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Research Article

Distribution and abundance of the ivy bee, *Colletes hederae* Schmidt & Westrich, 1993, in Sussex, southern England

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Abstract

The solitary ivy bee *Colletes hederae* has recently naturally colonised the British Isles. It was first recorded in Britain in Dorset, near the south coast, in 2001. By 2021 it had reached Scotland and Ireland. It had spread to Sussex, some 100km east of Dorset by 2004, but occurred only locally. In autumn 2020, to determine the distribution and abundance of the ivy bee in Sussex, we made three surveys of 100 insects foraging on ivy flowers at 57 locations during the female flight period. We found the ivy bee at all 57. It was the second most abundant insect (22%), being outnumbered by social wasps (*Vespula* spp. 42%), but was more numerous than honey bees (*Apis mellifera* 14%). In autumn 2021 we made a further presence or absence survey at 17 additional locations, and the ivy bee was seen at each one. The results show that the ivy bee is now found throughout Sussex and is abundant. Comparisons of site characteristics showed no significant effect of urban versus rural locations on ivy bee relative abundance. It was, however, significantly more relatively abundant on Downland compared to Weald and Coastal Plain locations, and on chalk and sand derived soils compared to clay and alluvium derived soils. Possible reasons for the success of *C. hederae* in Britain are discussed.

Key words: Britain, solitary bee, colonisation, presence and absence, *Hedera helix*

Introduction

Discussions of the status of bees in recent years have tended to be rather depressing, with well documented declines in both the diversity and abundance of bee species in Britain, as in many other countries (Williams 1982; Biesmeijer et al. 2006). Several species have become extinct in Britain, including the short haired bumble bee *Bombus subterraneus* L., 1758, last seen in 1988 (Benton 2006). Ollerton et al. (2014) noted the extinction of 13 bee species since 1853. One of these, the solitary bee *Andrena vaga* Panzer, 1799, has subsequently been rediscovered but remains very rare. Attempts to reintroduce *B. subterraneus* were made between 2012 and 2016, although these appear to have been unsuccessful (Gammans 2020). The rate of extinction was greatest in the early to mid 20th century, and has declined since then, possibly because the most vulnerable species had already been lost (Ollerton et al. 2014).

It is often implied in the popular media that there are simple and universal explanations for all of these declines, but this ignores the fact that some bees, such as the six most common British bumble bee species, remain very common, with some expanding their ranges (Benton 2006). In addition, one bumble bee species new to Britain, the tree bumble bee (*Bombus hypnorum* L. 1758), first recorded in 2001 after naturally colonizing from Europe, is thriving. It was first found near Southampton near the south coast and has rapidly expanded its range, is now commonly found throughout most of Britain, and had spread to Ireland by 2017 (Falk and Lewington 2015; O'Donnell 2018; Hill 2021).

Another naturally-colonising bee species new to Britain is the solitary *Colletes hederae* Schmidt & Westrich, 1993, known as the ivy bee. It utilises ivy (*Hedera helix* L., 1753) as its main foraging resource and its nest building and provisioning period occurs during the flowering period of ivy (Hennessy et al. 2021b). The species is relatively new to science, being described in 1993 (Schmidt and Westrich 1993), having previously been confused with several similar species (Kuhlmann et al. 2007; Else and Edwards 2018). *Colletes hederae* is native to mainland Europe and is a member of the *Colletes succinctus* species group of plasterer bees, so called because they line their underground cells with saliva which hardens into a cellophane-like material that protects the cell contents (Benton 2017 p 61). In Britain there are two closely related species, the sea aster bee *Colletes halophilus* Verhoeff, P.M.F., 1944 and the heather bee *C. succinctus* L., 1758, which, like *C. hederae*, are on the wing in late summer and into autumn (Else and Edwards 2018) although not as late as *C. hederae* (Kuhlmann et al. 2007). Zenz et al. (2021) concluded that all species in the *C. succinctus* group are relatively recently-diverged species.

The ivy bee was first recorded in Britain in September 2001, at Worth Matravers, Dorset, a few km inland from the south coast (Cross 2002). The initial discovery was followed by others nearby, suggesting that the introduction had taken place some time before 2001 (Else and Edwards 2018). By 2016 it had been recorded in north Wales, Lancashire and northern Yorkshire. By autumn 2020, it had been recorded on the northwest coast of England at Skinburness, Cumbria, on the south shore of the Solway Firth, at the same latitude inland at Wetheral near Carlisle, Cumbria, and on the northeast coast at Whitburn near Sunderland, Tyne and Wear, approximately 450-500 km from the first Dorset record in less than 20 years (National Biodiversity Network Trust 2023b). Its colonization of the British Isles has continued, as in 2021 it was recorded in Scotland, near Dunbar by the coast (National Biodiversity Network Trust 2023b), and Ireland, near Wexford on the south east coast (National Biodiversity Centre, Ireland, 2021) where it had probably been present for several years and it is now found in coastal areas of Counties Wexford and Wicklow (Ratnieks et al. 2022). In 2022 it was first recorded in the Isle of Man (National Biodiversity Network Trust 2023b).

