

Using citizen science to examine the nesting ecology of ground-nesting bees

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Abstract. Suitable nest sites are a crucial habitat requirement of ground-nesting bees, but empirical studies of fossorial solitary bee nesting ecology in the UK are few in number. This study used a citizen science approach to overcome the logistical and temporal barriers associated with this type of research and to gather data on the abiotic environment associated with the nesting aggregations of four fossorial solitary bee species in the UK. Three hundred and ninety-four records were submitted by the public between March and November 2017. Sixty percent (236) of these records were verified as indicative of active nesting aggregations of the target species. Overall, the species in this study demonstrated the capacity to nest within a broad range of environmental variables. Although *Colletes hederæ* (Schmidt and Westrich 1993) was often reported from sloped, unshaded sites, and *Andrena fulva* (Müller in Allioni 1766) was regularly associated with flat, shaded locations. This study demonstrated the efficacy of a citizen science approach in surmounting the intrinsic difficulties associated with studying solitary bee nest sites, which are both ephemeral and cryptic structures in the landscape.

Key words: citizen science; ground-nesting bees; nesting ecology; solitary bees.

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INTRODUCTION

Solitary bees constitute roughly 250 species of wild bee in the UK, but there remain significant knowledge gaps with regard to their ecology (Wood et al. 2016). This group encompasses many important pollinators, including those of high-value crops such as apples (Garratt et al. 2016), but is facing diversity loss (Biesmeijer et al. 2006), declines in relative abundance (Bartomeus et al. 2013), and extinctions (Ollerton et al. 2014). There are two principal resources that solitary bee populations require in order to survive and proliferate: suitable and robust nest sites for their offspring to successfully mature in, and sufficient forage material both for their own survival and to provision their young. The

foraging requirements of bees have been well studied (Strickler 1979, MacIvor et al. 2014, Dicks et al. 2015, Wood et al. 2016) as they are believed to be the principal limiting resource. However, within a landscape, Gathmann and Tschamntke (2002) have speculated that nest sites may be a limiting factor for solitary bees more often than forage, although it is clear that these resources must work in tandem. There is a lack of empirical research regarding the nesting requirements of fossorial solitary bees in the UK (but see Potts and Willmer 1997). Although there are multiple reasons for this gap, the difficulties associated with finding sufficient nest sites in the field and the lack of robust experimental methods are two of the most significant barriers. These issues are further compounded

by the short flight seasons of many UK solitary bees, which result in only a narrow window of time when active nest sites can be discovered and examined.

There are two main types of empirical study performed on ground-nesting bees' nesting ecology: those studies that focus on single species (Potts and Willmer 1997, Wuellner 1999, Julier and Roulston 2009, Xie et al. 2013) and those that examine the effects of nest site suitability on wider metrics such as species richness, abundance, and community composition (Grundel et al. 2010, Sardiñas and Kremen 2014, Martins et al. 2018). When the species-specific studies are taken together, it is clear that there may be significant interspecific diversity in solitary bee nest site preferences with regard to key environmental characteristics. Within the UK, Potts and Willmer (1997) empirically examined *Halictus rubicundus* (Halictidae) (Christ 1791) nest aggregations and identified a preference for softer soils with a moderate slope and southern aspect. Wuellner (1999) showed that the North American bee *Dieunomia triangulifera* (Vachel 1897) preferentially nests in areas of bare, compacted soil with a warm soil surface temperature and close to visual landmarks. A study in Chinese *Camellia oleifera* (Abel) orchards found that *Andrena camellia* (Wu 1977) preferred loose, moist, and low-temperature soil conditions (Xie et al. 2013). The abundance of *Peponapis pruinosa* (Say 1837), a specialist pollinator of pumpkin in the United States, has been shown to be negatively related to soil clay content and positively related to soil irrigation (Julier and Roulston 2009). In all these studies, nest temperature seems to be an important characteristic and comes through either directly, in that individuals are observed nesting in areas with particular soil temperatures (Wuellner 1999, Xie et al. 2013), or indirectly, where they are observed nesting at sites whose physical characteristics can potentially confer thermal benefits (Potts and Willmer 1997). Although the direction of preference appears to be mixed, a similar pattern emerges with respect to the physical characteristics of the soil, where these attributes appear to be uniformly important, but the specifics of what is preferred seem to vary on a species-to-species basis.

Across geographical contexts, the availability of ground-nesting resources has been shown to be a strong predictor of bee abundance (Potts et al. 2003, Sardiñas and Kremen 2014), species richness (Grundel et al. 2010), and community composition (Potts et al. 2005, Grundel et al. 2010). A recent study from Quebec, Canada, showed that bee diversity in apple orchards and blueberry and raspberry fields was influenced by the presence of suitable nesting resources (Martins et al. 2018). Again, the important characteristics of the nesting resource vary, but the availability of bare ground (Potts et al. 2005), sloped terrain (Sardiñas and Kremen 2014), sandy soils (Cane 1991), and soils with low organic matter content (Grundel et al. 2010) are factors that have proven to be important in at least some contexts.

