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Original article

Characteristics of black woodpecker cavities chosen and not chosen by honeybee swarms

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Abstract – The black woodpecker (*Dryocopus martius*) is an important excavator of tree cavities across much of the Palearctic. Honeybees (*Apis mellifera*) are frequent secondary occupants of black woodpecker cavities in managed forests dominated by beech (*Fagus sylvatica*) in Germany; however, it is unclear how well the tree holes fulfil the bees' requirements and whether honeybees discriminate among black woodpecker cavities according to their characteristics. Here we report on the tree diameter, cavity height above the ground, cavity entrance direction, cavity entrance size, cavity volume, and relative entrance position of $N = 20$ black woodpecker cavities, half of which were used at least once by honeybees within a previous 2 to 4-year monitoring period. Black woodpecker cavities chosen by honeybee swarms had higher volumes (median volume 41 L vs. 19 L) and smaller entrances (44 cm^2 vs. 67 cm^2) than cavities not recently chosen by bees, and entrances were positioned at the bottom rather than in the middle or top of the cavity body. We conclude that black woodpecker cavities can serve as suitable nest sites for honeybees, provided they have time to enlarge through secondary decay. The mapping, labelling, and long-term preservation of black woodpecker cavity trees can promote populations of wild-living honeybees in managed forests, which are otherwise largely depleted of suitable tree cavities.

***Apis mellifera* / *Dryocopus martius* / nest-site selection / tree cavities / secondary cavity use / forest management**

1. INTRODUCTION

The decline of old-growth trees with large cavities is a critical ecological and conservation issue worldwide (Lindenmayer et al. 2012). Tree cavities provide essential nesting and sheltering habitats for a wide array of fauna, including birds, bats, and invertebrates (Cockle et al. 2011). A particularly remarkable case of cavity-nesters is the western honeybee (*Apis mellifera*). While the species is typically considered in the context of beekeeping, wild honeybee colonies heavily rely on tree cavities for nesting (Seeley and Morse 1976; Rutschmann et al. 2025; Oleksa et al. 2013; Requier et al. 2020).

Compared to their tropical counterparts, honeybees living in temperate and cold climates face the challenge of surviving cold winters with

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little to no foraging opportunities and limited capacities for colony defence (Seeley 1985). This necessitates selecting a suitable cavity for nesting in advance—one that provides enough space to store honey as a winter food reserve, enables the bees to retain heat generated through collective thermoregulation, and offers protection against predators. In fact, the strong selection pressures of the winter season have shaped the evolution of specific nest site preferences in temperate European honeybees (Seeley 1985, 2010).

Cavity selection in honeybees takes place during swarming, their natural process of colony reproduction. When food resources are abundant and a colony becomes large in spring or early summer, it splits into two parts. The old queen and about 70% of the workers, typically around ten thousand, leave the nest to form a new colony. The departing swarm clusters temporarily near the original colony while a couple of hundred bees search the surroundings for suitable nesting sites. These scouts explore multiple potential cavities and assess their quality based on a suite of features including volume, height above ground, entrance size, entrance direction, and the presence of old wax combs from former colonies. After returning to the swarm, they advertise their findings using the waggle dance. Since dances for high-quality sites are repeated more often than dances for low-quality sites, relatively more fellow scouts are directed to the best cavity locations. The recruited nestmates then reinforce the advertisement, and a consensus for the best cavity gradually emerges. Once a quorum is reached for a particular nest site, the swarm departs to occupy the chosen cavity (reviewed by Seeley 2010).

The nest site preferences of honeybees adapted to temperate climate regions have been studied extensively in the context of a stable population of wild honeybees inhabiting old-growth forests in the Northeastern United States (Seeley and Morse 1976, 1978; Seeley 1977, 2010, 2019). These bees are the descendants of several European subspecies of honeybee introduced by settlers in the seventeenth and eighteenth centuries. The principal insight was that honeybee swarms prefer large cavities (at least 10 L, better > 20 L) that have a small entrance (12.5 cm^2 preferred over 75 cm^2) high above the forest floor (5 m height preferred over 1 m) (Seeley 2010). However, little is known about the nest site characteristics and cavity preferences of wild honeybee colonies in their native European range.

In Germany, honeybee swarms commonly use cavities excavated by black woodpeckers (*Dryocopus martius*) as nesting sites (Kohl and Rutschmann 2018; Kohl et al. 2022). Black woodpeckers are key creators of large cavities in central European forests managed for timber production (Johnsson et al. 1993; Sikora 2017). However, the winter survival rate of honeybee colonies in these cavities was found to be only about 16%, insufficient to sustain a stable population (Kohl et al. 2022). This raises questions about the suitability of black woodpecker cavities for honeybees. It has been suggested that they are merely chosen due to a lack of better alternatives, in which case they could be considered "ecological traps" (Kohl et al. 2023). In fact, freshly excavated black woodpecker cavities (BWCs) typically have a volume of only about 10 L (Kosiński and Walczak 2019), which is at the lower limit of what is acceptable for honeybee colonies. Moreover, their relatively large entrance holes may fail to prevent the intrusion of avian and mammalian predators during winter (Kohl et al. 2023). Interestingly, BWCs are not occupied randomly, suggesting that honeybee swarms select cavities with specific features (Kohl et al. 2022).

