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Pollinator effectiveness and fruit set in common ivy, *Hedera helix* (Araliaceae)

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Abstract Flowers of common ivy (*Hedera helix* L.) provide late season pollen and nectar for several insect groups, and its fruits are a winter and spring food source for frugivorous birds. Ivy benefits from insect pollination in order to set fruit, but it is unknown which flower-visiting insects are the most effective pollinators. Our observations suggest that *Vespula* wasps are potentially the most effective pollinators since they were frequent visitors, had relatively fast foraging rates, carried large numbers of pollen grains on their bodies and had the highest 'Pollination potential PP index' score (a measure of pollinator effectiveness) of all the insect groups examined. There was also a positive linear relationship between the proportion of ivy flowers that set fruit and wasp foraging activity in 0.5 m^2 quadrats. Visits by *Vespula* wasps may therefore be important for ensuring a supply of ivy fruits for birds.

Keywords Fruit set · Pollination · Pollinator effectiveness · *Vespula* · Wasps · Hedgerow

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Introduction

Ivy (*Hedera helix* L.) is a native climbing plant, common in UK hedges, which flowers unusually late in the year between September and November. The open flowers 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 Aculeata (bees and wasps), Diptera (true flies), and Lepidoptera (moths and butterflies; Knuth 1908; Free 1970; Ferrazzi 1988; Dirlbeck 1990; Proctor et al. 1996; Cross 2002; Metcalfe 2005; Vezza et al. 2006; Ollerton et al. 2007). 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 (Jacobs et al. 2009). Its flowers attract several insect taxa, which may vary in their contribution to pollination (as found in studies of other plants e.g. 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 number of pollen grains 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; Vázquez et al. 2005). Insects also carry different quantities of pollen on their bodies (Jennersten 1984; Yeboah Gyan and Woodell 1987; 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 1987; Herrera 1989; Vicens and Bosch 2000; Monzón et al. 2004) and vary in the amount of contact they make with the stigma of a flower (Vicens and Bosch 2000; Monzón et al. 2004; Stout 2007). These parameters have been used to investigate the 'potential' 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). Conversely, Vázquez et al. (2005) analysed data from several studies and concluded that visitation frequency may be more important than effectiveness on a per visit basis, with frequent visitors making the greatest contribution to pollination. In terms of per visit effectiveness, 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 1987; Thomson and Goodell 2001). Nevertheless, here we take a combined approach: indirect measurement of the pollination potential of flower visitors will be coupled with direct measurement of the frequency of their visits to flowers and the proportion of flowers that set fruit. The direct measurement approach is to determine whether relationships exist between pollinator visitation and fruit set (which has been demonstrated in some plants, e.g. Montalvo and Ackerman 1986; Klein et al. 2003), and will help provide an overall assessment of their contribution to ivy fruit production.

Materials and methods

Observations of insects visiting ivy and ivy fruit set were made in 2005 and 2007 in hedges on the Rothamsted Research farm and neighbouring areas of Hertfordshire, UK (51°48.9N, 0°21.5W, Ordnance Survey grid ref TL1314). Most flower visitors were assignable to five groups, which differed substantially in characteristics of morphology and behaviour that are likely to affect pollination. They thus approximated pollinator functional groups for our study system (e.g. Fenster et al. 2004). These were: bumblebees, honeybees, wasps, bristly flies (mainly calyptrate diptera) and large hoverflies (Table 1).

