly fly abundance and hawthorn flower density differed between crop types, with a steeper relationship in hedges adjacent to 'grass' compared to 'WOSR', therefore separate lines best described these data ($F_{1, 59} = 6.97$, $P = 0.011$, Figure 5.2).

Figure 5.2 Relationship between bristly fly abundance (log scale) and hawthorn flower density (log scale), in relation to adjacent crop type (‘WOSR’ and ‘grass’). Observations from 16 hedges on four separate dates. (From the fitted model excluding non-significant terms and with one outlier removed)



After fitting full models for all insect groups, no relationship was found between hawthorn fruit set and flower density (*P* >0.05 for all models), or the abundance of total bees ($F_{1, 10} = 3.24$, $P = 0.102$), large hoverflies ($F_{1, 10} = 0.01$, $P = 0.908$) or bristly flies ($F_{1, 10} = 3.10$, $P = 0.109$). The exception was the large solitary bee group, with evidence of a positive linear relationship between the proportion of hawthorn flowers that set fruit and large solitary bee abundance, which was best explained by a single line ($\hat{y} = 0.162 + 0.160x$, $r^2adj = 0.253$, $F_{1, 10} = 5.92$, $P = 0.035$, Figure 5.3) and was similar for both crop types ($F_{1, 10} = 0.09$, $P = 0.775$).

Figure 5.3 Relationship between the proportion of hawthorn flowers that set fruit and large solitary bee abundance (log scale) for 16 hedges. (From the fitted model excluding non-significant terms). Dotted lines represent 95% upper and lower confidence limits



5.3.3. Hawthorn fruit crop and the abundance of frugivorous birds

Haws comprised 92% of the fruit on all of the hedges; the remaining 8% were fruits of white bryony (*Bryonia dioica* Jacq.), dogwood (*Cornus sanguinea* L.), privet (*Ligustrum vulgare* L.), blackthorn (*Prunus spinosa* L.), *Rosa* spp., bramble (*Rubus fruticosus* agg.), elder (*Sambucus nigra* L.), woody nightshade (*Solanum dulcamara* L.), black bryony (*Tamus communis* L.) and guelder-rose (*Viburnum opulus* L.). Since haws were the most abundant fruit the analyses focused on looking for evidence of a relationship between haws and birds that were abundant in the hedges and/or known to include haws in their winter diet. Frugivorous birds observed in the hedges that eat haws (according to Snow and Snow, 1988) included blackbirds (33.9% of frugivores observed), robins (20.7%), fieldfares (5.1%), redwings (4.4%), song thrushes (1%), mistle thrushes (0.2%) and blue tits (34.7%). For analysis, the birds were placed into the following groups:

1. most abundant birds and therefore considered separately:

- blackbirds
- blue tits
- robins

2. birds often found together in flocks ‘migratory thrushes’:

- redwings and fieldfares

3. thrushes combined as a group ‘thrushes’:

- redwings, fieldfares, song thrushes, mistle thrushes, blackbirds

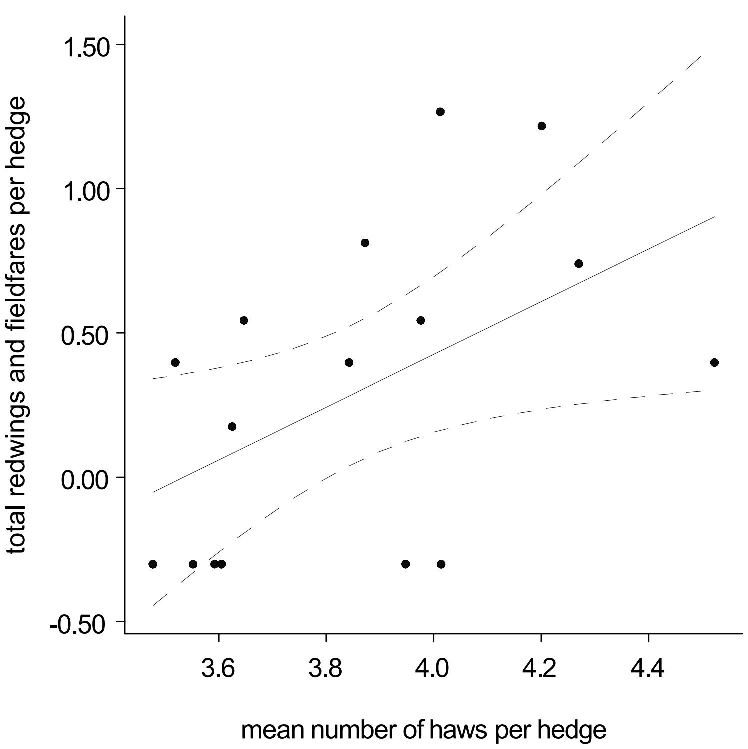
The seasonal average haw count represents a subsample of the haws present on hedges, since they were only counted in alternative 1m segments of the transects and from only the front. The number of fruits on the back of hedges at the start of the bird counts varied to those on the front for some hedges (Table 5.4), and the backs of some hedges were also cut during the experiment.

Table 5.4 Assessment of the abundance of fruits (haws) on the back of hedges

Site	Hedge	Grid reference	Similar no. berries on back of hedge at start of counts?	Reason for difference
Rothamsted	1. Black Horse	TL103132	fewer	Back of hedge cut regularly due to pavement
	2. Summerdells	TL119127	similar	
	3. Barnfield	TL118143	fewer	Back of hedge cut regularly due to footpath
	4. Little Hoos	TL124140	fewer	Back of hedge cut regularly due to footpath
	5. Annables	TL103145	similar	
	7. Fiddlers Hill	TL114165	fewer	Less hawthorn
	6. Thrales End	TL117168	fewer	Back of hedge cut
	8. Dodds Lane	TL053095	unknown	No access to back of hedge – private land
Loddington	1. Greengates	SK794025	unknown	Difficult to access back of hedge – dense scrub
	2. Churchills	SK791027	similar	
	3. Barrow Hill	SK798025	similar	
	4. Upper Pond	SK798016	similar	
	5. Top Collie	SK799025	similar	
	6. Pond Field	SK793011	similar	
	7. Collie's Hump	SK799026	similar	
	8. Cabins	SK797011	fewer	Less hawthorn

No relationship was found between the seasonal average number of haws and the abundance of blackbirds ($F_{1, 14} = 2.95$, $P = 0.108$), blue tits ($F_{1, 14} = 1.29$, $P = 0.274$) robins ($F_{1, 14} = 1.81$, $P = 0.200$) or 'thrushes' ($F_{1, 14} = 4.11$, $P = 0.062$). There was a positive linear relationship between 'migratory thrushes' and the number of haws ($\hat{y} = -3.23 + 0.914x$, $r^2adj = 0.20$, $F_{1, 14} = 4.75$, $P = 0.047$, Figure 5.4).

Figure 5.4 Relationship between the abundance of 'migratory thrushes' and the mean number of haws in 16 hedges over the winter (x and y axis on log scale). Dotted lines represent 95% upper and lower confidence limits for the mean response



5.4. Discussion

The effects of co-flowering plant species on pollination and seed set may range from facilitation to competition according to plant abundance (Rathcke, 1983). It might be expected that the large number of plants and flowers in a field of winter oilseed rape should exert competition on hawthorn for pollinators, since high abundance of co-flowering plants can exert competition on the plant that is less abundant (Muňoz and Cavieres, 2008). In my study, no effect of the presence of oilseed rape on pollinator activity, pollination or fruit set of hawthorn was found, and this neutral effect has also been observed for other plants (Aigner, 2004; Moragues and Traveset, 2005).

