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ORIGINAL RESEARCH

# Assessing concrete nest boxes for cavity-nesting bees

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## Abstract

Artificial nest boxes for solitary bees and other cavity-nesting Hymenoptera are increasingly used for a variety of purposes, including ecological research, crop pollination support and public outreach. Their attractivity and colonization success by cavity-nesting solitary bees depend on their design and placement, including hole dimensions, orientation and the neighboring habitats and available resources. While most bee nest boxes are made of wooden materials, we assessed here the suitability of perennial, concrete nest boxes for cavity-nesting bees. We carried out a three-year nesting survey of 52 custom-made nest boxes located in 11 different sites throughout France and totaling 2912 available holes of 6, 8, 10 or 12 mm in diameter. Concrete nest boxes successfully attracted reproductive females of solitary bee species and supported successful larval development until the emergence of new individuals. Preferred cavities were the smallest ones (6-8 mm), located at the lowest tested positions above ground (31-47 cm) and oriented southward. Local bee populations established in nest boxes steadily increased throughout the three successive seasons in nearly all study sites. The cavity-nesting bee communities were mostly composed of rather common and generalist species, but also comprised a foraging specialist. Additionally, two cleptoparasitic bee species were detected. All species belonged to the Megachilidae. We further discuss the effects of neighboring urban and natural habitats as potential source or sink of nesting bees, as well as opportunities of concrete nest boxes as tools for urban agriculture and more generally for the new biomimetic urban designs to restore local ecosystem services in cities.

**Keywords** Wild bees · Nesting behaviour · Trap nest · Bee hotel · Urban ecology · Biomimetic urban designs

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## Introduction

In the face of declining wild bee populations (Biesmeijer et al. 2006; Potts et al. 2010; Burkle et al. 2013; Zattara and Aizen 2021), it is important to understand their biology, behaviour and how populations are changing in response to the evolution of their environment. Bee nest boxes, also termed 'bee hotels', 'nesting aids' or 'nesting traps' (von Königslöw et al. 2019) may have several roles to play in this context (MacIvor and Packer 2015; MacIvor 2017; von Königslöw et al. 2019). Nest boxes are man-made refuges for cavity-nesting bee species, typically displaying a range of artificial holes or natural cavities where nesting females can build several brood cells in line. Cells are made of mud, resin, chewed leaves or pieces of cut leaves, depending on the bee species. Most common materials used to build nest boxes are drilled wood, hollow plant stems or pithy stems, including bamboo or reed, or tubes made up of a variety of materials such as paper, cardboard, glass or plastic (MacIvor 2017). They are often used as experimental tools in science to study host-parasite, host-predator and host-disease relations, to understand the biology, behaviour, life history traits and food preferences of bee species or to study biological invasions (MacIvor and Packer 2015; Geslin et al. 2020). They thus can serve as bioindicators of ecological changes and habitat quality (Gaston et al. 2005) and make it possible to monitor the evolution of local populations (Fortel et al. 2016; Geslin et al. 2020).

Nest boxes can also improve pollination services for plants, especially crops, when the intrinsic characteristics of nest boxes (e.g. cavity diameter and length) are designed to favour one or several species of interest (MacIvor 2017). Indeed, a growing number of solitary bees are now reared in nest boxes for commercial pollination purposes, including for instance some *Osmia* species for orchard pollination (Bosch and Kemp 2002; Koh et al. 2018; Boyle and Pitts-Singer 2019) and the alfalfa leafcutting bee *Megachile rotundata* for alfalfa seed crops pollination (Bosch and Kemp 2005).

Promoting wild (solitary) bee diversity and conservation is frequently invoked when setting up nest boxes, particularly in urban and peri-urban areas. However, nest boxes may often harbour more individuals of invasive alien species than endemic ones, e.g. the invasive giant resin bee *Megachile sculpturalis* or the alien wasps *Isodontia mexicana* (MacIvor and Packer 2015; Fortel et al. 2016; von Königslöw et al. 2019; Geslin et al. 2020), potentially competing with native bees for nesting cavities (Straffon-Díaz et al. 2021). Artificial nest boxes may also promote the proliferation of parasites, predators and diseases because nests are concentrated in the same area, which rarely exists naturally for non-gregarious species (MacIvor and Packer 2015). This therefore stresses the need for more research to identify best practices for optimising nest box benefits for local bee populations.

Last but not least, bee nest boxes are used to raise public awareness about the often overlooked existence of solitary bees and to observe their nesting behaviour (Hane and Korfmacher 2022). Nest boxes may therefore be viewed as useful tools for participatory science projects, assisting researchers in the study of the ecology, behaviour and diversity of solitary bee assemblages, while pursuing public outreach objectives at the same time. This can be particularly efficient in urbanized areas that can accommodate a substantial diversity of cavity-nesting bee species (Fortel et al. 2016; Fauviau et al. 2022).

The nest box occupancy or colonization success, often expressed as the percent of holes eventually occupied by bee nests after a predetermined exposure period, depends on a range of intrinsic and extrinsic nest box characteristics, as reviewed by MacIvor (2017).

Extrinsic characteristics such as the surrounding landscape composition and proximity to floral resources are obviously influential (Everaars et al. 2011; MacIvor and Packer 2015; Maclvor 2016), though their respective effects on occupancy appear difficult to disentangle owing to the multifaceted nature of the wild bee fauna in terms of foraging behavior and habitat preference. Conversely, the importance of some intrinsic nest box characteristics is well established, such as orientation of the openings respective to the sun (i.e. southward in the northern hemisphere) or hole diameter, with smaller holes (e.g. 4 to 8 mm) being usually attractive to more bees than larger ones (von Königslöw et al. 2019). Other intrinsic nest box characteristics remain poorly documented to date, such as shading, orientation to prevailing winds, or height above ground or vegetation (e.g. Budrienė et al. 2004; Everaars et al. 2011; Martins et al. 2012).

Nest box material is arguably another critical point for bee occupancy. Most studies that have compared nest boxes made-up of diverse materials found significant differences in terms of bee occupancy. Bee nests may be more abundant in drilled logs compared to hollow stems or commercial grooved boards (Fortel et al. 2016; González-Zamora et al. 2021). Likewise, the abundance of emerging bees may vary significantly among drilled logs or pithy stems from different plant species (Fortel et al. 2016), which illustrates the high variability of potential nesting outcomes from one box design to another.

