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Do nest sites limit wild honey bee colonies? Decoding swarm waggle dances to assess nest site availability

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Abstract

1. Nest sites are often considered to limit wild honey bee, *Apis mellifera*, colonies in Europe where wild colony densities are low (mean 0.26/km^2). Nest site availability can be challenging to quantify directly, especially in urban areas and farmland where colonies nest in different substrates.
2. Here we assess nest site availability indirectly across large areas (78.5 km^2) of mixed habitat (67% farmland, 25% urban and 8% woodland) by decoding 3310 waggle dances produced by scouts on swarms. During summers of 2021 and 2022, 14 artificial swarms were set up in two study areas in East Sussex, England.
3. Swarms advertised three to nine nest locations (mean of 5.5) at distances of 0.1–11.2 km (median 1.2 km) all within 0.4–15.2 daylight hours after dancing commenced (median 2.7). We estimated the total number of nest locations, including those not advertised, by quantifying the overlap in locations advertised by two swarms (a form of mark–recapture), which gave a mean density of approximately three nest sites per km^2.
4. The probability of swarms advertising nest sites per km^2, calculated using simulations of dance variation, was an average of 42% higher in urban areas (0.018/km^2), 78% higher in woodland (0.023/km^2) and 12% lower in farmland (0.011/km^2) than random expectation. After controlling for distance, swarms were still more likely than expected to advertise nest sites in woodland but only in one study area.
5. Our results indicate that nest sites do not limit wild colonies in the study areas given that our conservative estimate of nest site density (3/km^2) exceeds the density of wild colonies on nearby landed estates (2/km^2) and other locations in Europe (0.26/km^2).

KEYWORDS
Apis mellifera, artificial swarms, conservation, landscape ecology, nest site availability, waggle dance decoding, wild honey bees

INTRODUCTION

Wild honey bee, *Apis mellifera*, colonies naturally nest in tree cavities throughout their native range in Europe (Kohl & Rutschmann, 2018) and Africa (Kajobe & Roubik, 2006) and their introduced range in the Americas (Ratnieks et al., 1991; Seeley, 2007) and Oceania (Oldroyd et al., 1994). Wild colonies also nest in cavities in buildings and other man-made structures (Bila Dubaić et al., 2021; Boreham & Roubik, 1987; Morse et al., 1990) and occasionally in rock crevices (Taber, 1979; Wenner, 1989) and other substrates such as termite nests (Boreham & Roubik, 1987; McNally & Schneider, 1996; Ratnieks et al., 1991). Nest site availability is often considered to limit wild colonies in Europe (Carreck, 2008; Kohl et al., 2023; Kohl & Rutschmann, 2018; Niklasson et al., 2023; Oleksa et al., 2013). Wild honey bee colony density has been quantified at more than 40 locations worldwide and ranges from 0.1 to 24.2/km^2 with a global mean of 2.4/km^2, although densities are lower in Europe (mean 0.26/km^2, $n = 8$ locations) than other continents (Visick & Ratnieks, 2023). It is unclear whether this low European density is due to a shortage of nest sites or other limiting factors such as food availability or climate. Remm and Lõhmus (2011) found that tree cavities suitable for nesting by vertebrates occur at a median density of 16/ha in 133 forests worldwide and those densities were lowest (5.6/ha) in the Palearctic (most sites were in Europe). Not all cavities will be suitable for wild honey bee colonies, given that honey bee nesting requirements can differ from those of vertebrates (Oldroyd et al., 1994). Wild colonies typically use large cavities of 15–80 L (McNally & Schneider, 1996; Oldroyd et al., 1994; Ratnieks et al., 1991; Seeley, 1977) with small entrances of 10–60 cm^2 (Baum et al., 2005; Gambino et al., 1990; Oldroyd et al., 1994; Ratnieks et al., 1991; Seeley & Morse, 1976). Cavity-nesting passerines in Europe, such as the great tit (*Parus major*) and collard flycatcher (*Ficedula albicollis*), typically use small cavities of less than 5 L (Maziarz et al., 2015; Remm et al., 2006; Walankiewicz et al., 2007).

Honey bee nest site availability has only been quantified by a few studies in Europe and all are in forests where wild colonies are only nesting in trees. Based on limited data regarding volume, Requier et al. (2020) estimated that 0.4% of cavities in European forests are suitable. Combined with predicted cavity densities of 8.5–25.2/ha (Requier et al., 2020), this gives honey bee nest site densities ranging from 3.4 to 10.1/km^2 of forest in different European countries. Kohl et al. (2022) found that wild colonies primarily nested in cavities created by black woodpeckers, *Dryocopus martius*, in two German forests and that woodpecker nests suitable for honey bees (85% of nests) occur at densities of 1.4–3.7/km^2 (Kohl et al., 2022, Suppl.). Direct surveys of nest site density are impractical in urban areas and farmland where wild colonies are nesting in different substrates. Therefore, an indirect approach to quantify nest site availability would be advantageous.

Waggle dances are used by honey bee foragers to advertise the location of foraging resources (nectar, pollen, water and propolis; von Frisch, 1967). Waggle dances are also used by scout bees on swarms to advertise the location of nest sites (Lindauer, 1955; Seeley, 2010). Dance decoding has been used to study many applied aspects of honey bee foraging ecology, including seasonal changes in foraging distances and habitat preferences (Balfour & Ratnieks, 2017; Bänsch et al., 2020; Carr-Markell et al., 2020; Couvillon et al., 2014a; Couvillon et al., 2014b; Couvillon et al., 2015; Danner et al., 2016; Garbuzov et al., 2014; Garbuzov et al., 2015; Ohlinger et al., 2022; Ohlinger et al., 2024; Rutschmann et al., 2023; Samuelson et al., 2022; Silliman et al., 2022; Steele et al., 2022). In the context of swarming, dance decoding has been used to understand the process of nest site selection (Lindauer, 1955; Seeley, 2010) and swarm dispersal distances (Kohl & Rutschmann, 2018; Seeley & Morse, 1977; Schneider, 1995). However, as with foraging resources, dance decoding also has the potential to provide ecological information on the availability and distribution of nest locations.