The Bees Wasps and Ants Recording Society has an active project collecting records of the ivy bee (McCulloch 2021)

The ivy bee was first recorded in Sussex, a county on the south coast of England approximately 100-200 km east of Dorset, in 2004 (Sussex Biodiversity Record Centre 2018). It is not known whether it reached Sussex by range expansion from Dorset, from separate or additional colonisations from continental Europe, or both. Dellicour et al. (2014) conclude that range expansion in Europe, including to Britain, has not been associated with a large reduction in genetic diversity, as would be expected if colonization were by only a few individuals, as might occur at a single location. Based on simulations, their data were better explained by relatively high migration rates. Similar conclusions have recently been drawn for the colonising bumble bee *B. hypnorum* (Brock et al. 2021). The samples of British ivy bees used by Dellicour et al. (2014) were from five locations in southern England, including Eastbourne, Sussex, which is within the area of the current study.

In 2012, surveys of 200 or 300 insects visiting ivy flowers at eight locations in pairs of urban and rural sites near four Sussex towns showed that the ivy bee was not universally present, being seen in only five of these locations, and it was not abundant (Garbuzov and Ratnieks 2014). Overall, the ivy bee represented only 3% of the insects on ivy flowers, compared to honey bees (*Apis mellifera* L., 1758, 21%), bumble bees (*Bombus* spp., 3%), social wasps (mainly *Vespula vulgaris* L. 1758, 13%), hover flies (Syrphidae, 27%), other flies (29%) and butterflies (4%) (Garbuzov and Ratnieks 2014). By contrast, a 2019 survey of insects on ivy flowers on the University of Sussex campus and the adjacent village of Falmer found that the ivy bee was by now at 26%, both much more numerous and the most numerous insect, being slightly more abundant than honey bees, 23% (Hennessy et al. 2021b).

In Sussex, female ivy bees predominantly forage on ivy flowers for pollen, which comprised approximately 98.5% of the pollen grains in the scopae of females returning to their nests at three study locations (Hennessy et al. 2021b). In addition, the flight period of ivy bees in Sussex is well synchronized with ivy bloom, with females only on the wing during this period (Hennessy et al. 2021b). The ivy bee is thus proving to be a successful colonist in Britain and a numerically significant new addition to the British bee and insect fauna. Indeed, given that the honey bee also predominantly forages on ivy flowers in the autumn (Garbuzov and Ratnieks 2014; Hennessy et al. 2021b), the ivy bee rivals the honey bee in absolute numbers in Sussex at that time of year.

Data collated by the Sussex Biodiversity Record Centre and the Bees, Wasps and Ants Recording Society show that the ivy bee has been recorded from many sites in Sussex (National Biodiversity Network Trust 2023b). However, these data have been collected over a number of years, and only show presence or lack of data, rather than abundance or absence. The aims of this

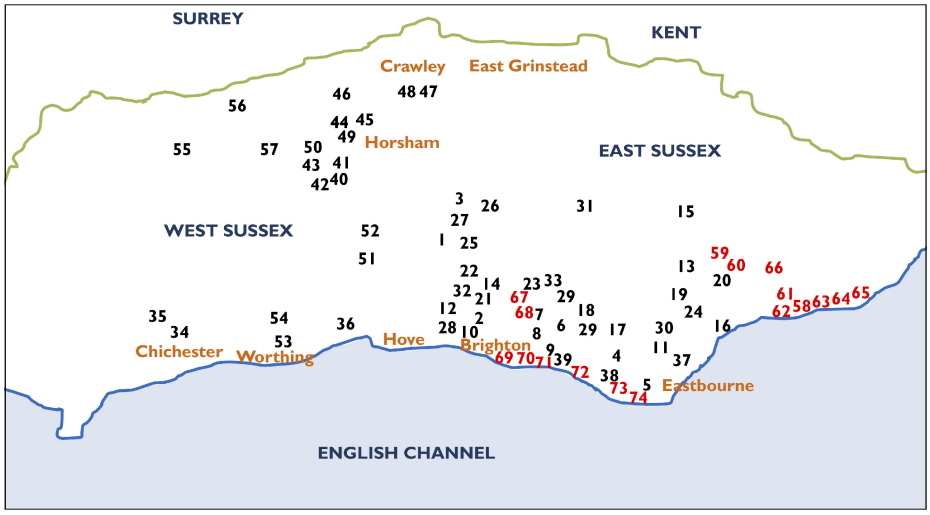

Figure 1. Locations of the 57 full survey study locations in 2020 (black) and 17 presence-absence study locations in 2021 (red) in East and West Sussex.

project, therefore, were to carry out a broad survey of the ivy bee in Sussex in order to determine how widespread and abundant the ivy bee is, and whether this showed any general pattern in relation to geographical, geological or land use features. To do this, we surveyed insects foraging on ivy flowers at 57 locations across Sussex in the autumn of 2020 using standardised methods. In addition, additional presence-absence data were gathered at 17 locations in 2021.