Insect activity on hawthorn was positively related to flower density as has been found in several studies of different plant species (Goulson et al., 1998; Grindeland et al., 2005; Feldman, 2006; Makino and Sakai, 2007), but in general, insect activity was not affected by adjacent crop type, with the exception of bristly flies. At hedges with low hawthorn flower densities the presence of oilseed rape increased fly densities relative to hawthorn hedges next to grass, whereas at hedges with high hawthorn flower densities the presence of oilseed rape decreased fly densities relative to hedges next to grass, suggesting that the interactions between their visits to hawthorn flowers and the presence of oilseed rape ranged along a continuum from facilitation to competition according to plant [or flower] abundance (as proposed by Rathcke, 1983). Large solitary bees were the only insect group whose abundance was positively related to hawthorn fruit set, which indicates that solitary bees are likely to be important pollinators of hawthorn. It was difficult to accurately identify large solitary bees on the wing, but the most common genera observed foraging on hawthorn were probably *Andrena*, followed by *Nomada*. It is expected that of these, female Andrenids have the greatest pollination value because they carry loosely packed pollen in scopae on their legs, which is likely to be available for pollination. *Nomada* are cleptoparasites with no requirement to collect pollen and probably contribute less to pollination. The phenology of *Andrena, Nomada* and other solitary bee species overlap well with hawthorn flowering, since hawthorn flowers relatively early in the year when solitary bee populations are strong, in comparison to social bees (honeybees and bumblebees) whose populations are still low (Proctor et al., 1996). The relationship between solitary bees and fruit set was similar regardless of adjacent crop type, suggesting it is unlikely that there were negative effects on fruit set due to heterospecific pollen transfer.

Experiments from Year 3 (2007) revealed that hawthorn was pollen limited in the hedges that were sampled, with flowers attaining a fruit set proportion of 0.37 when hand cross-pollinated, compared to 0.17 when open pollinated (see Chapter 2). In the present study, open pollinated flowers attained a fruit set proportion of 0.33, which is higher than that found for open pollinated flowers in previous experiments (see Chapter 2: Year 1, 2005 = 0.10; Year 3, 2007 = 0.17). From these results it would appear that open pollinated hawthorn flowers in hedges in the present study were less pollen limited than open pollinated hawthorn flowers in hedges in Years 1 and 3. This either reflects greater fruit set in the present study, or the methods used to calculate fruit set in Years 1 (2005) and 3 (2007) i.e. subsampling groups of buds, are not directly comparable with the method used in Year 2 (2006) i.e. whole hedge fruit set calculated using flower estimates obtained from a simulation model. I would argue that the fruit set data are not comparable and hawthorn flowers in hedges in this study are also likely to be pollen limited, as for hawthorn flowers studied in other locations. The relationship between solitary bee abundance and fruit set supports this, because hawthorn fruit set is higher on hedges where solitary bees are most abundant and lower where they are infrequent, presumably due to inadequate pollen delivery. There are limitations to using the subsampling method because it involves sampling a relatively small proportion of the flower/fruit population, but it could also be argued that there are limitations to calculating fruit set from the number of flowers on hedges as estimated using a simulation model. Also, the flowering duration of an individual hawthorn flower used in the simulation model was calculated from hedges in a subsequent year, rather than from hedges in the current study. The assumption was that the flowering duration would be similar across years, although this is not necessarily true. Whilst it would have been preferable to count each bud before anthesis on all hedges this was impractical, and the subsampling and simulation model methods were deemed suitable alternatives. For similar studies in the future I would recommend a scaled-up subsampling method. For example, the number of hawthorn buds present in 1m x hedge height sections could be counted before anthesis at 5m intervals along each transect.

Reasons for a neutral effect of winter oilseed rape on insect activity and hawthorn fruit set may be complex. Hawthorn flowers are not specialised, possessing a similar, open structure to those of oilseed rape. Both flowers are attractive to a range of generalist pollinators and therefore the oilseed rape flowers may not have been more attractive except in terms of abundance and the scale of the reward. The scale of this reward may be of relevance because oilseed rape was already at peak flowering when hawthorn started to flower and was moving into the declining stage of flowering, finishing at approximately the same time as hawthorn, if not slightly earlier. Consequently, the nectar flow may have been low and it may not have been a strong competitor with the flowers in the hedge. Despite this, insects were observed foraging on the winter oilseed rape in good numbers (Table 5.3), although social bees were more frequent on oilseed rape flowers and solitary bees were more frequent on hawthorn flowers. Unfortunately, it was not possible to compare statistically the activity of insects foraging on winter oilseed rape and adjacent hawthorn flowers because oilseed rape flower density was not recorded. Without statistical comparison of insect activity data from the crop and hedge, it is unclear whether solitary bees showed a significant preference for hawthorn flowers over oilseed rape flowers, or constancy to hawthorn (floral constancy has been observed in some solitary bee species to varying degrees, see Gross, 1992; Ne’eman, 2006), which might have helped explain the lack of a crop effect on solitary bee activity and hawthorn fruit set. Another consideration is the isolation distance between hawthorn hedges next to ‘grass’ and winter oilseed rape fields in the study. Oilseed rape provides an attractive source of nectar and pollen at the landscape scale, and since fields of oilseed rape were unavoidably close to hedges adjacent to ‘grass’ at both sites (within 500m at Rothamsted and within 300m at Loddington), mobile pollinators attracted initially by the oilseed rape may have been able to use the hedges of hawthorn equally, regardless of the immediate crop type. The abundance of workers of some bumblebees species foraging in field margins or experimental plots later in the season has been found to be positively related to the proportion of land in mass-flowering crops such as oilseed rape (Westphal et al., 2003; Herrmann et al., 2007) as a consequence of improved colony growth (Hermmann et al., 2007), which indicates a landscape scale effect of mass-flowering crops. Roy et al. (2003) observed that bees were more abundant on flowers in oilseed rape field margins than flowers in beet or maize field margins, and it is unclear whether this was due to local facilitative effects of the oilseed rape in individual fields, or whether the facilitative effects on pollinator visitation were operating at the landscape scale according to the proportion of different crop types grown. Bjerknes et al. (2007) suggest that co-flowering species could have positive effects on pollination by providing a food resource that increases overall pollinator densities in the landscape. My study did not consider this, but instead focused only one season, and did not take account of the presence of oilseed rape in the previous year, which may have boosted pollinator abundance.

Social bees were relatively infrequent visitors to hawthorn in this study, but honeybees are known to visit hawthorn (Guitián and Fuentes, 1992) and they were locally abundant on a hawthorn hedge in 2007, which was located approximately 20m from honeybee hives. Pollinators vary temporally and spatially (Fishbein and Venable 1996; Kandori, 2002; Ivey at al. 2003; Kudo and Kasagi, 2004) and in areas where they are more common, honeybees might be good pollinators of hawthorn flowers. Honeybees were present on the oilseed rape crop (Table 5.3), which raises the question of whether the oilseed rape competed with hawthorn at a landscape scale for honeybee visits. The oilseed rape may have attracted honeybees away from hawthorn flowers (irrespective of the immediate crop type), which might otherwise have resulted in greater hawthorn fruit set than from solitary bee pollination alone. Future work could involve testing this idea on a landscape scale, but it would require comparable hedges to be located in areas where winter oilseed rape is grown and where it is absent, which may be difficult to achieve in the UK.

