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Ancient, veteran and other listed trees as nest sites for wild-living honey bee, *Apis mellifera*, colonies

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Abstract

Wild-living honey bee (*Apis mellifera*) colonies naturally nest in old cavity-bearing trees throughout their range, but this important nesting habitat is in global decline. Here we determine the use of ancient, veteran and other listed trees as nest sites by wild-living honey bee colonies in Britain and investigate the effect of tree size, genus and management on occupancy. Over 1,000 trees of special interest (TSIs) were surveyed in southeast England using the Ancient Tree Inventory (ATI) of the Woodland Trust, a charity that protects and promotes trees in Britain. 2% of all TSIs and 4.4% of TSIs with cavities were occupied by wild-living honey bee colonies (n=21). Occupancy positively correlated with tree diameter, which is surprising given that the overall sample already had a large mean diameter of 1.3 m. Wild-living colonies occupied sweet chestnut (*Castanea sativa*) more frequently than expected (7% versus 2% overall), probably due to their large mean diameter (1.6 m) and proportion of trees with cavities (73%). Heights of occupied tree cavities (including non-ATI trees) ranged from 0 to 18.2 m with a median of 6.8 m, entrance size ranged from 2.2 to 322 cm² with a median of 33.8 cm² and entrance orientation was not significantly different from random.

Implications for insect conservation

Our results show that TSIs provide valuable nesting habitat for wild-living honey bee colonies in southeast England. Based on an occupancy rate of 2% and a recent estimate of 2 million TSIs in England, we estimate that TSIs support 40,000 wild-living honey bee colonies across Britain and that wild-living colonies are a significant component of total colony numbers in areas with a high density of TSIs (> $50/km^2$).

Keywords Wild-living honey bees · Apis mellifera · Ancient and veteran trees · Tree cavities · Woodland Trust

Introduction

Old trees have long been recognised for their cultural and historical value (Hooke 2010), for example the Major Oak in Sherwood Forest, England, is closely linked to the legend of Robin Hood and the Jaya Sri Maha Bodhi in Sri Lanka is believed to be descended from the tree under which Buddha attained enlightenment. More recently, attention has been focused on the role of old trees in ecosystems (Hall and Bunce 2011), where they contribute disproportionately to services such as carbon storage and microclimate control (Jacob et al. 2013). Old trees also provide a wide range of microhabitats such as cavities, bark pockets, deadwood and epiphytes (Kraus et al. 2016) used by many other species (Paillet et al. 2018). Mitchel et al. (2019) compiled a list of over 2,300 species spanning multiple major taxa (birds, mammals, invertebrates, bryophytes, fungi and lichens) associated with oaks (*Quercus* spp.) in the UK. Out of 1,600 records with data regarding tree age, 1,300 (81%) of species were reported to use mature or veteran trees.

Cavities are an important microhabitat that mainly develop in older trees. Ranius et al. (2009) found that less than 1% of pedunculate oaks (Q. robur) in southeast Sweden under 100 years old had cavities, whereas 50% aged 200 to 300 years and 100% aged over 400 years had cavities. Cavities can result from decay, damage, or excavation by primary nesters, most notably woodpeckers (family

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Picidae) (Lindenmayer and Laurance 2017) and can vary in size from a few millilitres, such as those excavated by wood-boring insects (Kraus et al. 2016), to several hundred litres, such as those used as denning sites by black bears in the US (Smith 1985). In Britain, tree cavities are used by birds, mammals, reptiles and invertebrates, although use often depends on context and season. For instance, several British birds, including blue tits (*Cyanistes caeruleus*) use tree cavities for nesting in the spring, but females often roost in ivy-covered branches and evergreen bushes during the winter (Stenning 2018). Similarly, in southern Scandinavia, female pine martens use tree cavities for denning and underground sites for resting (Brainerd et al. 1995).

Many insects also nest in tree cavities, including stingless bees (Meliponini) in tropical regions (Grüter 2020) and hornets (Vespa spp.) throughout the Northern Hemisphere (Nadolski 2012). The western honey bee (Apis mellifera) is an obligate cavity-nester throughout temperate Europe, North America and Oceania and a colony can occupy a cavity continuously for multiple years (Seeley and Morse 1978; Oldroyd et al. 1997; Baum et al. 2005; Seeley 2017). Honey bee colonies are kept in approximately 102 million managed hives worldwide (FAO, 2021) but there are probably two to three times as many colonies living wild in cavities in trees, buildings and rock crevices (Visick and Ratnieks 2023). Wild-living honey bee colonies, hereafter referred to as "wild colonies" (see discussion), naturally nest in old cavity-bearing trees throughout most of their range (Visick and Ratnieks 2023) but these are declining worldwide (Lindenmayer et al. 2012) due to increased mortality associated with urbanisation, poor management and climate change (Nolan et al. 2020). For example, most of the largest and oldest African baobabs (Adansonia digitata), which can live for over 2,000 years, have died or collapsed in the last two decades (Patrut et al. 2018).

Here we used the Ancient Tree Inventory (ATI) of the Woodland Trust, a charity that protects and promotes trees and woodland in Britain, to survey over 1,000 trees of special interest (TSIs) in 16 sites across southeast England and to determine the proportion with wild colonies nesting in them. TSIs are defined as old trees that usually exhibit veteran characteristics, such as a hollowing trunk, crown retrenchment and the presence of saproxylic fungi (ATF and WT, 2008). The main aim of this study was to assess the value of TSIs as a nesting habitat for wild honey bee colonies, which are considered to be rare in Europe (Jaffé et al. 2010; Kohl and Rutschmann 2018). We also investigated the effect of tree size, genus and management on wild colony occupancy. Lastly, we provide a brief description of tree cavities used by wild colonies in our study area including their size, height and entrance compass orientation.

Methods and background information

Honey bee nest site selection

Honey bee colonies are established by swarms mainly in spring and early summer. During the process of nest site selection, scout bees identify several potential nesting cavities within a few kilometres of their parental nest and the whole swarm moves into the one they determine is most suitable (Seeley 2010). When given a choice, swarms are more likely to choose cavities with a volume of 40 L, compared to 10 or 100 L, with a south-facing entrance (in the N. hemisphere) of 12.5cm², compared to north-facing and 75cm^2 , and prefer cavities that are 5 m above ground versus 1 m (Seelev and Morse 1978). The main cavity constraints are cavity volume and entrance size. Wild colonies have been shown to mainly use cavities between 15 and 80 L (McNally and Schneider 1996; Oldroyd et al. 1994; Ratnieks et al. 1991; Requier et al. 2020; Seeley and Morse 1976) with entrances between 10 and 60cm² (Seeley and Morse 1976; Gambino et al. 1990; Ratnieks et al. 1991; Oldroyd et al. 1994; Baum et al. 2005).