Here we decode 3310 waggle dances produced by scouts on 14 artificial swarms set up in two mixed urban–rural locations in East Sussex, England, to assess nest site availability. We determine the number of advertised nest locations and the distance of each from the swarm. We estimate the number and density of all nest locations, including those not advertised, using the logic of mark–recapture. We use simulations of dance variation to calculate nest site probability densities in farmland, urban and woodland land types and determine whether these deviated from expectations before and after controlling for the distance of each land type to where swarms were set up. Finally, we discuss the implications of our results to honey bee conservation and the factors limiting wild colonies in Britain and elsewhere in Europe.

METHODS

Study areas

Swarms were set up in two study areas near the towns of Eastbourne and Brighton in East Sussex, England. Study areas were 25 km apart and in each, there were four sites where swarms were set up (Figure 1). Three were close, within 0.5–1 km, with the other over 3 km away. Swarms were set up at different sites so that nest locations could be determined more accurately through triangulation. A total of seven swarms were set up in each study area (one or two at each site). Swarms were set up in Eastbourne in 2021 and 2022, whereas all swarms in Brighton were set up in 2022. Swarms were set up from mid-June to early August to avoid interference from natural swarms, which occur from April to June in the study area.

Swarm preparation

We used the long-established method of studying artificial swarms (Morse & Bosh, 1977; Simpson, 1962). A total of 1 kg of worker bees and a queen were removed from a strong colony at an apiary over 5 km from both study areas. Bees were kept in a well-ventilated box and stored in a cool (c. 20°C) dark room for at least 36 h. During this

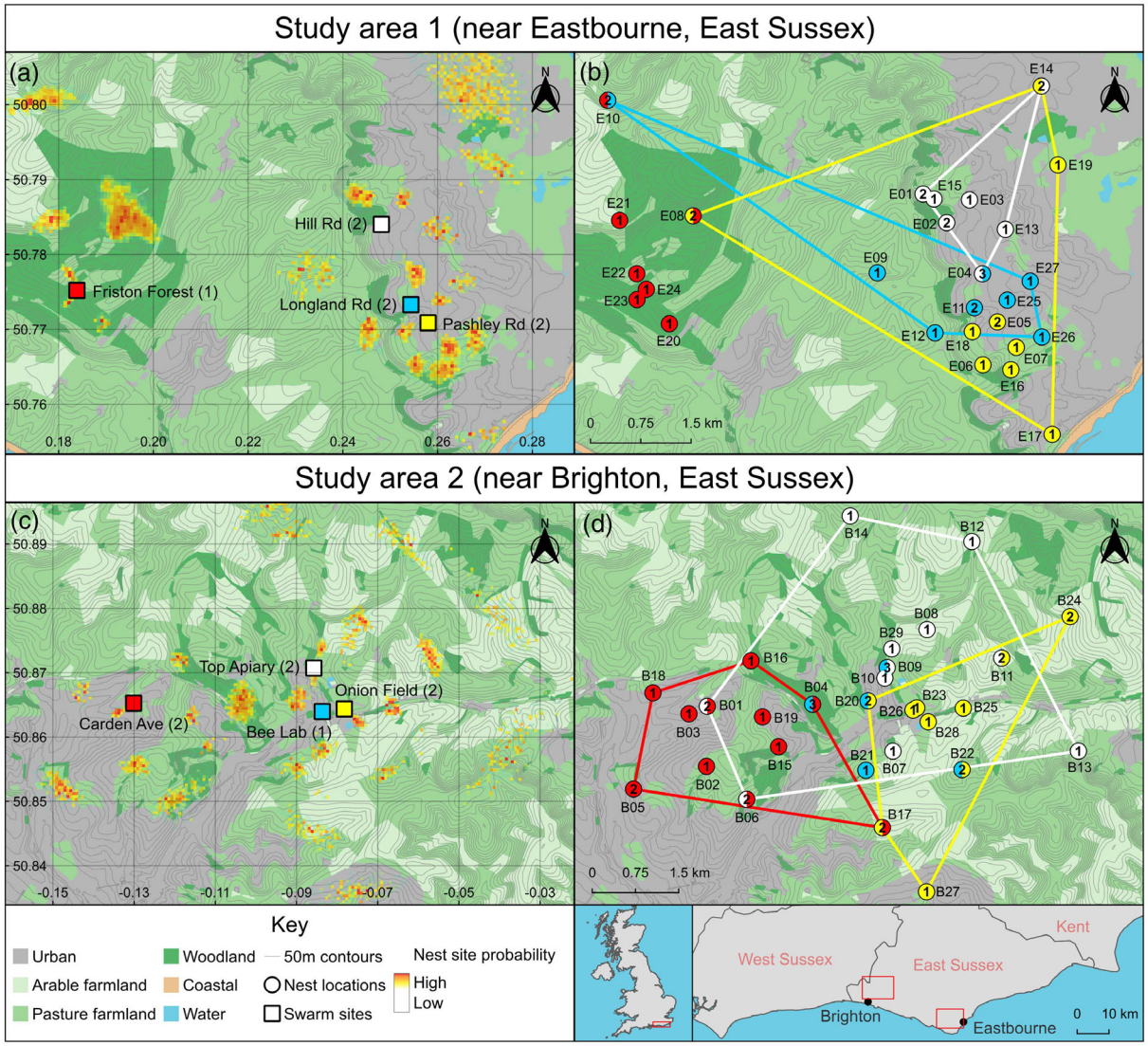

FIGURE 1 Study areas in East Sussex, England. (a and c) Sites where swarms were set up in each study area. The number of swarms set up at each site is shown in parentheses. Grids show latitude and longitude (decimal degrees). Heatmaps (yellow and red cells) for dances advertising the same nest locations were combined and normalised. Only cells with the highest probabilities (top 25%) are visible and these were averaged to produce nest locations (circles, $n = 56$) shown in (b) and (d). (b and d) The colour of each nest location corresponds with the site of the swarm that advertised it. Nest locations with two colours were advertised by swarms set up at different sites. The number inside each nest location shows how many swarms advertised it. Thirty-eight nest locations (68%) were advertised by one swarm, 15 (27%) by two and 3 (5%) by three. Polygons show minimum bounding areas used to estimate density at sites where two swarms were set up ($n = 6$). Map made in QGIS (v3.32.1).

period, bees were fed liberally with 50% sucrose solution. Following Seeley and Buhrman (1999), swarms were mounted on a 50 × 50 cm board attached to the top of a 150 cm post (Figure 2). A queen cage, digital clock and two glass jar feeders, each with 500 mL of 50% sucrose solution, were secured to the board. Swarms were set up in the morning (c. 11:00), and bees had usually clustered and started dancing by midday.