While the majority of nest boxes built for commercial or research purposes are made up of wooden materials, to our knowledge, concrete or other mineral materials have rarely been evaluated in the scientific literature – possibly because of the technical difficulty to manufacture standard nest boxes with such substrates. Among the exceptions, Martins et al. (2012) found that bees successfully nested in cardboards tubes inserted in holes drilled in vermiculite, i.e. a composite mineral substrate. Hole occupancy by bees was, however, five times less in the vermiculite substrate as compared to wooden controls. More recently, Shaw et al. (2021) evaluated the use by solitary bees of holes in bricks, known as 'Bee Bricks'. Authors have reported over two consecutive years the presence of nesting bees, holes being typically capped with mud, cut leaves and chewed leaves. Brick hole occupancy ranged from 1.3% (year 1) to 2.8% (year 2) out of several thousand available holes. Wooden control occupancy values, respectively 1.1% and 0.7%, were lower, but not significantly different from brick hole occupancies. The identity of nesting bee species, as well as their actual emergence success was not reported, however. Still, this latter study offers interesting new insights into the use of mineral (non-wooden) nest boxes by bees and their potential scientific and societal interest.

The overall objective of our study is to assess the suitability of concrete nest boxes for cavity-nesting bees, based on a three-year nesting survey involving a participatory research action. As a mineral substrate, one possible advantage of concrete for cavity-nesting insects is its resistance and durability, compared to wooden substrates that may need to be regularly replaced due to natural decomposition or degradation by weather and xylophagous insects. In line with these characteristics, concrete nest boxes may be further embedded into more sustainable urban designs and building restoration projects. They may for instance contribute to support the increasing demand for urban pollinators along with the development of urban agriculture in community allotments or on green roofs (e.g. Hofmann and Renner 2018). More broadly speaking, this is in line with the novel approach of 'biomimetic urban designs' that seeks to reconcile social and ecological issues by achieving positive net impacts on ecosystem services (Blanco et al. 2021). Biomimetic buildings most commonly focus on biophysical ecosystem services such as water collection or carbon sequestration through augmented vegetation covers around and on buildings, and more rarely consider fauna and habitat management schemes (Blanco et al. 2022). Still, one may eventually consider pollination services as a part of those biomimetic designs, by the inclusion of wild bee concrete nesting aids.

Judging from the apparent nesting flexibility of some cavity-nesting species, e.g. *Osmia bicornis* and *O. cornuta* (Fortel et al. 2016), we predicted that some species may thrive in concrete cavities. Specific objectives were (i) to ascertain the attractivity, establishment and development of cavity-nesting bee communities in concrete boxes, (ii) to determine the intrinsic characteristics that promote box occupancy, particularly hole diameter, height above the ground and cardinal orientation, (iii) to assess whether the presence of urban and natural habitats in their immediate vicinity may further act as a source of cavity-nesting bees and (iv) to provide a broad description of the bee community attracted by concrete nest boxes, including species occurrence frequencies, expected richness and conservation status. Strength and possible weaknesses of concrete bee boxes are finally discussed, along with future research perspectives.

## Materials and methods

### Concrete bee nest boxes

Nest boxes were designed and manufactured specially for the study using ultra high-performance fiber-reinforced concrete (UHPFC), also named SMART-UP (Vicat company, Isle-d’Abeau, France). The strength, durability and mechanical properties of the SMART-UP concrete make it a common material in construction and building technology, including for the construction of complex outdoor shapes and smaller decorative elements.

Concrete boxes were conceived as 25×25-cm wide removable modules that could be integrated into various kinds of urban furniture. Each box displays 56 holes 8-cm deep designed to offer nesting opportunities to cavity-nesting bees (Fig. 1). To guarantee a smooth finish of the inside of the holes, nest boxes were entirely molded in one piece with their holes, rather than having their holes drilled at a later stage. For the sake of the study, nest boxes were integrated into planters offering ornamental nectariferous and polliniferous plants such as lavender *Lavandula angustifolia*, rosemary *Rosmarinus officinalis* and thyme *Thymus vulgaris* and provided with educational displays about solitary bee nesting biology (Fig. 1). All boxes were identical in terms of hole number, diameters and distribution.

In each box, the 56 holes had diameters adapted to bee nesting (von Königslöw et al. 2019): 23 holes 6 mm in diameter, 11 holes 8 mm, 10 holes 10 mm and 12 holes 12 mm. The holes were arranged symmetrically, with respect to diameters, along a horizontal axis when the boxes are placed in the planters. On each planter, two boxes were exposed in the ‘lower’ position (holes arranged between 31 and 47 cm from the ground) and two others in the ‘higher’ position (holes between 49 and 65 cm from the ground), i.e. a total of four boxes and 224 holes per planter.

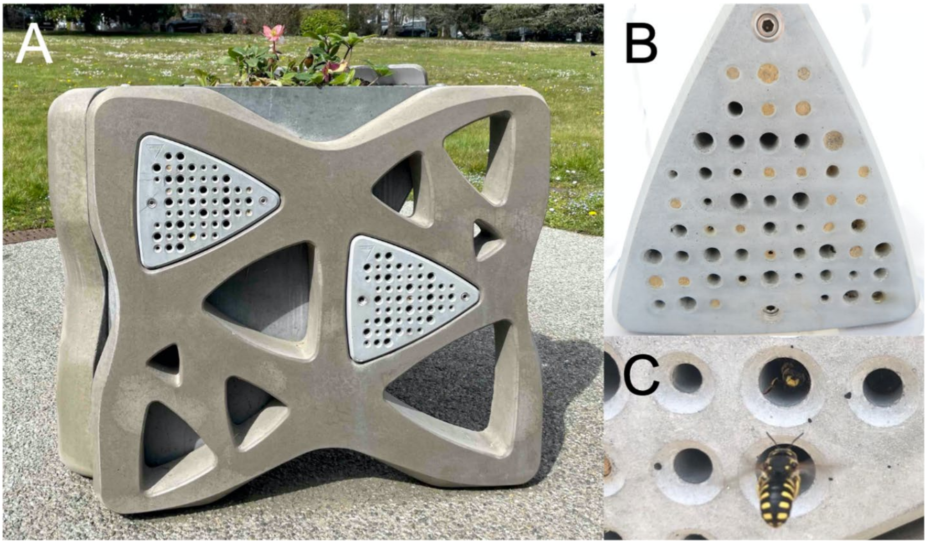


**Fig. 1** Example of concrete nest boxes placed in a planter. **(A)** Nest boxes display 23 holes of 6 mm in diameter, 11 holes 8 mm, 10 holes 10 mm and 12 holes 12 mm in diameter. They are placed either in the *lower* or the *higher* position (holes at 31–47 cm and 49–65 cm from the ground, respectively). **(B)** Holes capped with mud indicate the presence of potential nests of mason-bees like *Osmia* spp. **(C)** Nesting activity of *Anthidium sp.* in concrete cavities (photo provided by E. Salles, Vicat).

## Study sites

A total of 14 planters were surveyed during three consecutive years in 2018-20. Planters were spread over 11 sites among different regions of France and located 30 to 720 km apart from each other (with the exception of two sites located just 6 km apart, see Fig. S1 in the online Supplementary Information). Three sites held two planters, located at least 200 m apart from each other. Study sites were all located in temperate continental to oceanic biomes, except the southernmost ones (Colomiers and Portes-lès-Valence) which were on the edge of the Mediterranean biome characterized by a more diverse bee fauna.