The ancient tree inventory (ATI)

The Ancient Tree Inventory (ATI) is a citizen science project established in 2004 by The Ancient Tree Forum (ATF), Tree Register of the British Isles (TROBI) and The Woodland Trust (Nolan et al. 2020). Members of the public can add trees to an online database via the Woodland Trust's website (https://ati.woodlandtrust.org.uk) and records become public once they have been verified by an expert. Trees are classified as notable, veteran or ancient based on their age and the presence of veteran characteristics. Notable trees are the largest individuals of a species in an area but don't necessarily possess veteran characteristics (ATF and WT, 2008). Ancient and veteran trees both possess veteran characteristics but only the former have entered the ancient phase of the aging processes (ATF and WT, 2008).

ATI data access

The version of the Ancient Tree Inventory (ATI) used for this study has 169,101 public records across the UK (165,194 in Britain). Each record includes the tree's GPS location, species name, girth (m) at breast height (~1.5 m), veteran status (notable, veteran or ancient) and form (e.g., maiden, pollard and coppice). Trees listed as maiden show no signs of management, whereas other tree forms including pollards and divergent forms (e.g., coppice and multistem) have been cut either at the upper branches (pollard) or close to ground-level (divergent) to produce new shoots Fig. 1 Study area in southeast England. 1,052 trees of special interest (TSIs) (blue points) searched at 16 sites within the counties of Greater London (LND), Surrey (SRY), West Sussex (SXW), Kent (KNT) and East Sussex (SXE). Data provided by the Woodland Trust (2008)



Table 1 Breakdown of tree numbers and wild colony occupancy per site. The number in parentheses in column 6 indicates the percentage of TSIs searched at each site

| Study site | County | Area (km ²) | TSIs | TSIs per km ² | TSIs searched | TSI w/ cavities | TSI w/ bees | Occu- pancy |
|---------------------------------|----------------|-------------------------|------|-----------------------------|---------------|--------------------|----------------|----------------|
| | | | | | | | | rate (%) |
| Richmond Park | Greater London | 9 | 1353 | 150.3 | 141 (10) | 89 | 0 | 0 |
| Knepp Estate | West Sussex | 5.6 | 409 | 73 | 167 (41) | 53 | 1 | 0.6 |
| Hatchlands Park | Surrey | 0.8 | 404 | 505 | 231 (57) | 91 | 1 | 0.4 |
| Scotney Castle | Kent | 2 | 283 | 141.5 | 136 (48) | 57 | 2 | 1.5 |
| Knole Park | Kent | 3.7 | 247 | 66.8 | 80 (32) | 39 | 1 | 1.3 |
| Mote Park | Kent | 1.8 | 193 | 107.2 | 73 (38) | 42 | 4 | 5.5 |
| Sheffield Park | East Sussex | 1.2 | 111 | 92.5 | 29 (26) | 15 | 1 | 3.4 |
| Ashburnham Place | East Sussex | 1.0 | 91 | 91 | 29 (32) | 17 | 0 | 0 |
| Buxted Park | East Sussex | 0.8 | 54 | 67.5 | 36 (67) | 14 | 3 | 8.3 |
| Herstmonceux Castle | East Sussex | 1.1 | 52 | 47.3 | 42 (81) | 28 | 4 | 9.8 |
| Nymans | East Sussex | 2.8 | 41 | 14.6 | 17 (41) | 8 | 1 | 5.9 |
| Petworth Park | West Sussex | 1.1 | 41 | 37.3 | 35 (85) | 18 | 3 | 8.6 |
| Markstakes Common | East Sussex | 0.4 | 36 | 90 | 11 (31) | 2 | 0 | 0 |
| Firle Estate | East Sussex | 1.1 | 29 | 26.4 | 9 (31) | 5 | 0 | 0 |
| Stanmer Park | East Sussex | 1.3 | 24 | 18.5 | 12 (50) | 3 | 0 | 0 |
| Michelham Priory | East Sussex | 0.1 | 11 | 110 | 4 (36) | 0 | 0 | 0 |
| Total or mean (*) for all sites | | 33.8 | 3379 | 100* | 1052 (31) | 481 | 21 | 2* |

(WT, 2008). ATI data were accessed from either the Woodland Trust's website or a Shapefile of the data imported into QGIS (v3.16.11). This Shapefile was also uploaded to Arc-GIS Online so that it could be accessed in the field via a mobile app (ArcGIS Explorer, v20.0.1).

Choice of sites

The study area comprises much of southeast England, which is within the native range of *A. mellifera* (Carreck 2008), including the counties of East Sussex, West Sussex, Kent, Surrey and Greater London (Fig. 1). The study area contains a total of 18,204 recorded TSIs (as of April

2022). For practicality, sites chosen had a high density of TSIs (> $50/km^2$). Wood pasture, parkland and deer parks (hereafter referred to as "landed estates") were most suitable because they often have a high density of TSIs in Britain (Butler 2014; Nolan et al. 2020) and are usually open to the public. Landed estates make up approximately 2% of land cover in England, with almost 10,000 sites across the country (Natural England 2021). We combined ATI and landed estates data to identify sites in England with a high density of TSIs. We found a total of 896 sites with a TSI density exceeding $10/km^2$ and 499 exceeding $50/km^2$ (excluding sites with fewer than 5 TSIs) and chose to survey 16 from the former that were in our study area (Table 1). At each

site, trees were located using their photograph(s) and GPS location. If photographs were not available or the GPS was inaccurate, attribute data, such as species name and girth, were used to identify the tree. An average of 31% of all TSIs were searched at each site (Table 1) and trees were chosen at random when possible.

Wild colony survey

Most trees were surveyed on a total of 25 days in 2021 and 2022, although a small number of trees (n=8) were surveyed opportunistically as part of another study. Most surveys were carried out on warm days in early spring (March and early April) because honey bee forager traffic is easier to spot when trees are not in leaf. This is also before the honey bee swarming season, which starts in mid to late April in the study area. As such, our surveys give a conservative estimate of wild colony occupancy as many colonies die in winter, and surviving wild colonies produce an average of two swarms in late spring and early summer (Seeley 2019). Therefore, we would expect wild colony occupancy in summer to be two or three times that of early spring when most of our surveys were made. Trees were searched thoroughly from all angles and with binoculars as appropriate. Upon discovering a wild colony, workers were checked for pollen with binoculars to ensure that traffic was not caused by robbing remaining honey from a dead colony (Seeley 2007).