A video camera (Sony Handycam®) was set up on a tripod 2 m from the swarm and was made level and perpendicular to minimise parallax errors. Swarm activity was recorded from approximately 08:00 to 19:00 every day until departure. Queens were caged to stop swarms moving into their chosen nest site. Swarms were put back into the box in the evening following departure and then transferred into a hive or used again at the other study area. Swarms were used a maximum of twice (once per study area).

Waggle dance decoding

Every waggle dance recorded on a swarm was decoded, except for swarms which produced over 500 dances. In these cases, dances were decoded until they were all for a single location. At this point, it was unlikely that more locations would be advertised as the final decision had been made (Seeley, 2010). The angle and duration of up to six

FIGURE 2 Artificial swarm of approximately 5,000–10,000 bees mounted on a vertical 50 × 50 cm board in the study area near Brighton, East Sussex, England. The swarm and video camera (opposite) are 1.5 m above ground and 2 m apart. Inverted glass jars filled with 50% sucrose solution were secured above the swarm to keep the bees well-fed and obviate the need to forage and advertise flower patches. The queen is caged (not visible) to stop the swarm from departing to their chosen nest site. A digital clock was placed beside the swarm for azimuth calculations. The video camera was mounted on a tripod and protected from the elements by an umbrella. The swarm itself was set up in the shade to prevent light-dependent misdirection (Seeley & Buhrman, 1999) but was otherwise exposed to the elements.

consecutive waggle runs were recorded for each dance, excluding the first and last run, which are more variable (Couvillon et al., 2012). Angle was converted to bearing by adding the solar azimuth. Duration (s) was converted to distance (km) using a Bayesian calibration model by Schürch et al. (2013), who collected calibration data in our study area with the same local bees. We chose this site-specific model over the universal calibration by Schürch et al. (2019) because it performs better at longer distances (Carr-Markell & Spivak, 2021). We report the mean distance produced by the calibration model for each nest location.

Number and density of nest locations

Dances advertising the same location can exhibit considerable variation in waggle run angle and duration (Couvillon & Schürch, 2012). We refer to advertised nest sites as 'nest locations' because their exact position could not be easily determined. We decided to omit nest locations represented by fewer than five dances as the resulting locations would have been particularly inaccurate. Therefore, our estimate of the number of nest locations is conservative. The effect of date, dance numbers, scouting time and study area on the number of locations advertised by swarms was tested using linear models. We define scouting time as the number of daylight hours taken to advertise all nest locations once dancing had commenced. Analyses and plots were made using R v4.3.1 (R Core Team, 2023) and *ggplot2* (Wickham, 2016).

Heatmaps containing one thousand 50 × 50 m (0.0025 km^2) cells were generated for each dance using simulations of dance variation (Schürch et al., 2013). Heatmaps for dances advertising the same location were combined, including those from different swarms. Heatmaps were then normalised (cell values range from 0 to 1) or averaged (cell values sum to 1) for land type analyses. Cells in the normalised heatmaps with the highest values (>0.75) were averaged to determine the approximate location of each nest site (Figure 1).

The total number of nest locations (N), including those not advertised, was estimated at sites where two swarms had been set up ($n = 6$) using the logic of mark–recapture. Density was calculated by dividing our estimate ($\widehat{N}$) by the minimum bounding area of advertised locations at each site (Figure 1). We use a modified version of the Petersen estimator for mark–recapture, which is less biased at small sample sizes (Chapman, 1951).

$$\widehat{N} = \frac{(M+1)\cdot(C+1)}{R+1} - 1.$$

M and C are the number of locations advertised by swarms 1 and 2, respectively, and R is the number of locations advertised by both. For example, if swarms 1 and 2 advertise 3 and 4 locations, respectively, and 1 location was advertised by both then $\widehat{N}$ is 9 (see Section 4 for assumptions). This estimator can still produce significant negative bias at low $M \cdot C/N$, where N is a rough estimate of total nest site numbers based on existing information (Chapman, 1951). We estimate that $N = 24$, based on the mean number of nest locations advertised by natural swarms in Munich, Germany (Lindauer, 1955). Total nest site numbers are underestimated by an average of 37% when $M \cdot C/N = 1$, which decreases to 5% at $M \cdot C/N = 3$ and 2% at $M \cdot C/N = 4$ (Robson & Regier, 1964). Therefore, each of our artificial swarms would have to advertise approximately 10 nest locations to reduce estimator bias to a negligible level of 2%.

Effect of land type

Averaged heatmaps were clipped to a 5 km radius (78.5 km^2) from where swarms were set up in each study area (mean coordinates of swarm sites in Figure 1). Farmland (arable and pasture), urban areas and woodland were mapped in these areas using the Land Cover Map 2021 (Marston et al., 2022). The mean probability of swarms advertising nest sites per km^2 (nest site probability density) was calculated for each cell in the clipped heatmaps. The effect of land type on nest site probability density was tested using zero-inflated Gamma generalised linear models with study area included as an interaction term. We do not report p-values due to the large sample size (n = 58,440 cells) and increased risk of false positives. Instead, we report estimated marginal means (EMMs) and 95% confidence intervals for each land type and effect sizes (% difference) when compared to expected values or EMMs from other land types. EMMs are given before and after controlling for the distance of each land type to where the swarms were set up.