Relative abundance of insect groups foraging on ivy flowers

Observations of insect activity in 2–4 0.5 m^2 quadrats of flowering ivy in six hedges were made in 2005 and 2007 (Table 2) to examine relationships between insect visits and fruit set. The number and diversity of foraging insects visiting the quadrats were recorded. Quadrats were spaced at least 5 m apart and at heights between 0.5 and 1.7 m according to the presence of ivy in the hedge. Insect activity on each quadrat was monitored in two 10 min periods (morning and afternoon) twice weekly. We hypothesized that this would provide sufficient representation of flower visitation rates throughout the ivy flowering period. The number of flowers were counted in each quadrat on the same days that insect observations took place. Recording continued until over 90% of the flowers were without petals. Relative abundance of flower visitors was measured as the number of 'patch arrivals' in 10 min for each group. An 'arrival' was defined as an insect

Table 1 Groups of insects observed foraging on ivy flowers, and examples of the species, genera and families

Insect group	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 (Syrphidae)	
(a) Large >1 cm 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.)
(b) Small <1 cm or thin bodied	*Melanostoma* spp.
	Sphaerophoria scripta (L.)
	Syritta pipiens (L.)

Table 2 Location of 0.5 m² quadrats of flowering ivy on hedges, attributes, and weather conditions during insect activity observation

Year	Hedge id.	Hedge grid reference	Hedge aspect	Solar radiation (MJm⁻²)	Number of quadrats on hedge	Mean flower density per quadrat	Flower density ranges per quadrat	Date range of observations	Temperature range (°C)	Relative humidity range (%)	Cloud cover range (%)	Wind speed range (Beaufort Scale)
2005	1. Osier	TL109129	N	7.895	4	2,219	1,312–3,329	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	2,058	1,221–2,894					
	3. Little Hoos I	TL123137	WNW	4.185	3	3,737	3,079–4,163					
2007	4. Great Knott II	TL116139	ESE	10.463	3	2,164	1,691–2,568	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	3,466	3,110–3,650					
	6. Black Horse	TL104132	SE	10.370	3	4,062	3,523–4,708					

entering the quadrat, landing on a flower and commencing foraging. Pooled data from these observations were used to calculate the proportion of visits attributable to each insect group.

Flower visitation rates

Flower visitation rate data were collected for the insect groups most frequently found foraging on ivy (number of individuals observed: bumblebees = 11, honeybees = 20, wasps = 19, large hoverflies = 21, bristly flies = 20). These were used to assess the ability of insects to transfer pollen between flowers and umbels in a unit of time, which is relevant to the pollination effectiveness of the individual. Observations of insects visiting patches of ivy in full flower were made at Rothamsted farm at three locations (grid references: TL104132, TL124139 and TL134139), between 13th September 2007 and 5th October 2007 under the following weather conditions: temperature 13.1–22.2°C, relative humidity 41–92%, wind speed 1–3 (Beaufort Scale), cloud cover 10–80%. For a group of insects, we tried to observe a similar number of individuals at each of the three locations to control for any differences between patches that might influence foraging activity. The number of flowers each insect visited was recorded for up to 20 visits or 2 min, depending on which came first. 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.

Pollen carried on the bodies of insects

Twelve individuals from each of the main groups of flower-visiting insects were collected from patches of ivy in full flower at Rothamsted farm (Ordnance Survey grid references of patches TL134131, TL123137, TL124133). Bumblebees were 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. Insects for pollen analysis were collected from different patches of ivy to those where correlations between insect visits and fruit set were being explored (Table 2) to avoid depleting the local pollinator community. As with observations on insect visitation rates, a similar number of individuals from each insect group was 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 personal communication). 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 soaked in ethyl acetate, into the bag or tube. The insect samples were stored in a freezer at $-18°C$ until the pollen grains could be removed and counted.

Insects were placed in 50 ml 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 ~ 30 ml of 0.05% Triton X detergent solution (250 µl of Triton X in 500 ml distilled water). The Apex tubes were placed on a shaker and shaken at 250 rpm for 10 min 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 we considered that this was unlikely to be available for pollination.

The resulting pollen suspension was centrifuged at 14,000 rpm for 15 min. A double cavity slide was placed onto a hotplate and the pollen load was pipetted into one well of the slide (100 µl 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.

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 $40\times$; eyepiece magnification $10\times$). The grid lines of the counting graticule fitted the field of the microscope and allowed the majority of the total pollen load to be counted.