In this study, we aimed to describe the characteristics and diversity of BWCs available to secondary cavity nesters in managed forests dominated by beech trees in central Europe. By analysing cavities previously chosen or not chosen by honeybees, we tested the hypothesis that swarms exhibit preferences for certain cavity types. Our data provide insights into the nesting ecology of honeybees in temperate regions and inform forest management strategies for preserving suitable habitats.

2. MATERIAL AND METHODS

2.1. Study sites and tree cavities

We collected data on tree cavity characteristics in two study regions in southern Germany, in the Biosphere Reserve Swabian Alb (SA) in Baden-Württemberg, and in forests of the two adjacent counties Coburg and Lichtenfels (CL) in Bavaria. Almost all (99%) black woodpecker cavities in these regions are in beech (*Fagus sylvatica*) trees and are situated in 120–180-year-old forest stands (Sikora 2017). Random samples of $N = 197$ (SA) and $N = 250$ (CL) black woodpecker cavity trees had previously been monitored to study the population demography of wild-living honeybee colonies (SA 2017–2021, CL 2019–2021) (Kohl et al. 2022). Most of the listed trees had been mapped independently before, between 2004 and 2019 (Sikora et al. 2016; N. Wimmer, personal communication 2019). Still, new cavities were added during the bee monitoring study (Kohl et al. 2022), so the list contained cavities of different ages, including recently excavated and old (> 20 years) ones. To select cavities for this study, we first created two categories: (1) "bee tree cavities", which were occupied by honeybee colonies at least once during the 2 to 4-year monitoring periods ($N = 34$ for SA, $N = 29$ for CL), and (2) "non-bee tree cavities", which were never occupied by honeybees during the same period (see supplementary information, Figure SI3 for an overview of tree observations).

With the geographic coordinates of bee trees and non-bee trees at hand, we conducted a field trip to the SA in June 2022 and a trip to the forests around CL in August 2023. The final selection of study trees was made based on two criteria. First, we selected forest stands containing multiple cavity trees. This allowed us to investigate pairs of bee trees and non-bee trees that were spatially close enough to assume that all trees were in reach of honeybee swarms (see maps of the cavity trees, supplementary material Figures SI1 and SI2). Second, only cavities unoccupied by honeybees at the time of the visit were analysed. This way, we avoided triggering aggressive behaviour and were able to measure internal cavity dimensions. For each bee tree cavity selected, we identified and examined the nearest non-bee tree cavity. This resulted in the study of $N = 20$ cavity trees, $N = 10$ bee trees, and $N = 10$ non-bee trees. Six cavity pairs were in the SA and four pairs in CL. The mean distance between bee tree and non-bee tree cavities was 166 m (range 11–762 m).

2.2. Measurement of cavity characteristics

For each selected cavity tree, we determined—by direct measurement or by approximation—the following features: cavity volume, cavity entrance area, entrance position in relation to the cavity body (e.g. bottom, middle, or top), cavity height above the ground, tree diameter at breast height (DBH), and cavity entrance direction. Entrance direction was recorded by standing with the back to the tree and reading the direction pointing away from the entrance hole using a magnetic compass. To determine DBH, we wrapped a rope around the tree trunk at breast height, measured the length of the rope section with a folding rule, and calculated the tree diameter by dividing circumference by pi. To inspect the cavities, we alternated between one of us ascending the tree to the height of the cavity. We used the rope-climbing technique with a semi-static climbing rope pulled over a large side branch and fastened at the trunk. The height of the cavity entrance above the ground was determined by lowering a second rope. The non-climbing person marked the point where it touched the ground with a knot so that the marked section could later be measured using a folding rule. At the cavity, we measured the height (major, vertical axis $= a$) and width (minor, horizontal axis $= b$) of the entrance hole (Figure 1). The entrance area was calculated based on the formula for the area of an ellipse:

$$\pi \times a/2 \times b/2$$

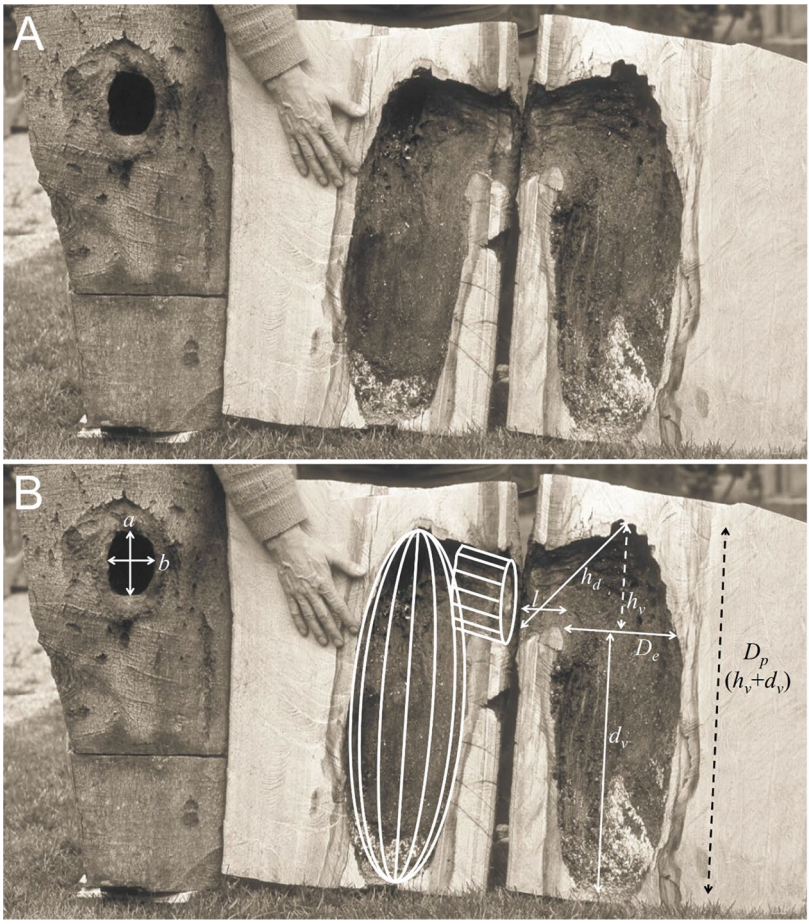

Figure 1. **A** Frontal view of the entrance of a black woodpecker cavity (left) and view of the interior of a black woodpecker cavity that was cut into two halves vertically (right). Both dissected cavities are in beech (*Fagus sylvatica*), which is the preferred nesting tree of the black woodpecker in central Europe. **B** The same image as above, with annotations showing the sections directly measured (solid lines) and inferred (dashed lines) in this study (see main text for description). On top of the left half of the vertically dissected cavity, the geometric approximation of cavity volume is illustrated (spheroid + cylinder). Photo credit: Luis G. Sikora.

The approximate volume of the cavities could only be determined indirectly. Based on photographs of dissected black woodpecker cavities (Figure 1A), we considered that the overall cavity volume is well described by combining the volumes of two geometrical bodies: a vertically elongated (prolate) spheroid for the actual cavity body and a horizontal cylinder fitting the entrance tube (Figure 1B). Adding the volume of the entrance tube was important because we had previously observed that bee colonies also use this part of the cavity for building wax combs. The volume of the entrance tube was calculated by multiplying the entrance area by the length of the entrance tube, l (= thickness of the cavity wall; directly measured with a ruler). Calculating the volume of the prolate spheroid representing the cavity body requires knowing its equatorial (D_e) and polar (D_p) diameters:

$$\frac{\pi}{6} \times {D_e}^2 \times D_p$$

We inserted a folding rule horizontally through the cavity entrance to measure the equatorial

diameter (D_e). By inserting the folding rule diagonally upwards, we measured the section between the bottom of the entrance and the roof of the cavity ("diagonal cavity height", h_d). We then used Pythagoras' theorem to determine the "vertical cavity height" (h_v) based on h_d, l, and D_e:

$$h_v = \sqrt{h_d{}^2 - (l + D_e/2)^2}$$

In turn, "vertical cavity depth" (d_v), from the entrance to the bottom, was assessed by lowering a weighted string to the cavity floor and measuring the relevant section of the string with a folding rule. The approximate total polar cavity diameter (D_p) was then obtained by adding vertical cavity height (h_v) and depth (d_v). Knowing the vertical cavity depth also allowed us to quantify the position of the entrance relative to the cavity body as a continuous variable theoretically ranging from 0 to 1, with higher values indicating entrance midpoints closer to the top of the cavity and lower values indicating entrance midpoints closer to the bottom:

$$(d_v + a/2)/D_p$$

2.3. Statistical analysis

The following analyses were performed using R (version 4.4.2; R Core Team 2024), and data were visualised using ggplot2, ggpol, and patchwork (Wickham 2016; Pedersen 2020; Tiedemann 2020). Since we analysed multiple features per cavity tree that were potentially correlated, we needed to use a multivariate two-sample test to simultaneously test the hypothesis that cavities chosen by honeybees (bee trees) differ from those not chosen by honeybees (non-bee trees) in any of the traits considered. The classic solution for this problem is Hotelling's T^2-test; however, not all response variables fulfilled the requirements of the two samples having similar variances and being normally distributed. We therefore used a non-parametric, permutation-based alternative, the two-sample energy ($\mathcal{E}$)-test to test whether the two multivariate samples stem from the same distribution (R-package, "energy") (Székely and Rizzo 2004; Rizzo and Szekely 2024). This test could be applied jointly to the five continuous variables. Unfortunately, data on internal cavity dimensions were missing for one of the ten bee tree cavities because its entrance was too small to insert a folding rule. Since the $\mathcal{E}$-test requires complete observations for all samples, we could only formally test differences in cavity traits between $N = 9$ bee trees and $N = 10$ non-bee trees. However, we also provide descriptive statistics and apply univariate Wilcoxon-Mann-Whitney tests (function "wilcox.test") for each variable separately for which we could include data for the bee tree with incomplete information. To test whether cavities in bee trees and non-bee trees differ in their distributions of entrance directions, we used circular statistics (Watson's two-sample test of homogeneity and Rayleigh test of uniformity, package "circular") (Agostinelli and Lund 2024).