Research on the effects of mass-flowering crops on bees has focused on bumblebees rather than honeybees or solitary bees, but it is thought that factors affecting solitary bee populations operate on a smaller, local scale. This is supported by evidence that they have shorter foraging ranges than social bees i.e. a few hundred metres (Gathmann and Tscharntke, 2002) and that solitary bee diversity is linked to the proportion of semi-natural habitats at small spatial scales i.e. 750m (Steffan-Dewenter et al., 2002). That solitary bee diversity and abundance are positively related to the proximity of semi-natural habitats has been documented in several studies (e.g. Steffan-Dewenter et al., 2002; Steffan-Dewenter, 2002; Albrecht et al., 2007; Williams and Kremen, 2007), and population sizes can be related to the availability of resources such as nest sites (Steffan-Dewenter and Schiele, 2008) and pollen and nectar (Williams and Kremen, 2007). The proximity to semi-natural habitats can also be important in terms of pollination service, and some plants have experienced reduced pollen deposition or seed production with increased distance from semi-natural habitats (e.g Steffan-Dewenter and Tscharntke, 1999; Klein et al., 2003a, 2003b; Kremen et al., 2004; Albrecht et al., 2007; Morandin and Winston, 2006). My conclusion is that factors in the local environment, such as nest site availability and forage within a few hundred metres of the hedges were probably more influential on the local abundance of solitary bees and hawthorn fruit set than the presence of oilseed rape.

Theoretically, plants with an abundant display of fruits should have an advantage over plants with smaller displays and should attract more birds (Snow, 1971; McKey, 1975; Howe and Estabrook, 1977; Pyke et al., 1977), as it is advantageous for birds to minimise time and therefore energy expenditure searching for fruits. Results for ‘migratory thrushes’ supports the hypothesis that large displays of fruits attract more birds since there was a significantly positive relationship between ‘migratory thrushes’ and the size of the haw crop, suggesting that these birds showed a preference for hedges with more haws. Similar relationships between bird abundance and the temporal and spatial availability of fruits have been found in other studies (Levey, 1988; Loiselle and Blake, 1991, 1993; Kinnaird et al., 1996; Moegenburg and Levey, 2003; Saracco et al., 2004; Telleria and Pérez-Tris, 2007; Telleria et al., 2008), and also for thrushes (Rey, 1995; Kwit et al., 2004; Jordano, 1993). There was not a statistically significant relationship between haw abundance and blackbirds, robins, blue tits or the combined ‘thrushes’ group. Other studies have also demonstrated interspecific differences between birds and their ability to track fruit resources (Rey, 1995; Telleria et al., 2008).

Redwings and fieldfares (or ‘migratory thrushes’) are gregarious and often travel together and feed in flocks. The ‘migratory thrushes’ group appeared to conform to the ‘ideal free distribution’ (Fretwell and Lucas, 1970), as discussed in Chapter 4, their abundance correlating positively with haw abundance in the hedges. By feeding in flocks birds are able to locate new areas of food as a result of social learning and an increased chance of encountering food when they are in large numbers (Krebs et al., 1972; Krebs, 1973; Giraldeau, 1984). Communal roosts are also a place where birds can learn the location of food patches according to the ‘information-centre hypothesis’ (Ward and Zahavi, 1973).

Redwings and fieldfares (or ‘migratory thrushes’) are gregarious and often travel together and feed in flocks. Birds that flock together have an advantage because they can find new patches of food more easily (Krebs et al., 1972; Krebs, 1973; Giraldeau, 1984), and to avoid intraspecific competition they should also benefit from feeding in large patches of fruit. These reasons could explain why they were often found in hedges with the best fruit resource. The observation that some birds preferred hedges with more haws did not necessarily mean that birds were consuming the fruits, but studies have shown that some large fruit crops tend to have more fruits removed from them than small fruit crops (Davidar and Morton, 1986; Sallabanks, 1993; Garcia et al., 2001; Ortiz-Pulido and Rico-Gray, 2000, Ortiz-Pulido et al., 2007), suggesting they do offer a good food resource. Haw abundance was variable enough between hedges to detect a positive increase in ‘migratory thrushes’ as the size of the haw crop increased, but future work could involve artificially manipulating the number of fruits on a hedge to look for relationships between fruit crops of different sizes and the abundance of frugivorous birds (e.g. Moegenburg and Levey, 2003). Future work on British hedges could also examine the temporal aspect of frugivory and competition for fruits, particularly since large numbers of migratory redwings and fieldfares arrive in October, which may exert competition for fruits on resident birds.

Overall, the presence of oilseed rape did not obviously affect the abundance of pollinators on hawthorn negatively or positively, and consequent quantity of hawthorn fruit available to birds in this study. It is important to note that fruit availability is also largely influenced by hedge management such as cutting regimes (Sparks and Martin, 1999; Croxton and Sparks, 2002), which affect the number of flowers on hedges before pollination has even taken place. Provided hedges are managed sensitively, my results suggest that hawthorn fruit availability is likely to be linked to the abundance of solitary bees on farmland, which are already documented as good pollinators of commercial fruit crops (Kuhn and Ambrose, 1984; Vicens and Bosch, 2000a; Javorek et al., 2002; Bosch et al., 2006; Gardner and Ascher, 2006). Hawthorn was shown to be pollen limited in a sample of British hedges (Chapter 2), which suggests there is scope for increasing the number of haws in hedges through an improved pollination service. If solitary bees are good pollinators of hawthorn, safeguarding their habitats by creating patches of bare ground for ground-nesting solitary bees such as *Andrena* (Gregory and Wright, 2005) and artificial nests for cavity-nesting solitary bees such as *Osmia* (Gaston et al., 2005) in close proximity to hedges, and by providing ‘pollen and nectar’ flower strips along field margins (Carvell et al., 2007) could be worth exploring as a way to ensure an abundant haw crop for birds.

6. General Discussion

6.1. Review of results

This project has shown that the flowers of fruit-bearing hedgerow plants attract a range of insects, providing them with pollen and nectar. It has also demonstrated that for some of these hedgerow plants, these insect visits are necessary for increased pollination and fruit set, and consequently help ensure a supply of food for frugivorous farmland birds. The results here are linked to the Objectives laid out in Chapter 1 (page 17; section 1.4).

