

The importance of soil and vegetation characteristics for establishing ground-nesting bee aggregations

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THE IMPORTANCE OF SOIL AND VEGETATION CHARACTERISTICS FOR ESTABLISHING GROUND-NESTING BEE AGGREGATIONS

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Abstract—Most bee species are ground-nesters, yet knowledge on the nesting behaviour of this diverse group remains sparse. Evidence on the effectiveness of ground-nesting bee species as crop pollinators is growing, but there is limited information on their nesting habits and preferences and how to manage habitats to enhance populations on farms. In this study, artificially prepared plots of bare soil were constructed with the aim to attract ground-nesting bees to nest in a commercial orchard in Kent, UK. Nine soil parameters were measured to determine their preferred soil properties: hydraulic conductivity, soil compaction, soil moisture, soil temperature, soil stoniness, soil organic matter, soil root biomass, soil texture and vegetation cover. Eighteen non-parasitic ground-nesting bee species (7 *Andrena*, 9 *Lasioglossum*, 1 *Halictus* and 1 *Colletes* spp.) were recorded in the study plots. Soil stoniness and soil temperature at 10cm depth were positively correlated, and vegetation cover and hydraulic conductivity were negatively correlated with the number of ground-nesting bees on the plots. We show that artificially created habitats can be exploited for nesting by several ground-nesting bee species. This study's findings can inform management practices to enhance ground-nesting bee populations in agricultural and urban areas.

Keywords—Hymenoptera, nest-site selection, solitary bees, pollination, ecosystem service

INTRODUCTION

Bees (Apoidea: Anthophila) provide essential pollination services to natural (Ollerton et al. 2011) and agricultural (Klein et al. 2007) ecosystems. There are approximately 20,000 known species globally which differ in their ecology, habit preference, body size, and appearance, diverging according to the plants on which they forage (Michener 2007). There are 277 bee species in the British Isles, and the great majority are ground-nesters, including species from *Andrena* Fabricius (68 species), *Lasioglossum* Curtis (33 species), *Halictus* Latreille (8 species), and *Colletes* Latreille (9 species) genera (Else & Edwards 2018). Sixty-four per cent of global bee species are ground-nesters (Cane & Neff 2011).

Yields of many insect-pollinated crops are managed via the addition of honeybees (*Apis mellifera* Linnaeus) (Goodwin et al. 2011; Rucker et al. 2012). However, studies increasingly indicate that the contribution of wild pollinators has been underestimated (Kleijn et al. 2015). Garratt et al. (2016) estimated the value of solitary bees for UK apple pollination at £51 million p.a. and the value of honeybees at £21 million p.a. Kleijn et al. (2015) estimated that 81% of the top 100 pollinator bee species were wild ground-nesters.

Ground-nesting bees need floral resources for nutrition, shelter, and appropriate nest sites for the development of their offspring and hibernation until emergence. Ways to provide floral resources for pollinators are comparatively well developed (Sheffield et al. 2008; Rosa & Miñarro 2014; Campbell et al. 2017); however, methods for

provisioning areas for ground-nesting bees are poorly understood (Antoine & Forest 2020). A recent review by Harmon-Threatt (2020) shows that information on nesting habits and preferences of ground-nesting bees was only available for 26% of the 527 species studied in the USA and Canada.

Since most of a ground-nesting bee's life cycle occurs underground, soil variables are highly likely to play a significant role in nesting bees' success and survival. Bare ground has been frequently linked with increases in fossorial bee nesting (Sardiñas & Kremen 2014). The nest locations of thirty-two bee species across the USA showed that ground-nesting bees did not nest in silt or clay soils but primarily in soils that were 33% - 94% sand (Cane 1991). Potts & Willmer (1997) studied a range of edaphic and microclimatic parameters involved in nesting of the ground-nesting bee *Halictus rubicundus* Christ. They observed that bees initially nested in soft soils, but gradually moved to hard soils as aggregations grew, probably because this provided a stronger nest structure, avoiding collapse. Soils with greater soil organic matter contents absorb and hold water and might make soils softer and easier for bees to dig (Bescansa et al. 2006). In addition, soil moisture is vital for the development of bee larvae (May 1972) but might also encourage the development of fungal pathogens inside nest cells affecting larval survival (Larsson 1991). The ground-nesting bee *Nomia melanderi* Cockerell is reported to prefer nesting beds in silty textured soils with good hydraulic conductivity, moist subsoils, and without surface vegetation (Johansen et al. 1978). Furthermore, nest temperature is also considered a significant component of nesting success as it determines the rate of egg and larval development (Miyano 1981) and influences the brood's emergence timing, which can be closely related to survivorship (Jeanne & Morgan 1992). *H. rubicundus* prefers to nest in warm soils and favours south-facing steep slopes, probably due to high sunlight absorption and a decreased likelihood of waterlogging compared to flat substrates (Potts & Wilmer 1997; Michener 2000).

A few studies have investigated entire communities of ground-nesting bees to understand nesting habitat characteristics (Potts et al. 2005; Sardiñas & Kremen 2014) and nest-site selection (e.g. Potts & Willmer 1997). Only a

handful of species' preferences in relation to the soil characteristics of nesting habitats are documented (Harmon-Threatt 2020) and these abiotic nesting preferences cannot be reliably extrapolated to most unstudied ground-nesting bee species.

The aim of this study was to 1) determine whether the provision of bare ground plots can provide a nesting resource for ground-nesting bees, 2) identify which species are attracted to artificially constructed nest sites, and 3) identify the preferred biotic and abiotic nesting factors that drive nest site selection of ground-nesting bees.