TABLE 1 Summary of 14 swarms set up in two study areas in East Sussex, England. Column 5 shows the number and percentage of waggle dances assigned to nest locations per swarm (2911 and 88% overall). Scouting and departure times are the number of daylight hours taken to advertise all nest locations and take-off, respectively, once dancing had commenced.

Site	Swarm	Date	Dances	No. assigned	Nest locations	Scouting (h)	Departure (h)
Eastbourne							
Hill Rd	1	23 June 2021	257	220 (86%)	4	13.9	18.7
Pashley Rd	1	21 July 2021	128	109 (85%)	4	3.3	11.6
Longland Rd	1	04 August 2021	204	176 (86%)	5	0.8	4.1
Hill Rd	2	22 June 2022	560	529 (94%)	5	0.6	14.3
Pashley Rd	2	27 June 2022	163	152 (93%)	6	8.3	14.5
Friston Forest	1	04 July 2022	278	252 (91%)	7	0.6	13.4
Longland Rd	2	01 August 2022	110	98 (89%)	5	2.2	27.4
Brighton							
Carden Ave	1	16 June 2022	205	177 (86%)	6	0.9	3.6
Top Apiary	1	16 June 2022	399	376 (94%)	9	11.4	14.2
Carden Ave	2	20 June 2022	156	133 (85%)	7	2.2	2.9
Bee Lab	1	28 June 2022	229	168 (73%)	5	15.2	18.1
Onion Field	1	08 July 2022	316	282 (89%)	6	0.4	3.8
Onion Field	2	05 August 2022	180	128 (71%)	5	13.2	16.2
Top Apiary	2	11 August 2022	125	111 (89%)	3	11.3	13.8

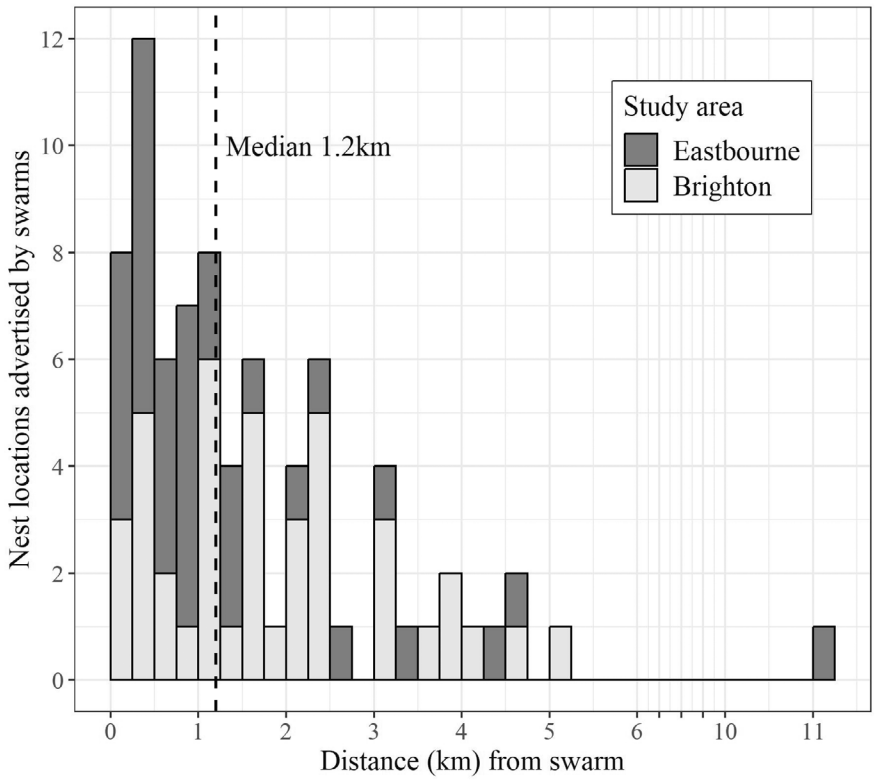

FIGURE 3 Distance of 56 nest locations indicated by waggle dance decoding of nest sites from 14 swarms. Nest locations were advertised by 1 ($n = 38$), 2 (30) and 3 (9) swarms ($n = 77$ distances in 250 m bins). Waggle run duration was converted to distance using a Bayesian calibration model by Schürch et al. (2013). Swarms advertised nest locations at distances of 0.1–11.2 km (median 1.2 km).

RESULTS

Number, density and distance of nest locations

A total of 3310 waggle dances were decoded in the summers of 2021 and 2022. Dance numbers ranged from 110 to 560 (mean 236) per swarm (Table 1) and 5 (see Section 2) to 393 (median 26) per nest location (Table S1). Swarms advertised three to nine nest locations (mean 5.5) at distances of 0.1–11.2 km (median 1.2; Figure 3) all within 0.4–15.2 daylight hours (median 2.7) after dancing commenced. Swarm departure occurred 2.9–27.4 daylight hours (median 12.6) after dancing commenced. Swarms set up later in the year advertised significantly fewer nest locations ($F_{1,12} = 6.3$, $p = 0.03$; Figure 4). Swarms advertised a mean of 6.1 (±0.5) nest locations in mid-June to early July ($n = 9$), which decreased to 4.4 (±0.4) in late July to early August ($n = 5$). The number of advertised locations was not affected by dance numbers ($F_{1,12} = 1.9$, $p = 0.19$), scouting time ($F_{1,12} = 0.4$, $p = 0.53$) or study area ($F_{1,12} = 0.77$, $p = 0.40$).