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 × flower

Table 3 Pollination potential (PP) index

PP index score = (PQN × PQL)/$\sum$(PQN × PQL for all insect groups)
where
PQN (pollinator quantity) = A × FVR
(A total no. arrivals to all quadrats over total sampling period, FVR mean flower visitation rate per minute)
PQL (pollinator quality) = mean number of pollen grains carried by insects on their bodies (instead of pollen grain deposition on stigmas since this was not recorded)

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 0–1) for each insect group observed at the patches of ivy in the study (Table 3). It is assumed that the closer the score is to 1, the greater the relative contribution of the insect group is to ivy pollination.

Ivy fruit set

Ivy fruit set was recorded on the same quadrats used to measure insect activity (Table 2). Before flowering, 20–30 umbels were selected at random and the average number of buds on an umbel 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 the records of Snow and Snow (1988) ivy fruit ripens from December to January, but the main bird feeding period does not start until January. We also observed that umbels of ivy fruits occasionally abscised later in the season, which may result in the fruits becoming available to ground-feeding animals. Fruit set was estimated by calculating the average number of fruits on 30 umbels selected at random 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 count of fruits set in the quadrat.

Hedges were selected according to the presence of flowering ivy, so there was no control for hedge aspect. To

account for any effects of solar radiation on insect activity and fruit set, solar radiation was measured using tube solarimeters (Delta-T, Cambridgeshire, UK) at each hedge on a sunny day in October, for incorporation into the statistical analysis. The solarimeters were placed on stands close to the hedge at a height of 1 m and readings were taken between sunrise ($\sim$0645 h) and sunset ($\sim$1920 h). 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.

Diurnal vs. nocturnal flower visitors

This study primarily investigated the role of diurnal flower-visiting insects in ivy pollination, but ivy flowers also receive nocturnal visits from moths (Knuth 1908). To assess the frequency 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 $\sim$1.5 m 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, although a few moth species do 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 (1850–0630 h). Filming was done under favourable conditions for moth activity: (temperature: 14.2–17.2°C, low wind speed of 1–2 on the Beaufort Scale, cloudy sky). To compare the number of nocturnal flower visitors with the number of diurnal flower visitors, two 10-min observations of insect activity on the quadrat were made in the morning and afternoon of the next day under the following weather conditions: temperature 16.5–18.0°C, wind speed 2 (Beaufort Scale), cloud cover 60–100%.

Statistical analysis

Pollen grain counts and flower visitation rates were compared among insect groups by ANOVA using GenStat (Payne et al. 2007), with log_e transformations where the assumptions of normality could be improved by the transformation. There was no blocking in the analyses and 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 total number of arrivals/10 min of different flower-visiting groups on ivy flowers in 2005 and 2007 were fitted using stepwise multiple regression (Payne et al. 2007). For each quadrat, a variable for 'patch arrivals' per flower was calculated. This was done by dividing the number of 'patch arrivals' from each insect group over the whole season by the number of flowers in the quadrat. This variable represents the pollination service received by flowers in each 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 for 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.

Results

Flower visitation rates

The groups of insects observed visiting quadrats of flowering ivy most frequently were wasps and bristly flies (Table 4). In general, flower visitation rates were recorded for the most frequent visitors to quadrats of ivy in farmland hedgerows. For example, for the hoverflies, only the behaviour of large hoverflies was observed because small hoverflies were relatively uncommon and from casual observation had low foraging rates and rarely touched the

Table 4 Relative abundance of insect groups visiting 0.5 m^2 patches of flowering ivy in 18 quadrats (measured by counting patch arrivals per 10 min and pooling data from all counts)