MATERIALS AND METHODS

STUDY SITE

The NIAB EMR commercial and experimental fruit farm in Southeast England (51°17'26"N 0°26'02"E) was used for the study. The farm has primarily level topography (< 2° slope) (DEFRA 2005), and the dominant soils are well-drained, non-calcareous Luvisols (IUSS Working Group WRB 2015) of the Malling and Fyfield series (Furneaux 1954). Eight south or southeast-facing bare soil plots were created in mid-February 2018, firstly by herbicide treatment to reduce vegetation growth, followed by the mechanical removal of surface vegetation and topsoil with a 0.91 m wide bucket digger. All sites were vegetated, primarily with a grass sward, before the construction of the bee plots. Each study plot was 10 x 2 m, and a slope of 10° (Appendix 1) was created in half of the plot by scraping off a 10 x 1 m section (0.88 m³ soil), which was then heaped and pressed onto the adjoining 10 x 1 m section. Plots were created in field headlands, orchard margins, and other uncropped land (see Appendix 2).

The growth of vegetation on plots was monitored visually as % estimates of flat and slope areas during the main solitary bee nesting period (April – July). When vegetation cover exceeded ≈10%, bare ground was reinstated by applying glyphosate at the recommended dose of 1,800 g/ha⁻¹. Eight glyphosate applications were made to all plots over the study period: 23 May 2018, 15 August 2018, 7 May 2019, 18 June 2019, 5 August 2019, 19 March 2020, 10 April 2020, and 24 June 2020.

MONITORING BEE SPECIES ON PLOTS

No nest monitoring took place before the bare plots were established. Following plot establishment, bee activity observations were carried out during sunny and/or mild weather above 10°C if cloud cover did not exceed 4 oktas. On cloudier days, (5 – 8 oktas), surveys were conducted if the temperature was above 14°C. Also, wind speeds were below Beaufort scale of 5, or 29 km/h (Pywell et al. 2005). Surveys took place between mid-April and May in 2018 and between mid-April and mid-August in 2019 and 2020. These months are within the active flight period of most of *Andrena*, *Halictus* and *Lasioglossum* mining-bee species in the UK (Else & Edwards 2018). Plots were surveyed twice weekly in 2018 and every two weeks in 2019 and 2020 (weather permitting, 10 surveys per year) in a randomised order on each date, so over the study period, plots were sampled at different times of the day, including both the morning and afternoon. Each plot was observed for 30 minutes while walking slowly around the perimeter. Once a bee arrived on the plot, it was collected using a sweep net (Watkins & Doncaster, Leominster, UK) and placed into a 5 ml clear plastic tube in an ice bucket where bees were kept inactive until the end of the observation period (Grixti et al. 2009). Subsequently, bees were identified to species level in the field. If this was not possible, photographs including the key characteristics were taken for later identification and confirmation by Mr Mike Edwards, a professional entomological consultant (Else & Edwards 2018). Bees that were not identifiable by photographs were grouped by their body length (Small = 3 – 5 mm, Medium = 5 – 7 mm). Bees were subsequently released next to the plot. Whenever notable numbers of kleptoparasites and wasps were observed, samples were collected for later identification in the laboratory.

BEE NESTING OBSERVATIONS

The number of bee nests on each plot's flat and slope sections prior to each 30-minute bee survey was recorded at each visit. Bee nests were distinguished from holes made by other invertebrates, including ants and earthworms, by the characteristic tumuli (volcano-shaped mounds of earth) that females make in the nest excavation phase. Ants also create similar soil structures, although these are usually formed of scattered soil

particles compared to solitary bee tumuli, which have a more organised and firm structure (K. Tsiolis personal observation). Nests were not counted if there was any doubt about the nest occupant. On each plot's flat and sloped sections, fifteen nest entrance holes were measured using digital callipers to the nearest tenth of a millimetre (Preciva IP54) in the 2019 and 2020 surveys. Starting from the edge of each plot, three nests were measured from the middle or nearest to the middle every two meters. Once a nest was measured, a 12 cm long plastic plant label was placed on the north side of the nest to ensure that it would not be measured again. The total number of bee nests on each plot was also recorded. Wind or rain can destroy tumuli throughout the season, and so the number of bee nests recorded fluctuated between counts. Therefore, peak nest density (the highest number of nests recorded on a plot section each year) was used in all analyses.

SOIL CHARACTERISTICS

From each plot, eight soil cores (D 10 cm x W 5 cm) were removed using a Buerkle soil sampler (Fisher Scientific International Inc., Hampton, US) in 2018 and 2020. Four samples were taken from each plot's sections (flat and slope). All samples were taken at least 2.4 m from each other and at least 30 cm away from the plot (Appendix 3). Soil water content was determined gravimetrically (80°C, five days; Martin-Vertedor & Dodd 2011). To measure root biomass, large aggregates were gently crushed with a mortar and pestle, and all visible root material was removed manually and weighed. The mass of root material was compared to the total weight per mass of each core to give root biomass in percentage. The stoniness of the samples was measured by hand sieving the sample through a 2 mm aperture test sieve for 30 seconds to separate the gravel fraction (Potts & Willmer 1997). The stones were weighed and calculated as a percentage of the total soil weight. Two grams of the remaining non-gravel fraction of each sample was then used to determine organic matter content by loss on ignition (550°C, 7 hrs; Goldin, 1987). From two soil samples per slope and two per flat section collected in 2018, the percentage content by mass of gravel (> 2.0 mm), sand (0.05 – 2.0 mm), silt (0.002 – 0.05 mm) and clay (< 0.002 mm) was determined by sedimentation using the Bouyoucos hydrometer method (Lesikar et al. 2005). These

measurements were used to determine soil texture according to the USDA texture classification system (Soil Survey Staff 2014). Hydraulic conductivity was measured from three samples per slope and three per flat section using mini disc infiltrometers (METER Group Inc., Washington, US). The devices were placed where soil cracks, bee nests and ant nests were absent. A suction rate of 2 cm s⁻¹ was chosen except for plot 5, where a suction rate of 6 cm s⁻¹ was used due to the high sandy soil texture of the plot. Water infiltration was recorded every 3 minutes (measurements were taken in 2018 and 2020).