Collectively, these studies show that nesting resources are important for the survival and proliferation of ground-nesting bees. But, due to geographical differences in community composition and interspecific differences in nest site preferences, a one-size-fits-all approach will not be sufficient in this context. This conclusion was also reached by Kim et al. (2006) who found that across agricultural landscapes, ground-nesting bee density was impacted by proximity to seminatural habitat and edaphic factors of the individual sites. However, species differed in their response to the specific measured variables.

In this study, we use a citizen science approach to circumvent the logistical and temporal issues associated with in situ solitary bee nesting research and attempt to identify and examine nesting aggregations on a national scale. Citizen science is an effective method of upscaling research projects, both temporally and spatially, by capturing far more data than could be achieved by one individual (Pocock and Evans 2014). It is also an excellent way to engage and educate the public about their local wildlife and scientific research (Kremen et al. 2011). Bees are currently enjoying a popular status both in the media and with the wider public, although this interest tends to center around honeybees and, to a lesser extent, bumblebees. This zeitgeist presents us with the opportunity to test the limits of this interest and investigate whether people are willing to learn about and invest in lesser-known bees at a large scale.

This project set out to address three questions: (1) Can citizen science be used to examine the nesting aggregations of solitary bee species? (2) Do *Andrena fulva*, *Andrena cineraria* (Linnaeus 1758), *H. rubicundus*, or *Colletes hederæ* exhibit any associations with environmental characteristics in choosing a nest site? (3) Do broadscale environmental variables affect the nest aggregation size of these four solitary bee species?

METHODS

Project design

Citizen science data can vary in quality (Aceves-Bueno et al. 2017), so this project was designed to optimize the chances of receiving high-quality data based on the citizen science literature. This involved three fundamental design decisions. Firstly, the study was narrowed to four distinctive species (Delaney et al. 2008). Second, the participants were asked to record simple data that could be gauged by eye. Finally, the protocol did not require the participant to make a large time commitment (Pocock and Evans 2014, Birkin and Goulson 2015).

A process of elimination protocol was used to identify four ground-nesting solitary bee species for inclusion in the project. Within this selection process, we aimed to identify species that were already recorded by the public, nest in aggregations, and have been recorded in the East of England. The October 2015–October 2016 UK solitary bee iRecord (brc.ac.uk/iRecord) submissions were examined according to these criteria, and the following 10 species were pulled out: from the Colletidae family *C. hederæ* and *Colletes succinctus* (Linnaeus 1758); from the Andrenidae *Andrena clarkella* (Kirby 1802), *A. fulva*, and *A. cineraria*; from the Halictidae *H. rubicundus*, *Halictus tumulorum* (Linnaeus 1758), and *Lasioglossum morio* (Fabricius 1793); from the Melittidae *Dasypoda hirtipes* (Fabricius 1793); and from the Apidae *Anthophora bimaculata* (Panzer 1798). From this list of 10, four species with differing flight periods and that could be identified from photographs were chosen. In addition, *H. rubicundus* was chosen because empirical, UK-based data on nest site preferences for it are available (Potts and Willmer 1997) and this project could build upon that knowledge. *C. hederæ* was already the subject of a large-scale citizen

science project run by the Bee, Wasps and Ants Recording Society (BWARS).

Once these four species were identified, a simple protocol for recording nesting aggregation data was designed. A project-specific website (thesolitarybeeproject.org) was created and launched both as an information tool and a portal for record submission. The website provided training instructions for participants. It also contained further context detailing what participants should look for and how to identify bee nests and aggregations and described potential confusion structures such as worm casts. It also provided descriptions and photographs of each of the four target species and links to further resources. The project focused on three principal environmental variables that have been shown to impact nest site suitability: shade (Potts and Willmer 1997), slope (Sardiñas and Kremen 2014), and ground cover (Wuellner 1999). A printable information sheet (Appendix S1), which included details on how to identify each of the four species and quantify the nest site characteristics, was provided to participants via the website (including example photographs of the three different categories of shadiness and diagrams depicting the three levels of slope). Participants were asked to upload a photograph of the bee and the nest site for validation purposes. This was not made compulsory so as not to deter participants confident with bee identification. Participants were also provided with space to add additional commentary or detail to the record. The project ran from 3 March to 3 November 2017. Participants were asked to answer the following multiple-choice questions and to identify on a map where the aggregation occurred:

1. How many nests were there?
 - a. 1–10
 - b. 11–30
 - c. 31–50
 - d. 51+
2. How sloped was the ground the aggregation was on?
 - a. Flat
 - b. Sloped
 - c. Vertical

3. How shady was the aggregation?
 - a. Aggregation was completely in the open
 - b. Aggregation was adjacent to trees or buildings that could provide shade
 - c. Aggregation was completely shaded by trees or other structures
4. What was the ground cover like?
 - a. Bare earth
 - b. Lawn
 - c. Under mulch
 - d. Other

Data validation

Verification of citizen science records by a trained expert increases the accuracy of the data (Gardiner et al. 2012) and so records in this project went through a process of expert validation before being accepted for analysis. Records submitted with a photograph were accepted if the specimen in the image was accurately identified and the bee had been observed at a nest site. Records without photographs were only accepted if there was adequate descriptive commentary that established that the bee had been observed nesting and that the species identification was correct. Due to these criteria, many submissions without photographs were ultimately rejected because they lacked enough detail to establish validity. Records were also immediately rejected if there were any missing data from the submission.