Materials and methods

Fifty-seven locations across Sussex were surveyed in order to cover a range of land use types including urban, suburban and rural, a range of key geological formations from the South Downs (chalk) to the Weald (heavy clays and sand), and coastal to inland sites, near sea level and at higher elevation on the South Downs (Figure 1; Supplementary material Table S1). Ivy is a woody climber, and at different sites its substrate varied, but overall included hedges, tree trunks, utility poles, garden and field edge walls, and the walls of buildings (Figure 2). The size of the survey location varied according to the density of the flowering ivy and abundance of insects. If necessary, the location was split into sub-locations up to a few hundred metres apart to include sufficient ivy flowers, but the sites were all small in relation to the likely foraging flight range of several hundred metres or more (Zurbuchen et al. 2010). The sites included some of the locations originally surveyed by Garbuzov and Ratnieks (2014).

These locations were surveyed on three occasions between the weeks beginning 21 September and 12 October 2020. The actual days chosen for observations were dependent on the weather. To ensure that foraging insects would be active, observations were made during suitable weather conditions (13–23 °C, wind < 5 Beaufort, usually fully or partly sunny). At each survey, 100 insects foraging on ivy flowers were recorded by walking

Figure 2. Typical substrates for flowering ivy surveyed in the study: a. gravestones; b. brick walls; c. domestic hedges; d. fallen trees (Photos: Norman Carreck).

slowly around the study area past the flowering ivy, identifying and recording insects in the following categories: male ivy bees; female ivy bees with visible pollen; female ivy bees without visible pollen; honey bees; bumble bees; other bees; social wasps; hover flies; other flies; butterflies; and other insects.

Although ivy bees are similar in size to honey bees, they are very distinctive in body colour and other features. Males are also noticeably different to females in appearance, having longer antennae and a smaller body. The closely-related species *Colletes halophilus* (sea aster bee) and *Colletes succinctus* (heather bee) have both also been recorded in Sussex, but there is no danger of misidentification. *Colletes halophilus* is rare, only recorded at three Sussex locations, all by the coast, the nearest of which was 3 km from one of our study locations (National Biodiversity Network Trust 2023a), but our data from this location were gathered in mid October, after the flight period of *C. halophilus* (Kuhlmann et al. 2007). *Colletes succinctus* is also little recorded in Sussex, with only two records within 2 km of two of our study locations (National Biodiversity Network Trust 2023c). However, the flight period of *C. succinctus* is somewhat earlier than for *C. halophilus* and does not overlap with our surveys of insects on ivy flowers. Our surveying

began at the earliest on 21 September, and at many locations a week later. The last record for *C. succinctus* in southeast England (n = 63 records in the counties of Sussex, Surrey, Kent, Hampshire and Dorset, National Biodiversity Network Trust 2023c) was 20 September.

To maximise the chances of observing ivy bees, the survey period included the periods of high and peak ivy bee foraging activity on ivy. In addition, sites 13, 14, 40 and 41 were sampled weekly, to cover almost the whole ivy flowering period, from 31 August to 22 November 2020 in order to provide a more complete and precise phenological picture.

In addition, in 2021 observations were made of ivy flowers at 17 additional locations in East Sussex (Figure 1; Table S1) from 10-14 October. The aim was simply to determine whether the ivy bee was present or not. Unlike in 2020, no attempt was made to quantify the number of ivy bees or to identify other insects. The observer (FLWR) located convenient patches of ivy in bloom. The patch was observed during very good or excellent weather conditions when numerous insects were foraging on the ivy flowers. The method was to observe up to 100 insects to determine whether any were ivy bees (present) or not (provisionally absent). In practice, however, many fewer insects were counted because a foraging ivy bee was always quickly seen. When an ivy bee was seen, no more insects were observed as the survey had done its job. The number of the first ivy bee seen in the sequence of insects was recorded.

Results

Presence and absence of the ivy bee

The ivy bee was observed on ivy flowers in all 57 study locations in East and West Sussex in 2020. The proportion of the insects observed foraging on ivy that were ivy bees varied considerably, however, from 54.6% at Loxwood (Site 56) down to 0.3% at Barnham (Site 34), with an overall mean of 22.0%. Other insects averaged: honey bees (*Apis mellifera,* 13.6%); bumble bees (*Bombus* spp., 0.5%); social wasps (*Vespula* spp., 41.9%); hover flies (Syrphidae, 9.7%); other flies (10.9%), butterflies (0.3%) and other insects (1.1%). Confirming its ubiquity in 2020, the ivy bee was swiftly detected in all 17 additional locations in East Sussex surveyed in 2021 (Table S2). The mean rank of detecting an ivy bee among the insects seen foraging on ivy flowers was 5.9 (range 1–14), indicating that it was abundant at all sites.