Soil compaction (unconfined compression strength; kg/cm²) was assessed in 2018 and 2020 by taking three probing readings per slope and flat section using an electronic recording cone penetrometer (Solutions for Research Ltd, Bedfordshire, UK). Readings were taken at 2.5 cm intervals and the mathematical mean calculated for those collected from the top 10 cm. the cone index was corrected for soil moisture content (measured using a MO750 model soil moisture meter; Extech Instruments Corp., New Hampshire, U.S.) according to Busscher et al. (1997).

Soil moisture and soil temperature were recorded twice in spring and twice in summer of 2020 as the mean of four positions per flat and slope sections. The HH2 moisture meter and a WET-2 sensor (Delta-T Devices Ltd., Cambridge, UK) were used. In addition, soil temperature was also measured in each plot every two hours from 28/03/20 to 12/08/20 by burying an iButton ThermoChron® data logger (model DS1921G-F5# ($\pm 0.5^\circ\text{C}$), Premier Farnell Ltd., Leeds, UK) at 10 cm depth (following Potts & Willmer et al. 1997) in the centre of each of the two plot sections. In situ soil measurements were made for the top 10 cm because this is the typical depth at which the brood cells of ground-nesting bees are found.

VEGETATION COVER

Percentage vegetation cover was visually monitored, using a 50 cm² quadrat, from the beginning of the plot creation. It was noted that there was an accumulation of moss and thatch on the soil surface from the spring of 2020. Hence this was recorded twice in the spring and twice in the summer of 2020, following the systematic method used for soil sampling (Appendix 3).

STATISTICAL ANALYSES

R studio (Version 1.2.5019; RStudio Team 2019) was used for all statistical analyses. Soil texture was plotted on soil texture triangles in the R package 'plotrix'. Peak nest density was tested with the Shapiro–Wilk test, it was not normally distributed, and non-parametric statistical approaches were used.

Two Generalised Linear Mixed Effect Models (GLMMs, R package: lme4) were used to determine whether there was a significant relationship (positive or negative) between peak nest density (response) and soil variables measured (predictor). A negative binomial distribution was used due to excessive overdispersion with the Poisson distribution. Soil variables, year, and gradient (flat vs slope) were set as fixed effects, and plot was set as a random effect. The variance inflation factor (R package: car) was used to identify variables with high multicollinearity. No multicollinearity was located (all variables VIF < 3). A few variables were only measured in 2020 (soil temperature and moisture (WET sensor) and vegetation cover), and as a result, a second GLMM was used, including all variables measured in 2020. After examination of model fit, a Poisson distribution was preferred, measured soil variables and gradient were set as fixed effects, and plot as a random effect. The variance inflation factor (R package: car) was used to identify variables with high multicollinearity, and as a result, soil water content and root biomass were removed due to high multi-collinearity (VIF > 10). As soil texture is determined by the percentage of sand, silt, and clay particles, there is high multi-collinearity between these measurements (VIF > 10). The effects of multi-collinearity were avoided using data for sand (highest percentage) for both models.

To explore the effects of slope, year and plot using data from all three years, a Kruskal-Wallis rank test was used to determine whether there was a significant change in peak nest density between years and between plots. The Dunn's Test of Multiple Comparisons (R package: rstatix) was used to identify which plots significantly differed from which. A Mann-Whitney U test was used to identify whether the slope section of plots showed significantly greater peak nest density than the flat section.

The data collected from the soil temperature data loggers were divided into four periods for analysis: early morning: 01:00 – 05:00, late morning: 07:00 – 11:00, afternoon: 13:00 – 17:00, and night: 19:00 – 23:00. A Kruskal-Wallis rank test was used to test whether there was a significant difference between the four periods, and a Dunn's Test of Multiple Comparisons (R package: rstatix) to identify significant differences between time periods.

To determine the range of each variable that bees can tolerate for nesting, the minimum and maximum values of each soil variable were calculated. Additionally, the value of soil variables at plots with the highest peak nest density was used to establish a potential optimum value promoting bee nesting.

RESULTS

BEE ACTIVITY

Over the three years of sampling, 870 bee specimens were identified (122 in 2018, 397 in 2019 and 351 in 2020), belonging to 26 species (14 in 2018, 14 in 2019 and 19 in 2020) (Appendix 4). Five hundred bee specimens were identified to species level and the remainder to genus level. The most abundant bee species (non-kleptoparasitic) was *Lasioglossum malachurum* Kirby (39.4%), second most abundant *Lasioglossum calceatum* Scopoli / *Lasioglossum albipes* Fabricius (10.2%), and third most abundant *Andrena flavipes* Panzer (6.2%) (Fig. 1). Eleven species, representing 49.7% of the total number of bee specimens, were kleptoparasites: *Sphecodes* spp. (79.2%) and *Nomada* spp. (14.8%) (Fig. 1). Furthermore, thirteen wasp species were recorded, representing 12% of the total number of specimens (Appendix 4).