Swarms advertised a total of 56 unique nest locations across the two study areas (Eastbourne 27, Brighton 29; Figure 1). Thirty-eight nest locations (68%) were advertised by one swarm, 15 (27%) by two and 3 (5%) by three. The total number of nest locations, including those not advertised, was estimated at six sites using the logic of mark–recapture and ranged from 9 to 20 (mean 15.5; Figure 5). 'Recapture' rates were low, with swarms only advertising one or two of the same nest locations. Advertised nest locations occurred over areas ranging from 2 to 20 km^2 (mean 9.3), which resulted in estimated densities of 1–4.7 available nest sites per km^2 (mean 2.4; Table 2). Swarms advertised an average of 5.5 nest locations, which is less than the 10 required to avoid significant negative bias in the mark–recapture calculations (see Section 2). As a result, total nest site numbers were likely underestimated by c. 30% (Robson & Regier, 1964; Table 2), making the actual average density approximately 3/km^2.

Effect of land type

The most common land type in both study areas was pasture farmland (Eastbourne 57% and Brighton 48%), followed by urban areas (Eastbourne 26% and Brighton 23%), arable farmland (Eastbourne 6% and Brighton 23%) and woodland (Eastbourne 11% and Brighton 6%). Nest site probability densities averaged 42% higher in urban areas (Eastbourne 0.019 ± 0.0006 and Brighton 0.017 ± 0.0005), 78% higher in woodland (Eastbourne 0.028 ± 0.0013 and Brighton 0.018 ± 0.0010) and 12% lower in farmland (Eastbourne 0.011 ± 0.0002 and Brighton 0.011/

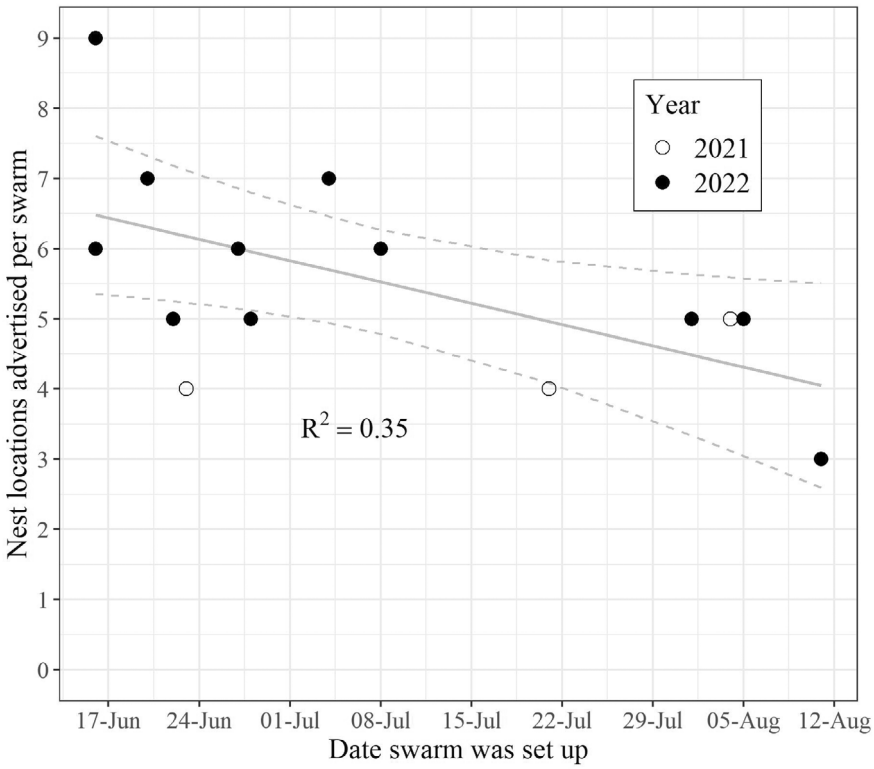

FIGURE 4 Number of nest locations advertised per swarm throughout the study period. Fourteen swarms were set up from mid-June to early August in 2021 and 2022. Swarms set up later in the summer advertised significantly fewer nest locations ($p = 0.027$). Swarms advertised an average of 6.1 (±0.5) nest locations in mid-June to early July ($n = 9$), which decreased to 4.4 (±0.4) in late July to early August ($n = 5$). Fitted values (solid line), 95% confidence intervals (dashed line) and R^2 were produced using a linear model.

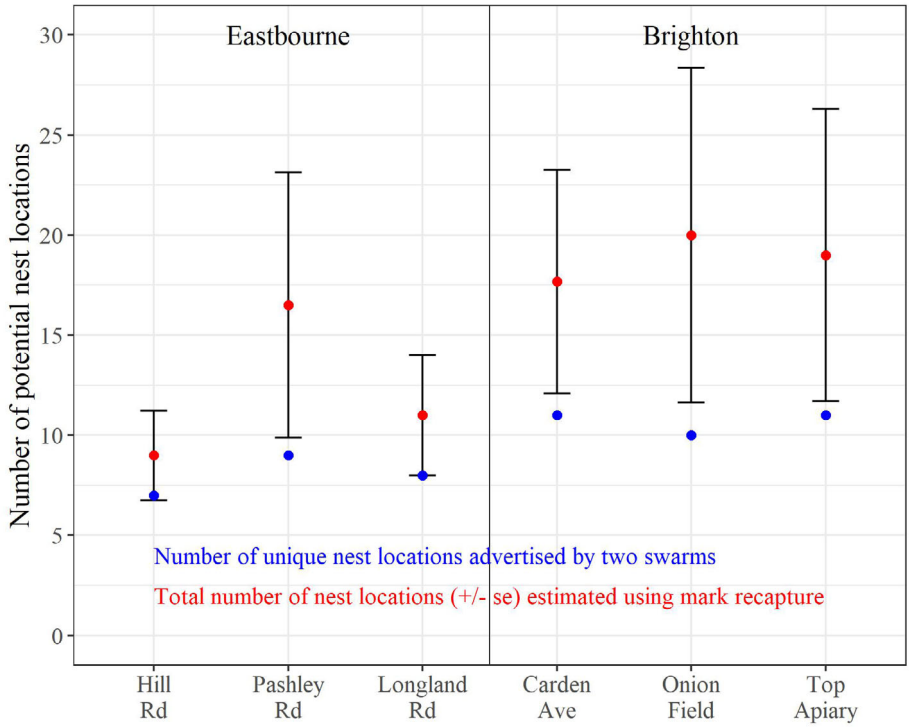

FIGURE 5 Total number of nest locations estimated using mark–recapture. The number of unique nest locations advertised by two swarms set up at the same site (blue points) was calculated as $M + C - R$, where M and C are the number of locations advertised by swarms 1 and 2, respectively, and R is the number of locations advertised by both. The estimated total number of nest locations, including those not advertised, (red points) +/− standard error (vertical bars) was calculated using the Chapman estimator for mark–recapture, $\frac{(M+1)\cdot(C+1)}{R+1} - 1$.