Effect of urban vs rural land use type

Sussex does not have large cities or heavy industry, and despite its proximity to London, ranges from surprisingly rural landscapes with a low human population to densely built up urban and suburban areas, especially the coastal conurbation of Worthing, Brighton and Hove, the coastal towns of

Eastbourne and Hastings, and the Horsham, Crawley, Haywards Heath area to the north. Dividing the 57 sites into "urban & suburban" (n = 22) versus "rural & village" (n = 35) shows that there was no difference in the abundance of the ivy bee between these two (mean and range 19.5%, 0.6–44.7%, and 23.6%, 0.3–51.2%, respectively; Mann-Whitney U = 336.5, P = 0.430).

Effects of region and soil type

Sussex has a varied geology, which affects both the natural flora and the physical characteristics of the resulting soils (Brandon 2003; 2022), which might, therefore, affect its suitability as a habitat for a ground nesting bee species such as *C. hederae*. The South Downs are a range of low hills running east to west composed of chalk, and reaching a maximum height of *c.* 250 m, producing light, well drained soils (Brandon 2022). To the north of these is an undulating area known as the Weald, consisting of a range of bands of several types of clay, which produce heavy, cold, poorly drained soils, but also, and in contrast, sandstones which produce light, sandy soils (Brandon 2003). Rivers flow from the north to south cutting through these strata producing valleys, and to the south of the downland is a coastal plain. Both of these areas have land at or slightly below sea level, with alluvial soils. The sites chosen for the study covered the range of these landscape types: Downland (21 sites), Weald (28) and Coastal Plain (8); and soil types: chalk (19 sites), clay (18), sand (9) and alluvium (11).

When the sites were divided into the three landscapes types, relative abundance of ivy bees was greatest in the Downland locations (mean 30.5%, range 13.7–50.3%) followed by Weald (mean 18.6%, range 0.6–51.2%) and Coastal Plain (mean 11.9%, range 0.3–34.7%) (Kruskal Wallis: H = 12.88, df = 2, P = 0.002).

Similarly, when the sites were divided into the four principal soil types, there was a significant trend that abundance of ivy bees was greatest in the locations with chalk-derived soils and lowest on clay or alluvial soils (Chalk: mean 31.2%, range 3.6–49.0%; Clay: mean 16.1%, range 0.6–32.9%; Sand: mean 25.2%, range 1.0–51.2%; and Alluvium: mean 13.3%, range 0.3–34.7%; Kruskal Wallis: H = 14.34, df = 3, P = 0.003).

Abundance over the flowering period of ivy

The mean proportion of insects that were ivy bee males, females carrying pollen, and females without pollen over the period of observations at the four sites that were observed weekly from September to November throughout the ivy flowering period are shown in Figure 3. Ivy bee males had already been observed foraging on other plants species, including various Asteraceae and great willowherb, *Epilobium hirsutum* L. 1753, for several weeks before the first ivy flowers were open (Figure 4a), so were very abundant at the start of ivy flowering, and declined steadily thereafter. Females appeared later and their relative abundance increased for several weeks and then too

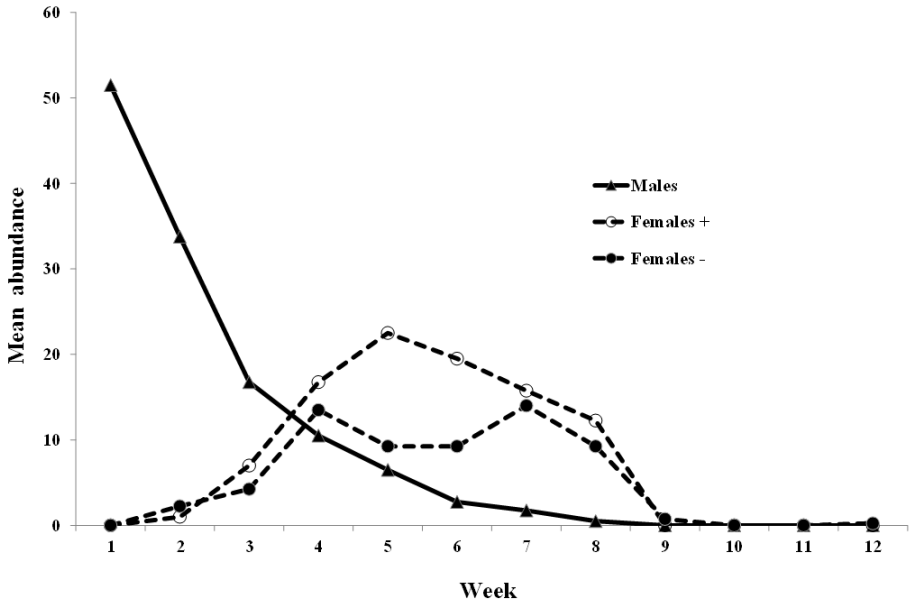

Figure 3. Mean proportion of insects foraging on ivy flowers that were ivy bee males, females with visible pollen on the scopa (+), and females without visible pollen (-), over twelve weeks of observations at sites 13, 14, 40 and 41 which were observed over the full period for female ivy bee activity from September to November 2020 (Week 1 is 31 August to 6 September).