## Nest box placement

All sites were private plots operated by the box designer (Vicat company) and its subsidiaries. They were typically sites of concrete activity embedded in a landscape mosaic composed of agricultural plots. Some sites also include in the direct vicinity of nest boxes (within a 50-m radius) either (i) extents of natural habitats (grasslands, hedgerows and other semi-natural elements), (ii) built-up and (sub-)urbanized areas, or (iii) both natural habitats and urbanized areas. The potential contribution of those natural and urbanized areas as possible habitat sources of cavity-nesting bees was assessed as an environmental factor liable to influence colonization success (see below *Data analyses*). The prevailing orientation of planters, either southwards or northwards, was also recorded, inasmuch as orientation is expected to be an important driver of nest occupancy. Five out of 14 planters were moved away by 50 to 100-m from one season to the next due to changes in access conditions. In this case, the information on placement (orientation and presence of nearby urbanized areas and natural habitats) was updated, resulting in a total of 19 different placement combinations. Statistical analyses took into account these placement changes with respect to each individual planter.

## Nesting surveys

The nesting surveys were intended to document the percent occupancy of holes by bee nests. They were carried out as a participatory research action by volunteer staff of the plot owner company who systematically reported capped holes at the end of each season of 2018-20. Participants were taught to recognize typical bee nest caps, made up of mud, cut or chewed leaves, plant fibers or resin. Holes obstructed by plugs of thin herbaceous twigs or other materials, likely originating from wasps or other arthropods, were noted as not available to nesting bees.

## Emergence surveys

Emergence surveys were intended to (i) validate and assess the accuracy of the participatory nesting surveys provided by engaged volunteers, (ii) ascertain the presence of bee nests, (iii) evaluate their emergence success and (iv) characterize the bee species nesting community in the tested concrete nest boxes. After each nesting season, a subset of boxes with evidence of nesting activity were removed from planters to enter an emergence routine survey throughout the season $n+1$ following box exposure in season $n$, i.e. in 2019, 2020 and 2021. A single one out of the four nest boxes per planter was removed, and no nest box was removed from planters with obviously very few nesting activity. Boxes removed from planters were replaced by new ones, while the others remained in place for the next season.

Removed boxes were all gathered at the same location (Bees & Environment unit, INRAE research center, Avignon, France), stored individually in 30×30×30 cm collapsible insect rearing cages and placed in an insect-proof tunnel to protect them from heavy rains or strong wind. Cages were carefully checked every other day for the presence of newly emerged individuals. All individuals were collected for later identification to species level by a network of taxonomist experts recognized by the French *National Inventory of Natural Heritage* (INPN – Inventaire National du Patrimoine Naturel, Muséum National d’Histoire Naturelle, Paris, France). The emergence surveys lasted from the first recorded emergence, typically around mid-February, until at least July and after no new emergence was recorded from any caged box over a period of six consecutive weeks. Boxes were carefully inspected before and after the emergence period in order to double-check hole occupancy data returned by the participatory nesting surveys, and to keep track of holes with caps removed, excavated or bored (successful emergence) vs. those that remained intact (no obvious emergence).

The study was primarily designed to monitor nest boxes as a whole and assess broad patterns of colonization and emergence success of the local cavity-nesting bee fauna. It was therefore not possible to obtain at this stage the high-resolution monitoring of individual nests to document thorough reproductive success values for each species (offspring size per nest or per nesting female), nor the species-specific nesting preferences with regard to the hole characteristics.

## Data analyses

*Validation of the participatory nesting survey data.* As a preliminary precaution, we performed a Pearson correlation test to compare the percent occupancies of nest boxes observed prior to emergences with those actually returned by the participatory nesting surveys on the same boxes ($n=29$ boxes, see results). Occupancies were defined as the proportion of capped holes in each nest box, setting apart unavailable holes likely to have been obstructed or clearly occupied by non-bee arthropods. Additionally, in order to detect potential biases arising from participatory surveys, a paired t-test was performed to compare occupancy values obtained from unexperimented volunteers with those obtained from our own observations.

*Interannual establishment and development of nesting activity.* In a second step, we assessed whether the nesting activity would overall increase year after year, as one might expect under the hypothesis of population or community establishment and development. To do so, we used the occupancy binary nesting data at individual hole level (occupied vs. unoccupied), and computed the overall evolution of occupancy probabilities throughout study years by the mean of a binomial generalized linear mixed model (GLMM). The study year, ranging from 1 to 3, was implemented as a fixed effect in the model, while specifying a random grouping structure to account for the non-independency of nesting data originating from the same planter, nest box and hole diameter category.

*Intrinsic nest box characteristics that promote occupancy.* After confirmation of the establishment and development of a nesting activity, we sought to assess which nest box intrinsic characteristics would promote their occupancy. We focused on three candidate correlates of occupancy as a part of a GLMM modelling framework: hole diameter (as a continuous quantitative variable, in mm), height above ground (*low* vs. *high* box positioning) and prevailing orientation (*southward* vs. *northward* placement). We also considered all the two-way interactions between these candidate correlates, as occupancy may respond differently to a given correlate conditionally on another one.

For the sake of parsimony, we favored a stepwise model simplification approach to identify the smallest subset of relevant correlates and statistical interactions. We first computed a *full model*, comprising all three candidate correlates as fixed variables, as well as their two-way interactions. The planter identity was specified as a random grouping variable. The temporal dependency of repeated observations on the same planter was further accounted for by allowing random slopes across years. Second, we simplified the full model down to the *minimum adequate model*, i.e. the model that returned the most parsimonious tradeoff between complexity and fit to data, as given by the Akaike Information Criterion (AIC). We used a backward stepwise model simplification, deleting sequentially the terms that did not contribute to reduce AIC, starting from interaction terms first, and maintaining simple terms whenever they were involved in a relevant interaction. Third, we performed Wald tests to assess the significance of each term in the minimal adequate occupancy model.

*Environmental factors acting as a source of nesting bees.* Once the intrinsic nest box factors accounting for occupancy variations had been satisfactorily identified, we tested whether the presence of urban and natural habitats in the immediate vicinity of a planter might further act as a source of cavity-nesting bees. To do so, we implemented into the minimum adequate occupancy model the information on presence or absence of urbanized areas and of natural habitats as additional fixed binary factors. A significant positive effect might be interpreted as a source of cavity-nesting bees, indicative of a relevant placement for nest boxes to assist population expansion or restore connectivity among habitats.

*Emergence success and description of the cavity-nesting bee community.* In a final step, we summed up the results of the emergence surveys to provide an overview of the cavity bee communities who successfully nested in the concrete boxes. We computed summary data on emergence success (proportion of capped holes with evidence of emergence), species occurrence frequencies, average observed species richness as well as total expected cumulative species richness.