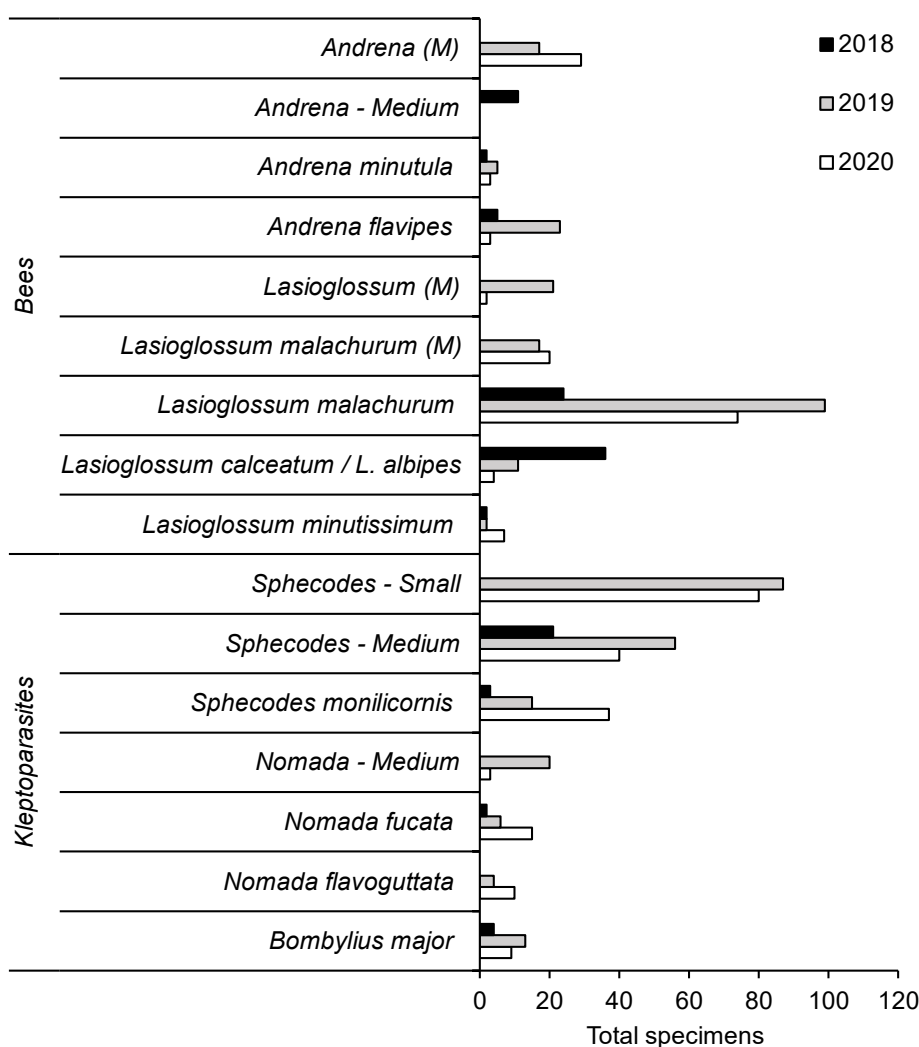


Figure 1: Total number of bees and kleptoparasites (> 10 individuals in total) sampled from all eight artificially created nesting plots in 2018, 2019 and 2020. Specimens that were only possible to identify to genus were grouped by their body length (small = 3 – 5 mm, medium = 5 – 7 mm, large = 7+ mm), and male specimens (M) were recorded separately.

NEST DENSITY

Peak nest density on plots did not significantly differ between years (Kruskal-Wallis rank test / $P = 0.605$; Fig. 2A). However, some plots attracted greater numbers of ground-nesting bees (Kruskal-Wallis rank test / $P < 0.000$; Fig. 2B) than others. The peak nest density on plot 5 was significantly less than on plot 2 ($P = 0.010$), 7 ($P < 0.000$) and 8 ($P = 0.001$), and the peak nest density on plot 7 was significantly larger than plot 1 ($P = 0.013$) (Dunn's Test of Multiple Comparisons). There was no significant difference in peak nest density between flat and slope sections (Mann-Whitney U test / $P = 0.243$; Fig. 2C). The mean diameter of nest entrances, measured in 2019 and 2020, was 3.08 ± 0.03 mm ($N = 1,295$, see Appendix 5), indicating that even though there were different species on the plots nest entrances were of similar size.

SOIL CHARACTERISTICS

Measurements of abiotic soil variables from 2018 and 2020 are summarised in Table 1. The ranges (min-max) of soil variables where bees were observed to nest were; $4.1 - 14.6$ kgf cm⁻² for soil compaction, $5.1e-5 - 5.35e-4$ (cm s⁻¹) for hydraulic conductivity, $1.0 - 34.6\%$ for stoniness, $3.6 - 15.9\%$ for organic matter, $25.5 - 29.9^\circ\text{C}$ for soil temperature, $13.5 - 19.7\%$ for soil moisture, $29.3 - 70.2\%$ for vegetation cover and $0 - 0.1\%$ for root biomass. Bees also tended to nest where vegetation cover on plots was $5 - 73\%$ thatch, then bare ground $5 - 95\%$, moss $0 - 58\%$ and finally green vegetation $0 - 27\%$ (see Appendix 8).

The soil texture of study plots was mostly sandy-loam or sandy-clay-loam, except for plot 5, which was in the sandy category (see soil texture triangles in Appendix 6). The ranges of soil textures where bees mostly nested were sand $48.4 - 70.9\%$, silt $9.4 - 34.4\%$ and clay $12.82 - 23.6\%$.