3. RESULTS

The cavities of bee trees and non-bee trees significantly differed when jointly comparing the five characteristics cavity volume, entrance size, entrance position, cavity height above ground, and tree DBH (multivariate two-sample $\mathcal{E}$-test of equal distributions; sample sizes: 9, 10; permutations 9999; $\mathcal{E}$-statistic = 147.9, $P = 0.0225$). The overall estimated median volume of black woodpecker cavities was 32.8 L ($N = 19$). The cavities chosen by bees ($N = 9$) tended to be larger (median 41.1 L, range 12.7–161.9 L) than those not chosen by bees ($N = 10$) (median 19.4 L, range 2–61.1 L) ($P = 0.0175$, one-sided Wilcoxon test). The overall median entrance size was 60.9 cm^2 ($N = 20$), with bee tree cavities ($N = 10$) having smaller minimum and median entrances (median 44.1 cm^2, range 1.4–75.4 cm^2) than control cavities (median 67 cm^2, range 28.3–78.5 cm^2) ($P = 0.0992$, one-sided Wilcoxon test). The entrances in bee tree cavities tended to be closer to the bottom than the top of the cavity ($P = 0.0782$,

one-sided Wilcoxon test). The median position was at 32.7% of the vertical cavity diameter (the bottom third, range 18.3–59.7%, $N=9$). In non-bee tree cavities, entrance position varied more widely (median 55.3%, range 14.8%–85.4%, $N=10$). Considering all cavities ($N=20$), height above the ground ranged between 7.7 and 17.6 m, with a median of 8.5 m. The median height above ground was 9.3 m in bee-tree cavities and 7.7 m in non-bee tree cavities, indicating no clear difference in entrance height between the two groups ($P=0.7054$, Wilcoxon test). Likewise, tree DBH did not differ between the two groups ($P=0.5964$, Wilcoxon test); the overall median DBH was 62.9 cm ($N=20$), the median DBH of bee tree cavities was 65.6 cm ($N=10$), and the median DBH of non-bee tree cavities was 62.4 cm ($N=10$). Both the smallest (DBH 58.6 cm) and the largest tree observed (DBH 92.6 cm) were bee trees.

The distributions of entrance directions of cavities in bee trees ($N=10$) and non-bee trees ($N=10$) did not differ significantly (Watson's two-sample test of homogeneity, test statistic: 0.033, $P>0.10$). Overall, cavity entrances did not concentrate at any one compass direction (Rayleigh test of uniformity with general unimodal alternative, test statistic 0.2272, $P=0.3606$).

4. DISCUSSION

Colonies of western honeybees living in regions with temperate or cold climates have specific nesting site requirements, with cavity volume being among the most important criteria (Seeley 1977). A key finding of our survey is that BWCs clearly constitute a source of suitable nesting sites for honeybees in relation to volume. While freshly excavated BWCs hold only around 10 L (Kosiński and Walczak 2019), our median volume estimate of 33 L in a sample of 19 BWCs of mixed (albeit unknown) age (ca. 0–20 years) shows that the tree holes increase considerably in size over time. The exceptional value of BWCs becomes clear when considering that most other tree cavities are probably much smaller in volume. Although quantitative data on the size distribution of random samples of tree cavities are rare, the following two examples provide a valuable reference. In a sample of 113 tree cavities used by various cavity-nesting species in riverine forests in central Estonia, the mean cavity volume was only 5 L (range 0.3–38 L) (Remm et al. 2006, Appendix A, "occupied cavities"). In Swedish boreal forests, measurements of $N=59$ cavities suggest a mean cavity volume of ca. 4.4 L (weighted mean based on cavities in managed and unmanaged forests) (Michon 2014; Andersson et al. 2018). In both the Estonian and the Swedish study system, the black woodpecker is among the species excavating tree holes and woodpecker cavities make up 88% and > 90% of all cavities, respectively. The finding that most cavities are rather too small for honeybees aligns with the results of Seeley (1977): among 14 tree cavities randomly dissected from a stand of mixed deciduous forest in Vermont, USA, only 2 (14%) were suitable for honeybees by volume (> 20 L).

Not only is the average BWC more spacious than expected. Honeybee swarms apparently discriminate among BWCs and select those that are especially large. Strikingly, the volume distribution of the nine bee tree cavities measured by us (median 41 L, range 13–162 L) closely corresponds to the volume distribution of 21 dissected bee tree cavities from forests in New York State (median 45 L, range 12–443 L) (Seeley and Morse 1976). This match suggests that preferences for cavity size in honeybees living in regions with long winters are highly conserved.

Another important feature of cavities for honeybees is entrance size (Seeley and Morse 1978). Entrances must allow the easy passage of foragers but be small enough to prevent excessive heat loss and exclude predators. In the woodlands of New York State, which are home to a stable population of wild colonies (Seeley 1978, 2017), the median entrance size of honeybee nests is approximately 25 cm^2 ($N=33$) (Seeley and Morse 1976). In a choice experiment between nest boxes with entrances of 12.5 cm^2 or 75 cm^2 area, honeybee swarms preferred the former (Seeley and Morse 1978). Being the largest woodpecker in the Palaearctic, black woodpeckers excavate

cavities with relatively large entrances of about 80 cm^2 (Kosiński and Walczak 2019; see also supplementary information, Figure SI4). As a comparison, in Remm et al.'s sample of 517 tree cavities (449 of which were woodpecker cavities), the median entrance area was only between 12.6 and 19.6 cm^2 (extracted from the histogram Figure 2 in Remm et al. 2006). This suggests that honeybee nest scouts face a dilemma: black woodpecker cavities are highly attractive considering volume, but relatively unattractive considering entrance size. In fact, they do not always provide sufficient protection from intruders, as shown by the observation that wild colonies nesting in black woodpecker cavities are often plundered by great tits, woodpeckers, and pine martens during winter (Kohl et al. 2023). From the bees' perspective, it is fortunate that once black woodpecker cavities are no longer in use and renovated by woodpeckers, host trees narrow down the entrances with bark and eventually overgrow the tree holes completely (Sikora 2007). The difference in entrance size distributions between cavities chosen and not chosen by honeybees shows that swarms indeed specifically select BWCs with smaller entrances. The extreme example is a cavity whose entrance was narrowed down by tree bark to a small vertical slit (tree A247, see supplementary information, Figure SI5). This cavity was the only one reoccupied by swarms every single year in our 4-year monitoring study at the Swabian Alb.