All analyses were carried out using R (R Core Team 2022). GLMMs were computed using the package *glmmTMB* version 1.1.4 (Brooks et al. 2017). Expected richness estimates were obtained using the package *vegan* version 2.6-2 (Oksanen et al. 2022). Expected cumulative richness curve was plotted using the package *iNEXT* version 3.0.0 (Hsieh et al. 2022).

## Results

### Nesting surveys and emergence surveys

The 14 planters totaled 52 nest boxes on display in the first year, 49 in the second year and 45 in the third year, i.e. a total of 2912, 2744 and 2520 holes, respectively. This led to 7866 binary hole occupancy records (occupied vs. unoccupied) out of 8176 (96.2%), considering that about 3.8% of the holes were judged unavailable to bees due to occupancy by other arthropods or other types of obstruction.

A subset of 8, 6 and 15 nest boxes with at least one occupied hole were removed at the end of the first, second and third study year, respectively, for the emergence surveys (in total, 29 boxes from 11 sites). A total of 686 newly emerged individuals were collected out of the emergence cages and identified to 11 different species, all from the Megachilidae (see below). Wasps, flies or other arthropods were seldom collected, suggesting that, overall, they marginally influenced the surveys.

### Validation of the participatory nesting survey data

Volunteer participants returned consistent and reliable occupancy data, closely correlated with those recorded by our observations on the same nest boxes (Spearman rank correlation tests, $n=29$ boxes, $R=0.98$, $P<0.001$). Errors appeared trivial, and generally biased towards a slight 3.0% underestimation by volunteer participants (Fig. 2). A paired t-test indicated that this difference was not significant – though close to the statistical significance threshold ($t=-1.98$, $n=29$ boxes, $P=0.056$). This bias mostly occurred due to undetected, inconspicuous caps that were positioned deeper inside holes, but was considered too subtle to affect the overall nesting statistics.

### Interannual establishment and development of nesting activity

The average hole occupancy steadily increased over time, from 2.9 to 11.6%, and then to 25.3% for the first, second and third year, respectively. The binomial GLMM confirmed

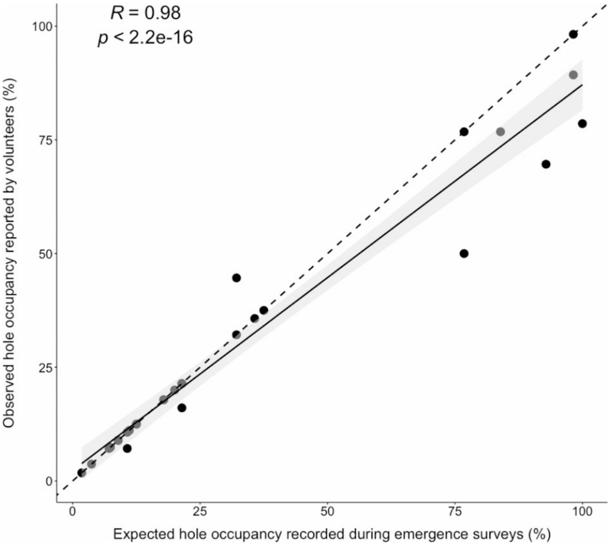


**Fig. 2** Correlation between observed occupancy recorded by volunteer participants and expected occupancy recorded during the bee emergence survey of the same 29 boxes. The straight line and shaded area stand for the *expected*-vs-*observed* correlation and its standard error, respectively. The dashed line indicates the 1-to-1 reference slope for perfect match between expected and observed occupancy records. Most deviations from expectations occur slightly below the reference slope, meaning that volunteers tended to slightly underestimate actual occupancy

a highly significant temporal increase of nest occupancy throughout the nesting surveys (n = 7866 holes, z = 23.43, P < 0.001). A tremendous variability among sites and years was observed, however, with occupancy eventually reaching 70,5 to 98,8% on the third year in three sites, while remaining below 20% in most of other sites.

## Intrinsic nest box characteristics that promoted occupancy

All three candidate correlates of hole occupancy contributed to explain a significant part of total deviance (GLMM, accounting for interannual and site variabilities as random variables). After model simplification, the minimum adequate occupancy model retained hole diameter, height above ground, orientation as well as highly significant two-way interactions between height and orientation on one hand and hole diameter and orientation on the other hand (Table 1). The holes with smaller diameter, and with a southward prevailing orientation, had significantly higher probabilities of occupancy overall. Although the height factor (boxes set at *higher* vs. *lower* positions) was not significant per se, it significantly interacted with orientation in a way that reveals a strong preference of nesting bees for lower boxes when exposed southward, while no clear height preference appeared when boxes were exposed northward (Fig. 3). Likewise, orientation and hole diameter revealed a strong and significant two-way interaction, with steadily decreasing occupancy probabilities as diameters increased in southward nest boxes, while no clear diameter pattern appeared in northward nest boxes (Fig. 3).

## Environmental factors acting as a source of nesting bees

The occupancy pattern returned by the minimum adequate model could be further refined by adding the environmental variables. The presence of urban and natural habitats in the immediate vicinity contributed to produce a fittest model (AIC reduced from 3398.3 to 3377.3), though not completely in accordance with initial expectations. Nearby natural

**Table 1** Results of the binomial GLMMs testing for the effects of concrete nest box characteristics on hole occupancy. Details of the minimum adequate occupancy model are shown first, with hole diameter as a continuous explanatory variable and box position and orientation as bimodal categorical variables (focus modalities are given in parentheses). The two-way interactions noted '×', as well as interannual trends, are further depicted in Fig. 3. In a second part, the minimum adequate model was implemented with two candidate environmental (extrinsic) variables, indicating the presence or absence of urbanized or natural areas in the close vicinity of the planters. Models are based on 7866 individual hole occupancy (occupied/unoccupied) observations reported from 14 planters in 11 surveyed sites (in total 19 different placement combinations regarding orientation and extrinsic variables). Each planter supported four concrete nest boxes and was surveyed for two to three consecutive years

| Explanatory variables (focus modalities) | Estimates | SE | Z | P |
|---|---|---|---|---|
| *Minimum adequate occupancy model: effects of intrinsic nest box characteristics on occupancy* | | | | |
| Intercept (lower position, northward orientation) | -3.343 | 0.5819 | -5.746 | < **0.001** |
| Position (higher *minus* lower) | 0.190 | 0.1516 | 1.254 | 0.210 |
| Prevailing orientation (southward *minus* northward) | 2.481 | 0.5156 | 4.811 | < **0.001** |
| Hole diameter | −0.068 | 0.0323 | −2.092 | **0.036** |
| Position (higher) × Orientation (southward) | -0.613 | 0.1948 | -3.149 | **0.002** |
| Orientation (southward) × Hole diameter | -0.226 | 0.0441 | -5.123 | < **0.001** |
| *Minimum adequate occupancy model, implemented with environmental (extrinsic) explanatory variables* | | | | |
| Intercept (lower position, northward orientation) | -2.933 | 0.494 | -5.934 | < **0.001** |
| Position (higher *minus* lower) | 0.166 | 0.152 | 1.090 | 0.276 |
| Prevailing orientation (southward *minus* northward) | 2.551 | 0.499 | 5.111 | < **0.001** |
| Hole diameter | -0.068 | 0.0324 | -2.096 | **0.036** |
| Presence of urbanized areas | -2.000 | 0.451 | -4.429 | < **0.001** |
| Presence of natural areas | 0.369 | 0.720 | 0.513 | 0.608 |
| Position (higher) × Orientation (southward) | -0.583 | 0.195 | -2.988 | **0.003** |
| Orientation (southward) × Hole diameter | -0.225 | 0.044 | -5.112 | < **0.001** |