The highest peak nest density was recorded at 8.6 kgf cm⁻² for soil compaction, $2.4e-4$ (cm s⁻¹) for hydraulic conductivity, 19.8% for stoniness, 3.8% for organic matter, 28.5°C for soil temperature, 13.6% for soil moisture, 40.6% for vegetation cover, 0.02% for root biomass, and for soil texture; sand 60.4% , silt 22.2% , and clay 17.4% (sandy-loam category).

There was a significant difference in soil temperature between early morning ($16.7 \pm 0.06^\circ\text{C}$

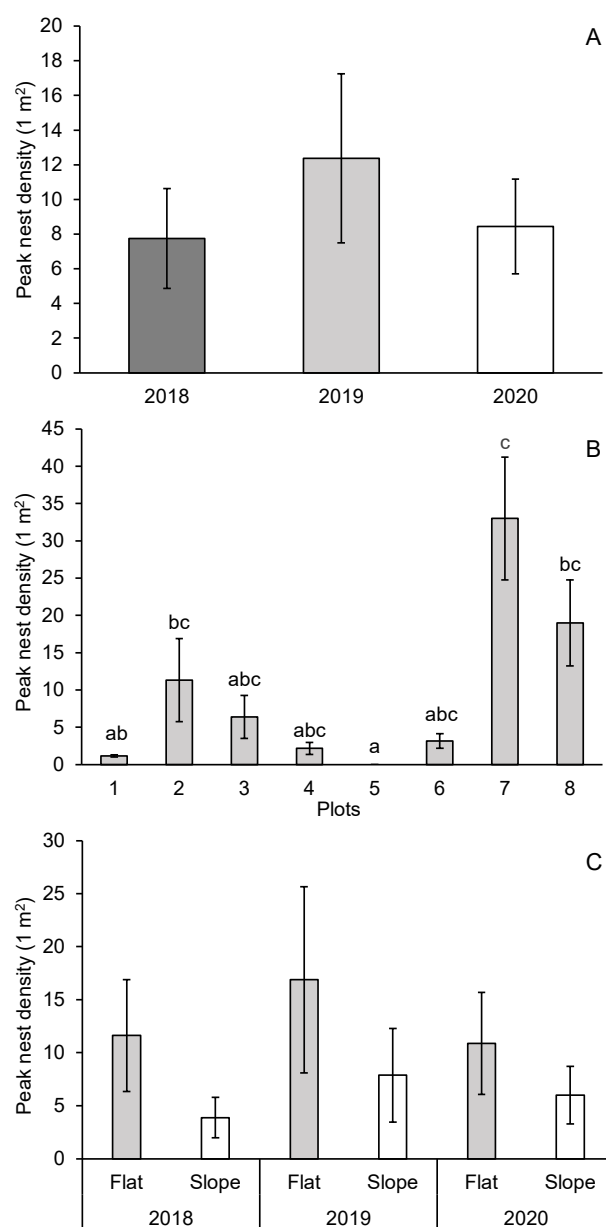


Figure 2: (A) Mean (\pm SE, $N = 8$) peak nest density for ground-nesting bees in artificially created nesting plots in 2018, 2019 and 2020. Peak nesting density was used because nest identification varies at each assessment depending on recent rain events, which can destroy the tumuli. There was no difference between years. (B) Mean (\pm SE, $N = 8$) peak nest density for ground-nesting bees in artificially created nesting plots over three years (2018 – 2020). Different letters indicate significant differences between plots ($P < 0.05$) according to Dunn's Test of Multiple Comparisons. (C) Mean (\pm SE, $N = 8$) peak nest density on the artificially created nesting plots over three years (2018 – 2020) on the flat and 10-degree sloped area. There was no difference between the flat and slope sections.

Table 1: Mean \pm SE, range and optimum values for soil and vegetation variables measured from eight study plots in 2018 and 2020.

	Variables	Mean \pm SE (N)	Range (Min – Max)	Optimum value
Bee nests	Peak nest density (1 m ²)	9.3 \pm 2.2 (28)	1 – 38	38
Plot characteristics	Hydraulic conductivity (cm s ⁻¹)	1.9e-4 \pm 1.5e-5 (84)	5.1e-5 – 5.35e-4	2.4e-4
	Soil compaction (kgf cm ⁻²)	9.0 \pm 0.3 (84)	4.1 – 14.6	8.6
	Soil water content (%)	16.0 \pm 0.1 (224)	13.5 – 19.7	13.6
	Soil temperature (°C)	27.5 \pm 0.1 (224)	25.5 – 29.9	28.5
Vegetation cover	Green vegetation (%)	2.4 \pm 0.4 (192)	0 – 27	0.9
	Thatch (%)	48.9 \pm 1.5 (192)	5 – 73	34.6
	Moss (%)	9.5 \pm 0.9 (192)	0 – 58	5.1
	Bare ground (%)	39.2 \pm 1.5 (192)	5 – 95	59.4
Soil Composition	Organic matter (%)	5.7 \pm 0.2 (112)	3.6 – 15.9	3.8
	Stoniness (%)	14.4 \pm 1.0 (112)	1 – 34.6	19.8
	Root biomass (%)	1.9e-2 \pm 3.0e-3 (32)	0 – 0.1	0.02
	Texture - Sand (%)	60.6 \pm 1.2 (16)	48.4 – 70.9	60.4
	Texture - Silt (%)	21.7 \pm 1.3 (16)	9.4 – 34.4	22.2
	Texture - Clay (%)	17.8 \pm 0.6 (16)	12.82 – 23.6	17.4

($N = 6,480$)), late morning ($17.0 \pm 0.06^\circ\text{C}$ ($N = 6,480$)), afternoon ($21.8 \pm 0.07^\circ\text{C}$ ($N = 6,480$)), and night ($20.1 \pm 0.07^\circ\text{C}$ ($N = 6,480$)) (Kruskal-Wallis rank test / $P < 0.000$; Appendix 7).