Participant recruitment

Immediately preceding and proceeding the launch of the project, it was advertised through BWARS and through the personal contacts of those involved in the project. This resulted in the project being target marketed to either those with a professional interest, for example, university contacts, or amateurs who are members of a wildlife recording society and are accustomed to wildlife recording. At the beginning of June 2017, three months into the project, a press release was circulated to local and national media outlets by the university press office. This press release resulted in a number of local and national radio and television appearances and newspaper articles about The Solitary Bee Project. In this way,

the project was marketed to a much wider group of potential participants from this point on.

Data analysis

A random forest algorithm was developed as a classification model (500 trees) to attempt to predict the number of nests in an aggregation (categorical outcome of 1–10; 11–30; 31–50 or 51+ nests) based on the species, shade, slope, and ground cover. Random forest is a machine learning approach that iteratively uses a different subset of the data to create multiple decision trees. In this way, it combines many classifications trees in order to produce more accurate classifications and is a robust method of examining variable importance and modeling interactions between variables (Cutler et al. 2007). We added a random variable of numbers between 1 and 100, generated by R to the model, so that the relative contributions of the other variables could be examined. All analyses were carried out in R version 3.5.1 (R Core Team 2018). The R package randomForest was used for the random forest analysis (Liaw and Wiener 2002).

RESULTS

Summary of records

In total, The Solitary Bee Project collected 394 records from across the UK and Ireland in 2017. Two hundred and thirty-six of these records were assessed as being accurate and indicative of an active nesting aggregation (Fig. 1). There was substantial variability in the number of accurate records submitted per species. Close to ten times more accurate records were received for *A. fulva* compared with *H. rubicundus* (105 and 11 accurate records, respectively). There were also marked interspecific differences in the proportion of accurate records submitted, where again *A. fulva* had the highest proportion (74% of records were accurate) and *H. rubicundus* the lowest (21% of records were accurate; Table 1).

Solitary bee nest sites

Records were used to build a picture of the areas in which the four species were nesting in terms of their shade (Fig. 2), slope (Fig. 3), and ground cover (Fig. 4).

Andrena fulva.—The ground cover of *A. fulva* aggregations was reported to be grass in 56% of