habitats tended to increase occupancy probability, but not in a significant way. Furthermore, nearby urban habitats exerted a highly significant decreasing effect on occupancy, which goes against the hypothesis of urban areas as a source of cavity-nesting bees (Fig. 4).

## Emergence success and description of the cavity-nesting bee community

Average emergence statistics were computed for the 17 boxes out of 29 which had at least ten occupied holes (Table S1 in the online Supplementary Information). The emergence success, i.e. the percentage of occupied holes eventually displaying evidence of successful emergence, was higher for boxes with a single or two seasons of exposure (88.0 ± 16.0%,

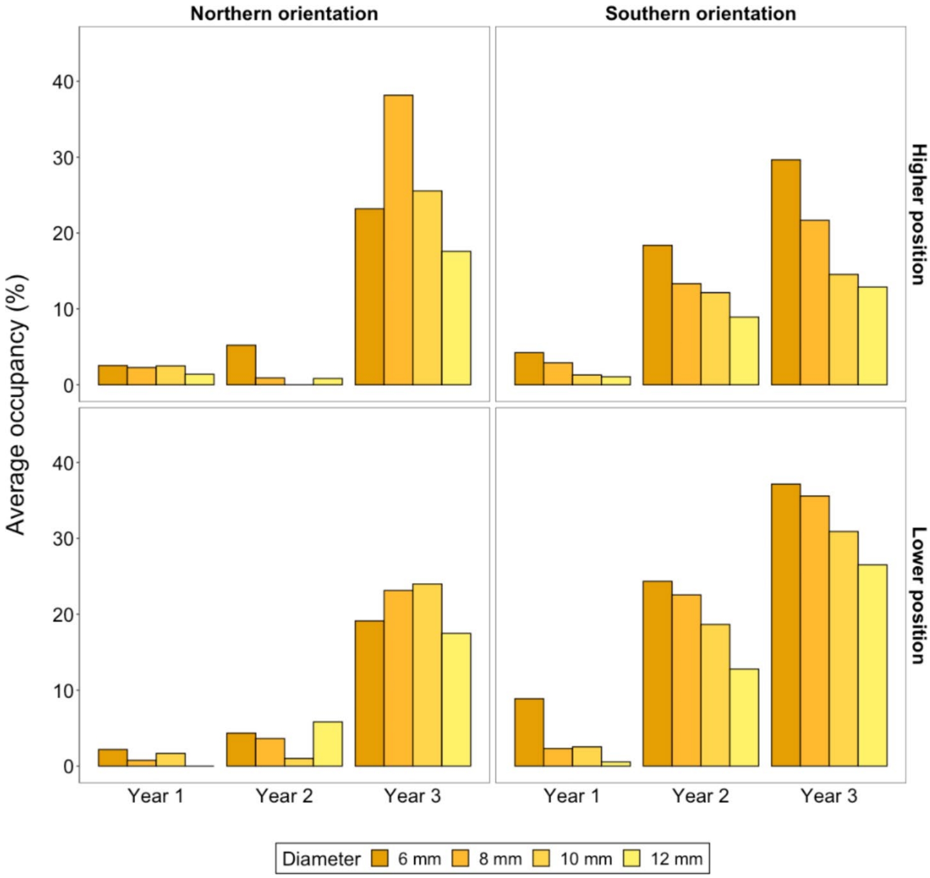
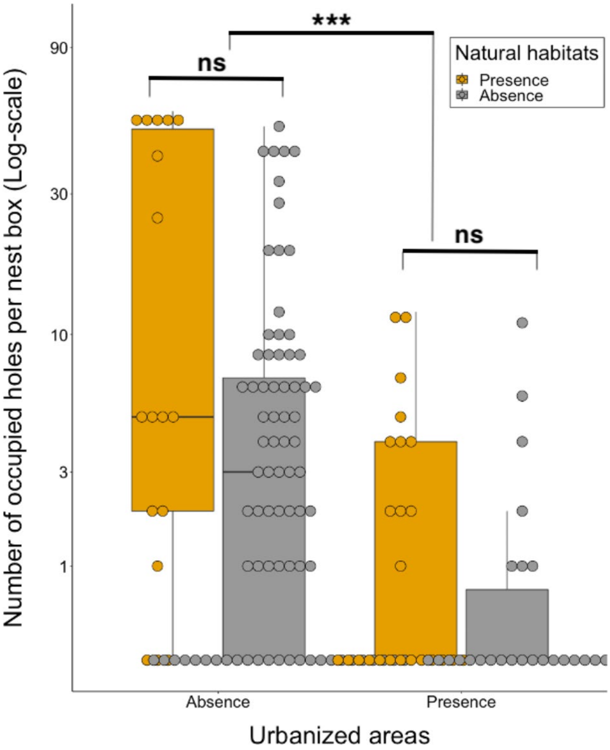


**Fig. 3** Average nest box hole occupancy (%) by study year (first to third nest box exposure year), hole diameter (6, 8, 10 and 12 mm), height above ground (*low* vs. *high* positions) and prevailing orientation (*southward* vs. *northward*)

n = 5, range [60.0%; 100%]) compared to boxes collected after three seasons of exposure (62.6 ± 13.7%, n = 12, range [38.5%; 83.3%]). This means that a small, but cumulative, proportion of occupied holes may actually not represent viable nests leading to new emerging individuals. Based on the latter proportion of 37.4% (100% – 62.6%) of non-emerging nests after three consecutive seasons, this cumulative emergence failure may be tentatively estimated to about 12.5% per year (37.4%/3). Further investigations made after the survey, however, revealed that the vast majority (93%) of those non-emerged nests were empty holes (false nests or fake nests, see Discussion).