SUBSTRATE PARAMETERS AND NEST DENSITY

The model which included variables measured in 2018 and 2020, showed no significant correlation with peak nest density (Appendix 9). The model which included variables measured only in 2020, indicated that hydraulic conductivity (GLMM, $P = 0.028$), soil temperature ($P = 0.007$), stoniness ($P = 0.009$) and vegetation cover ($P = 0.005$) were significantly correlated with peak nest density (Tab. 2).

DISCUSSION

Artificial and ecological experimental studies investigating the nesting preference of ground-nesting bee species are limited (Orr et al. 2022). This study demonstrates that the provision of bare ground plots can provide a nesting resource for ground-nesting bees. The key nesting factors influencing nest site selection and peak nest density were stoniness, soil temperature, hydraulic conductivity, and vegetation cover.

Hydraulic conductivity and vegetation cover had a negative relationship, and soil temperature and stoniness had a significant positive relationship with peak bee nest numbers (Tab. 2).

SPECIES USING THE NESTING SITES

The 18 non-parasitic ground-nesting bee species identified were 7 *Andrena*, 9 *Lasioglossum*, 1 *Halictus* and 1 *Colletes* spp. (Appendix 4) representing 15% of mining bee species in Britain and Ireland (Else & Edwards 2018). Fortel et al. (2016) used human-made bare ground bee nesting structures and attracted 31 non-parasitic ground-nesting bee species within two years. This, and the present study, indicate that many ground-nesting bee species have similar nesting requirements. However, it is important to consider that in this study, 83.8% of recorded non-parasitic bee specimens (identified to species level) belonged to four bee species, *L. malachurum* Kirby (62.1%), *L. calceatum* Scopoli / *L. albipes* Fabricius (13.5%), and *Andrena flavipes* Panzer (8.2%). These species may have dominated the plots as fast colonisers rather than because such plots and soil characteristics are more suitable for them than other bee species. The remaining recorded bee species might establish

Table 2: GLMM analyses of soil variables for 2020 only. The variables which had significant correlation with peak nest density were hydraulic conductivity, soil stoniness, soil temperature and vegetation cover. Significant variables: 0 ‘*’ / 0.001 ‘***’ / 0.01 ‘**’ / 0.05 ‘.’**

Variables	Estimate	Std. Error	z value	P value	VIF
Slope	0.338	0.351	0.963	0.335	1.890
Hydraulic conductivity	-1.273	0.580	-2.194	0.028 *	1.355
Soil compaction	-0.060	0.332	-0.182	0.856	1.562
Soil organic matter	0.279	0.300	0.930	0.352	1.538
Soil stoniness	0.632	0.245	2.578	0.009 **	1.793
Soil texture (sand)	0.628	0.585	1.074	0.283	1.373
Soil temperature (WET)	0.968	0.359	2.699	0.007 **	1.367
Soil moisture (WET)	0.162	0.404	0.401	0.688	1.239
Vegetation cover	-0.669	0.238	-2.815	0.005 **	1.645

more slowly, so longer studies are necessary to capture their potential for colonisation.

In this study, 93% of identified bee specimens (species level) belonged to 9 species (non-kleptoparasites) which included bivoltine (spring and summer brood per year; *A. dorsata* Kirby, *A. flavipes* Panzer and *A. minutula* Kirby), and eusocial (*Lasioglossum pauxillum* Schenck, *L. malachurum* Kirby, *L. calceatum* Scopoli, *L. albipes* Fabricius, *Lasioglossum morio* Fabricius and *Halictus tumulorum* Linnaeus) species (Else & Edwards 2018). Moreover, the mean nest entrance diameter (3.08 ± 0.03 mm, Appendix 5) indicated that small *Lasioglossum*, *Halictus* and *Andrena* species were utilising the plots rather than larger Andrenids, such as *Andrena cineraria* Linnaeus, *Andrena haemorrhoa* Fabricius, and *Andrena nitida* Müller (6+ mm, K. Tsiolis, personal observation). The preference for these species to nest in bare soil needs further investigation.

Kleptoparasitic species arrived at the same time as bees from the first year of plot establishment. The most abundant genus was *Sphecodes* (79%) which are mainly kleptoparasites of *Halictus* and *Lasioglossum* genera in the Palearctic. The second most abundant was *Nomada* (15%) which predominantly attack the *Andrena* genus (Else & Edwards 2018).

ABIOTIC FACTORS AND NEST SITE-SELECTION

Nest excavation is a significant investment for most ground-nesting Hymenoptera, encompassing energy and time costs (Michener & Rettenmeyer 1956; McCorquodale 1989). Nevertheless, firmer soils can be beneficial for ground-nesting bees. Potts & Wilmer (1997) noted that soft soils are initially selected, but as the nest aggregation grows, they favour harder soils which support larger nest architecture.

There was a significant negative correlation between hydraulic conductivity and peak nest density (Tab. 2). A faster hydraulic conductivity rate increases drainage, resulting in soils with limited water content and may be favourable to ground-nesting bees as waterlogging is reduced. Johansen et al. (1978) reported that increased water infiltration is favoured by alkali bees (*Nomia* spp.) for nesting. Faster hydraulic conductivity rates could also be linked to soils with a greater percentage of stoniness enabling nest construction as observed in earwig (*Forficula auricularia* Linnaeus) nests (Lamb 1976). Conversely, more rapid hydraulic conductivity in sandy or very soft soils could result in nest collapse. In this study, plot 5 was sandy, had the highest rate of hydraulic conductivity (0.0011 cm s^{-1}) and no bee nests were observed (Fig. 2B). This variable can also be influenced by soil compaction as the shape, size,

and connectivity of microscale pores contribute to water flow in soils (Ebina et al. 2004).