6.1.1. Requirement of hedgerow plants for insect pollination

There was mixed evidence in the literature on the mode of reproduction and the requirement for insect pollination of some of the plants I studied (see Table 1.2, pages 24-26, and Chapter 2) and these were investigated further (Objective 1). Chapter 2 revealed that hawthorn, blackthorn and ivy all benefit from flower visits from insects in order to set fruit, showing reduced fruit set when flower-visiting insects were excluded by bagging flowers for the duration of flowering. Exposing flowers to insects for half the time had little effect on fruit set. There was little effect of excluding flower-visiting insects on the fruit set of individual plants of bramble and dog rose that were studied, but both dog rose (Graham and Primavesi, 1993) and bramble (Edees and Newton, 1988) are taxonomically complex and may exhibit variable modes of reproduction, ranging in self-fertility and the degree to which they require insect pollinators for fruit set. The number of seeds produced in multi-seeded fruits such as dog rose, bramble and ivy are probably also a consequence of levels of pollination. This is less important for single-seeded fruits of blackthorn and hawthorn, but for multi-seeded fruits, fruit architecture may be affected by the number of seeds, and future work could investigate this further. Twenty years prior to my study, Yeboah Gyan and Woodell (1987b) investigated blackthorn, hawthorn, bramble and dog rose pollination in the UK. Since then insect populations have shown declines (Benton et al., 2002; Biesmeijer et al., 2006; Shortall et al., in press), which may have affected current levels of pollination of hedgerow flowers. The fruit production of blackthorn and hawthorn on the hedges in this study was shown to be pollen limited, which is a common phenomenon among flowering plants (Burd, 1994; Ashman et al., 2004; Knight, T. M. et al., 2005), and if typical of hedges across the UK suggests that the hedgerow fruit yields could be greater with improved pollination. The evidence was more complicated for ivy. It did not appear to be pollen limited in the bagging study in Chapter 2, although only terminal inflorescences not lateral inflorescences were used in this study. This contrasts with the findings of Chapter 3 where wasp visits were significantly correlated with the fruit set of all inflorescences (on the same hedges), suggesting pollen limitation is occurring in some places.

6.1.2. Pollination effectiveness of flower-visiting insects

Objective 2 was to examine which insect groups had the greatest value for pollinating fruit-bearing hedgerow plants. This was assessed for blackthorn, hawthorn and ivy since they all were shown to have a requirement for insect pollination (Chapter 2). Blackthorn fruit set was not related to the activity of any insect group, yet when pollination value parameters were measured, bumblebees, bristly flies and solitary bees showed the greatest potential for pollinating blackthorn flowers on the study hedges. The relative abundance of different insect groups foraging on blackthorn flowers was highly variable between hedges, suggesting that the contribution of a particular insect group to blackthorn pollination may vary according to their local density (Chapter 4). I propose two explanations for the lack of a relationship between insect activity and fruit set. Firstly, it may have been that any relationship was obscured because overall there was very low (insufficient) pollen delivery due to low pollinator densities (affecting the 'quantity' component of pollination). Blackthorn produces abundant flowers, a strategy that may ensure a good supply of ovaries in case of loss of fruitlets through inadequate pollination for example (Stephenson, 1979; Ehrlén, 1991; Guitián, 1993), and pollinator densities per flower and the proportion of flowers setting fruit was generally low. Secondly, blackthorn also reproduces vegetatively, which may affect the 'quality' component of pollination, i.e. insect visits may be adequate, but if the pollen delivered to flowers by insects has originated from flowers on a single clone then geitonogamy (pollination between flowers on the same plant) could result in limited fruit set (e.g. Hessing, 1988; de Jong et al., 1993; Honnay et al., 2006). Hawthorn set some fruit in the absence of insect visits. For hedges in this study, fruit set was correlated with solitary bee activity, suggesting that these are excellent pollinators of hawthorn (Chapter 5; Figure 5.3). Ollerton et al. (2007) hypothesised that ivy flowers were 'functionally specialized' for wasp pollination. The results from Chapter 3 agree with this idea, since wasps made more contact with the reproductive organs of the flower, carried thousands of pollen grains on their bodies, visited flowers in rapid succession, and their activity was positively related to the proportion of ivy flowers that set fruit (Chapter 3, Figure 3.4) as noted earlier. These hedgerow plant species, all of which are native to the UK, and the flower visitors that pollinate are well synchronised in time; as expected for such mutualistic relationships: blackthorn flowering coincides with a time when bumblebee queens and solitary bees are emerging from hibernation and require pollen and nectar to build nests, hawthorn flowering overlaps with solitary bee populations, and ivy flowers at the end of the season, when insects are preparing for hibernation and wasp colonies are producing sexuals (Spradbery, 1973) and are actively seeking nectar.

6.1.3. Effect of hedge aspect on blackthorn pollination and fruit set

Hedge aspect (or the amount of solar radiation reaching a hedge) was hypothesised to have a modifying effect on the activity of flower-visiting insects and hence the pollination and fruit set of hedgerow fruits (Objective 3). There was evidence of greater solitary bee activity on blackthorn flowers on warm hedges, but the activity of other insect groups was similar irrespective of hedge aspect. There was little evidence of a relationship between insect abundance and blackthorn fruit set (Chapter 4). The activity of the majority of insects responded positively to flower density. Insect activity was frequently influenced by the site, with more bumblebees and solitary bees on blackthorn in hedges at Rothamsted and local farms compared to hedges at Loddington. The majority of bumblebees observed collecting pollen and nectar were queens. Blackthorn is one of the earliest plants to flower and is likely to be a good forage resource for nest-founding bumblebee queens and solitary bee females who have emerged from hibernation. The differences in bumblebee and solitary bee densities on blackthorn hedges may be due to landscape factors, such as the slightly higher proportion of land in semi-natural habitats at Rothamsted, where four out of eight ‘Rothamsted’ hedges were located (21% in Year 1, 2004-2005), compared to Loddington (11% in Year 1, 2004-

2005), which may provide more habitats for bumblebees. Alternatively, hedges at Rothamsted were situated close to urban areas compared to Loddington farm, which is situated away from urban areas. Gardens may provide good habitats for bumblebees when compared to an intensive agricultural landscape. For example, gardens are known to be important nesting sites of bumblebees (Osborne et al., 2008b). Bumblebee populations are also known to be positively influenced by the proportion of mass-flowering crops in a landscape (Westphal et al., 2003; Herrmann et al., 2007), and there may have been a greater proportion of mass-flowering crops at Rothamsted in the previous year compared to Loddington, but this was not investigated further. Bristly flies were observed at higher densities on hedges at Loddington compared to hedges at Rothamsted and local farms. This may be due to the greater proportion of pasture at Loddington (12% in Year 1, 2004-2005) compared to Rothamsted, which only had a small amount of winter pasture, and consequent habitat availability for bristly flies associated with dung (Skidmore, 1978). In terms of the proportion of blackthorn flowers that set fruit, it appeared that ‘warm’ hedges showed greater fruit set, but this was only apparent at Loddington and could largely be attributed to high fruit set on one hedge. My conclusion is that factors other than hedge aspect are likely to be more important in determining blackthorn fruit set, and these will be discussed later.