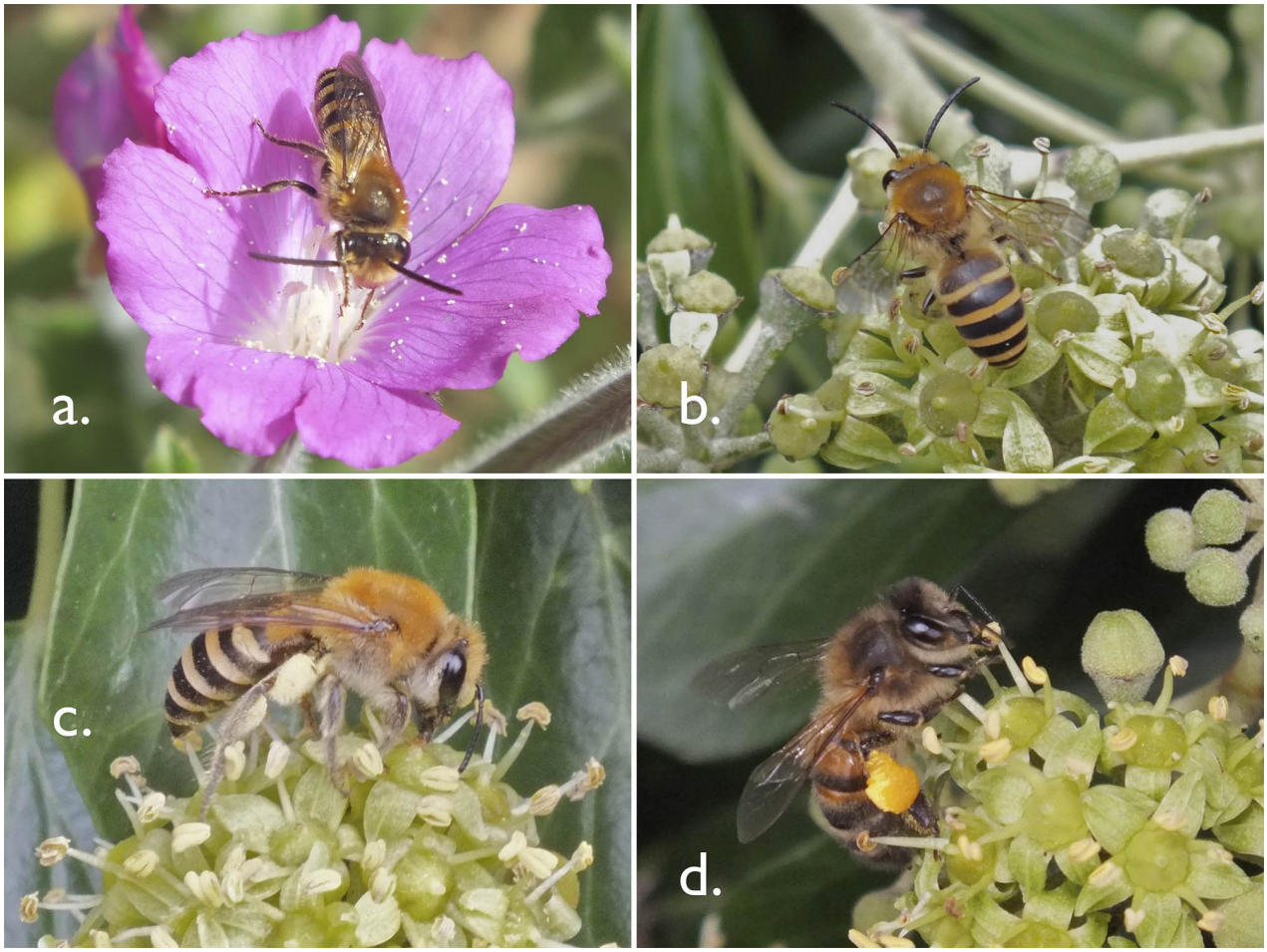

Figure 4. a. Male ivy bee foraging on great willowherb (*Epilobium hirsutum*) flowers prior to flowering of ivy. b. Male ivy bee foraging for nectar on early flowering ivy. c. Female ivy bee foraging for pollen on green phase ivy flowers. d. Honey bee foraging for pollen on green phase ivy flowers. As can be seen, male and female ivy bees are distinctive and can easily be distinguished from worker honey bees, which are of similar size to female ivy bees. Male ivy bees are smaller. Photos: Francis Ratnieks.

declined. By 2 November, no ivy bees were seen, although ivy was in flower for several weeks afterwards and was being visited by other insects, including honey bees, for both nectar and pollen.