Soil moisture ranged between 2.7 and 37.8% during the nesting activity of 32 ground-nesting bee species (Cane 1991), suggesting soil moisture content might be species-specific, but bees can tolerate a range of soil moisture. High fatality of *Andrena vaga* Panzer and local population decline (Fellendorf et al. 2004) and delayed emergence of male *Calliopsis pugionis* Cockerell (Visscher et al. 1994) resulted from waterlogged soils. Soils considered suitable for bee nesting are neither waterlogged nor too dry, and moderating moisture levels will contribute to successful larva development and minimal risk of brood cell desiccation (Potts & Wilmer 1997).

Soil texture influences soil temperature, moisture, and oxygen availability, which may impact bee survival inside a nest (Harmon-Threatt 2020). Ground-nesting bees, including *Halictus*, *Lasioglossum* and *Andrena* species, nest in clay-loam, sandy-loam, and silt-loam but not silt or clay soils (Cane 1991). Potts & Wilmer (1997) reported that *H. rubicundus* nested in sand/loamy and sand/sandy-loam soils, although texture was not correlated to nest numbers. Harmon-Threatt (2020) reviewed the soil preferences of 527 species in the USA and Canada. Soil texture was only reported in 48 descriptions, but 75% of bee species were nesting in sand or sandy-loam soils. The review also highlighted the lack of qualitative data on soil texture preferences. Bees in our study were also primarily nested in sandy-loam and sandy-clay-loam soils.

Stoniness had a significant correlation with peak nest density. Potts & Wilmer (1997) reported that 57% of nests of *H. rubicundus* were associated with stones which had higher temperatures compared to nests without stones. Soils of bee nests constructed under stones in halictid aggregations were 2–3°C warmer (at 5 cm) during the afternoon compared to bare soil (Packer et al. 1989). To test this, Cane (2015) introduced pebble mulch treatments to *H. rubicundus* nesting aggregations and found that 70% of bees built nests in plots with pebbles compared to bare soil control. Stones may also offer protection from parasitism (Potts & Wilmer 1997) and/or could serve as visual landmarks (Brünnert et al. 1994).

Organic matter softens soils, reducing compaction (Hamza & Anderson 2005) and darkens soil (Jackson 2014), improving the absorbance of solar radiation. Conversely, thick layers of organic matter may create a waterlogged environment (Bescansa et al. 2006). Although organic matter did not impact peak nest density in this study, soil from nesting sites of *L. malachurum* contained 0.004% (\pm 0.0012) organic matter (Polidori et al. 2010), and Grundel et al. (2010) found bee nest density negatively correlated with organic matter.

Increased vegetation results in greater soil moisture and lower soil temperature (Wuellner 1999; Anderson & Harmon-Threatt 2016). Wuellner (1999) reported that the ground-nesting bee, *Dieunomia triangulifera* Vachal, preferred nesting in soil with little to no vegetation, attributed to roots which disturb digging and may grow into nests. The findings of this study suggested a significant negative impact of vegetation cover but no negative impact of root biomass on bee nesting (Tab. 2).

This study intended to treat vegetation with herbicides at early growth stages to keep soil bare. However, this was not always possible due to weather conditions, and at times considerable amounts of vegetation grew and became thatch ($48.9 \pm 1.5\%$ (N=192)) after herbicide treatment. Additionally, the growth of moss was recorded ($9.5 \pm 0.9\%$ (N=192)) in the third year of the study. Both habitat types could significantly affect bee nesting and should be carefully managed in future studies.

As solitary bees are ectothermic (Stone & Willmer 1989), they cannot reliably control nest temperature. Belowground, low temperatures can result in slower nest founding and construction (e.g. *L. malachurum* (Weissel et al. 2006)). Additionally, nest entrance temperature sometimes facilitated by “chimneys” may initiate foraging (Norden 1984), as observed in this study by small *Lasioglossum* species which positioned themselves inside their ‘chimneys’ (see Appendix 10) for 1–2 minutes in the morning before leaving their nest (K. Tsiolis, personal observation). This study has shown that the average soil temperature during late morning hours (07:00 – 11:00) was at 17.0°C and 21.8 °C during afternoon hours (13:00 – 17:00).

There was no significant difference in the number of bee nests between the 10° gradient slope and flat sections of our study plots. However, it should be acknowledged that the slope sections of plots were created artificially in 2018, and the soil was not as compacted as on the flat sections. Soil compaction of slopes had increased by 2020 (Table 1), but longer-term studies are needed to determine if any further soil compaction occurred and the impact on peak nest density. Soil compaction also influences other variables, such as soil moisture (Soane & Ouwerkerk 1994) and hydraulic conductivity (Horton et al. 1994). The latter was shown to influence nesting in this study. Furthermore, it is possible that increasing slope gradient beyond >10° would be more beneficial for bee nesting; many bee nesting aggregations are often found in steep slopes such as riverbanks and drainage ditches (Michener 2007).

MANAGEMENT OF GROUND-NESTING BEE POPULATIONS

The availability of nesting and food resources are vital to sustaining bee populations; hence, both need to be considered as part of effective management for ground-nesting bees (Potts et al. 2003; Grundel et al. 2010; Murray et al. 2012). The provision of additional food resources in the form of nectar and pollen, such as flower strips (Haaland et al. 2011; Wratten et al. 2012), field margins (Rands & Whitney 2010), hedgerows (Garratt et al. 2017) and semi-natural land near farms (Martins et al. 2015) are highly beneficial for bees and improve bee abundance and diversity (Garibaldi et al. 2014; Venturini et al. 2016; Fountain 2022). Nevertheless, the nesting preferences of ground-nesting bees are under-researched (Antoine & Forest 2020).