A total of 11 species were recorded over the three years of survey (5 species in the first year, 8 in the second year and 8 in the third year). Setting apart cleptoparasitic species, a maximum of three species were recorded in a given nest box after a single exposure season, and up to four species after two or three consecutive seasons. The total extrapolated species richness one may expect to cover throughout the survey does not vary much among richness estimates, typically ranging from 12 to 13 species (Chao: 11.6 ± 1.3; first-order Jack-

**Fig. 4** Average nest box hole occupancy (%, log-scale) as a function of the presence or absence of urban and natural habitats in the direct vicinity. The presence of urban areas exerted a significant negative effect on nest box occupancy (***), while the positive trend for natural habitats was not statistically significant (ns), see text and Table 1 for details. Bars delineate the median and quartiles, and vertical lines the 95% confidence intervals



knife: 12.9 ± 1.3; Bootstrap: 12.1 ± 1.0), while the extrapolated species accumulation curve predicts that a ceiling has probably already been reached over the surveyed sites (Fig. 5).

All sampled species belong to the Megachilidae and included medium to large species (body length 6 to 17 mm), typically nesting either in pre-existing plant or mineral cavities (Table 2). Most of them (8 out of 11 species) are known to be polylectic, collecting pollen on a variety of unrelated plants. One exception is *Hoplitis adunca*, an oligolectic species specializing on pollen from *Echium* sp. (Boraginaceae). Two other species, *Coelioxys echinata* and *C. inermis*, are cleptoparasites known to occur in nests of *Megachile centuncularis* and *M. rotundata*, respectively.

Nine of the 11 species were found in at least two sites (range [2; 6]), which underlines a certain consistency in the identity of species that nested in concrete nest boxes (Table 2, Table S2). The most abundant and frequently collected species was *H. adunca*, being found in six of the 11 sites (256 individuals, 37.3%), followed by *Osmia bicornis* (5 sites, 213 individuals, 31%) and *O. caerulescens* (5 sites, 76 individuals, 11.1%).

## Discussion

The design of artificial nest boxes made of concrete is an original concept to our knowledge. We found in this study that concrete nest boxes succeed to attract reproductive females of several solitary bee species and support successful larval development until the emergence of new, viable individuals. Preferred cavities were the smallest ones (6–8 mm in diameter),

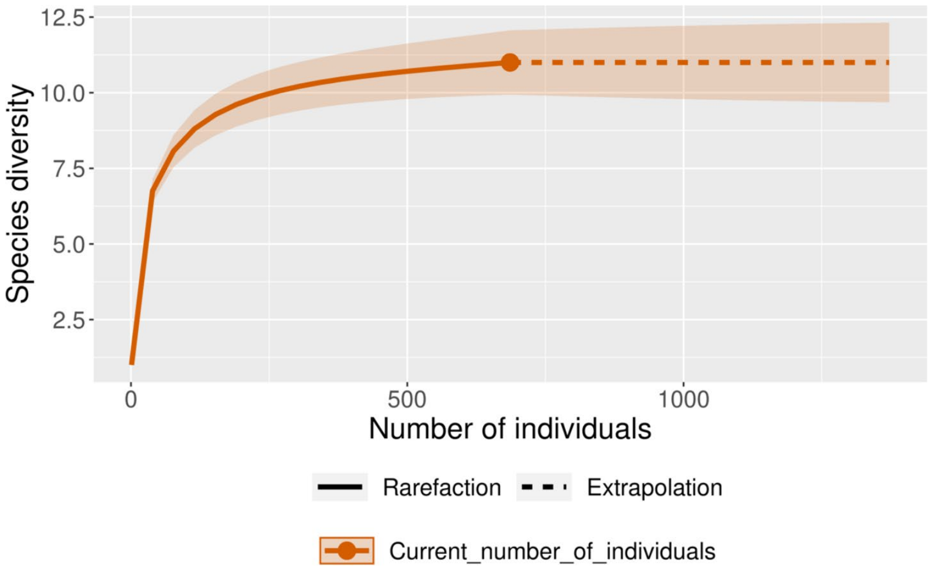


**Fig. 5** Cumulative bee species richness as a function of collected individuals from the 29 nest boxes that have entered the emergence survey. The extrapolated part of the curve (dotted line) does not predict any increase of species richness from the 11 surveyed sites

located at the lowest tested positions above ground (31–47 cm) and oriented southward. Local colonization rates steadily increased throughout the three consecutive seasons in nest boxes for nearly all study sites. The sampled nesting bee community appears not very diversified, with rather common and generalist species that typically nest in wood or hollow stems (rubicolous) or pre-existing cavities, but at least one of them is known to be foraging specialists. Much research remains to be done to understand the potential effect of neighboring habitats as potential source or sink of the nesting bees. In that respect, opportunities of concrete nest boxes as tools for urban agriculture are further discussed.

## Interannual establishment and development of nesting activity

Owing to an effective participatory monitoring program, we found that concrete nest boxes obviously succeeded in attracting and hosting conspecific nesting bees, which eventually developed into local bee populations. Most of the experimental planters were colonized in the first year of exposure, and all were colonized after three years. The average hole occupancy followed an increasing trajectory from one year to the next, with many conspecific individuals emerging from the same nest box in a given year – for instance up to 75 *Osmia bicornis* (sex ratio 1.7 male for 1 female) were collected from a single nest box on the third year (Table S2). Several species, including *O. bicornis*, are gregarious or even philopatric, i.e. young bees build their nests close to the parental nest (Fortel et al. 2016), thus forming rapidly growing aggregations in the same area. Olfactory cues mays also play a role in attracting nesting bees close to already existing conspecific nests, either made during the current season or a previous one (Pitts-Singer 2007).

**Table 2** Descriptive results of emergence surveys by species. Results include global species occurrence data in concrete nest boxes (individual numbers, relative abundance in % and number of occurrences out of the 11 study sites) and species life history traits related to body size, phenology, pollen specialization (lectism) and nesting habits. Except when otherwise stated, body size data come from Amiet et al. (2004) and other life history traits from Scheuchl and Willner (2016)