Data recorded for each tree included their ID number, presence of suitable cavities and presence of a wild colony. We considered cavities with an entrance area between 10 and 60cm² to be suitable for a wild colony (Seeley and Morse 1976; Gambino et al. 1990; Ratnieks et al. 1991; Oldroyd et al. 1994; Baum et al. 2005) and entrance sizes were approximated from ground-level (for unoccupied tree cavities). These data were then combined with ATI attributes using the tree's ID number. Diameter at breast height (DBH) was used for analyses of tree size and was calculated by dividing girth by π . An Ancient coppice hornbeam (*Car*pinus betulus) at Herstmonceux Castle, East Sussex, had a recorded girth of 17 m (5.4 m DBH) so was removed from analyses of diameter on occupancy. Analyses of tree taxonomy were carried out at the genus-level and all genera represented by fewer than 20 trees were listed as "other". Tree forms were sorted into three main categories: maiden, pollard (including natural and lapsed) and other (including coppice, multi-stem, phoenix, and stump). Species was not recorded for two trees and form was not recorded for 328 trees so these were excluded from their respective analyses.

Nest site characteristics

Nest site characteristics, including entrance location, origin, size, height and compass orientation, were recorded for all occupied tree cavities in the study area, regardless of whether the tree was listed on the ATI or not. Entrance locations included the main trunk, branches, base and co-dominant stems. The base is the lowest part of the main trunk and co-dominant stems are two or more stems of similar size that grow vertically from the same point of origin on the main trunk. Entrance size (cm²) was measured by mounting a camera on a telescopic pole and photographing the entrance at 90 degrees and at a standard distance of 0.5 m. Entrance area was measured using ImageJ (Schneider et al. 2012) and the origin of the entrance (e.g., excavation, decay or damage) was recorded. Honey bees at the nest entrance were used for scale (length of c. 13 mm) if a photo could not be taken from a known distance. Entrance height (m) was measured using either a tape measure (< 2 m), a telescopic pole (2-15 m) or a clinometer (>15 m). Location, height and compass orientation were only recorded for the main nest site entrance (with the most forager traffic), whereas origin and size were recorded for all entrances (maximum of two).

Statistical analyses

All analyses were performed in R (v4.2.2) (R Core Team 2022) and plots were made using ggplot2 (Wickham 2016). Generalised linear models (GLMs), with the family argument set to "binomial", were used to test for the effect of DBH, veteran status, genus and tree form on wild colony occupancy. Models with and without a variable were compared using their Akaike information criterion (AIC). A lower AIC indicates that a model fits the data better, although a difference in AIC (Δ AIC) of less than 2 is considered nonsignificant. In addition, the effect of tree genus, veteran status and form on wild colony occupancy was investigated using a similar methodology to Oleksa et al. (2013). The observed frequency of wild colonies in each tree category was compared to expected frequencies generated from 50,000 random samples of the data (Table 2). P values were generated using the Poisson probability density function:

$$f(x) = \frac{\lambda^x}{x!} e^{-\lambda}$$

where *x* is the observed frequency and *y* is the mean expected frequency.

Results

TSI diversity in the study area

The 8 most common TSI genera surveyed were *Quercus* (n=687), *Castanea* (n=86), *Fagus* (n=73), *Fraxinus* (n=35), *Pinus* (n=24), *Acer* (n=22), *Tilia* (n=22) and *Aesculus* (n=21) (Table 2), which accounted for over 90% of all trees searched. Other genera present in our survey included *Cedrus* (n=11), *Betula* (n=9), *Carpinus* (n=10), *Taxus* (n=9) and *Platanus* (n=8). Within the oaks (*Quercus* spp.), 10 species were surveyed including *Q. petraea* (n=30), *Q. cerris* (n=6) and *Q. ilex* (n=4), with the vast majority *Q. robur* (n=608).

Wild colony occupancy

A total of 1052 TSIs were searched across 16 sites in southeast England. 481 (45.7%) had cavities and 21 (2%, 4.4% of TSIs with cavities) contained a wild honey bee colony (Table 1). An additional 15 trees not listed on the ATI contained wild colonies. In total, 36 bee trees and 38 wild colonies were identified during the study (two trees contained two wild colonies). Greater tree diameter (DBH) correlated positively with wild colony occupancy ($\Delta AIC=16.6$). Diameter ranged from 0.26 to 2.95 m with a mean of 1.3 m in unoccupied TSIs (n=1030) compared to 1.7 m in occupied TSIs (n=21) (Fig. 2).

Oak (Ouercus spp.) was the most common genus, with a total of 687 searched and 10 occupied by wild colonies, which is slightly lower than random expectation (1.5% versus 2% overall) (x=10, y=13.7, P=0.072). Out of the 86 sweet chestnuts (Castanea sativa) searched, 6 were occupied by a wild colony, which is 3.5 times as many as expected (7% versus 2% overall) (x=6, y=1.7, P=0.006). Sweet chestnuts had the greatest mean diameter (1.6 m) and proportion of trees with cavities (73%) of the 8 most common genera surveyed (Table 2). Wild colonies were also found in beech (Fagus), ash (Fraxinus), pine (Pinus) and lime (Tilia), but the observed number of colonies matched expected frequencies in each case (Table 2). Maiden (unmanaged) tree forms were occupied more frequently than expected (2.7% versus 2%) (x=15, y=11, P=0.054), although this result was borderline significant. Despite these results, binomial models were not significantly better at predicting wild colony occupancy when tree genus ($\Delta AIC = -4.9$) or form ($\Delta AIC = -3.8$) were included. In addition, veteran status did not significantly affect wild colony occupancy ($\Delta AIC=-3.5$) (Table 2).

Nest site characteristics

The 38 wild colonies located in the study area occupied tree cavities with a range of different characteristics. 15 wild colonies (39%) occupied cavities with an entrance located on the trunk, 12 (32%) on a branch, 9 (24%) on a co-dominant stem and 2 (5%) at the base. Entrance height and compass orientation were recorded for 36 wild colonies.