Fig 2

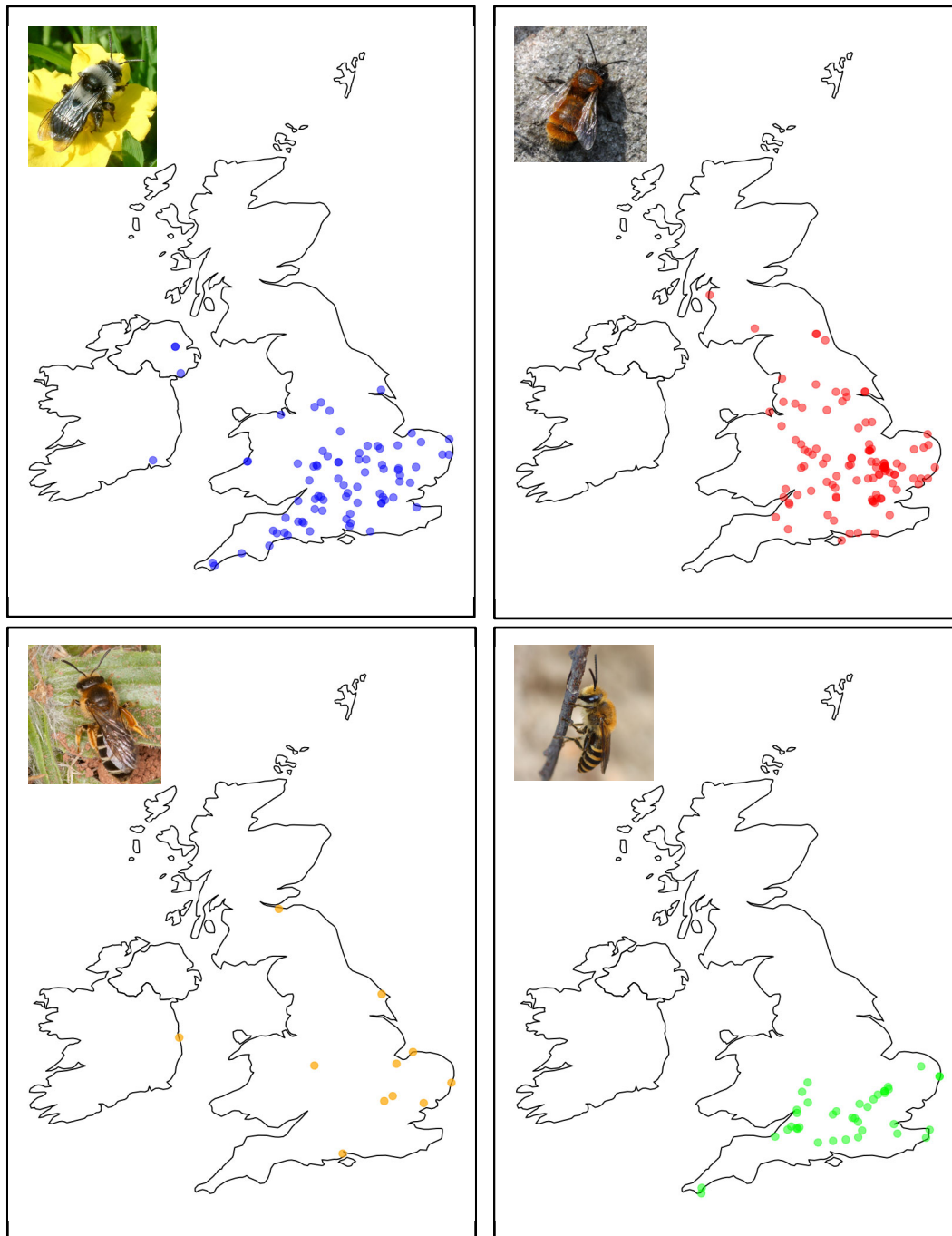


Fig. 1. Distribution maps for the records submitted for each species. *Andrena cineraria*, blue dots ($n = 81$); *Andrena fulva*, red dots ($n = 105$); *Halictus rubicundus*, orange dots ($n = 11$); *Colletes hederæ*, green dots ($n = 39$). Photographs: Thomas Ings.

aggregations and bare in 34% of aggregations. Eighty-two percent of records reported this species to be nesting in flat ground with no slope. The records also indicated that *A. fulva* has a broad tolerance for shade with 68% of

aggregations reported to be experiencing at least partial shade. However, only 10% of aggregations were reported to be in full shade.

Andrena cineraria.—Fifty-three percent of *A. cineraria* aggregations were reported to be

Table 1. Summary of records by species.

Species	Total records	Accurate records
<i>Andrena fulva</i>	142	105 (74%)
<i>Andrena cineraria</i>	128	81 (63%)
<i>Halictus rubicundus</i>	53	11 (21%)
<i>Colletes hederæ</i>	71	39 (55%)

fully in the open, and 44% were reported to experience some shade. Just 3% of aggregations were reported as fully shaded. Sixty-seven percent of *A. cineraria* aggregations occurred on flat ground, and 30% were sloped. Sixty-four percent of aggregations were reported to be in a grassy area, and 30% occurred in bare ground. This reflects a very similar pattern to *A. fulva*.

Halictus rubicundus.—From the 11 accurate records of *H. rubicundus* aggregations, 54% occurred on flat ground and 36% on sloped ground. Most records (74%) specified that the ground was bare. No strong trend manifested in terms of shade with 45% of records specifying the aggregation to be in the open and a further

45% specifying the aggregation to be in partial shade.

Colletes hederæ.—A majority (74%) of *C. hederæ* aggregations were reported to be fully exposed to sunlight, while no aggregations were in full shade. Aggregations occurred equally on flat ground and on sloped ground. Sixty-two percent of recorded aggregations reported grass as the primary ground cover, with 36% recorded as bare.

Participant reach

The media attention three months into the project resulted in what might be considered a high-quantity, low-accuracy scenario where in the first month post-press 230 of the 394 total records were submitted. In the first three months of the project, a total of 95 records were received, of which 82% were verified as accurate and 70% included one or more photographs (Table 2). In comparison, of the records submitted in the three months post-media, only 49% were validated and taken