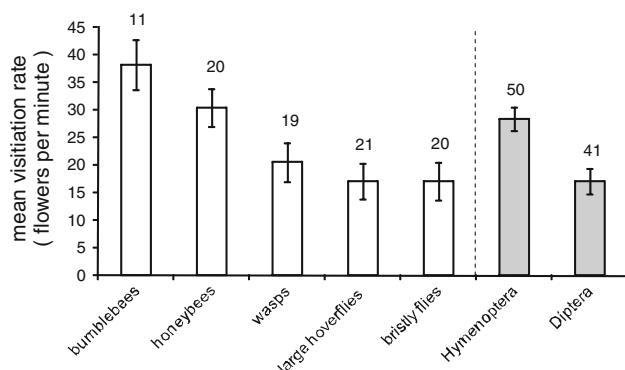| Insect group	Total number of visits over season	Proportion of visits (%)	Mean ± SE number of visits per quadrat
Wasps	1,435	54.67	79.72 ± 9.45
Bristly flies	881	33.56	48.94 ± 6.61
Large hoverflies >1 cm	140	5.33	7.78 ± 1.98
Small hoverflies <1 cm	68	2.59	3.78 ± 1.26
Honeybees	57	2.17	3.17 ± 0.58
Bumblebees	42	1.60	2.33 ± 0.60
Small solitary bees <1 cm	2	0.08	0.11 ± 0.08
Total insects	2,625	100	145.83 ± 15.59

stigma of the flower. Honeybees and bumblebees were infrequent visitors to the quadrats, but data on their behaviour 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 higher flower visitation rate than Diptera (large hoverflies and bristly flies; $F_{1.86} = 48.32$, $P < 0.001$, Fig. 1). Large hoverflies and bristly flies visited a similar number of flowers per minute ($F_{1.86} = 0$, $P = 0.992$, Fig. 1). Bees (bumblebees and honeybees) visited more flowers per minute than wasps ($F_{1.86} = 31.38$, $P < 0.001$, Fig. 1). Of the bees, bumblebees had a higher visitation rate to flowers than honeybees ($F_{1.86} = 7.28$, $P = 0.008$, Fig. 1).

Although not quantified specifically, further observations revealed that bristly flies, hoverflies and bees made less contact with the stigma than wasps when foraging. Bristly flies, hoverflies and bees possess long proboscises and were able to forage with their bodies held away from the stigma. The exception was bumblebees, which occasionally contacted stigmas with their metasoma 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.

Pollen carried on the bodies of insects

Hymenoptera (bumblebees, honeybees and wasps) carried more ivy pollen grains on their bodies than Diptera (large hoverflies and bristly flies; $F_{1.55} = 30.55$, $P < 0.001$, Fig. 2). Large hoverflies carried more pollen grains on their bodies than bristly flies ($F_{1.55} = 5.03$, $P = 0.029$, Fig. 2). There was no difference in pollen grain load between wasps and bees (bumblebees and honeybees; $F_{1.55} = 1.00$,

$P = 0.321$, Fig. 2), or between bumblebees and honeybees ($F_{1.55} = 1.79$, $P = 0.187$, Fig. 2).
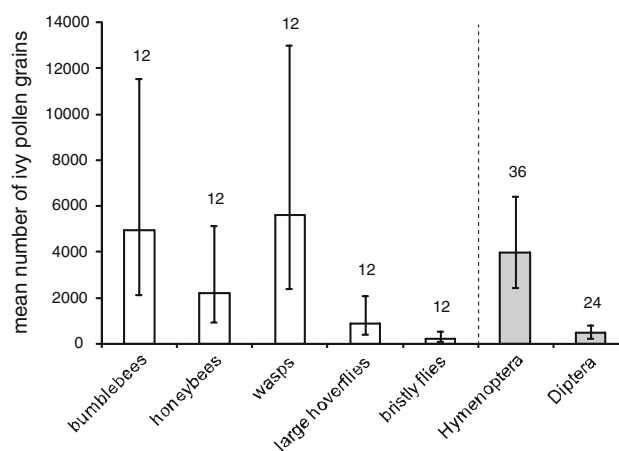
Pollination potential (PP) index

The majority of the insect groups had low PP index scores. The exception was wasps, which had a high score of 0.9 (Table 5).