Table 2 Tree occupancy by wild honey bee colonies. The number in parentheses in column 4 and 5 indicates the percentage of trees in each category with cavities and wild honey bee colonies, respectively. The observed number of wild colonies in each category were compared with expected values generated from 50,000 random samples of the data. P values were generated using the Poisson probability density function. Asterisks show P values that exceed significance thresholds of 0.05 (*), 0.01(**) and 0.001(***)

| Tree category | No. trees | Mean DBH (m) | No. cavities | Obs. no. colonies | Exp. no. colonies | P value |
|----------------|-----------|-----------------|--------------|-------------------|-------------------|---------|
| Genus | | | | | | |
| Quercus | 687 | 1.3 | 339 (49) | 10 (1.5) | 13.7 | 0.072 |
| Castanea | 86 | 1.6 | 63 (73) | 6 (7) | 1.7 | 0.006** |
| Fagus | 73 | 1.4 | 33 (45) | 1 (1.4) | 1.5 | 0.339 |
| Fraxinus | 35 | 1 | 12 (34) | 1 (2.9) | 0.7 | 0.348 |
| Pinus | 24 | 0.9 | 3 (13) | 1 (4.2) | 0.5 | 0.295 |
| Acer | 22 | 1 | 2 (9) | 0 (0) | 0.4 | 0.643 |
| Tilia | 22 | 1.5 | 3 (14) | 1 (4.5) | 0.4 | 0.282 |
| Aesculus | 21 | 1.3 | 11 (52) | 0 (0) | 0.4 | 0.657 |
| Other genera | 80 | 1.3 | 15 (19) | 1 (1.3) | 1.6 | 0.323 |
| Veteran status | | | | | | |
| Veteran | 732 | 1.3 | 369 (50) | 16 (2.2) | 14.6 | 0.093 |
| Notable | 209 | 1.1 | 46 (22) | 3 (1.4) | 4.2 | 0.187 |
| Ancient | 111 | 1.7 | 66 (60) | 2 (1.8) | 2.2 | 0.268 |
| Form | | | | | | |
| Maiden | 553 | 1.4 | 261 (47) | 15 (2.7) | 11 | 0.054 |
| Pollard | 143 | 1.5 | 77 (54) | 3 (2.1) | 2.9 | 0.223 |
| Other forms | 39 | 1.4 | 13 (33) | 1 (2.6) | 0.8 | 0.358 |
| All trees | 1052 | 1.3 | 481 (46) | 21 (2) | | |

Fig. 2 Diameter at breast height (DBH) of trees of special interest (TSIs) with and without wild honey bee colonies. Diameter ranged from 0.26 to 2.95 m with a mean of 1.3 m in TSIs not containing bees (n = 1030) and 1.7 m in TSIs containing bees (n = 21). Occupancy positively correlated with diameter (Δ AIC = 16.6)



Height ranged from 0 to 18.2 m with a median of 6.8 m and compass orientation was not significantly different from random (Rayleigh test, R=0.05, P=0.9). Origin and size were recorded for 32 nest entrances. 21 (66%) entrances were branch holes originating from either decay (n=11) or mechanical damage (n=10), 8 (25%) were the result of excavation by woodpeckers and 3 (9%) formed between buttresses at the base of the tree. Entrance size ranged from 2.2 to 322cm² with a median of 33.8cm². 9 wild colonies (28%) occupied cavities with entrance areas outside the typical range reported in the literature (10 to 60cm²) (Seeley and Morse 1976; Gambino et al. 1990; Ratnieks et al. 1991; Oldroyd et al. 1994; Baum et al. 2005).

Discussion

Occupancy of TSIs by wild colonies

Our results show that approximately 2% of trees of special interest (TSIs), listed on the Ancient Tree Inventory (ATI) in southeast England, are used as nest sites by wild colonies. Based on this occupancy rate and the current number of TSI records, we estimate that there are approximately 350 wild colonies nesting in listed TSIs in our study area and approximately 3,300 across Britain. However, the ATI is far from complete and Nolan et al. (2022) estimate that there could be 2 million ancient and veteran trees in England alone (62% of Britain), so the number of wild colonies nesting

in old trees in Britain could be over 40,000. This is a rough estimate based on the assumption that the results from our study area apply more widely in Britain. This is a reasonable assumption given that wild colonies are present throughout Britain (Thompson 2012; Seeley and Chilcott 2020) and that tree diversity in our study area largely reflects that of the whole ATI (Nolan et al. 2020). In addition, wild colony occupancy is probably two or three times higher in the summer than in early spring when most trees were surveyed, so this figure is probably an underestimate (see below). There are approximately 288,000 managed honey bee colonies in Britain (1.4/km²) (NBU, 2022) and our results suggest that wild colony numbers may approach or even exceed those of managed colonies on sites with a high density of TSIs $(>50/km^2)$, of which there are approximately 500 in England alone (see methods). This will have implications for the role of natural selection on colony survival and the contribution of wild colonies to pollination services in these areas.

Wild colonies occupied 4.4% of TSIs with cavities, which falls within the range of occupancy rates reported elsewhere in Europe. For example, Oleksa et al. (2013) found that wild colonies occupied 1.3% of cavity-bearing trees along rural avenues in Poland and Kohl et al. (2022) found that wild colonies occupied 14.1% of old black woodpecker (*Dryocopus martius*) nests in two German beech forests at least once during a 4-year period. Our study is most comparable with Oleksa et al. (2013) who studied a range of tree genera (predominantly *Tilia*, *Acer*, *Carpinus*, *Fraxinus* and *Quercus*) in rural areas. There are also studies from Australia

and the Americas that have reported high occupancy rates (>25%) of artificial nest boxes by wild colonies (Coelho and Sullivan 1994; Soderquist et al. 1996; Liébana et al. 2013; Lindenmayer et al. 2016). However, nest boxes are designed to be attractive to cavity-nesting animals and it is unlikely that natural cavities are occupied as frequently in these areas (Broughton et al. 2015; Saunders et al. 2021).

In Europe, wild colonies appear to occupy only a small proportion of available tree cavities at any given time (Oleksa et al. 2013; Kohl and Rutschmann 2018; Kohl et al. 2022). In our study, most trees were searched before the honey bee swarming season and we mainly report tree occupancy by established colonies that survived the previous winter, a period of overall reduction in colony numbers. Wild colony occupancy in two German beech forests dropped from an average of 9.6% in September to an average of 1.4% in April following an average winter mortality of 84% (Kohl et al. 2022). However, wild colonies were mainly nesting in old black woodpecker nests (Kohl and Rutschmann 2018; Kohl et al. 2022), which have an average volume of only 10 L (Kosiński and Walczak 2019). Cavities of at least 15 L are required to store the quantity of honey required to overwinter in temperate regions (Seeley 1985) so it is possible that the wild colonies in this study experienced higher mortality than usual. In addition, the study area consisted of forest dominated by beech (Fagus sylvatica), which is wind pollinated and does not produce nectar (Jarić et al. 2013) so it is possible that colony survival was also limited by floral resources (Rutschmann et al. 2023).