| Species | Nb. Collected Individuals (relative abundance; site occurrence) | Body size males/females (mm) | Voltinism$^{a}$ | Flight period (month ID) | Lectism | Nesting substrate | Nest materials |
|---|---|---|---|---|---|---|---|
| Anthidium florentinum | 8 (1.2% ; 1/11) | 14–20 / 13–15 | uni$^{c}$ | VI-VIII | polylectic$^{c}$ | pre-existing cavity | trichomes, leaves |
| Anthidium manicatum | 17 (2.5% ; 2/11) | 10–16 / 10–13 | uni$^{c}$ | VI-VIII | polylectic$^{c}$ | pre-existing cavity | trichomes, leaves |
| Coelioxys echinata | 3 (0.4% ; 2/11) | 6–7 / 6–8 | uni | VII-VIII | parasitic | Cleptoparasite (host species : *Megachile rotundata*) | |
| Coelioxys inermis | 1 (0.1% ; 1/11) | 9–10 / 9–10 | bi | V-X | parasitic | Cleptoparasite (host species : *Megachile centuncularis*, *M. versicolor*) | |
| Hoplitis adunca | 256 (37.3% ; 6/11) | 9-12$^{b}$ / 9-11$^{b}$ | uni | VI-IX | oligolectic | pre-existing cavity, rubicolous$^{d}$ | Wood particles, petals, sand, soil$^{d}$ |
| Megachile apicalis | 26 (3.8% ; 3/11) | 7–8 / 8–9 | uni | VI-VIII | polylectic | pre-existing cavity, rubicolous, helical | leaves |
| Megachile centuncularis | 5 (0.7% ; 2/11) | 9–11 / 11–12 | bi | V-X | polylectic | pre-existing cavity, rubicolous | leaves |
| Megachile rotundata | 12 (1.7% ; 2/11) | 7–8 / 8–9 | uni | VI-IX | polylectic | pre-existing cavity, rubicolous, woodcutting | leaves, petals |
| Osmia bicornis | 213 (31.0% ; 5/11) | 8–12 / 8–12 | uni | III-VII | polylectic | pre-existing cavity, rubicolous, woodcutting | mud (clay, soil) |
| Osmia caerulescens | 76 (11.1% ; 5/11) | 7–9 / 8–10 | bi, tri | III-X | polylectic | pre-existing cavity, rubicolous, woodcutting | leaves |
| Osmia cornuta | 69 (10.1% ; 4/11) | 11–13 / 12–15 | uni | II-VI | polylectic | pre-existing cavity, rubicolous, woodcutting | mud (clay, soil) |

a : uni=univoltism ; bi=bivoltism ; tri=trivoltism ; b : Müller (2016) ; c : Coiffait-Gombault et al. (2016) ; d : Müller (2022)

## Intrinsic nest box characteristics that promote occupancy

The most attractive and rapidly colonized holes for cavity nesting bees were the smallest ones (6 mm diameter), oriented southward, and located at the lowest position above ground (31 to 47 cm). While the hole size and orientation preferences were already documented in the literature (von Königslöw et al. 2019), the preference for rather low positions appears to be a new observation. In previous bee nesting studies, the most commonly used cavities were often also the ones with the smallest diameters (< 8 mm) because there are more small bees than large ones (reviewed by von Königslöw et al. (2019). In their study, carried out with reeds and bamboos, von Königslöw et al. (2019) modelled the probability of cavity occupancy as a function of diameter and found that holes of 6 mm in diameter had about 30% chance of being colonized, against only 15% and 7.4% for those 9 and 12 mm in diameter, respectively. In our study, occupancies did not decrease as steeply with increasing diameter, but still eventually reached a nearly two-fold difference between smallest and largest ones (14.6%, 12.9%, 10.6%, and 8.2% respectively for 6 mm, 8 mm, 10 and 12 mm diameter holes). Bees may even use smaller cavities in wood or hollow stems, with e.g. *Hylaeus* spp. preferring holes with a diameter between 3 and 4.3 mm (Budrienė et al. 2004) or *Ceratina* sp. nesting in holes between 2.6 and 5 mm (González-Zamora et al. 2021). It is unclear, however, whether concrete nest boxes would have attracted more diverse bee species with smaller holes (< 6 mm), and these may also be technically difficult to produce.

Not surprisingly, our study carried out in the northern hemisphere revealed that mean occupancies were nearly twice greater in southward nest boxes (15.0%) compared to northward ones (8.6%), most probably owing to better thermal inertia. Temperature inside an artificial nest box depends partly on the type of shelter and the material used, but also on the amount and timing of sunlight (Youngsteadt and Favre 2022). The orientation strongly impacts the internal temperature. It is generally recommended to orient nest boxes to the southeast and prefer a shaded location in the afternoon so that nests heat up more quickly with the morning sun. This increases the number of hours of foraging for adults, while avoiding the risks of extreme temperatures in the afternoon in situations of heatwave, which can be deadly for brood (MacIvor 2017; von Königslöw et al. 2019; Youngsteadt and Favre 2022). Yet, Wilson et al. (2020) found that *Megachile rotundata* preferred cooler, northward cavities when nesting in plastic nest boxes – which might be related to poorer thermal buffering of plastic cavities compared to concrete ones in our study. Nesting obviously depends on a complex interplay between material thermal properties, orientation, and shading, which remain to be elucidated. Importantly, our study is mostly indicative of temperate climates (see *Material and Methods*). The thermal properties of concrete nest boxes might lead to different nesting outcomes in hotter climates like the Mediterranean one. Thermal properties of concrete boxes should be the subject of a more targeted study in relation with nesting bee thermotolerance, especially in the current context of global warming and increasing heatwave frequencies and intensities in the southern regions.

Finally, hole depth is another nest box characteristic that appears critical for promoting occupancy. Depth effect has not been investigated herein because all nest boxes used in this study had standard holes of 8-cm in depth. Still, this depth appears somehow limiting given the recommended 15-cm depth in other studies (MacIvor and Packer 2015; von Königslöw et al. 2019). Shallow holes hold less cells and may lead to male-dominated sex-ratios (MacIvor 2017), among others because male cells are preferentially placed in the outermost positions, while female cells are located deeper in the nest for better protection against parasites and predators. Indeed, our survey returned a skewed sex-ratio with 1.64 males per female (426 M: 260 F, Table S1). Furthermore, we collected on average 2.0 individuals per successful nest, i.e. nests with evidence of viable emergence (686 individuals out of 346 successful nests, Table S1), which is arguably low. For comparison, *Osmia bicornis* may build about three brood cells and *Heriades truncorum* and *Osmia lignaria* about five brood cells in a cavity 15-cm deep (Bosch and Kemp 2001; MacIvor 2017; von Königslöw et al. 2019). Likewise, *Megachile gomphrenoides* (Torretta et al. 2012) and *Megachile cephalotes* (Akram et al. 2022) may build up to 7 or 8 brood cells in cavities 10-cm and 15-cm deep, respectively. Nevertheless, we may not draw firm conclusions on optimal hole depth in our study, owing to possibly inaccurate census of new emerging bees. Nests made in concrete boxes cannot be opened – as one would do with reeds or cardboard nesting tubes – in order to properly count cells or new emerging individuals. On several boxes, we even collected fewer individuals than the actual number of successful nests (Table S1). Some newly emerged individuals remained obviously undetected because they took refuge at the bottom of their original nest or of an adjacent hole.

It is also important to note that two species (set apart cleptoparasitic ones) are known in the literature to be possibly bivoltine, i.e. with two generations per year (Table 2). Therefore, our monitoring design, based on a simple diachronic comparison of nest presence at the beginning and the end of the nesting season, may have failed to cover all their active nests. Colonization and emergence values reported herein may therefore be somehow underestimated for these species.