TABLE 2 Overlap in nest locations advertised by two swarms was quantified at six sites to estimate the total number of nest locations. Our estimate ($\widehat{N}$) was calculated using the Chapman estimator for mark–recapture, $\frac{(M+1)\cdot(C+1)}{R+1} - 1$, where M and C are the number of nest locations advertised by swarms 1 and 2, respectively, and R is the number of locations advertised by both. Estimator bias was calculated using the formula, $100 \cdot e^{-M \cdot C/N}$, where N is a rough estimate of total nest site numbers ($N = 24$; see Section 2; Robson & Regier, 1964). Area (km^2) is the minimum bounding area of advertised locations (polygons in Figure 1).

Site	Swarm 1	Swarm 2	Interval (d)	M	C	R	$\widehat{N}$	SE	% bias	Area (km^2)	Density ($\widehat{N}$/km^2)
Eastbourne											
Hill Rd	23 June 2021	22 June 2022	364	4	5	2	9	2.2	−43.5	1.9	4.7
Pashley Rd	21 July 2021	27 June 2022	341	4	6	1	16.5	6.6	−36.8	14.1	1.2
Longland Rd	04 August 2021	01 August 2022	362	5	5	2	11	3	−35.3	5.0	2.2
Brighton											
Carden Ave	16 June 2022	20 June 2022	4	6	7	2	17.6	5.6	−17.4	7.5	2.4
Onion Field	08 July 2022	05 August 2022	28	6	5	1	20	8.4	−28.7	7.2	2.7
Top Apiary	16 June 2022	11 August 2022	56	9	3	1	19	7.3	−32.5	19.9	1.0

km^2 ± 0.0002) than random expectation (0.013 in 78.5 km^2 study areas; Figure 6). Swarms were approximately twice as likely to advertise nest sites (per km^2) in urban areas and woodland than farmland. Nest site probability densities in woodland remained higher than expected after controlling for distance in Eastbourne (0.029 ± 0.0011) but not Brighton (0.008 ± 0.0004). Nest site probability densities in urban areas were close to random expectation after controlling for distance (Eastbourne 0.010 ± 0.0002 and Brighton 0.012 ± 0.0003).

DISCUSSION

Our results show that decoding swarm waggle dances can be used to assess honey bee nest site availability, just as decoding forager dances can be used to study honey bee foraging ecology. Swarms advertised three to nine nest locations (mean 5.5), which is lower than previous studies. Swarms set up by Seeley and Buhrman (1999) in upstate New York advertised 5–13 nest locations (mean 9.7). Swarms set up by Schneider (1995) in Costa Rica advertised

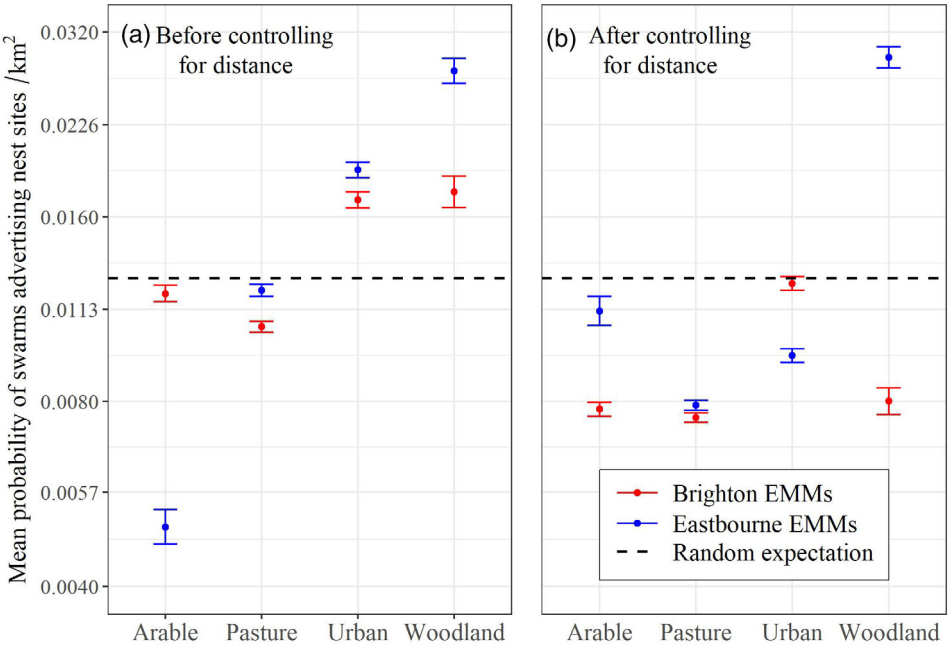

FIGURE 6 Effect of land type on nest site probability density. The Y-axis is on a log scale. Points show estimated marginal means (EMMs) produced by zero-inflated generalised linear models before (a) and after (b) controlling for the distance of each land type to where swarms were set up. Error bars show 95% confidence intervals. Dashed lines show the expected nest site probability density in each 78.5 km^2 study area (0.013/km^2). (a) Nest site probability densities averaged 42% higher in urban areas (0.018/km^2), 78% higher in woodland (0.023/km^2) and 12% lower in arable and pasture farmland (0.011/km^2) than expected. (b) Nest site probability densities were still higher in woodland after controlling for distance but only in the Eastbourne study area.