Discussion

The results show that the ivy bee is now very well established in Sussex, being present in all 57 locations surveyed in 2020 which included 32 in the county of East Sussex and 25 in West Sussex and all 17 additional locations in East Sussex in 2021. In addition, the ivy bee was one of the three most numerous visitors to ivy flowers during its flight period at 22%, lower than *Vespula* sp. wasps at 42%, but higher than honey bees at 14%. This is in good agreement with the 2019 data from several sites in Sussex (Hennessy et al. 2021b), which found that ivy bees comprised 26% of visitors. Although insect populations fluctuate greatly from year to year, these overall means of the ivy bee as 26% and 22% of all insect visitors to ivy in 2019 and 2020 respectively, compared to 3% in 2012 (Garbuzov and Ratnieks 2014) seem to represent a genuine and substantial increase in abundance over eight years. In addition, the ivy bee was observed in all 57 sites visited in 2020, and the 17 visited in 2021, compared to only five of eight locations in 2012, suggesting that it has become universally distributed in Sussex wherever ivy is found. Ivy is almost ubiquitous in Sussex. Garbuzov and Ratnieks (2014) had previously found that ivy was present in six out of 10 0.2 km × 0.2 km quadrats in rural locations and 10 out of 10 urban locations surveyed in East Sussex.

The main aim of our study was to determine how widely distributed the ivy bee was in Sussex. This could potentially have been done in other ways, such as by using malaise or pan traps or by looking for nesting sites. However, as ivy bees, especially females, predominantly forage on ivy (Else and Edwards 2018), we concluded that a suitable and practical way was to observe insects foraging on it. In addition, given that in autumn honey bees also mainly forage on ivy in the study area this also gave us an opportunity to compare the abundance of the ivy bee relative to its main competitor, the honey bee, and other flower visiting insects.

Among the other insects, social wasps were present at all 57 sites and were frequently very numerous, ranging from a maximum of 93.1% at Tilgate Park (Site 48) to a minimum of 2.0% at Glynde (Site 29). The high abundance, plus the variability, probably represent the presence or absence of nearby nests, which may each contain as many as several thousand workers in the early autumn when colony populations are at a maximum (Spradbery 1973). Because we recorded 100 insects at each observation rather than attempting to obtain an absolute measure of abundance, ivy bees appear to be relatively less numerous at sites where there was a large wasp population (Table S1). There is, however, also a possibility that the presence of wasps deters ivy bees from foraging, either through competition

for nectar, or through direct predation. Further work to investigate the relationships between ivy bees, social wasps and other flower visitors to determine whether or not the presence of wasps deters ivy bees from foraging would be of interest.

One reason why the ivy bee has been so successful in Britain is presumably because its needs are simple and are met. It nests in habitats that are very common, such as areas of short grass and bare soil, flat or sloping, which is abundantly provided by road verges, gardens, lawns and pasture (Maher et al. 2019; Clark 2020, 2022). In addition, it forages on a superabundant resource at a time of year where there are relatively few other competing flower-visitors flying. The major exceptions to this are social wasps and the honey bee. In the autumn, certainly in the area around the University of Sussex, honey bees forage primarily on ivy, gathering approximately 90% of their pollen from ivy flowers at that time, although most individual worker bees are actually gathering nectar alone (Garbuzov and Ratnieks 2014; Hennessy et al. 2021b). Kirk and Howes (2012) point out that ivy forms the last important nectar source for honey bees before overwintering. In 2020, however, at only 16 out of 57 sites studied (28%) was the honey bee more numerous than the ivy bee. At most sites there were more ivy bees than honey bees, and at 9 sites (16%), no honey bees were seen at all. The local presence or absence of honey bees probably reflects the location of colonies managed by beekeepers, but recent work (Visick *personal communication*) indicates that there are many wild honey bee colonies living in old trees and buildings in Sussex.

The ivy bee is well suited to foraging on ivy in the study area, with its female flight period coinciding with and contained within the ivy flowering period, meaning that it has little need for other food sources. The climate of this part of southern England generally produces periods of fine autumn weather sufficient to enable it to make its nests and forage for food to provision them. Although the period when an individual ivy inflorescence produces pollen is relatively short, the flowers produce nectar over a longer period, passing from a green phase through a green/brown phase and then a brown phase, whilst still remaining attractive to insects (Vezza et al. 2006). In addition, whilst ivy in a sunny location may complete flowering and set fruit rapidly, plants in shady positions, often on the other side of the same hedge, will produce inflorescences long afterwards. This means that nectar and pollen are continuously available over a period of approximately three months, easily sufficient for the flight period of ivy bees, which, being univoltine (Dellicour et al. 2014), have a short flight period in contrast to colonial bumble bees which forage over a long period, multi-voltine solitary species, or the honey bee which can forage, flowers and weather permitting, all year round.

As a new arrival to Britain, the ivy bee is, by definition, an alien species. Goodenough (2010) has pointed out that the relationships between alien

and native species are complex, and are rarely entirely beneficial or entirely harmful. It is important to consider whether, on the one hand, the ivy bee is competing with other insects visiting ivy, or, on the other, whether it is beneficial through contributing to ivy pollination. One reason for the rapid expansion of an alien species in a new territory might be if the new species comes to occupy a vacant ecological niche, for example a habitat which has not yet been exploited as a nest site, or a food source that is unused. Clearly this is not the case with the ivy bee, since ivy is already visited by many insects during flowering. However, ivy is a very abundant and extensive resource, found in a variety of different environments throughout Britain and Ireland (Preston et al. 2002). Therefore, although ivy flowers are not a vacant niche, the niche is large and is almost certainly underutilized. This is demonstrated by further research in the study area during autumn 2021 which showed that approximately half the pollen and nectar produced by ivy flowers were uncollected by insects (Harris et al. 2023).