Population status of honey bee colonies in our study area

Typical honey bee populations consist of both wild and managed colonies (Thompson 2012; Youngsteadt et al. 2015; Rangel et al. 2020; Hinshaw et al. 2015; Bila Dubaić et al. 2021; Kohl et al. 2023). Although, wild colonies have been shown to form isolated populations in Australia (Oldroyd et al. 1997), Africa (McNally and Schneider 1996) and North America (Seeley 2007). Clearly, the colonies living in tree cavities in our study do not form an isolated wild population as all are within mating range of managed hives (up to 15 km, Jensen et al. 2005), but we still refer to honey bees living in tree cavities as "wild" at the colony-level. In some areas, colonies are not able to survive in the wild and many die during the winter and are replaced by swarms from managed hives the following spring and summer (Kohl et al. 2022). However, this is not the case in our study area. Most of the colonies in our study area are being monitored as part of a long-term study to determine colony survival. Preliminary data from the first three field seasons suggests that approximately half of all colonies in tree cavities survive the winter (ODV, unpublished data). Therefore, we estimate that wild colony occupancy is two or three times higher in the summer compared to early spring, given that half of the colonies survive the winter, and each should go on to produce an average of two swarms (Seeley 2019; Kohl et al. 2022). In cases where survival rates are low (~10%), such as those reported in some locations in Europe (Kohl et al. 2022; Lang et al. 2022), wild colony occupancy might be up to ten times higher in summer than early spring. Preliminary data from our study area indicates that winter mortality is less extreme than reported elsewhere in Europe and that our estimate of wild colony occupancy in the summer is reasonably accurate.

Effect of tree diameter on wild colony occupancy

Wild colony occupancy positively correlated with tree diameter, which probably reflects the positive trend in cavity presence and size with tree diameter and age reported elsewhere (Lindenmayer et al. 2000; Ranius et al. 2009). We searched trees with a mean diameter of 1.3 m, which is twice as large as those surveyed by Oldroyd et al. (1994) in Australia and by Oleksa et al. (2013) in Poland. However, unlike these studies, we did not search a random sample of trees at each site. Instead, we focused on TSIs, which will include many of the oldest trees in an area (ATF and WT, 2008) and subsequently have a higher average diameter. Interestingly, the mean diameter of trees containing bees (1.7 m) was also twice as large, on average, when compared with previous studies (Avitabile et al. 1978; Baum et al. 2005; Gambino et al. 1990; Oldroyd et al. 1994; Oleksa et al. 2013; Seeley and Radcliffe 2018). Our results show that there is no saturation in the relationship between tree diameter and wild colony occupancy, given that this trend persists in a sample of trees that were twice as large as previous studies (Oldroyd et al. 1994; Oleksa et al. 2013). It seems that wild colonies will readily nest in large trees if they are present. Indeed, we found a wild colony in the largest tree we surveyed: an ancient oak at Petworth Park, West Sussex, with a recorded girth of 9.3 m (3 m DBH). It would take centuries to replace the habitats provided by the largest trees on the ATI, so it is particularly important that these individuals are conserved.

Effect of tree genus, veteran status and form on wild colony occupancy

Tree genus, veteran status and form had little effect on wild colony occupancy. This is consistent with previous studies that have shown that bee trees reflect the most abundant trees in an area. For example, Seeley and Morse (1976), Avitabile et al. (1978) and Gambino et al. (1990) found that the most common tree used for nesting by wild colonies in New York, Connecticut and California, respectively, were oaks (*Quercus* spp.), which are the dominant hardwood in each state. Oaks were also dominant in our study area and were occupied by wild colonies slightly less than expected (1.5% versus 2% overall). Wild colonies occupied sweet chestnuts (*Castanea sativa*) significantly more frequently than expected (7% versus 2% overall), which is probably due to their large mean diameter (1.6 m) and high proportion of trees with cavities (73%). Sweet chestnut trees are native to southern Europe but occur across Britain as individual trees or small groups in significant locations, such as landed estates, and are also common in southeast England as coppice woodland (Jarman et al. 2019).

Wild colonies occupied maiden trees more frequently than expected (2.7% versus 2% overall), although this result was only borderline significant. Maidens are trees that have no signs of historical management (WT, 2008), including coppicing and pollarding. Here preference as a bee tree cannot be attributed to mean diameter or the proportion of trees with cavities because these were not different from average. It is possible that cavities provided by divergent tree forms (e.g., coppice and multi-stem) are of poorer quality than maiden trees, perhaps in terms of cavity volume. Divergent tree forms branch at lower heights which means there is a greater chance of cavities developing in branches instead of the trunk which limits their maximum volume.

Nest site limitation and competition

We estimated that roughly half of all TSIs had cavities that were suitable for wild colonies. However, this is almost certainly an overestimate as cavity suitability was based on entrance size but not volume, which is an important factor but difficult to quantify. Seeley (2010) was able to directly measure cavity volume by felling and dissecting trees in a 0.32km² plot of managed forest in Vermont and found that only 2 trees (14%, 6/km²) had cavities larger than 20 L. Nevertheless, at 6 cavities/km², this exceeds wild colony densities of 1/km² in forests in neighbouring New York State (Seeley 2007; Seeley and Radcliffe 2018). Similarly, in unpublished work by the authors, cavities were measured in a 0.33km² area of cork oak (Q. suber) groves in Andalucía, southern Spain, and 8 trees (14%, 24/km²) had cavities of 15 to 80 L with entrances between 10 and 60 cm². Given that wild colonies occur at a density of approximately 2/km² in our study area in southeast England (ODV, unpublished data) and a high percentage of trees appeared to have suitable cavities, it is unlikely that nest site availability limits wild colony numbers in our study sites.