3–23 nest sites (mean 12.2). Both locations contained large areas of unmanaged woodland containing many trees with cavities (Schneider, 1995; Seeley & Buhrman, 1999). Therefore, it is not surprising that swarms advertised more nest locations than in our study areas, which averaged only 8% of woodland most of which is managed.

Natural swarms observed by Lindauer (1955) in Munich, Germany, advertised 13–34 nest locations (mean 24), over four times as many in our study. However, natural swarms are larger than those prepared artificial and may begin looking for nest sites before leaving the parental colony (Seeley, 2010; von Frisch & Lindauer, 1956). Our swarms consisted of 5,000–10,000 bees, which is smaller than most natural swarms in northern latitudes (Fell et al., 1977; Morse & Bosh, 1977). In addition, we only considered locations represented by at least five dances. Therefore, dance decoding of artificial swarms will provide a conservative estimate for nest site numbers.

Using the logic of mark–recapture, we estimated the total number of nest locations, including those not advertised, by quantifying the overlap in locations advertised by two swarms. This assumes that all nest locations, that exceed a given quality threshold and elicit dancing, had an equal chance of being found by swarms. However, closer locations are more likely to be found and may be overrepresented by dance decoding. Half of all advertised locations were within 1.2 km (Figure 3), although we did observe long-distance locations up to 11.2 km (E10; Figure 1). This is within the distance that the waggle dance can communicate, which occurs in foraging but rarely (Beekman & Ratnieks, 2000; Eckert, 1933; Steele et al., 2022; von Frisch, 1967), and indicates that swarms have the capacity to scout large areas in a relatively short period of time.

We also assumed that all nest sites were available to both swarms (i.e., nest site 'mortality' was zero). Queens were caged to stop swarms moving into their chosen nest site and rendering it unavailable to other swarms, so this source of error is absent. It is possible that nest sites were occupied by natural swarms between surveys, which would result in decreased recapture rates and an overestimate of nest site numbers and density. However, this is unlikely because swarms were set up in mid to late summer when most natural swarming in the study area is over. In addition, recapture rates were relatively constant, despite considerable variation in the interval between swarms (Table 2). Therefore, we are confident that nest site availability remained constant throughout the study period and that our estimate of nest site numbers and density is conservative.

Implications for honey bee conservation: do nest sites limit wild colonies?

Honey bee nest site density was estimated to be approximately 3/km^2 in both study areas, which falls within the range of densities reported in European forests (1.4–10.1/km^2; Kohl et al., 2022, suppl.; Requier et al., 2020). Our study was done after the main swarming

season but before winter mortality, at the time of maximum prior occupation of nest sites by wild colonies in our study areas. Therefore, our estimate of three nest sites per km^2 was in addition to those already occupied.

Wild colonies occur at densities of approximately 2/km^2 on landed estates near the study area (authors, unpublished), where high-quality nest sites are more abundant than in the wider landscape due to high densities of veteran trees (Visick & Ratnieks, 2024). Therefore, 2/km^2 probably represents the maximum density that wild colonies could occur in the study area. Indeed, the density of colonies that survive the winter on estates is closer to 1/km^2 (authors, unpublished). Wild colony densities reported elsewhere in Europe are as low as 0.1/km^2 (Kohl et al., 2022; Kohl & Rutschmann, 2018; Oleksa et al., 2013) and lower than that of managed hives (mean 1.2/km^2; Visick & Ratnieks, 2023). Overall, this strongly suggests that nest sites do not limit wild colonies in our study area, given that our conservative estimate of nest site density (3/km^2) exceeds wild colony densities recorded nearby and elsewhere in Europe.

Our results show that swarms advertised significantly fewer nest locations in late summer (Figure 4). This was not due to differences in day length because the number of advertised locations was not affected by scouting time, which we calculated within daylight hours. There is no clear explanation for this result. Nest site availability might decrease later in the year if a larger proportion of cavities are occupied by natural swarms. However, swarming in the study area is over by mid-June so that most cavities occupied that year would be occupied before our data collection began. In addition, all 14 swarms departed for their chosen nest site after a relatively brief period of house hunting (mean 12.6 daylight hours), even in late summer. If nest sites were in short supply, one would expect the process to take longer.

Nest sites have been shown to limit several cavity-nesting birds in managed forests by studies that have recorded changes in breeding density after manipulating nest site availability (reviewed by Newton, 1994; Weibe, 2011). Nest site limitation in wild honey bee colonies is based on circumstantial evidence. For example, high occupancy rates (>25%) of bird nest boxes by honey bee swarms have been reported in Australia (Soderquist et al., 1996; Lindenmayer et al., 2016) and the Americas (Coelho & Sullivan 1994; Liébana et al. 2013). However, without data on colony density and nest site availability, it is impossible to determine whether colony numbers have increased in response to additional nest sites or whether colonies have simply switched from nesting in variable-quality natural sites to highly attractive artificial sites (Broughton et al., 2015; Newton, 1994; Saunders et al., 2021). Indeed, the low occupancy (<10%) of natural tree cavities by wild colonies (Kohl & Rutschmann, 2018; Oldroyd et al., 1994; Oleksa et al., 2013; Visick & Ratnieks, 2024) strongly suggests that nest sites are not limiting. However, experimental manipulations of nest site availability are needed to conclusively determine whether nest sites are limiting (Newton, 1994). In the case of the honey bee, one obvious factor limiting wild colonies in Europe is food supply, particularly in late summer when competition with managed colonies is likely at its greatest (Couvillon et al., 2014a; Rutschmann et al., 2023).

Effect of land use

Nest locations were well distributed across land types (Figure 1). Nest site probability densities were higher in urban areas and woodland than expected (Figure 6). After controlling for distance, nest site probability densities in urban areas were close to expected values. Most swarms were set up in residential gardens and may have been more likely to advertised nearby nest sites. In urban areas, wild colonies have been shown to nest in cavities in buildings and other man-made structures, such as water meters (Baum et al., 2008; Boreham & Roubik, 1987) and window shutters (Bila Dubaić et al., 2021), with typically fewer nest sites in trees (Baum et al., 2008; Bila Dubaić et al., 2021; Boreham & Roubik, 1987). Nest sites available in urban areas likely differ to those in more natural habitats (e.g., woodland) but our results show that they are still readily advertised by swarms.