Besides larger volumes and smaller entrances, older black woodpecker cavities are more suitable for honeybees with respect to a third variable, the relative position of the entrance. Experimental analyses with nest boxes have shown that honeybees prefer cavities with entrances at the bottom over those with entrances at the top of the cavity body (Seeley and Morse 1978). This may help maintain a warmer and more stable microclimate by reducing convective heat loss through the entrance. Unfortunately, freshly excavated woodpecker cavities have their entrances at the top. However, given time and fungal decay, the cavity roof can expand upwards so that the entrance "moves down" (Sikora 2007). In agreement with the data of 21 natural nesting cavities dissected in forests of New York State (Seeley and Morse 1976), the BWCs selected by honeybees in our study tended to have their entrance at the bottom rather than the top of the cavity. It is unclear, however, whether the bees specifically discriminate BWCs based on entrance position, or whether the apparent preference for entrances at the bottom of the cavities is simply a by-product of selecting large cavities. Interestingly, in our sample of $N = 19$ BWCs, a Pearson correlation showed no significant relationship between cavity volume and relative entrance position ($r = -0.18$, $P = 0.47$), suggesting that honeybee swarms might be evaluating both variables independently.

Since the black woodpecker creates holes in living sapwood, its host trees can live for many (> 20) years after the cavities have been excavated (Wesołowski 2011; Sikora 2024). Cavity-nesting species differ in nest site preferences, and communities of secondary cavity occupants can change in time alongside changes in the characteristics of woodpecker cavities (Edworthy et al. 2018). Our results regarding the bees' preferences for BWCs with higher cavity volumes, smaller entrances, and lower entrances support previous data suggesting that the honeybee is a species occurring later in the temporal succession of BWC users (Sikora 2007). The insight for forest nature conservation is that mapping and labelling black woodpecker cavity trees and specifically their long-term preservation can increase the availability of suitable nesting sites for wild honeybee colonies in managed forests.

Although previous studies have shown that honeybees also have a preference regarding the height of the cavity above the ground and the compass direction of the cavity entrance (Seeley and Morse 1978), it is not surprising that there was no significant difference in our study between bee tree and non-bee tree cavities regarding these variables. Honeybee swarms prefer cavities situated several metres above the ground, likely because these are less easily spotted by mammals than ground-level nests (Seeley 2019). Since the black woodpecker has the same preference