6.1.4. Effect of adjacent crop type on hawthorn pollination and fruit set

It was also hypothesised that the presence of a mass-flowering crop such as winter oilseed rape, which is an attractive pollen and nectar source for a range of insects, would influence the abundance of insects visiting hedgerow flowers and subsequent hedgerow fruit set, when compared to flowers in hedges next to a cereal crop, pasture or set aside (Objective 4). This could either be through competition for pollinators (e.g. Chittka and Schürkens, 2001; Brown et al., 2002; Muňoz and Cavieres, 2008; Moragues and Traveset, 2005), or facilitation of pollination by attracting pollinators into the field and onto hawthorn flowers in the hedge (e.g. Moragues and Traveset, 2005; Laverty, 1992; Johnson et al., 2003; Ghazoul, 2006), but the study revealed a neutral effect of adjacent crop type on hawthorn (Chapter 5). Insect activity responded positively to flower density as with the blackthorn study, but their activity was generally similar irrespective of the adjacent crop type. The only group of insects that showed differences between adjacent crop types in relation to hawthorn flower density were bristly flies. For bristly fly visits at least, the interactions between their visits to hawthorn flowers and the presence of oilseed rape ranged along a continuum from facilitation to competition according to plant [or flower] abundance (as proposed by Rathcke, 1983). At hedges with low hawthorn flower densities the effect of winter oilseed rape appeared to facilitate visits to hawthorn flowers, whilst at hedges with high hawthorn flower densities, the effect of winter oilseed rape appeared to be competitive, with fewer bristly fly visits to hawthorn flowers per hedge than in hedges of the same hawthorn flower densities that were next to grass (Chapter 5, Figure 5.2). However, there was no correlation between bristly fly visits and fruit set, and the proportion of hawthorn flowers that set fruit was similar between hedges regardless of adjacent crop type. Proportion of fruit set was positively related to the activity of large solitary bees, whose populations may be more closely tied to the proportion of semi-natural habitats and the proximity of nest sites and floral resources, particularly at small spatial scales (Steffan-Dewenter et al., 2001; 2002; Steffan-Dewenter, 2002, Albrecht et al., 2007; Williams and Kremen, 2007; Steffan-Dewenter and Schiele, 2008).

6.1.5. Fruit and bird abundance in hedges

Objective 5 was to examine relationships between fruit and bird abundance in hedges. Relationships were apparent for some bird species, in particular the larger thrushes. It was not possible to assess whether birds were consuming fruits, but it was possible to comment on whether hedges with high fruit yields were more attractive as a habitat to frugivorous birds than those with lower fruit yields. Numbers of fieldfares, song thrushes and blackbirds, combined as a group, showed a positive relationship with the abundance of sloes, and the total abundance of all fruits in hedges (Chapter 4, Figure 4.8). Numbers of migratory thrushes (redwings and fieldfares) also showed a positive relationship with the abundance of haws in hedges (Chapter 5, Figure 5.4). These data imply either that these birds can assess the fruit resource to visit patches that are most profitable, or they stay for longer in large patches. Relationships between the abundance of fruits and frugivorous birds have been documented by other researchers (Levey, 1988; Loiselle and Blake, 1991, 1993; Rey, 1995; Kinnaird et al., 1996; Moegenburg and Levey, 2003; Kwit et al., 2004; Saracco et al., 2004; Telleria and Pérez-Tris, 2007; Telleria et al., 2008). The relationship between migratory thrushes (redwings and fieldfares) and fruits is perhaps unsurprising: they are gregarious birds and are often seen together, they have a close association with hedgerow fruits since they migrate to the UK to overwinter in farmland where they can take advantage of these fruits, or feed on invertebrates in open fields when the weather is mild (Simms, 1978).

Fruits have evolved to offer birds a food reward and in turn birds disseminate their seeds (Snow, 1971; McKey, 1975). Although hedges are planted by humans, there may be some regeneration of hedgerows via the dispersal of seeds by frugivores (Sarlöv-Herlin, 2001). Birds select fruits according to several criteria (reviewed in Chapter 1), but feeding experiments by Sorensen (1984) revealed that blackbirds preferred autumn fruits that were more easily digested over any other fruit characteristic because they could consume greater quantities of these over time. Sorensen (1984) showed that the preferred seeds were ones that were regurgitated (hawthorn, blackthorn and ivy) and had a short passage time, compared to defecated seeds (elder, bramble and dog rose), which had a long passage time. It may be coincidental that the three regurgitated fruits with a quick passage time are insect pollinated and the seeds with a long passage time are self-pollinated, or it could imply co-evolution between pollinators, birds and fruits to optimise plant gene flow. For example, elder, bramble and dog rose fruits are likely to have limited gene flow from pollination, since these plants readily set fruits through self-pollination (Chapter 2). Hawthorn, blackthorn and ivy flowers require cross-pollination, predominantly through insect visits, to set fruit (Chapter 2) resulting in high gene flow in comparison to self-pollinated fruits. The restricted gene flow of self-pollinated elder, bramble and dog rose fruits may be compensated for by the long passage time in a bird’s gut resulting in fruits (and hence genes) being dispersed further in the landscape. Equally, the high gene flow resulting from the cross-pollination of hawthorn, blackthorn and ivy flowers may be negated by the short passage time of their seeds in a bird’s gut, which must result in only short distance seed dispersal and gene flow.

The results of this project have highlighted the links between hedgerow flowers, pollinating insects, fruits and birds. The flowering succession of some fruit-bearing hedgerow plants is well synchronised with the flight activity of their pollinators. For example, blackthorn flowers in March when bumblebee queens and solitary bees are emerging from hibernation and require pollen and nectar to found their colonies; hawthorn flowers in May when *Andrenid* solitary bees reach peak activity; and ivy flowers late from August to November when wasp colonies are producing males and queens (Spradbery, 1973) and may have extra demand for food. A relationship was found between the size of the blackthorn and hawthorn fruit crop and the abundance of frugivorous birds in hedges, in particular the migratory thrushes (redwings and fieldfares). This suggests that hedges bearing an abundant supply of fruits provide an attractive habitat for these birds, probably due to the presence of a food resource.

6.2. Comments on the study design

Ideally some of the studies would have involved greater sample sizes i.e. more hedges or groups of buds, and greater sampling intensity of flower-visiting insects. For the blackthorn study (Chapter 4) in particular this could have helped establish whether sampling limitations or biological factors were behind the absence of a relationship between insect activity and blackthorn fruit set, but the sample sizes were deemed reasonable for the time and labour available. In the same blackthorn study, some hedges chosen earlier in the year could not be used since it became apparent during the blackthorn flowering period that they had insufficient flowers for experiments to be done. It required experience to determine which hedges were likely to produce flowers, and this was gained in Year 1 and was used for selecting hedges for experiments in subsequent years. Some hedges were also accidentally cut during the bird and fruit survey period and had to be removed from the analysis, reducing the available degrees of freedom for testing the effects of some factors that may have been of interest e.g.

aspect and site (although it was still possible to test for main effects i.e. the relationship between fruits and birds). There are also limitations to monitoring plants and insects over single years (Chapter 4 and Chapter 5), and over a limited number of sites (i.e. two sites: Rothamsted and local farms, and Loddington), since pollinator communities and hence the extent to which they affect seed set may vary temporally and spatially (e.g. Aigner, 2004; Larson and Barrett, 1999; Dudash and Fenster, 1997), meaning it is difficult to make generalisations. When possible, methods were developed over the years to improve data collection. For example, statistical power analysis using data from experiments where groups of buds were marked to determine fruit set in Year 1 was used to calculate sample sizes for subsequent experiments in Year 3. For the hawthorn study in Year 2 (Chapter 5), a better method than the one used in the blackthorn study in Year 1 for assessing flower density was developed (Chapter 4), and the sampling intensity of flower visitors to hawthorn was increased.

6.3. Directions for future research

6.3.1. Effect of pollination on fruit characteristics

Using a set of pollination treatments, this project has established that insect visitors are required for the fruit set of a range of fruit-bearing hedgerow plants (Chapter 2). Some of the fruits from these experiments were harvested with the intention of exploring the effects of the pollination treatments (e.g. complete and partial exclusion of pollinators, and supplemental cross-pollination) on fruit characteristics of the multi-seeded fruits bramble, dog rose and ivy, such as pulp to seed ratio, which may be of importance to birds when choosing fruits (Howe and Vande Kerchove, 1979; Herrera, 1981;

Moermond and Denslow, 1983; Sallabanks, 1993). Unfortunately there was no time available, but this could be considered in future experiments, to assess whether the pollination environment could affect the *quality* of fruit available to birds.