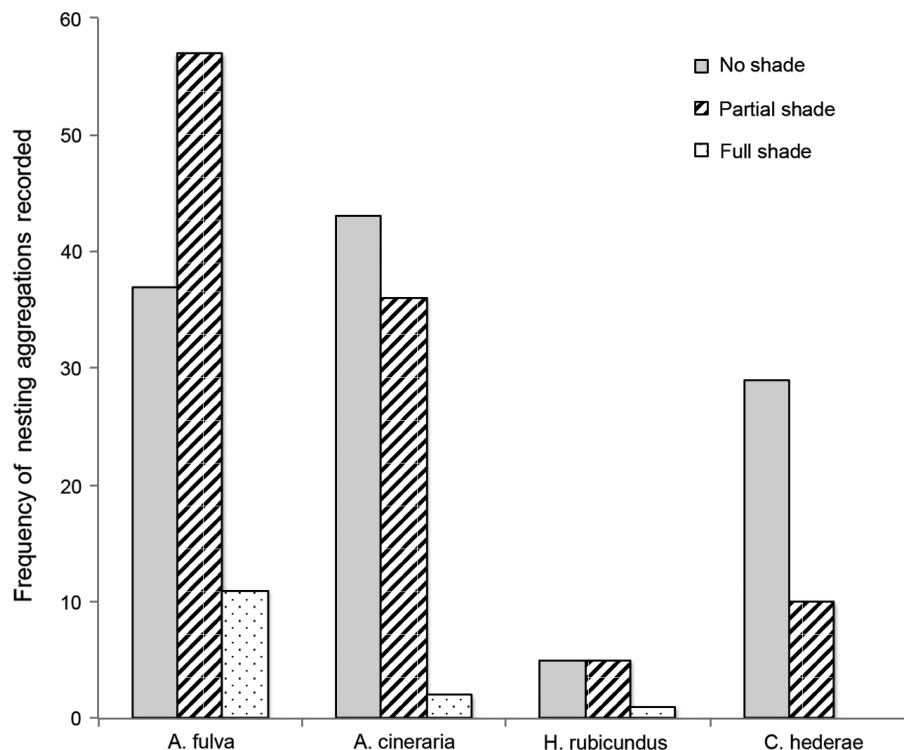


Fig. 2. Frequency distribution of the number of verified records of nesting aggregations in shade, partial shade, and full shade for each of the four study species ($n = 236$).

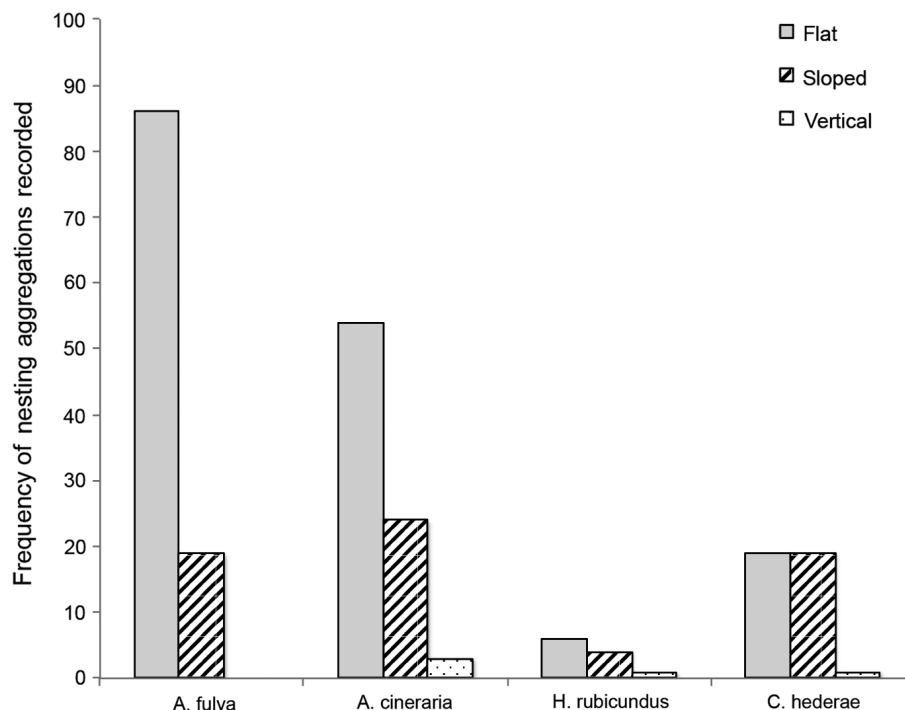


Fig. 3. Frequency distribution of the number of verified records of nesting aggregations in flat, sloped, and vertical terrain for each of the four study species ($n = 236$).

through for data analysis. Not only were many of the records removed from the analysis, but the percentage of records with accompanying images dropped to 33% (Table 2).

Predicting the aggregation size

The random forest algorithm could not successfully predict the size of an aggregation and had an out-of-the-bag error rate of 57.63%. This value represents the average of the errors associated with each iteration (classification tree) and is based on the correlation between the observed aggregation size and the predicted aggregation size. The variable importance plot shows that the random variable inserted into the model was the main driver of the model (Fig. 5). Therefore, none of the measured variables are considered to be useful predictors of the number of nests in an aggregation.