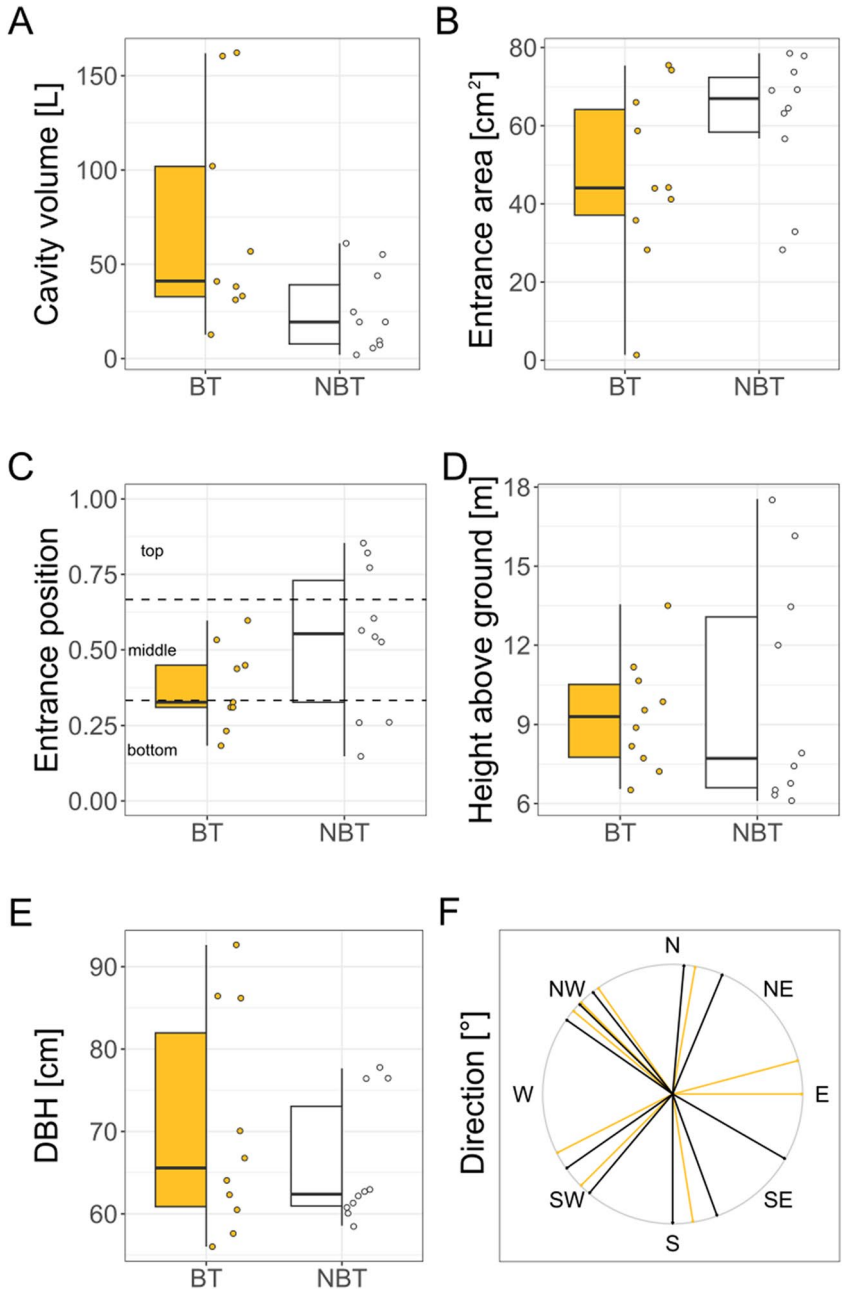

Figure 2. Characteristics of black woodpecker cavities (or of the respective cavity trees) that were selected by honeybee swarms (bee trees, BT) or not selected by bees (non-bee trees, NBT) in the same monitoring periods. Standard box plots alongside raw data points are provided for continuous variables. **A** Estimated volume of the cavity, **B** area of the entrance hole, **C** relative position of the entrance hole in relation to the cavity body, **D** height of the cavity entrance above the ground, **E** diameter at breast height of the cavity tree, and **F** compass direction of the entrance hole (yellow arrows, cavities in bee trees; black arrows, cavities in non-bee trees).

(Kosiński and Walczak 2019; Zawadzki 2024), most of its cavities will be suitable with respect to this variable from the bees' perspective anyway. Honeybees disproportionately select cavities whose entrances face south, likely due to energetic advantages under temperate climatic conditions (Seeley and Morse 1978). However, honeybee nest entrances can face any direction, and the preference for south only becomes evident when considering large samples. For example, among 285 tree cavities with bees discovered by citizen scientists throughout Germany, southward-facing entrances made up 20% (Rutschmann et al. 2025). This is a significantly—but not strikingly—higher frequency compared to the 12.5% expected for a random distribution across the eight cardinal and intercardinal directions (north, north-west, etc.). We did not find a direction bias in our study of black woodpecker cavities, probably due to the small sample size and because entrance direction is probably less important for the bees than cavity volume or entrance size.

When interpreting the differences we found between cavities chosen and not chosen by honeybees, two caveats of our methods need to be considered. All the studied cavities were excavated by the same species and, therefore, were likely similar in their shapes. However, we do not know whether all cavity bodies, especially those of the larger cavities, matched the shape of a spheroid, so our cavity volume data must be considered estimates only. The second caveat is that the distinction of "bee trees" and "non-bee trees" was not based on complete occupation histories of each cavity tree but on censuses in the years 2017–2020 (Swabian Alb) and 2019–2020 (Coburg/Lichtenfels) only. The cavity measurements, in turn, were performed in the years 2022 and 2023, respectively, meaning that some cavity trees classified as "non-bee tree" might have been occupied by bees in any of the years outside our monitoring period. Furthermore, our method of climbing the trees and inserting folding rules only allowed us to study cavities that were unoccupied at the time of investigation. We had to reject several cavities currently occupied by bees. These two factors mean that our classification of bee tree and non-bee trees was not 100% sharp, and our sample of bee trees was likely biased by lacking the very best cavities in our study regions from the bees' perspective. The likely result of these shortcomings is that the difference between cavities chosen and not chosen by bees was underestimated in our study.

A previous monitoring study showed that wild-living honeybee colonies occupying BWCs in German forests have an annual survival rate of only about 11%, which is too low for the population to sustain itself (Kohl et al. 2022). The results of our cavity survey, however, do not support the idea that the low survival is explained by poor nesting sites, as previously speculated (Kohl et al. 2022, 2023). Specifically, black woodpecker cavities selected by bees were sufficiently large to store enough honey for the winter, and some cavities had much smaller entrances than would be expected from freshly excavated cavities. Another (albeit indirect) argument against the ecological trap hypothesis is that wild-living honeybee colonies living in German cities have a similarly low annual survival rate as those living in managed forests, despite the bees in urban areas not primarily using woodpecker cavities for nesting (40% of colonies use hollow spaces in buildings) (Rutschmann et al. 2025).

Even if BWCs can be suitable nest sites for honeybees, our results suggest that there are too few high-quality cavities per unit forest area. Population monitoring showed that only a fraction of all black woodpecker cavities is ever occupied by bees (Kohl et al. 2022). We can now conclude that this is not simply because honeybees prefer nest sites previously occupied by bees, but because not all of the cavities are acceptable for the bees in the first place. The densities of all cavity trees monitored in the two study areas were 1.42 trees per km^2 at SA and 3.67 trees per km^2 at CL, and the percentage of trees used at least once by honeybees during that study was 17.3% (24 out of 197) and 11.6% (29 out of 250), respectively (Kohl et al. 2022). Hence, the densities of BWCs suitable for honeybees might only be 0.25 and 0.43 cavities per km^2 in the two German forest regions.