Swarms were over twice as likely to advertise nest sites in woodland than expected after controlling for distance, but only in Eastbourne. In mixed landscapes, woodland patches might provide higher quality nest sites than those closer by in other land types. Swarms set up in Eastbourne advertised nest locations over 4 km away in (E08; Figure 1) or near (E10; Figure 1) Friston forest, which (as of 2024) has stands ranging from 29 to 104 years (mean 73) plus a selection of 'notable' trees, which are likely much older. Kohl and Rutschmann (2018) showed that wild colonies readily nest in cavities in relatively young beech trees (80 years, 0.4 m diameter) created by black woodpeckers. The green woodpecker (*Picus viridis*) is the largest woodpecker in Britain and excavates cavities of up to 7 L (Brown et al., 1999; Glue & Boswell, 1994) but may also provide access to larger existing cavities.

Advantages and disadvantages of using swarms to assess nest site availability

Swarms can be used to assess nest site availability in any land type, including urban areas where honey bee colonies frequently nest (Baum et al., 2008; Bila Dubaić et al., 2021; Boreham & Roubik, 1987; Morse et al., 1990). Surveying nest sites directly in urban areas would be impractical due to the lack of access and sheer number of potential nest sites to survey in buildings, many of which may not have obvious entrance holes like those in trees. Using swarms also enables nest site availability to be quantified over large areas. In our study, half of all advertised locations were within 1.2 km (4.5 km^2) and all were found by swarms within a median of 2.7 daylight hours (Table 1) after dancing commenced. By comparison, it took the authors over 30 h to find every suitable honey bee nest site in 0.3 km^2 of cork oak groves in Andalusia, southern Spain (authors, submitted).

Another important advantage of using swarms is that nest site availability is less likely to be overestimated because it accurately

reflects the nest sites that are acceptable. Scout bees determine whether a cavity is suitable by integrating several cavity parameters and only advertise those that are acceptable (Seeley, 2010). Researchers can determine whether a cavity is suitable by using important criteria such as entrance size, which is usually estimated at ground level (Oldroyd et al., 1994; Oleksa et al., 2013; Visick & Ratnieks, 2024) and often leads to overestimates as not all entrance holes lead to a suitable cavity. For example, the density of suitable black woodpecker nests was estimated to be 1.4–3.7/km^2 in two German forests (Kohl et al., 2022, Suppl.) but wild colony densities did not exceed 0.36/km^2 over a 4-year period (Kohl et al., 2022), suggesting that nest sites were not limiting. However, black woodpeckers excavate small cavities (c. 10 L) with large entrances (c. 50 cm^2; Kosiński & Walczak, 2019; Remm et al., 2006) that provide little protection from depredators in winter (Kohl et al., 2023). Therefore, the actual density of high-quality nest sites that permit winter survival is probably much lower in German forests than previously estimated.

A disadvantage of using swarms to assess nest site availability is that dance decoding can only provide the approximate location of nest sites. Therefore, it can be challenging to determine land type (e.g., woodland, urban) or cavity type (e.g., tree, building) in patchy landscapes. This is especially the case with distant nest sites as any variation in waggle run duration and angle translates to a larger area. In addition, calibration data are rarely available for distances beyond 1 km (Kohl & Rutschmann, 2021). We used calibration data from Schürch et al. (2013) who trained bees to feeders at distances of up to 1.3 km. However, 44% of advertised locations exceeded this distance and might have been communicated via a different waggle duration function (Kohl & Rutschmann, 2021). These limitations only relate to inferences made regarding land type and do not affect our estimate of nest site numbers or density given that nest sites show up as discrete areas of dancing regardless of the calibration used to convert waggle run duration to distance.

Implications for other cavity-nesting species

In the case of decoding forager dances, honey bees forage for pollen and nectar as do many other species of flower-visiting insects. Indeed, foraging hot spots shown by honey bee dance decoding (Couvillon et al., 2014a) were found to include areas within grassland nature reserves (Couvillon et al., 2014b) with many other flower-visiting insects including bumble bees, butterflies, hover-flies and other flies (Balfour et al., 2015). Could decoding swarm dances similarly provide information relevant to other cavity-nesting species? There are many cavity-nesting species in Britain and elsewhere including birds, mammals and other social insects. However, their requirements vary considerably from those of honey bee swarms that typically chose cavities of 40 L (Seeley, 1977). In contrast, a pair of great tits will typically require a cavity of less than 5 L (Maziarz et al., 2015). One insect, however, that does require large cavities is the hornet, *Vespa crabro* (Nadolski, 2012). Overall, decoding swarm dances will not usually provide information as directly relevant to other cavity-nesting species as decoding forager dances can do for flower-visiting insects (Couvillon & Ratnieks, 2015), especially given that honey bees are generalist foragers and visit a wide range of flower species and varieties. Nectar and pollen are generic resources for many species, but nest sites vary in suitability across species and honey bees have special not general requirements.

CONCLUDING REMARKS

Previous studies have shown that researchers who eavesdrop on honey bee communication by decoding waggle dances can learn valuable lessons about honey bee foraging ecology and the challenges that colonies face in obtaining food. In the current study, we show that eavesdropping on swarms can also provide important information on the conservation of wild honey bee colonies regarding nest site availability. Encouragingly, our results show that the availability of nest sites deemed suitable by scout bees themselves exceeds that needed to house the population of wild colonies. This is despite England having a lower percentage area of woodland than most other European countries.

AUTHOR CONTRIBUTIONS

Oliver D. Visick: Conceptualization; methodology; formal analysis; data curation; visualization; writing – original draft; project administration. **Idris Adams:** Data curation. **Phoebe Ney:** Data curation. **Francesco S. Marzano:** Data curation. **Francis L. W. Ratnieks:** Conceptualization; methodology; supervision; funding acquisition; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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