Relationship between insect visits and fruit set

Stepwise multiple regression revealed a significantly positive relationship between the total number of wasp 'patch arrivals' per flower per 10 min and the proportion of flowers setting fruit ($\hat{y} = 0.083 + 2.216x$, $F_{1.16} = 5.03$, $P = 0.039$, $r^2\mathrm{adj} = 0.192$, Fig. 3). No other variables (bees, small hoverflies, large hoverflies, bristly flies, solar radiation, last day of flowering) were selected by the model as significantly relating to fruit set. Wasp arrivals explained only 19% of the variation in fruit set ($r^2\mathrm{adj} = 0.192$). The remaining 81% variation is difficult to explain as it could be due to factors unrelated to pollination, for example, hedge orientation and weather conditions. We do not have enough information on all the different factors to reach a useful conclusion. Relationships between insect activity and flower density were generally positive, although not statistically significant.

Diurnal vs. nocturnal flower visitors

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 20 min. Only three moths were observed in the

Fig. 1 Mean flower visitation rates of individual insects of a range of taxonomic groups visiting ivy flowers (± 95% confidence intervals). Values above columns = no. insects observed

Fig. 2 Mean number of ivy pollen grains carried on the bodies of insects visiting ivy flowers back-transformed from the log$_e$ scale (± 95% confidence intervals). Values above columns = no. insects sampled

Table 5 Pollination potential (PP) index scores for each group of insects visiting ivy flowers

Insect group	PQN (pollination quantity)		PQL (pollination quality)	PP (Pollination Potential) index score
	A (abundance)	FVR (flower visitation rate: flowers min^{-1})	PG (number of pollen grains on body)	
Honeybees	57	30.42	2,208	0.02
Bumblebees	42	38.24	4,964	0.04
Wasps	1,435	20.59	5,597	0.90
Large hoverflies >1 cm	140	17.11	889	0.01
Bristly flies	881	17.08	228	0.02

patch and they spent little time foraging on flowers: one moth remained still for 2 h 10 min from 2120 to 2330 h.
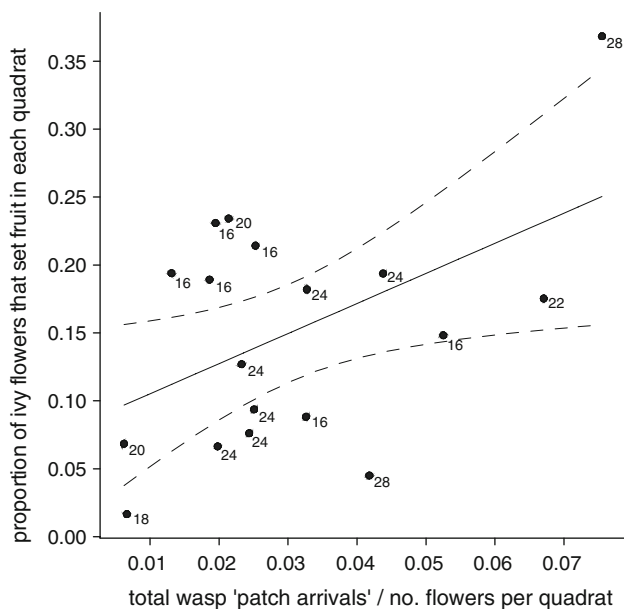
Discussion

Indirect assessments of the effectiveness of groups of flower visitors as pollinators of ivy showed that Hymenoptera (honeybees, bumblebees and wasps) carried more ivy pollen on their bodies than Diptera, and had faster visitation rates to flowers. Bumblebees, honeybees and wasps carried a similar amount of pollen on their bodies. Bees had higher flower visitation rates than wasps did, but wasps were abundant, carried large quantities of pollen