It is questionable whether a stable population of wild honeybees can exist under such low densities of nesting sites. Seeley estimated that the density of wild colonies in forests in New York State is at least around 1 colony per km^2, meaning that the density of available nesting cavities is at least that high (Seeley 2019). Deer parks, wood pastures, and parklands in South England, which have been found to harbour a stable metapopulation of wild honeybee colonies, offer suitable cavities for bees at estimated densities of 15–20 per km^2 (Visick and Ratnieks 2026). The pool of nesting cavities in these conservation areas is also much more diverse compared to those available in managed forests in Germany. For example, at least seven different genera of trees contain cavities suitable for honeybees in English wood pastures (Visick and Ratnieks 2024), whereas 99% of BWCs in our study system are in beech (*Fagus sylvatica*) trees (Sikora 2017). Furthermore, many of the trees in the English wood pastures are very old, both in relative and absolute terms, as indicated by an average bee tree DBH of 1.7 m. The average DBH of BWC trees with bees in our study was only 0.7 m. Besides woodpecker-excavated holes, these veteran and ancient trees in England often contain large non-excavated cavities. Although these figures demonstrate that managed forests are relatively poor habitats for wild honeybees in terms of cavity abundance and diversity, they also underline the significance of the black woodpecker as a keystone species in such landscapes.

Studies of tree cavities, as the one presented here, are naturally hampered by the difficulty in accessing tree holes. Due to a small sample of studied cavities, the imprecise measurement of cavity volume, and the imperfect distinction between bee trees and non-bee trees, our study lacks the statistical power to detect subtle preferences of honeybees for certain cavity traits. Nevertheless, our first cavity survey provided interesting insights and raises several questions. For example, honeybee swarms choosing BWCs apparently face a dilemma in that it is difficult to optimise cavity volume and entrance size. We generally do not know how honeybee scouts weigh various variables when assessing potential nesting cavities. This issue could be investigated using experiments in which swarms are offered pairs of nest boxes varying in two variables at a time, one being at the optimum and the other at a borderline acceptable state (Seeley and Morse 1978). Another important question is how the large variation in cavity traits affects the bees' survival and reproduction in the wild. Measuring dozens of bee tree cavities and subsequently documenting the survival of colonies nesting there could be a way to investigate this in the field. Furthermore, to fully understand the context of honeybees' nest site preferences, it is important to collect data on the characteristics of large random samples of cavities, including those other than BWCs. New technical solutions, such as a recently presented pole-mounted 3D-scanner (Visick and Ratnieks 2025) and drone-based robotic inspection systems (Steich et al. 2016), will enable more precise and efficient measurement of tree cavities.

Managed forests often cover significant portions of land; in Germany, they make up almost one-third of the country. Regarding the question of how wild honeybee populations can be promoted in managed forests, we hypothesise that the low density of suitable nesting sites, not the quality of selected nest cavities per se, is a limiting factor. Following the examples of studies on cavity-nesting birds (Thompson et al. 2023), it would be interesting to test whether the supplementation of managed forests with nest boxes tailored to the bees' preferences will increase the density and survival of wild honeybee colonies.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https://doi.org/10.1007/s13592-026-01268-2.

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AUTHOR CONTRIBUTION

BR and PLK were involved in conceptualisation, methodology, investigation, formal analysis, visualization, writing – original draft, writing – review & editing.

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DATA AVAILABILITY

The data that support the findings of this study are available in the Supplementary Material.

DECLARATIONS

Ethics approval No honeybees were harmed during this study, as we used non-invasive monitoring methods. Ethical approval was therefore not required.

Conflict of interest The authors declare no competing interests.

REFERENCES

Agostinelli C, Lund U (2024) R package "circular": circular statistics (version 0.5–1)

Andersson J, Domingo Gómez E, Michon S, Roberge J-M (2018) Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. Scand J Forest Res 33:233–244. https://doi.org/10.1080/02827581.2017.1360389

Cockle KL, Martin K, Wesołowski T (2011) Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Front Ecol Environ 9:377–382. https://doi.org/10.1890/110013

Edworthy AB, Trzcinski MK, Cockle KL et al (2018) Tree cavity occupancy by nesting vertebrates across cavity age. J Wildl Manag 82:639–648. https://doi.org/10.1002/jwmg.21398

Johnsson K, Nilsson SG, Tjernberg M (1993) Characteristics and utilization of old Black Woodpecker *Dryocopus martius* holes by hole-nesting species. Ibis 135:410–416. https://doi.org/10.1111/j.1474-919X.1993.tb02113.x

Kohl PL, Rutschmann B (2018) The neglected bee trees: European beech forests as a home for feral honey bee colonies. PeerJ 6:e4602. https://doi.org/10.7717/peerj.4602

Kohl PL, Rutschmann B, Steffan-Dewenter I (2022) Population demography of feral honeybee colonies in central European forests. R Soc Open Sci 9:220565. https://doi.org/10.1098/rsos.220565

Kohl PL, Rutschmann B, Sikora LG et al (2023) Parasites, depredators, and limited resources as potential drivers of winter mortality of feral honeybee colonies in German forests. Oecologia 202:465–480. https://doi.org/10.1007/s00442-023-05399-6