There are several initiatives in Britain and elsewhere that install log hives and other artificial cavities in parks and forests under the assumption that natural nest sites are lacking (https://www.justbeeecohives.com; https://www. logbeehives.co.uk; https://beekindhives.uk). However, our results strongly suggest that, in many places, there is no need to supplement honey bee nest sites because natural cavities in trees are likely in sufficient numbers. Indeed, we identified 499 sites in England where the density of TSIs exceed 50/km². Interestingly, these types of areas are often chosen for log hive installation (https://www.freelivingbees. com/projects), probably because wild colonies are already present and artificial cavities are quickly colonised by swarms (Tofilski and Oleksa 2013, University of Dundee 2023), although this does not necessarily mean that natural nest sites are lacking (Broughton et al. 2015; Saunders et al. 2021). Log hives and man-made tree cavities provide a more natural alternative to modern beekeeping (Powell 2016), but probably have limited value in honey bee conservation. We propose that a better way of helping wild honey bee colonies is by conserving natural nest sites that are already present in old trees.

We observed several other species using TSIs as nest sites including doves and pigeons (Columba spp.), grey squirrels (Sciurus carolinensis), jackdaws (Corvus monedula), little owls (Athene noctua), ring-necked parakeets (Psittacula krameri) and hornets (Vespa crabro). These include introduced species (grey squirrels, ring-necked parakeets and little owls) or species often considered pests (pigeons and jackdaws). The vast majority (>90%) of TSIs appeared to be unoccupied. This suggests that nest site availability does not limit cavity-nesting taxa in our study sites and indicates that competition among species may be low, although it is possible that less conspicuous cavity-nesters were overlooked. It is also unlikely that the cavity requirements of honey bees overlap greatly with other cavity-nesters in the study area given that even large birds (e.g., pigeons and jackdaws) that require similar cavity volumes (>15 L) generally use cavities with larger entrances (Valera et al. 2019) which are not usually chosen by honey bee swarms (Seeley and Morse 1978). However, the European hornet can have large colonies exceeding 20 L in volume (Nadolski 2012) and were observed to occupy tree cavities previously used by wild colonies in our study. Hornets also predate on honey bees, but are unlikely to be sufficiently abundant in the study area to greatly affect honey bees. The invasive Asian hornet (Vespa velutina) has become established in several European countries (Lioy et al. 2022) since it was first detected in France in 2004 and is becoming established in the study area as of September 2023 (DEFRA, 2023). The Asian hornet does not usually nest in cavities (Bo Choi et al. 2012; Diéguez-Antón et al. 2022), instead building an external nest with a robust paper envelope (Feàs Sanchez and

Charles 2019), but is a more voracious predator of honey bees and may pose a threat to wild colonies in the future.

Value of the ATI

The Ancient Tree Inventory (ATI) is building into a comprehensive database of old trees and currently (2023) has almost 200,000 records across the UK (Nolan et al. 2020; WT, 2008), but it is still far from complete and there could be 10 times as many trees yet to record according to a recent estimate by Nolan et al. (2022). As with all citizen science projects, records are biased towards areas with greater human activity where old trees are more likely to be noticed, such as landed estates which made up most of our study sites. Wild colonies were present in 12 out of the 16 sites surveyed (Table 1), although they were not always nesting in TSIs. Our results show that TSIs are generally larger than the average tree used as nest sites by wild colonies elsewhere in the world and that wild colonies readily nest in other trees associated with TSIs but not listed on the ATI themselves, presumably because they are younger and do not possess veteran characteristics that develop with age. In some cases these trees were within a few meters of a TSI, so it is unlikely that they were missed by a recorder. Despite these biases, the ATI and other tree databases (e.g., https:// www.monumentaltrees.com), might be a useful tool for identifying areas where wild honey bee colonies and other species may occur.

The main aims of the ATI are to protect old trees in Britain and to promote their value to wildlife (WT, 2008; ATF and WT, 2009). Indeed, the Woodland Trust emphasise the value of ancient and veteran trees to wildlife on their website (WT, 2008) and in their tree guides (ATF and WT, 2009). On the ATI recording form (WT, 2008), recorders are encouraged to note the presence of wildlife associated with TSIs including fungi, epiphytes, bats and invertebrates. Approximately half of all records have this information, although it is currently limited to fungi and epiphytes. Here we provide a clear example of how TSIs are valuable to wildlife in Britain in that they provide nesting habitat for an important native pollinator: the honey bee. As noted above, we estimate that there could be over 40,000 wild colonies nesting in TSIs in Britain, when the list is completed, and there are likely many more wild colonies nesting in buildings and other man-made structures. Our results serve to also make it clear that in Britain, as in many other parts of the world (Visick and Ratnieks 2023), honey bee colonies still exist in natural habitats with little interference from humans. Our results should encourage other ATI recorders to look out for honey bee colonies and other invertebrates using TSIs and make the most out of this valuable database and citizen science project.

Authors' contributions ODV wrote the main manuscript text, collected data, did statistical analyses and made tables and figures. FLWR help conceptualise the project and provided feedback on multiple drafts.

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Declarations

Competing interests 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.

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References

- Ancient Tree Forum and Woodland Trust (2009) Ancient Tree Guide No. 6: The special wildlife of trees. https://www.woodlandtrust. org.uk/publications/2009/12/special-wild-livinglife-of-ancienttrees/ accessed 1st March 2023
- Ancient Tree Forum and Woodland Trust (2008) Ancient Tree Guide No. 4: What are ancient, veteran and other trees of special interest? https://www.woodlandtrust.org.uk/publications/2008/11/ what-are-ancient-veteran-and-trees-of-special-interest/ accessed 1st March 2023
- Avitabile A, Stafstrom DP, Donovan KJ (1978) Natural nest sites of honeybee colonies in trees in Connecticut, USA. J Apic Res 17:222–226
- Baum KA, Rubink WL, Pinto MA, Coulson RN (2005) Spatial and temporal distribution and nest site characteristics of feral honey bee (Hymenoptera: Apidae) colonies in a coastal prairie landscape. Environ Entomol 34:610–618
- Bila Dubaić J, Simonović S, Plećaš M, Stanisavljević L, Davidović S, Tanasković M, Ćetković A (2021) Unprecedented density and persistence of feral honey bees in urban environments of a large SE-European city (Belgrade, Serbia). Insects 12:1127
- Bo Choi M, Martin SJ, Wook Lee J (2012) Distribution, spread, and impact of the invasive hornet *Vespa Velutina* in South Korea. J Asia Pac Entomol 15:473–477
- Brainerd SM, Helldin JO, Lindström ER, Rolstad E, Rolstad J, Storch I (1995) Pine marten (*Martes martes*) selection of resting and denning sites in Scandinavian managed forests. Ann Zool Fenn 32:151–157
- Broughton RK, Hebda G, Maziarz M, Smith KW, Smith L, Hinsley SA (2015) Nest-site competition between bumblebees (Bombidae), social wasps (Vespidae) and cavity-nesting birds in Britain and the Western Palearctic. Bird Study 62:427–437
- Butler J (2014) Mapping ancient and other trees of special interest: UK citizens' contribution to world tree heritage. European

wood-pastures in transition (ed. By Hartel, T. and Plieninger, T.), Routledge, Oxfordshire, England, pp. 203–217.