6.3.2. Further exploration of plant-pollinator interactions

In this project, assessments have been made of which groups of insects might have the greatest pollination value for blackthorn, hawthorn and ivy. To some extent this assessment is limited to plants in the hedges in this project, since the relative abundance of pollinators and hence their overall effectiveness as pollinators could vary spatially and temporally. For example, hawthorn fruit set was shown to be positively related to the density of large solitary bees (Chapter 5), yet honeybees could also have been good pollinators of hawthorn but were rarely observed on the hedges in that study. Perhaps in areas where honeybees are abundant they do contribute to hawthorn fruit set. There was no time to measure the same pollination value parameters that were measured for blackthorn and ivy, so future research could investigate this further to determine whether colonies of honeybees on farmland could also ensure hawthorn fruit availability. Plant-pollinator interactions in the UK are also changing over time, for example there is now a localised association of the solitary bee *Colletes hederae* Schmidt & Westrich and ivy along the South coast of England. This bee is new to the UK, has a monolectic pollen diet of ivy flowers (Cross, 2002) and can be found nesting in dense aggregations under stands of ivy (S. Roberts, pers. comm.). As far as I am aware, no assessment has yet been made of its pollination value to ivy flowers in the UK or elsewhere, or its potentially competitive interaction with wasps, which are ‘functionally specialised’ pollinators of ivy (Chapter 3; Ollerton et al., 2007).

It has not been possible to conclusively establish whether it is pollen ‘quantity’ i.e. the frequency of flower visits from insects, or pollen ‘quality’ i.e. the origin of pollen on the bodies of flower-visiting insects, or both, that is currently limiting fruit set in blackthorn. The next step would be to examine blackthorn present in hedges using genetic analysis to determine whether clonal populations exist within hedges, which could be leading to geitonogamy (pollination between flowers on the same plant) and low fruit set. If possible, this technique could also be used to establish the paternity of seed within the mature fruits (which can only be a consequence of cross-pollination) and pollen on the bodies of insects foraging on blackthorn flowers to explore pollen movement around the landscape and whether localised pollinator activity or the distance between blackthorn plants could also be restricting fruit set. Molecular techniques have been used by other researchers to determine reproductive success and mating patterns in populations of plants that may be restricted by clonal reproduction (e.g. Eriksson and Bremer, 1993; Honnay et al., 2006; Araki et al., 2007; Llaurens et al., 2008). If clonal populations are restricting the availability of blackthorn fruits then it could be argued that birds would benefit if the vegetative spread of blackthorn in hedges was controlled, and if the blackthorn planted in hedges was genetically diverse.

In order to determine the pollination requirements of hedgerow plants, bagging experiments were designed to exclude insects from flowers, and surveys of insect activity over the flowering period showed that for some plant species, variations in insect activity related to variations in fruit set. Further experimentation could be done to examine the relationship between insect flower visits and fruit set by attempting to augment pollinator populations in the surrounding area, e.g. by placing honeybee hives near hedges (see Fries and Stark, 1983; Stern, 2001), or by providing solitary bees with nesting habitats such as artificial nests or areas of bare ground (e.g. Gregory and Wright, 2005; Gaston et al., 2005). This could also be scaled up into investigating landscape effects on the pollination and fruit set of hedgerow plants e.g. whether a high proportion of semi-natural environments in a landscape has a positive effect on hedgerow fruit set. This suggestion arises out of the conclusion that it could be the availability of habitats for solitary bees that determine hawthorn fruit availability. The effects of landscape structure on the pollination and fruit set of hedgerow flowers could vary according to which group of insects are the main pollinators. Positive relationships have been observed between landscape complexity or the proportion of semi-natural habitats and solitary bee abundance and diversity, particularly at small spatial scales (Steffan-Dewenter et al., 2001; Steffan-Dewenter, 2002; Steffan-Dewenter and Schiele, 2008). Honeybees and bumblebees respond to factors in the landscape at a much larger scale than solitary bees, with higher honeybee densities on experimental flowering plots in areas where the landscape has fewer semi-natural habitats, perhaps because this represents the only available forage source (Steffan-Dewenter et al., 2001; 2002), and higher bumblebee densities with increasing proportions of mass-flowering crops in the landscape (Westphal et al., 2003; Herrmann et al., 2007). Steffan-Dewenter et al. (2001) were unable to detect whether the proportion of semi-natural habitats had positive effects on the seed set of wild plants. They suggested this was due to increased seed predation with increasing landscape complexity counteracting any positive effects on seed set, the fact that the pollinators respond differently to landscape structure at varying spatial scales, and that pollinator foraging behaviour changes with increasing landscape complexity. If landscape effects on the pollination and fruit set of hedgerow plants were to be tested, it would be interesting to compare pollinator densities and hedgerow fruit set on farms with a high proportion of land in agri-environment schemes that benefit pollinators to those without. Albrecht et al. (2007) did a similar, field- and landscape-scale experiment in Switzerland on herbaceous plants and found that pollinator visitation and seed set of some plants was greater in meadows that were managed within agri-environment schemes compared to intensively managed meadows. In general, this positive effect declined with increasing distance from extensively managed meadows. I have also hypothesised that the proximity of farmland to urban gardens could affect bumblebee densities on blackthorn. Therefore a study could be done examining pollinator densities and fruit set of blackthorn in hedges on farmland near to urban areas compared to hedges on farmland that is isolated from urban areas.

6.4. The future for the pollination of hedgerow flowers and fruit availability for birds

It is unknown whether fruit abundance may be limiting frugivorous farmland bird populations in the UK over the winter. Migratory thrush populations are affected by the variable weather in breeding areas and are hunted in areas of Europe (Milwright, 2002a; 2000b), which may be exerting more pressure on populations of redwings and fieldfares than fruit availability. However, winter food availability is important for the survival of granivorous birds over the winter (Siriwardena et al., 2007; 2008) and the importance of fruits for assisting fat deposits has been highlighted by (Berthold 1976; 1996). A study by Swann (1980) of the weights of fieldfares and blackbirds, suggested that the depletion i.e. reduced availability of a fruit supply was linked to fieldfares losing weight or dying. In the same study the condition of blackbirds was buffered against this by their catholic food choices and ability to eat food provided by humans in gardens such as raisins, cheese, bread and fat, which fieldfares did not possess. Taking these factors into account, it would seem prudent to provide a plentiful winter supply of fruits for frugivores such as fieldfares and redwings, which this project suggests can be achieved through improved pollination services by insects.

Recent agricultural practice in the UK has resulted in declines of insects, including pollinators (reviewed in Chapter 1), some of which have been identified in this thesis as having a role in the pollination of fruit-bearing hedgerow plants. For example, bees are probably important pollinators of blackthorn and hawthorn, and yet their diversity in Britain has been declining over the last 30 years (Biesmeijer et al. 2006). Bristly flies (e.g. Calliphoridae, Bibionidae) may also be fairly good pollinators of blackthorn and possibly hawthorn, but there is evidence that the abundance in Southern Britain has decreased significantly over the last 30 years or so (Shortall et al. in press). Wasps appeared to be effective pollinators of ivy in hedges in my study, but declines have been recorded in *V. germanica* from the late 1970s to early 1980s (Archer, 2001) and in *Vespid* wasps from 1973 to 2002 (Shortall et al. in press). If pollinators continue to suffer declines then the worst case scenario is that fewer hedgerow flowers would set fruit, affecting the fruit supply for birds, and perhaps ultimately the survival of birds through the British winter.