Kosiński Z, Walczak Ł (2019) Does cavity reuse affect timing of reproduction and fledgling success in the black woodpecker? J Ornithol 160:79–89. https://doi.org/10.1007/s10336-018-1585-5

Lindenmayer DB, Laurance WF, Franklin JF (2012) Global decline in large old trees. Science 338:1305–1306. https://doi.org/10.1126/science.1231070

Michon S (2014) Comparison of tree cavity abundance and characteristics in managed and unmanaged Swedish boreal forest. Master degree thesis, Swedish University of Agricultural Sciences

Oleksa A, Gawroński R, Tofilski A (2013) Rural avenues as a refuge for feral honey bee population. J Insect Conserv 17:465–472. https://doi.org/10.1007/s10841-012-9528-6

Pedersen TL (2020) Patchwork: the composer of plots. R Package Version 1(1):1

R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Remm J, Lõhmus A, Remm K (2006) Tree cavities in riverine forests: what determines their occurrence and use by hole-nesting passerines? For Ecol Manage 221:267–277. https://doi.org/10.1016/j.foreco.2005.10.015

Requier F, Paillet Y, Laroche F et al (2020) Contribution of European forests to safeguard wild honeybee populations. Conserv Lett 13:e12693. https://doi.org/10.1111/conl.12693

Rizzo M, Szekely G (2024) energy: E-statistics: multivariate inference via the energy of data

Rutschmann B, Remter F, Roth S (2025) Monitoring free-living honeybee colonies in Germany: insights into habitat preferences, survival rates, and citizen science reliability. Ecol Evol 15:e71469. https://doi.org/10.1002/ece3.71469

Seeley T (1977) Measurement of nest cavity volume by the honey bee (*Apis mellifera*). Behav Ecol Sociobiol 2:201–227. https://doi.org/10.1007/BF00361902

Seeley TD (1978) Life history strategy of the honey bee, Apis mellifera. Oecologia 32:109–118. https://doi.org/10.1007/BF00344695

Seeley TD (1985) Honeybee Ecology: A Study of Adaptation in Social Life. Princeton University Press

Seeley TD (2010) Honeybee Democracy. Princeton University Press

Seeley TD (2017) Life-history traits of wild honey bee colonies living in forests around Ithaca, NY, USA. Apidologie 48:743–754. https://doi.org/10.1007/s13592-017-0519-1

Seeley TD (2019) The Lives of Bees: The Untold Story of the Honey Bee in the Wild. Princeton University Press

Seeley TD, Morse RA (1976) The nest of the honey bee (*Apis mellifera* L.). Insectes Soc 23:495–512. https://doi.org/10.1007/BF02223477

Seeley TD, Morse RA (1978) Nest site selection by the honey bee, *Apis mellifera*. Insectes Soc 25:323–337. https://doi.org/10.1007/BF02224297

Sikora LG (2007) Entwicklung und Veränderung von Schwarzspecht-Höhlenbäumen zwischen 1997 und 2007 im östlichen Schurwald (Baden-Württemberg). Deutsche Wildtier Stiftung, Hamburg

Sikora LG (2017) Density, distribution and development of black woodpecker Dryocopus martius cavities and their use in forests in Baden-Württemberg, with additional notes on the black woodpecker population (in German). Charadrius 53:77–82

Sikora LG (2024) The black woodpecker Dryocopus martius and its cavity trees in the Swabian Alb biosphere reserve. Vogelwelt 142:17–23

Sikora LG, Schnitt D, Kinser A (2016) Folgeuntersuchung von Schwarzspecht-Höhlenbäumen im Biosphärengebiet Schwäbische Alb. Deutsche Wildtier Stiftung, Hamburg

Steich K, Kamel M, Beardsley P, et al (2016) Tree cavity inspection using aerial robots. In: 2016 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS). IEEE, Daejeon, South Korea, pp 4856–4862. https://doi.org/10.1109/IROS.2016.7759713

Székely GJ, Rizzo ML (2004) Testing for equal distributions in high dimension. Interstat 5:1249–1272

Thompson EK, Keenan RJ, Kelly LT (2023) The use of nest boxes to support bird conservation in commercially managed forests: a systematic review. For Ecol Manage 550:121504. https://doi.org/10.1016/j.foreco.2023.121504

Tiedemann F (2020) Ggpol: visualizing social science data with'ggplot2'. R Package Version 00(7):216–229

Visick OD, Ratnieks FLW (2024) Ancient, veteran and other listed trees as nest sites for wild-living honey bee, *Apis mellifera*, colonies. J Insect Conserv 28:153–163. https://doi.org/10.1007/s10841-023-00530-7

Visick OD, Ratnieks FLW (2025) Non-destructive measurement of tree cavity volume relating to nest sites for wild honey bee colonies and other species. J Apic Res 0:1–13. https://doi.org/10.1080/00218839.2025.2556076

Visick OD, Ratnieks FLW (2026) Density and survival of wild honey bee colonies in English wood pasture, parkland and deer parks. Apidologie 57:5. https://doi.org/10.1007/s13592-025-01234-4

Wesołowski T (2011) "Lifespan" of woodpecker-made holes in a primeval temperate forest: a thirty year study. For Ecol Manage 262:1846–1852. https://doi.org/10.1016/j.foreco.2011.08.001

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York

Zawadzki G (2024) Nesting-tree preferences of the black woodpecker—the biggest cavity excavator in a conifer-dominated forests