It is unknown how far the ivy bee flies between its forage sites and its nest sites. From the known ranges of solitary bees of its body size it has been suggested that it is likely to be less than a few hundred metres (Gathmann and Tscharntke 2002), but there are anecdotal reports that it may fly up to 0.5 km (Schmid-Egger et al. 1995), and Else and Edwards (2018) note that nesting aggregations may be a considerable distance from ivy sources, forcing the bees to fly long distances. The bee has certainly colonised Britain at a rate of *c.* 25–50 km per year, but there is no information about the dispersal range of young females. For the bee to be successful, it is therefore vital for suitable nest sites to be available close to areas of forage (Westrich 1996), in this case flowering ivy. Although in our project, deliberately searching for nest sites was not part of the protocol, it is nevertheless surprising that in view of the abundance and ubiquity of the ivy bees foraging on ivy, only one nest aggregation site was found by any of the observers during the study. This was at Magham Down (Site 13), on a roadside within the area surveyed. Ground nesting solitary bees often nest on south facing slopes without excessive vegetation, and in well drained soils (Edwards 1995; Benton 2017, p 59), and Ratnieks et al. (2022) found seven aggregations in an area of sand dunes in Co. Wexford, Ireland. In a citizen science study, however, Maher et al. (2019) found considerable variation in nest location; most ivy bee nest sites were sunny, either flat or sloping, and usually grass covered. A nest aggregation in a domestic garden in Falmer village has been observed for more than five years (Ratnieks, unpublished observations; Hennessy et al. 2020) and consistently hosts several thousand nest holes. It comprises an area of some 50 m^2 of rough domestic lawn on a gentle south west facing slope on a light chalk derived soil. Else and Edwards (2018) and Clark (2020) have described similar nesting situations in southern England. Given a suitable site, a single ivy bee female can provision up to 18 cells (Bischoff et al. 2005; Benton and

Fremlin 2018), and Clark (2022) estimated that a single female can produce 10 female offspring. This is many more than its close relative, the sea aster bee *C. halophilus* (Rooijakkers and Sommeijer 2009), giving it the ability to build up populations rapidly. The ivy bee is clearly successful at dispersing from a location, and in the process of colonisation there is likely to be natural selection for colonising ability, as has been observed in other exotic species such as the Africanised honey bee in America and the cane toad *Bufo marinus* Schneider, 1799 nin Australia (Ratnieks 1990; Shine et al. 2011).

Müller and Weibel (2020) observed that the ivy bee overwinters as a half grown larva rather than as a prepupa or imago, as is common in most ground nesting solitary bee species. They speculate that the waterproof cell lining protects any remaining food reserves from fungal attack and desiccation, meaning that the larva does not need to complete its growth before the onset of winter, allowing the bee to complete its active season very late in the year when a sudden drop in temperature might be expected. The waterproof cell lining, which is unique to the Colletidae (Torchio et al. 1988; Almeida 2008) is likely to mean that the ivy bee is less prone to flooding of its nest than other solitary bees.

In our study we had many well drained sites on chalk or sand, but we also had sites on the heavy clays of the Weald, and low lying sites on alluvial soils, both of which may be seasonally wet and even flooded (Brandon 2003), and therefore expected to be less suitable for ground nesting bees. Nonetheless, we observed ivy bees at all of these sites. There was evidence of more ivy bees on the chalk downland sites than on the clay and alluvial sites, but there was much variation. We suggest, therefore, that due to its waterproof nest the ivy bee may be capable of nesting in many different soil substrates. The fact that the clay soils on the Weald are cold in spring may be a disadvantage to solitary bee species which emerge in the spring, but this is likely to be irrelevant to the ivy bees, which do not emerge until the end of summer or early autumn, when all soils will be warm.

Another factor which could have aided the spread and population build-up of the ivy bee in Britain is that as a new arrival it appears to have few pests, diseases and predators. In mainland Europe a major parasite of ivy bees is the meloid blister beetle *Stenoria analis* Schaum, 1859. This can lay hundreds or thousands of eggs, and young larvae can be carried by adult male bees into a nesting aggregation (Vereecken and Mahe 2007), where they can reach high densities. In a study in Switzerland, Müller and Weibel (2020) found that eight (29%) of the 28 cells that they had excavated contained only beetle parasites instead of ivy bee larvae. Although *S. analis* has not yet been recorded in Britain, Falk and Lewington (2015) state that it has been found in the Channel Islands, and it is also found in western France (Vereecken and Mahe 2007) and the Netherlands (Moenen 2009). We expect therefore that it is only a matter of time before this parasite reaches Britain, and that if it does become established it could spread

rapidly and probably check or reduce ivy bee populations. *Stenoria analis* is known to also parasitise other bee species, including the Nationally Notable (Falk 1991) sea aster bee *C. halophilus* (Moenen 2009), so it is also possible that if it were to become established in the ivy bee population it could also cause harm to other *Colletes* species which are not abundant. In particular, *C. halophilus* is restricted in its range in Britain to the south east and east coast of England (Sussex Biodiversity Records Centre 2018; National Biodiversity Network Trust 2023a).