DISCUSSION

The Solitary Bee Project collected 236 accurate records of solitary bee nest site locations of four species from across the UK. Although the

resolution of the data was not fine enough to identify any influence of environmental factors on aggregation size, the project did reveal some interesting trends in terms of where these four species nest in a landscape. All species were found to have broad tolerances for the measured environmental characteristics, but they did exhibit some significant interspecific differences in nest site characteristics. Furthermore, these results suggest that interspecific differences may be reduced when species are closely related and have similar flight seasons. This study took a novel approach to overcoming the logistical barriers associated with solitary bee nesting research and showed that citizen science can be an effective tool in this context, although data resolution would benefit from some methodological changes in the future. There was substantial engagement with the project and the near 400 submitted nest site records reflect the engagement the public had with this lesser-known but important group of bees. The data collected by this study are indicative of presence only, and future research could be strengthened by the explicit collection and consideration of absence

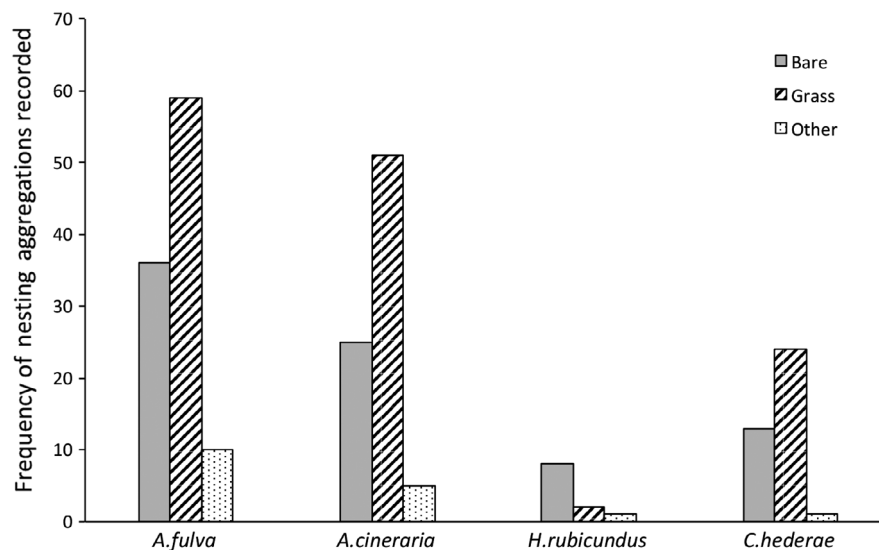


Fig. 4. Frequency distribution of the ground cover (bare, grass, other) of the verified records of nesting aggregations for each of the four study species ($n = 236$).

data. However, this would be difficult to achieve using a citizen science approach as it would require systematic and repeated surveying of specific geographic areas whether bees were present and nesting or not. This burden of effort would likely deter potential participants.

Shade

Nest sites that are in full sun are understood to be attractive to ground-nesting species as they experience increased soil temperature (Brockmann 1979, Potts and Willmer 1997). *C. hederæ* followed this trend and was most often reported from sites that experienced no shade (Fig. 2). However, there was evidence that all species could tolerate some level of shade, including *H. rubicundus* which has previously been found to show a strong preference for sites in full sun (Potts and Willmer 1997). In fact, *A. fulva* was found to nest in open spaces in very few cases



Fig. 5. Variable importance plot. This plot illustrates a list of the most predictive variables in descending order. In this case, the random variable, which is listed first, contributes the most to the model.

(Fig. 2), which indicates that there may be benefits to nesting in a shaded site that outweigh the disadvantages. In this study, a number of participants reported *A. fulva* to be nesting near and, in some

Table 2. Summary description of submitted records.

Parameter	No. of records	No. of valid records	No. of records with photographs
Overall	394	236 (60%)	174 (44%)
Before media	95	73 (82%)	62 (70%)
After media	299	125 (49%)	84 (33%)

cases, directly beneath, trees. Although *A. fulva* is polylectic, a study of their pollen loads in Cardiff, Wales, found that females were primarily foraging on flowering trees such as maple and cherry (Paxton 1991), and so the tendency of *A. fulva* to nest in shaded areas may be a function of their decision to nest in close proximity to forage material. As *A. fulva* is active in early spring, when flowering plants are scarce, there may be more pressure on it than summer flying species to construct a nest close to abundant foraging resources. Trees can also alter the soil environment in ways that may facilitate nesting. For example, fossorial insects do not nest in hard-packed soil (Gliński et al. 2011, Srba and Heneberg 2012), but tree roots can break up compacted or hardened soil layers, which may make the area habitable. Trees also help to mitigate extremes in soil surface temperature (Edmondson et al. 2016), which may be beneficial to larvae developing underground (Potts and Willmer 1997).

Slope

Sloped, south-facing ground experiences higher soil temperatures, and this is thought to confer significant benefit to species that nest in these areas (Potts and Willmer 1997). In this study, the majority of *C. hederæ* nesting sites were reported to be on sloped ground, in line with previous findings for this species (Bischoff et al. 2004, Falk 2015). Conversely, most *A. fulva* nesting sites occurred on flat ground (Fig. 2), a tendency that has previously been noted for other *Andrena* species that occur in North America (Youssef and Bohart 1968). Neither *H. rubicundus* nor *A. cineraria* demonstrated a trend for any particular terrain gradient. This mixed picture is not unusual. When Srba and Heneberg (2012) examined the nest sites of five species of digger wasp (four sphecids and one crabronid), they also identified interspecific differences in the slope of the nesting areas, noting that there were preferences for both sloped and flat terrain. Potts and Willmer's (1997) study of *H. rubicundus* nesting aggregations found that across sites, there was no correlation between slope and nesting density; however, within a site this species nested at higher densities in areas with steeper slopes. So, although these species possess the capacity to nest in variously sloped ground, these may not represent optimal nest sites and further study is required to untangle this relationship.