- Carreck NL (2008) Are honey bees (*Apis mellifera* L.) native to the British Isles? J Apic Res 47:318–322
- Coelho J, Sullivan J (1994) Colonization of wildlife nest boxes by honey bee swarms. Am Bee J 134:697–699
- Department for Environment Food & Rural Affairs (2023) Asian hornet: UK sightings. Animal and plant health. https://www.gov. uk/government/publications/asian-hornet-uk-sightings accessed 20th September 2023
- Diéguez-Antón A, Escuredo O, Seijo MC, Rodríguez-Flores MS (2022) Embryo, relocation and secondary nests of the invasive species *Vespa Velutina* in Galicia (NW Spain). Animals 12:2781
- Feàs Sanchez X, Charles RJ (2019) Notes on the nest architecture and colony composition in winter of the yellow-legged Asian hornet, *Vespa Velutina* Lepeletier 1836 (Hym.: Vespidae), in its introduced habitat in Galicia (NW Spain). Insects 10:237
- Food and Agriculture Organization of the United Nations (2021) Beehive production. FAOSTAT statistical database. https://www.fao. org/faostat/en/#data/QCL accessed 9th September 2023
- Gambino P, Hoelmer K, Daly HV (1990) Nest sites of feral honey bees nests in Trees. Apidologie 57:35–45
- Grüter C (2020) Stingless bees: their behaviour, ecology and evolution. Springer Nature Switzerland AG, Cham, Switzerland
- Hall SJG, Bunce RGH (2011) Mature trees as keystone structures in Holarctic ecosystems – a quantitative species comparison in a northern English park. Plant Ecol Divers 4:243–250
- Hinshaw C, Evans KC, Rosa C, López-Uribe MM (2015) The role of pathogen dynamics and immune gene expression in the survival of feral honey bees. Front Ecol Evol 8:e594263
- Hooke D (2010) Trees in Anglo-Saxon England: literature, lore and landscape. Boydell & Brewer, Woodbridge, England
- Jacob M, Bade C, Calvete H, Dittrich S, Leuschner C, Hauck M (2013) Significance of over-mature and decaying trees for carbon stocks in a central European natural spruce forest. Ecosystems 16:336–346
- Jaffé R, Dietmann V, Allsopp MH, Costa C, Crewe RM, Dall'Olio R, De la Rúa P, El-Niweiri MAA, Fries I, Kezic N, Meusel MS, Paxton RJ, Shaibi T, Stolle E, Moritz RFA (2010) Estimación de la densidad de colonias de abejas en su rango natural para cerrar la brecha en los censos del declive de polinizadores. Conserv Biol 24:583–593
- Jarié S, MacUkanovic-Jocie M, Mitroviél M, Pavlovié P (2013) The melliferous potential of forest and meadow plant communities on Mount Tara (Serbia). Plant-Insect Interact 42:724–732
- Jarman R, Chambers FM, Webb J (2019) Landscapes of sweet chestnut (*Castanea sativa*) in Britain — their ancient origins. Landsc History 40:5–40
- Jensen AB, Palmer KA, Chaline N, Raine NE, Tofilski A, Martin SJ, Pedersen BV, Boomsma JJ, Ratnieks FLW (2005) Quantifying honey bee mating range and isolation in semi-isolated valleys by DNA microsatellite paternity analysis. Conserv Genet 6:527–537
- Kohl PL, Rutschmann B (2018) The neglected bee trees: European beech forests as a home for feral honey bee colonies. PeerJ 6:e4602
- Kohl PL, Rutschmann B, Steffan-Dewenter I (2022) Population demography of feral honeybee colonies in central European forests. Royal Soc Open Sci 9:220565
- Kohl PL, D'Alvise P, Rutschmann B, Roth S, Remter F, Steffan-Dewenter I, Hasselmann M (2023) Reduced parasite burden in feral honeybee colonies. Ecol Solutions Evid 4:e12264
- Kosiński Z, Walczak Ł (2019) Does cavity reuse affect timing of reproduction and fledgling success in the Black Woodpecker? J Ornithol 160:79–89
- Kraus D, Bütler R, Krumm F, Lachat T, Larrieu L, Mergner U, Paillet Y, Rydkvist T, Schuck A, Winter S (2016) Catalogue of tree