In terms of hedgerow management, the outlook for the availability of hedgerow fruits is improving. Despite extensive hedgerow loss since the 1970s (Barr et al., 1981; 1986), by the 1990s hedgerow removal had slowed, with no difference in the extent of hedges from 1990 to 1998 (Haines-Young et al., 2000). Although hedgerow loss has undoubtedly affected habitats available to wildlife, the way current hedges are managed can be just as important. If possible, hedges should not be cut post-harvest, before birds have eaten the fruits (Sparks and Robinson, 1999) and this is now prohibited in the UK. They should not be trimmed too frequently (i.e. annually) because this can substantially reduce fruit availability of most fruit-bearing plants (Maudsley et al., 2000; Sparks and Martin, 1999; Croxton and Sparks, 2002) and biennial late winter cutting in February is preferable (Maudsley et al., 2000). Sparks and Martin (1999) estimated that in 1997, the hawthorn yield available to birds in British hedgerows may have been 20,000 tonnes, but if these hedges were managed with the aim of optimising fruit production, the yield could have been 1.5 million tonnes. Of course, this did not take account of the services provided by pollinators and what could be achieved if the pollination service increased. The importance of hedges to wildlife is now recognised by the UK Government, and this is reflected in Defra's 2005 Environmental Stewardship Scheme. There are various hedgerow management options for farmers, which may be helpful for improving existing hedgerow habitats for both pollinators and birds. These include maintaining the height of hedges, cutting the hedge no more than once every two years, avoiding cutting in the bird-breeding season and rotational cutting i.e. only cutting a portion of the hedges at one time (Defra, 2005).

To remedy negative environmental effects of the initial CAP policy of intensification, CAP reforms introduced the idea of agri-environment schemes and the encouragement of farming in a more environmentally sustainable way (Lloyd, 2000). Agenda 2000 resulted in 'cross compliance' where amongst other measures, farmers were required to maintain hedges in order to receive subsidies (Harris, 2000) and set-aside (land taken out of agricultural production) was introduced to help reduce agricultural surpluses. In 2005, set aside covered 559,000ha (Defra Statistics, 2005). Defra's 2005 Environmental Stewardship Scheme has provided farmers with options for set aside land and the creation of wildlife habitats (Defra 2005; Defra and the RPA, 2006). Several of these options have positive benefits for pollinators by providing pollen and nectar e.g. natural regeneration (Kells et al., 2001; Pywell et al., 2005); wildflower, and pollen and nectar mixes (Pywell et al., 2005; Carvell et al., 2006b, 2007); and the wild bird seed mixture for birds, since the flowering of plants such as kale, *Brassica oleracea*, provide forage (Parish and Sotherton, 2004). All of these measures should increase the area of semi-natural habitats in the landscape. Isolation of plants from semi-natural habitats is known to negatively affect pollinator diversity, abundance, visitation rate and plant reproductive success (Steffan-Dewenter and Tscharntke, 1999; Steffan-Dewenter, 2002; Steffan-Dewenter et al., 2002; Klein et al., 2003a, 2003b; Kremen et al., 2004; Kleijn and van Langevelde, 2006; Morandin and Winston, 2006; Albrecht et al., 2007; Williams and Kremen, 2007; Ricketts et al., 2008), and this effect can become apparent at short distances from semi-natural habitats (Kohler et al., 2008). This suggests that increasing the heterogeneity of agricultural areas at small spatial scales i.e. within a few hundred metres, should be encouraged to support pollinators and safeguard the ecosystem service they provide. However, in 2007 set-aside was suspended by the European Union due to concern over food shortages, and it is now permissible to turn set-aside land over to crop production. This is likely to reduce the availability of semi-natural habitats for pollinators and other farmland wildlife, possibly with detrimental consequences for ecosystem services such as pollination and the availability of hedgerow fruits. Hedges may become even more important as wildlife habitats or refuges.

This PhD project has developed the understanding of links between hedgerow flowers, pollinating insects, fruits and birds. It has shown that some hedgerow plants depend on insect pollination, and that different groups of insects are differentially effective at pollination and boosting fruit availability. It also highlights the need to manage agricultural land to support pollinator populations in order to secure a fruit supply for frugivorous birds from late summer, through winter and into spring.

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Appendix A. Testing meshes for the passage of airborne pollen and their effectiveness as barriers to flower-visiting insects

A.1. Methods

The amount of airborne pollen passing through muslin, nylon and tulle bags was assessed using sticky slides to trap pollen inside bags at a hedge of flowering blackthorn at Loddington farm (Leicestershire, UK, SK805026) in Year 2. For each treatment a block of florist's foam (oasis) was placed on top of a bamboo cane and four slides coated in petroleum jelly were pushed into it to trap pollen from all directions. A wire cage was constructed around this and a muslin, nylon or tulle bag was placed over the top and secured with a twist tie and insulating tape. A 5cm x 10cm yellow insect sticky trap was also placed in each bag to check whether pollinating insects were able to pass through the mesh bag (although without blackthorn flowers inside the bag they may not have been attracted inside) (Plate A.1 bagged slides and Plate A.2 open slides). Three groups, each comprising bamboo canes with sticky slide treatments inside one muslin bag, one nylon bag, one tulle bag and one unbagged (as a control), were positioned close to the hedge at regular intervals along its length. After five days, the slides were collected and taken to the laboratory for pollen grain counts. The experiment was not repeated on any other of the remaining plant species due to time constraints, but it was assumed that the permeability of the bags to pollen would be similar if not greater since the pollen grains are of a similar size to blackthorn or smaller: blackthorn = 43µm, hawthorn = 37µm, ivy = 30µm, dog rose = 24µm, bramble = 26µm (Kirk, 1994).

Each slide was prepared for pollen grain counts by placing a cover slip on the slide, using a few drops of Gelvatol as a mountant. The number of blackthorn pollen grains in each of six evenly spaced traverses of the slide was counted using a grid eyepiece graticule, under a microscope objective magnification of x 40 and an eyepiece magnification of x 10. The mean number of pollen grains was calculated for each treatment.

The effectiveness of muslin and tulle as barriers to flower-visiting insects was also tested again in Year 3 using flowers on blackthorn hedges that were used for experiments listed in Chapter 2. At each hedge in the study, a muslin bag and an additional tulle bag (each containing an 8cm x 5cm yellow insect sticky trap) were placed over flowers. At the end of flowering, the number of insects on the sticky trap was counted.

Plate A.1 Bagged slides

Plate A.2 Open slides

A.2. Results

Table A.1 shows the mean number of pollen grains per treatment that were caught by the sticky slides, and the number of insects trapped on the insect sticky traps within the bags. The tulle bag allowed approximately 40% of the airborne pollen grains through when compared with the open control, whereas muslin allowed approximately 3% and nylon allowed approximately 5% of the number of pollen grains through. Virtually no insects entered the bags. Table A.2 shows the number of insects caught on yellow insect sticky traps that were inside bags containing blackthorn flowers. Very few insects were caught on the sticky traps and they were all very small (<2mm).