Ground cover

Seventy-four percent of *H. rubicundus* nest sites were found in bare ground, but for the other three species (*A. fulva*, *A. cineraria*, and *C. hederæ*), grass was reported as the primary ground cover of the aggregation in the majority of records. Bare ground has been shown to encourage solitary bee nesting (Gregory and Wright 2005, Dicks et al. 2010), but the results of this study show the capacity of some species to nest in grassy areas. For *A. fulva* and *A. cineraria*, many participants reported the aggregations to be in mown lawn or grazed grass, indicating that these species can tolerate significant anthropogenic disturbance to the surface area of the nest site. This is supported by the fact that many of the aggregations recorded in bare ground occurred on footpaths with frequent pedestrian or vehicular traffic. These findings are in line with descriptions of typical nesting sites for these species as detailed in field guides and species' profiles (Falk 2015). Although little work has been done on the impact of disturbance on solitary bee nest sites, Ullmann et al. (2016) found that tilling the soil to a depth of 40 cm delayed the emergence of the squash bee *P. pruinosa* in an agricultural landscape. However, roughly 50% of the bees survived the management and so these results, taken with the results of this study, suggest that highly disturbed landscapes in both rural and urban landscapes can potentially contribute to the persistence of ground-nesting solitary bee populations. This may indicate that these species have a broad tolerance for the surface characteristics of the ground they nest in and that other factors are more important for optimizing their nest site location. Srba and Heneberg (2012) studied the nest site characteristics of five species of digger wasp and found a general trend of preference for low vegetation cover with some species more strongly selecting for this than others. However, they noted that one species showed no preference for vegetation cover and dug nests in areas with up to 80% cover. The authors did identify strong interspecific differences in the wasps' soil requirements. Evidence shows that edaphic factors such as soil particle size (Cane 1991) and organic matter content (Grundel et al. 2010) can drive the presence and density of fossorial bees and wasps and so it is possible that the subterranean environment is

a more dominant feature compared to the surface characteristics for some species.

Interspecific similarities and differences

Overall, *A. fulva* and *A. cineraria* nest sites exhibited similar trends in terms of their environmental characteristics. Furthermore, these two species were sometimes reported to be nesting together, a scenario observed by the authors of this paper. This, taken with previous work (Youssef and Bohart 1968), suggests that these closely related species with strongly overlapping flight seasons favor similar nesting conditions. This pattern has also been identified in the Colletidae family, where steep, south-facing, sandy slopes are preferred (Bischoff et al. 2004). This tentatively suggests that phylogenetic relatedness could potentially play a role in defining the nest site requirements of a species, but more research with the specific aim of testing this hypothesis is required.

There seemed to be some inter-familial differences, with the majority of *C. hederæ* and *A. fulva* nest sites having values for slope and shade in opposite directions. Furthermore, *H. rubicundus* was the only species for which bare soil was identified as the primary ground cover in the majority of records. Summarizing previous work on species from different families demonstrates some divergences in their preferred nest site characteristics (Potts and Willmer 1997, Wuellner 1999, Julier and Roulston 2009, Xie et al. 2013). These differences may have originally manifested for many reasons. Although all species have a common goal of finding a nest site that is suitable for larval development and subsequent survival of offspring, they may differ significantly in what constitutes optimal soil for digging and what is the optimal position for forage. There is a high degree of morphological diversity within the ground-nesting solitary bees, particularly with regard to body size. Smaller bees are likely to have shorter foraging ranges (Greenleaf et al. 2007) and so may be more restricted in requiring a nest site in close proximity to suitable food resources. Furthermore, monolecitic and oligolectic species may be constrained by the presence of their food plants. Body size may also impact the ability of an individual to excavate nests in harder soils. Indeed, Cane (1991) found that larger bees tend to nest in soils with higher clay content, and nesting in these conditions results in higher energy costs (Srba and Heneberg

2012). Species' flight periods may also play a role. Spring flying species such as *A. fulva* and *A. cineraria* have to cope with lower soil temperatures, which will alter the digging conditions (Xie et al. 2013). For example, soils with larger particles, such as sand, freeze more easily than those with a higher proportion of fine particles such as clay. In this way, clay-rich soils may be easier to dig in the spring, while in the summer months sandy soils represent a lower energy excavation. The closely related digger wasps *Ammophila pubescens* and *Ammophila sabulosa* have been shown to preferentially nest in areas where the soil has a low gravel content (Srba and Heneberg 2012).