The parameters that need to be considered in construction are 1) soil hydraulic conductivity between $5.1\text{e-}5$ – $5.35\text{e-}4$ cm s⁻¹ with the optimal value at $2.4\text{e-}4$ cm s⁻¹, 2) soil temperature between 25.5 – 29.9°C with the optimal value at 28.5°C, 3) soil stoniness between 1 – 34.6% with optimal value at 19.8%, and 4) vegetation cover between 29.3 – 70.2% with optimal value at 40.6% as they are factors in nesting of recorded *Andrena*, *Lasioglossum*, *Halictus* and *Colletes* species. However, there is a strong relationship between soil variables, which should be considered in creating such habitats.

Our approach to nest site creation could be used to support the conservation of bees or even promote pollination in systems where ground-nesting bees are important pollinators, such as apples (Garratt et al. 2016). Providing both food and nesting resources would potentially increase bee abundance and diversity (Kline & Joshi 2020; Fountain 2022); which is essential for inter-annual stability in pollinator communities (Senapathi et al. 2021). Where both appropriate food resources and nesting habitats exist, ground-nesting bees could remain and multiply for many years. Examples of long-lived ground-nesting aggregations are *Panurginus polytrichus* Cockerell for 20 years (Neff 2003), and *L. malachurum* Kirby for 37 years (Stöckhert cited in Michener 1974). Populations of the alkali bee (*N. melanderi* Cockerell), the world's only intensively managed ground-nesting bee due to its value for pollinating alfalfa (*Medicago sativa* L.), grew nine-fold (16.7 million females) over eight years (Cane 2008). Nevertheless, it should be acknowledged that bees tend to nest near their parental nests (philopatry), and the nest density could be caused by both soil characteristics and the propensity to nest at natal sites (Michener et al. 1958).

Though not directly tested in this study, farming practices should be considered in the process of enhancing the population of ground-nesting bees in agricultural landscapes. For instance, minimum or no-till practices should be favoured, as 10-20 cm tillage may directly kill and have a negative impact on the following year's emergence of ground-nesting bees (Shuler et al. 2005). Pesticide use, including ground-applied herbicides, should be minimised to prevent exposure during foraging (Brown & Paxton 2009; Bloom et al. 2021) and nesting. A recent study has shown that contamination of nesting soils of the ground-nesting solitary squash bee (*Eucera pruinosa* Scopoli) with a neonicotinoid (Imidacloprid, 18 mL/100 m row) insecticide; resulted in bees initiating 85% fewer nests, harvesting 5.3 times less pollen and producing 89% fewer offspring compared to untreated control soils (Willis & Raine 2021).

Individuals interested in undertaking a similar study would be encouraged to be patient and spend in the field as much time as possible to familiarise themselves with the identification of

bee nests and observe nesting behaviours that may play a significant role in understanding bee nesting preferences. There were several challenges during this study which should be considered for future experiments. The ability of the surveyor to identify bee nests was significantly reduced after heavy rain. As a result, it is suggested to pay close attention to the weather forecast and count nests after a minimum of 1-2 weeks of warm, dry weather during peak activity and before rainfall. Recording soil compaction was not a straightforward process due to the high percentage of stoniness at the site, which resulted in recording and discarding many false readings. Moreover, it was decided to mark assessed nests with plant labels, but it was soon realised that some labels were destroyed and removed by wildlife (possibly badgers). Vegetation cover is also a factor that requires close attention with the aim to control it at early growth stages to prevent accumulation of thatch on the plots, which could significantly influence bee nesting. This study could have been improved by recording the availability of bare ground cover and food resources near study plots for the entire duration of the study, as they can both influence bee nesting. This is particularly significant when such experiments take place in agricultural landscapes, which often experience frequent local habitat changes. This additional data would have helped with interpretations of findings.

CONCLUSION

A critical component for sustaining ground-nesting bee populations is the availability of suitable nesting resources, which can be a limiting factor in both urban and agricultural environments. This study provides new insights into the nesting needs of ground-nesting bees. It shows that artificially created bare ground plots could help provide nesting resources for several ground-nesting bee species if key abiotic conditions are considered. Further research is needed to enrich the current limited knowledge on nesting preferences of these important ground-nesting bees and allow the improvement and sustainable enhancement of their populations in agricultural and urban environments. Nevertheless, the findings of this study can contribute to raising farmers' awareness of the nesting needs of ground-nesting bee species, can

inform agri-environment schemes rewarding good practices, and support environmental policy.

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APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix 1. Map of bare ground bee nesting plots and a photograph of a plot at NIAB EMR.

Appendix 2. Surrounding habitat type and dominant local vegetation type of plots.

Appendix 3. Soil sampling method.

Appendix 4. Bee and wasp species sampled from plots in each year of the study.

Appendix 5. Mean diameter of nests' entrance on flat and slope sections of plots.

Appendix 6. Soil texture of flat and sloping areas of plots.

Appendix 7. Mean soil temperature (°C) of plots in the morning, afternoon, and night hours.

Appendix 8. Mean percentage of plot's vegetation cover.

Appendix 9. Summary of GLMM analyses of soil variables measured both in 2018 and 2020.

Appendix 10. Examples of solitary ground-nesting bee nests with "chimneys".

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