Table A.1 Mean number of pollen grains per treatment, at three locations along a hedge of blackthorn at Loddington, Leicestershire, UK

Treatment	Average number of pollen grains	Insects on sticky traps
open (control)	877	n/a
tulle (1.2 mm mesh)	341	1 thrip
nylon (0.7mm mesh)	51	0
muslin (0.5mm mesh)	26	0

Table A.2 Number of insects on 8cm x 5cm sticky traps inside mesh bags on blackthorn hedges

Field	Grid reference	Insects on yellow sticky trap inside muslin bag	Insects on yellow sticky trap inside tulle bag
Black Horse	TL105134	3 small aphids (1mm)	2 small wasps (2mm), 1 thrip, 1 pollen beetle
Annables I	TL102147	0	0
Annables II	TL100143	0	4 small wasps (2mm), 2 thrips
Cooters End	TL125156	0	0
Little Hoos	TL124140	0	1 thrip
Great Harpenden	TL124138	0	0

A.3. Discussion

The bags did impede the passage of airborne pollen to some extent, and of these tulle allowed the highest number of pollen grains through. All bags were very effective at excluding all but the smallest of insect visitors, and the number of these trapped within the bags was very low. The conclusion is that the bags are pollinating insect-proof, but the contribution of wind pollination to fruit set may be underestimated. It is impossible to exclude insects completely without using bags and the tulle bag was the most practical and reliable way of testing for fruit set in the absence of insects.

Appendix B. Timing of pollen presentation for blackthorn and ivy

B.1. Methods

Flowers of blackthorn and ivy were randomly selected and the anthers wiped with sticky tape to determine if the anthers were dehiscing. This was repeated on several flowers throughout the day from dawn until dusk for blackthorn, and over a 24 hour period for ivy (because ivy flowers are known to be visited by nocturnal insects).

B.2. Results

Blackthorn anthers presented pollen continuously from dawn (0620h) until dusk (1950h) (Table B.1). Ivy anthers presented pollen continuously for 24 hours (Table B.2).

Table B.1 Results of experiments on blackthorn on 22/04/05 to determine timing of pollen presentation

Time	Evidence of the presence of pollen grains from the anthers of 20 flowers wiped with sticky tape (yes/no)
0620h	yes
0750h	yes
0920h	yes
1050h	yes
1220h	yes
1350h	yes
1520h	yes
1650h	yes
1820h	yes
1950h	yes

Table B.2 Results of experiments on ivy on 25/09/07 to determine timing of pollen presentation

Time	Evidence of the presence of pollen grains from the anthers of flowers on 10 inflorescences wiped with sticky tape (yes/no)
0600h	yes
0730h	yes
0900h	yes
1030h	yes
1200h	yes
1330h	yes
1500h	yes
1630h	yes
1800h	yes
1930h	yes
2100	yes
2230	yes
2400	yes
0300	yes

Appendix C

Table C.1 Location and attributes of hedges containing dog rose where insect exclusion experiments were done, with sample sizes (Chapter 2, Year 1, 2005)

Site	Hedge id.	Grid reference	Aspect	Warm/cool	Adjacent crop type	No. of bagged inflorescences (approx. 3 buds per inflorescence)	No. of open inflorescences (approx. 3 buds per inflorescence)
Rothamsted	1. Thrales End C	TL123168	WNW	warm	cereal	10	10
	2. Annables D	TL098154	SW	warm	WOSR	9	9
	3. Little Hoos	TL123137	WNW	warm	WOSR	8	8
Loddington	1. Paradise	SK799019	WNW	warm	WOSR	10	10

Table C.2 Location and attributes of hedges containing bramble where insect exclusion experiments were done, with sample sizes (Chapter 2, Year 1, 2005)

Site	Hedge id.	Grid reference	Aspect	Warm/cool	Adjacent crop type	No. of bagged inflorescences (unknown no. buds per inflorescence)	No. of open inflorescences (unknown no. buds per inflorescence)
Rothamsted	1. Thrales End C	TL123168	WNW	warm	cereal	10	10
	2. Great Knott	TL118135	WNW	warm	cereal	9	9
	3. Annables D	TL098154	SW	warm	WOSR	9	9
Loddington	1. 44 Acre	SK798016	SSW	warm	cereal	8	8
	2. Bottom Collie W	SK805026	SSW	warm	WOSR	5	5
	3. Paradise	SK799019	WNW	warm	WOSR	10	10

Table C.3 Location and attributes of hedges where pollen limitation in blackthorn, and the effects of manipulating the exposure of blackthorn flowers to pollinators on fruit set was studied, with sample sizes (Chapter 2, Year 3, 2007). The uneven number of experimental units per hedge reflects an uneven distribution of blackthorn in bud across hedges

Site	Hedge id.	Grid reference	Aspect	Warm/cool	Adjacent crop type	No. of groups of buds per treatment (approx. 30 buds per group)				
						M100	T100	T50	OP	XP
Rothamsted	1. Annables I	TL102147	WSW/SW	warm	cereal	10	10	10	10	10
	2. Annables II	TL100143	WNW	warm	cereal	9	9	9	9	9
	3. Black Horse	TL105134	SE	warm	pasture	9	9	9	9	9
	4. Cooters End	TL125156	SW	warm	field beans (not in flower)	8	8	8	8	8
	5. Little Hoos	TL124140	SW	warm	cereal + setaside grassland (few flowers)	5	5	5	5	5
	6. Great Harpenden	TL124138	SE	warm	field beans (not in flower)	9	9	9	9	9

Table C.4 Location and attributes of hedges where pollen limitation in hawthorn, and the effects of manipulating the exposure of hawthorn flowers to pollinators on fruit set was studied, with sample sizes (Chapter 2, Year 3, 2007)

Site	Hedge id.	Grid reference	Aspect	Warm/cool	Adjacent crop type	No. of inflorescences per treatment (approx. 15 buds per inflorescence)				
						M100	T100	T50	OP	XP
Rothamsted	1. Annables	TL103144	SW	warm	setaside grassland (few flowers)	11	11	11	11	11
	2. Thrales End	TL123168	WNW	warm	cereal	11	11	11	11	11
	3. Black Horse	TL109131	SSW	warm	cereal	11	11	11	11	11
	4. Horse Paddock	TL119162	SW	warm	cereal	11	11	11	11	11
	5. Fiddlers Hill	TL114164	NW	cool	cereal	11	11	11	11	11
	6. Little Hoos	TL124140	SW	warm	cereal + setaside grassland (few flowers)	11	11	11	11	11

Table C.5 Location and attributes of hedges where pollen limitation in ivy, and the effects of manipulating the exposure of ivy flowers to pollinators on fruit set was studied, with sample sizes (Chapter 2, Year 3, 2007)

Site	Hedge id.	Grid reference	Aspect	Warm/cool	Adjacent crop type	No. of inflorescences per treatment (approx. 30 buds per inflorescence)				
						M100	T100	T50	OP	XP
Rothamsted	1. Great Knott II	TL116139	ESE	cool	Bare field or crop at seedling stage	6	6	6	6	6
	2. Little Hoos II	TL124139	NW	cool	Bare field or crop at seedling stage	6	6	6	6	6
	3. Black Horse	TL104132	SE	warm	Bare field or crop at seedling stage	6	6	6	6	6