Although there is evidence to suggest that phylogenetic relatedness can help determine nesting requirements, Cane (1991) found that ground-nesting bees exhibit substantial variability in their preferences for soil grain size. They also noted that the species with more similar preferences did not necessarily align along taxonomic relationships. The resolution may be that in certain families, for example, Colletidae and Andrenidae, taxonomic relatedness does help to delineate nesting preferences, but this is not true for all fossorial families. Looking ahead, significantly more research is required to gain a clear understanding of how these factors interact.

Aggregation size

The data collected did not distinguish any differences in environmental conditions for different sized aggregations. This may have been due to the broad nature of the questions asked, which is an inherent risk when designing hypothesis-led citizen science projects. There is a careful balance to be struck between establishing complexity in the methods for scientific robustness but maintaining simplicity in order to encourage participation and ensure accurate reporting. The categorical nature of the questions seemed to have a negative effect on data resolution as the categories were constrained. This was especially apparent with the *C. hederæ* data for which 77% of records reported the nest site to consist of more than 51 nests (the highest category). A separate, fine-scale study of a subset of the aggregations revealed a wide range in the mean number of nests per square meter (S. Maher, F. Manco and T. C. Ings, *unpublished data*). For example, *A. fulva* had a mean highest nest density of eight nests per square meter and *C. hederæ*

49 nests per square meter. So, measuring the number of nests in an aggregation on a continuous scale would likely have improved the resolution.

Participant recruitment

There have been inherent and long-standing difficulties with the communication of science in mainstream media (Bell 1994, Barron and Brown 2012, Mehr 2015), and the drop in accurate records following the national media attention of this project demonstrates some of the issues that can arise. However, the project's appearance in the media did, overall, result in a higher number of accurate records being submitted in absolute terms. The impact of media coverage can possibly be tempered by careful planning of the project, for example, by simplifying the actions and by having clear, concise, and readily available instructions. The records collected in this project were submitted anonymously and so there was little opportunity to engage directly with participants or to offer feedback on their submissions through the website. However, participants could engage with project researchers via email or through social media profiles that were set up specifically for the project. These profiles also offered a way for participants to keep track of the project and its progress and were regularly updated with distribution maps of the submitted records. Social media has been acknowledged as an important tool for citizen science endeavors for engaging participants and creating a sense of community around a project (Stafford et al. 2010, Dickinson et al. 2012). We found that exploiting social media platforms as forums in which potential participants could ask questions and clarify instructions with researchers directly was of great help. In some cases, participants would share a potential record with researchers via social media to get feedback before submitting the data through the website proper, rendering these records more accurate. That said, whether or not citizen science data are accurate, greater engagement represents more people learning about, and becoming aware of, solitary bees, which is in itself an important function of citizen science.

For future endeavors, we have found that citizen science can be a useful tool for the study of solitary bee nesting ecology and this exact approach could be enlisted for any distinctive species that can be accurately identified from

photographs. However, the variability in the number and quality of records for the different species in this study raises an important consideration. *A. fulva* was the most successful species, while *H. rubicundus* performed poorly. This is most likely a reflection of the fact that *A. fulva* is a relatively large and physically distinctive species, which is easy for amateurs to become familiar with and identify in the field, whereas *H. rubicundus* is smaller and far less charismatic. This indicates that for the many solitary species which are difficult to identify, it may be useful for participants to be able to submit specimens to researchers for identification. In cases where this is not possible, citizen science can still be used to examine nesting ecology in general terms without specific connection of the nesting site to an individual species. Furthermore, the capacity of the public to find and record active nesting aggregations could be harnessed to develop databases of nest site locations for further investigation by scientists, thereby removing one of the most significant logistical barriers associated with studying this topic.

CONCLUSION

This study represents the first instance of using citizen science as a tool to examine solitary bee nesting ecology and illustrated the efficacy of a citizen science approach in this context. On the whole, this study demonstrated the capacity of the four target species to tolerate a broad range of environmental variables, although questions remain around whether these conditions impact the nesting density of bees. Srba and Heneberg (2012) in their study of digger wasp nesting found that some variables may be used to identify usable nesting areas and that others are important for determining nest density at a suitable site, and the results from this study may be a reflection of this process. Most *C. hederæ* nest aggregations occurred at sloped sites in full sun, whereas the majority of *A. fulva* sites were found in flat, shaded areas. The distance to forage and phylogenetic relatedness may play a role in determining the nest site requirements of a ground-nesting species, but more empirical research is required. Despite not being able to discriminate the effects of the measured environmental variables on aggregation size, we believe that by calculating the total number of nests or

nest density on a continuous scale, the data resolution required for this analysis could be achieved. The location, size, and nesting density of solitary bee aggregations are likely determined by complex interactions between the abiotic environment, foraging resources, phylogeny, parasite load, and natal nest site fidelity, and more empirical studies are needed to elucidate these forces. A better understanding of solitary bee nesting ecology will assist us in developing robust conservation practices and policy going forward as, in order to protect anything, we must first understand what needs protecting.

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