microhabitats – reference field list. Intergrate + Technical Paper. 16p

- Lang U, Albouy V, Zewen C (2022) Comparative monitoring of freeliving honey bee colonies in three western European regions. Nat Bee Husb Magazine 23:23–31
- Liébana MS, Sarasola JH, Santillán MÁ (2013) Nest-box occupancy by neotropical raptors in a native forest of central Argentina. J Raptor Res 47:208–213
- Lindenmayer DB, Laurance WF (2017) The ecology, distribution, conservation and management of large old trees. Biol Rev 92:1434–1458
- Lindenmayer DB, Cunningham RB, Pope ML, Gibbons P, Donnelly CF (2000) Cavity sizes and types in Australian eucalypts from wet and dry forest types a simple of rule of thumb for estimating size and number of cavities. For Ecol Manag 137:139–150
- Lindenmayer DB, Laurance WF, Franklin JF (2012) Ecology: global decline in large old trees. Science 338:1305–1306
- Lindenmayer DB, Crane M, Blanchard W, Okada S, Montague-Drake R (2016) Do nest boxes in restored woodlands promote the conservation of hollow-dependent fauna? Restor Ecol 24:244–251
- Lioy S, Bergamino C, Porporato M (2022) The invasive hornet *Vespa Velutina*: distribution, impacts and management options. CABI Reviews.
- McNally LC, Schneider SS (1996) Spatial distribution and nesting biology of colonies of the African honey bee *Apis mellifera scutellata* (Hymenoptera: Apidae) in Botswana, Africa. Environ Entomol 25:643–652
- Mitchel RJ, Bellamy PE, Ellis CJ, Hewison RJ, Hodgetts NG, Lason GR, Littlewood NA, Newey S, Stockan JA, Taylor AFS (2019) Collapsing foundations: the ecology of the British oak, implications of its decline and mitigation options. Biol Conserv 233:316–327
- Nadolski J (2012) Structure of nests and colony sizes of the European hornet (*Vespa crabro*) and Saxon wasp (*Dolichovespula Saxonica*) (Hymenoptera: Vespinae) in urban conditions. Sociobiology 59:1075–1120
- National Bee Unit (2022) Hive count. Beebase: Beekeeping information resource for beekeepers. https://nationalbeeunit.com/index. cfm?pageid=362 accessed 27th September 2023
- Natural England (2021) Wood pasture and parkland (England). Natural England open data publication. https://naturalengland-defra. opendata.arcgis.com/datasets/Defra::wood-pasture-and-parkland-england accessed 19th September 2023
- Nolan V, Reader T, Gilbert F, Atkinson N (2020) The ancient tree inventory: a summary of the results of a 15 year citizen science project recording ancient, veteran and notable trees across the UK. Biodivers Conserv 29:3103–3129
- Nolan V, Gilbert F, Reed T, Reader T (2022) Distribution models calibrated with Independent field data predict two million ancient and veteran trees in England. Ecol Appl 32:e2695
- Oldroyd BP, Lawler SH, Crozier RH (1994) Do feral honey bees (*Apis mellifera*) and regent parrots (*Polytelis anthopeplus*) compete for nest sites? Aust J Ecol 19:444–450
- Oldroyd BP, Thexton EG, Lawler SH, Crozier RH (1997) Population demography of Australian feral bees (*Apis mellifera*). Oecologia 111:381–387
- Oleksa A, Gawroński R, Tofilski A (2013) Rural avenues as a refuge for feral honey bee population. J Insect Conserv 17:465–472
- Paillet Y, Archaux F, du Puy S, Bouget C, Boulanger V, Debaive N, Gilg O, Gosselin F, Guilbert E (2018) The indicator side of tree microhabitats: a multi-taxon approach based on bats, birds and saproxylic beetles. J Appl Ecol 55:2147–2159
- Patrut A, Woodborne S, Patrut RT, Rakosky, Laszlo R, Lowly DA, Hall G, von Reden KF (2018) The demise of the largest and oldest African baobabs. Nat Plants 4:423–426

- Powell J (2016) Tree beekeeping field guide. Natural Beekeeping Trust, Frome, England
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rangel J, Traver B, Stoner M, Hatter A, Trevelline B, Garza C, Shepherd T, Seeley TD, Wenzel J (2020) Genetic diversity of wild and managed honey bees (*Apis mellifera*) in Southwestern Pennsylvania, and prevalence of the microsporidian gut pathogens *Nosema ceranae* and *N. apis*. Apidologie 51:802–814
- Ranius T, Niklasson M, Berg N (2009) Development of tree hollows in pedunculate oak (*Quercus robur*). For Ecol Manag 257:303–310
- Ratnieks FLW, Piery MA, Cuadriello I (1991) The natural nest and nest density of the africanzed honey bee (Hymenoptera, Apidae) near Tapachula, Chiapas, Mexico. Can Entomol 123:353–359
- Requier F, Paillet Y, Laroche F, Rutschmann B, Zhang J, Lombardi F, Svoboda M, Steffan-Dewenter I (2020) Contribution of European forests to safeguard wild-living honeybee populations. Conserv Lett 13:e12693
- Rutschmann B, Kohl PL, Steffan-Dewenter I (2023) Foraging distances, habitat preferences and seasonal colony performance of honeybees in central European forest landscapes. J Appl Ecol 60:1056–1066
- Saunders ME, Goodwin EK, Santos KCBS, Sonter CA, Rader R (2021) Cavity occupancy by wild-living honey bees: need for evidence of ecological impacts. Front Ecol Environ 19:349–354
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. Nat Methods 9:671–675
- Seeley TD (1985) Honeybee ecology: a study of adaptation in social life. Princeton University Press, Princeton, New York
- Seeley TD (2007) Honey bees of the Arnot Forest: a population of feral colonies persisting with *Varroa destructor* in the northeastern United States. Apidologie 38:19–29
- Seeley TD (2010) Honey bee Democracy. Princeton University Press, Princeton, New York
- Seeley TD (2017) Life-history traits of wild-living honey bee colonies living in forests around Ithaca, NY, USA. Apidologie 48:743–754
- Seeley TD (2019) The lives of bees. Princeton University Press, Princeton, New York
- Seeley TD, Chilcott AB (2020) In search of wild-living colonies of honey bees in the Scottish highlands. Beecraft 6:8–11

- Seeley TD, Morse RA (1976) The nest of the honey bee (*Apis mellifera* L). Insectes Sociaux 4:495–512
- Seeley TD, Morse RA (1978) Nest site selection by the honey bee, *Apis mellifera*. Insectes Sociaux 25:323–337
- Seeley TD, Radcliffe RW (2018) Deep forest bee hunting. Am Bee J 158:871–877
- Smith TR (1985) Ecology of black bears in a bottomland hardwood forest in Arkansas [PhD thesis]. University of Tennessee, Knoxville, United States
- Soderquist T, Traill B, Faris F, Beasley K (1996) Using nest boxes to survey for the brush-tailed phascogale *Phascogale Tapoatafa*. Vic Naturalist 113:256–261
- Stenning M (2018) The blue tit. Bloomsbury Publishing, London, England
- Thompson CE (2012) The health and status of the feral honeybee (*Apis mellifera* Sp) and *Apis mellifera mellifera* population of the UK [PhD thesis]. The University of Leeds, Leeds, England
- Tofilski A, Oleksa A (2013) There are still Bee Trees in Europe. Bee World 90:18–19
- University of Dundee (2023), August 4 It was meant to bee 3D-printed log hive proves popular with local bees [press release]. https:// www.dundee.ac.uk/stories/it-was-meant-bee-3d-printed-loghive-proves-popular-local-bees accessed 21st September 2023
- Valera F, Václav R, Calero-Torralbo MA, Martínez T, Veiga J (2019) Natural cavity restoration as an alternative to nest box supplementation. Restor Ecol 27:220–227
- Visick OD, Ratnieks FLW (2023) Density of wild honey bee, *Apis mellifera*, colonies worldwide. Ecol Evol 13:e10609
- Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer Publishing, New York City, New York
- Woodland Trust (2008) Ancient Tree Inventory. https://ati.woodlandtrust.org.uk accessed April 25th 2022
- Youngsteadt E, Appler RH, Lopez-Uribe MM, Tarpy DR, Frank SD (2015) Urbanization increases pathogen pressure on feral and managed honey bees. PLoS ONE 10:e0142031

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