Fig. 3 Relationship between the proportion of ivy flowers that set mature fruit in 18 × 0.5 m² quadrats and the total number of wasp 'patch arrivals' per quadrat recorded over the flowering period (Sept to Nov)/no. flowers per quadrat. *Dotted lines* represent 95% upper and lower confidence limits for the mean response. Each data point is annotated to show the number of 10-min censuses each quadrat received

grains on their bodies, had relatively high flower visitation rates and were frequently observed making contact with the stigma during foraging. The frequency of wasp visits to flowers in quadrats also correlated with the proportion of ivy flowers that set fruit. The mean proportional fruit set per quadrat was generally low (0.15). This is in contrast to a study of ivy fruit set under different pollination scenarios, which found that mean proportional fruit set per umbel was high (0.45; Jacobs et al. 2009). The latter study only scored fruit set of terminal umbels to test pollination scenarios and since terminal umbels are the first to flower they may receive more insect visits and hence achieve greater fruit set. Here we include not only terminal umbels in our measure of fruit set but also lateral umbels, which may be more susceptible to pollen limitation.

Together, abundance and high visitation rates combined to make wasps the most important pollinators. Indeed their PP index score was much higher than any other group of flower visitors, and only visitation by wasps correlated with the reproductive success of ivy. These results support the hypothesis of Ollerton et al. (2007) 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. Ollerton et al. (2007) also observed that wasps were abundant on ivy and carried more pollen on their bodies than calliphorid flies and hoverflies.

Wasp workers 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 influencing their 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 (Collett 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 recruitment of colony members through the processes described above, their ability to remember where to find food, 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.

The relative abundance and hence effectiveness of pollinators can vary temporally and spatially (Fishbein and Venable 1996; Kandori 2002; Ivey et al. 2003; Kudo and Kasagi 2004). Whilst wasps are potentially the most valuable pollinators of ivy in hedges in this study, at other sites different flower visitors may assume greater importance for ivy pollination. Wasp visitation may be limited by the proximity of ivy flowers to a nest and the foraging range of wasps. For one Vespid wasp species, *Vespula pensylvanica* (de Saussure), foraging range has been recorded as within 2,000 ft (610 m) of the nest to a carbohydrate source for the majority of workers, but up to 3,293 ft (1.04 km) for some individuals (Akre et al. 1973). Translocation experiments showed workers could return to the nest from at least 1.4 miles (2.25 km; Akre et al. 1973) and if wasps are able to forage this far, they could be capable of long distance pollen transfer. We observed variation in pollinator communities between patches of ivy on farmland and one patch of ivy near gardens: wasps were frequent visitors to ivy on the Rothamsted farm but bumblebees were infrequent visitors. The reverse was true for ivy flowering in a residential area with bumblebees observed making frequent visits to ivy relative to wasps. 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 potential pollinator communities with the arrival of *Colletes hederae* Schmidt and Westrich, a solitary bee species new to the UK, which favours ivy flowers as a pollen source (Müller and Kuhlmann 2008). This species has been recorded along the South coast since 2001 (Cross 2002) and recent records show that it is colonising suitable areas inland (http://www.bwars.com/maps_bees.htm). In some locations there may be thousands of nests of *C. hederae* close to patches of ivy (S. Roberts personal communication), which may have

implications for pollination and fruit availability in these areas.

Compared to diurnal flower visitors, nocturnal visitors were only observed for one night and for one quadrat. It appeared that they probably contribute little to ivy pollination and fruit set at the location studied, but due to the small sample size, further experimentation is desirable. Visits from butterflies and moths were infrequently observed and nocturnal filming suggested that moths were fairly inactive foragers, especially in comparison to diurnal insects.

There is also scope for further investigation of whether pollinator activity affects not only the quantity 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 and suggested that smaller fruits containing fewer seeds would be the optimal food resource. As far as we are 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 Kerckhove 1980; Herrera 1981; Moermond and Denslow 1983; Sallabanks 1993).

This paper 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. Ivy flowers late in the year and may have evolved to benefit from wasp pollination since this is when the number of bees is diminishing, but it is the time when wasp colonies are producing males and queens (Spradbery 1973) and their requirements for nectar increase.

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