The ivy bee has also been expanding its range over continental Europe, with records from Austria, Belgium, Croatia, France (including Corsica), Germany, Greece, Italy (including Sardinia), Luxembourg, the Netherlands, Serbia, Slovenia, Spain and Switzerland (Else and Roberts 2019) and it has recently been found for the first time in both Slovakia and the Czech Republic (Bogusch et al. 2021). Climate change is often given as a reason for species range expansion, and indeed Hopfenmüller (2014) suggested that climate change could explain the expansion of the ivy bee throughout Bavaria, Germany. In a modelling study of the effects of climate change on a range of solitary bee species, however, Roberts et al. (2011) considered that the ivy bee currently only occupies a part of its present potential range, given current climatic limitations on both the bee and on the ivy plant. They concluded that warming of the climate could aid the northern expansion of the ivy plant, and therefore could increase the potential range of the ivy bee. The climate of southern Scotland, the furthest north in Britain that the ivy bee has yet reached, is considerably colder than that of Sussex, both now and a few decades ago before climate changes, suggesting that the bee is capable of living in a wide range of different climatic conditions, although Edwards (2022) suggests that the bee is on the northern edge of its range and that warmth may be a restricting resource. If the ivy bee's colonisation of Britain had been as a result of climate change, it would presumably have remained restricted to warmer regions in southern Britain.

As well as being an important food resource for flower visiting insects, ivy flowers result in ivy berries which are an important winter and early spring resource for a large range of bird species (Jacobs et al. 2009). Jacobs et al. (2009) found that fruit set was reduced when insect visitors were excluded from flowers, and concluded that insect pollination of ivy was beneficial. They also concluded that at the time of their study (before the arrival of the ivy bee to their study locations) the key pollinators were likely to be wasps, due to their abundance (Jacobs et al. 2010). An increasing number of ivy bees could therefore possibly be beneficial through increased pollination and through increasing berry production, increasing food for birds during the winter. However, further studies would be needed to determine whether ivy bees are now a major pollinator of ivy. In addition, given the diversity and numbers of insects that visit ivy flowers, and given that it is the main nectar and pollen source in autumn in Britain, it is

unlikely that ivy was generally underpollinated before the arrival of the ivy bee. We are unaware of any studies exploring whether ivy is underpollinated in terms of maximising berry production, rather than simply requiring insect pollination.

With the current concern about the global decline of bee species in both abundance and diversity, it is pleasing that the ivy bee is thriving in Sussex, is now widespread in Britain, and in 2021 reached both Scotland and Ireland. This begs a contrast between the ivy bee's success, and the increasing rarity of many other bee species. Rasmussen et al. (2022) compared bee species in two 20-year data sets collected 100 years apart in the Danish island of Lolland. They concluded that bee species with a narrow feeding range were more likely to have declined than generalists. By any measure, the ivy bee has a narrow feeding range, although a very abundant one. Although early emerging males forage on a range of flowers before ivy blooms, females forage almost exclusively on ivy (Müller and Kuhlmann 2008; Teppner and Brosch 2015; Else and Roberts 2019; Hennessy et al. 2021b; Zenz et al. 2021; Ratnieks et al. 2022). This reliance of *C. hederae* on a single flower species is an effective strategy, however, simply because ivy is such a ubiquitous and plentiful forage source. In a recent study of the extremely rare solitary bee *Anthophora retusa* L., 1758 which has one of its three known British locations within our study area of Sussex, Hennessy et al. (2021a) concluded that its choice of forage sources could not be a limiting factor for its population, because it mainly foraged on common plants such ground ivy (*Glechoma hederacea* L. 1753 which is not related to *H. helix*). A narrow feeding range may therefore not be a barrier to the success of a bee species if the key forage source is a very common plant, such as ivy, just as foraging on abundant plants such as *G. hederacea* may not by itself be a recipe for success.

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Author's contribution

Conceptualization: N.L.C. and F.L.W.R.; methodolgy: F.L.W.R.; N.L.C. and M.G.; Data collection: all authors; writing – original draft preparation: N.L.C.; writing – review and editing: F.L.W.R. and N.L.C. All authors have read and agreed to the published version of the manuscript.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Descriptions of sites used in the 2020 surveys, and percentage abundance of ivy bees, honey bees and wasps (mean of three surveys, 100 insects counted in each).

Table S2. Descriptions of sites used in the 2021 surveys, presence of ivy bees and number in sequence of the first ivy bee seen.

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