### Environmental factors acting as a source or sink of nesting bees

Beyond the above-discussed nest box intrinsic characteristics, many environmental factors are liable to influence bee nesting activity. The present study did not aim to cover them all. We focused on two habitats whose presence in the close vicinity is liable to influence nest box occupancy, namely natural habitats and urbanized areas. Urbanization in particular is known to act as an ecological filter, affecting soil-nesting bee species more drastically than cavity-nesting ones (Fauviau et al. 2022). Yet, we found that the presence of urbanized areas in the close vicinity had an overall negative effect on nest box occupancy. Instead of acting as a source of cavity-nesting bees, urbanized areas may produce a nesting dilution effect. Indeed, human-made infrastructures may provide cavity-nesting species with many nesting opportunities (Maclvor 2016) similar to those offered by the concrete nest boxes.

Conversely, the presence of semi-natural areas or urban green spaces in the close vicinity is another important criterion for promoting bee diversity in nest boxes (Maclvor 2016). As central place foragers, bees will forage back and forth between their nest and neighboring foraging areas. This makes the proximity of adequate floral resources an essential condition for successful nest establishment. In our study, nearby natural habitats tended to increase the probability of occupancy, but not in a significant way. However, with only 19 different nest box placement combinations in total, obtained from 14 planters located in 11 surveyed sites, our study was unlikely to reach sufficient statistical power to fully address the influence of surrounding habitats and their potential interactions. This issue remains to be resolved using a more extensive sampling network to inform on the adequate placement to maximize nest boxes occupancy.

### Emergence success and description of the cavity-nesting bee community

The emergence surveys indicate that concrete nest boxes offer suitable conditions for the development of larvae and the emergence of viable offspring from most bee nests. The apparent emergence success gradually decreased over time, but this was an inherent bias in our experimental design. Each year, a small subset of nests (about 12.5%) apparently failed to produce viable individuals – as no emergence was observed from them. As these nests remain capped from one year to the next, their proportion increased over time, so that estimates of emergence success appeared overly low in boxes surveyed after three successive years of exposure (62.6%) compared to those surveyed after only a single or two consecutive years of exposure (88.0%).

Brood loss due to disease or parasitism is a possible hypothesis to explain failing nests. There is little data in the literature with comparable accuracy for emergence success, but some similar results have been reported, e.g. 83% survival in *Osmia cornuta* (Kehrberger and Holzschuh 2019) or 85.2% in *O. bicornis* (2,889 out of 3,394 offsprings in Persson et al. 2018). Average brood loss rarely exceeds 20% in wild bees (Minckley and Danforth 2019), which is consistent with our findings. However, in our study, we called failing nests those nests for which the cap remained intact, i.e. with no evidence of emergence. On the contrary, brood loss is most often attributable to natural enemies that feed on provisioned pollen or prey on the eggs or larvae (Minckley and Danforth 2019), and therefore bore or excavate the nest cap either before or after preying on the nest content.

Alternatively, we hypothesize here that most of our so-called failing nests were actually false or fake nests. In a subsequent emergence trial involving nine identical concrete nest boxes, we excavated 45 holes whose cap remained intact throughout the season (10 holes capped with mud and 35 with chewed leaves). Two of them harbored a potentially parasitic bombyliid (Diptera) larvae, one harbored a couple of empty cells, while all the other 42 capped holes (93%) were actually completely empty, containing no brood cell, pollen, larvae or any other organism. This observation points to obvious underestimations of emergence success in our study. It is already known that some females may leave incomplete or abandoned nests (MacIvor 2016). In our study, as many neighboring holes were offered on display, some females may sometimes have capped a wrong hole, or cap several additional holes around their actual nest in order to confuse parasites or predators through prey dilution effect. In line with this fake nest hypothesis, some cavity-nesting bee species may leave an empty cell, also called vestibular, at the outermost position of the nest in order to keep their brood out of reach of potential oviposition by parasitic wasps (Münster-Swendsen and Calabuig 2000; Velez et al. 2017).

Regardless of the underlying biological explanation behind empty nests, it highlights the risk of the accumulation of false or fake nests that could over time saturate nest boxes. This may be viewed as a limitation of continuous use of concrete nest boxes in practice, which would require a regular maintenance scheme to support nesting dynamics, such as a hole cleaning every two to three years, which could also help to limit parasitism and the spread of diseases (Youngsteadt and Favre 2022).

The bee community that nested in concrete nest boxes appears overall not much diversified, with mostly common and generalist species, though one of them is also known to be a foraging specialists. In comparison to the 11 species we recorded, an average of 24 species were found in nest boxes composed of wooden supports or hollow stems in urban or peri-urban environments (Pereira-Peixoto et al. 2014; MacIvor and Packer 2015; Fortel et al. 2016; von Königslöw et al. 2019). Furthermore, the species accumulation curve (Fig. 5) indicates that a ceiling was virtually reached, and richness estimators predict hardly more than a couple of additional species to be expected in the sampled sites. However, there is a high chance that more cavity nesting species may be eventually detected in concrete nest boxes if they were set up in a wider range of sites, including parks or more natural areas that may provide a source of more diverse cavity-nesting species.

The species assemblages that nested in concrete nest boxes did not appear singular from a taxonomic or functional point of view. All the species are considered to be relatively common and do not benefit from a particular conservation status at the European level ("Lower Concern" category of the IUCN – the International Union for the Conservation of Nature). They have a wide and ubiquitous range on French and European territories – except for *Anthidium florentinum* which is a rather Mediterranean species that was, indeed, collected in one of the southernmost sites of the study. Likewise, the majority of recorded species are polylectic, i.e. foraging on different genera of flowering plants for pollen in an unspecialized way, which is also a functional trait favored in highly anthropic areas (Fauviau et al. 2022). Still, one species, *Hoplitis adunca*, is known to be oligolectic on the pollen of *Echium* spp. (Boraginaceae). Food specialization is often associated with ecological fragility because specialist species cannot survive locally without the presence of their preferred host plant (Biesmeijer et al. 2006). The presence of nesting opportunities such as artificial nest boxes may then be viewed as an asset for the maintenance of such local populations.

Two cleptoparasitic bee species (*Coelioxys inermis* and *C. echinata*) were also observed in boxes that had been exposed for two or three years, which is indicative of complex species interactions. Cleptoparasitic bees are dependent on the prior establishment of a population of their host species, in this case *Megachile centuncularis* and *M. rotundata*, respectively. Indeed, the two cleptoparasitic species were reported in the same nest box than their respective host. The number of cleptoparasitic species may increase over time in nest boxes, although individual numbers are definitely too low in this study to test this hypothesis. The installation of cleptoparasitic bees also testifies to a certain stability of parasitized populations over time if they are maintained despite the cost generated by cleptoparasitism (Sheffield et al. 2013).

Interestingly, not a single individual of the invasive giant resin bee *Megachile sculpturalis* was recorded during our three years of survey, in spite of its rapid expansion from the south of France northward (Le Féon et al. 2018). Indeed, 16 specimens of this bee species were previously collected in wooden nest boxes by Fortel et al. (2016), close to our southernmost sampling sites. This species appears to be largely dependent on wood as a nesting substrate, and nest boxes made of concrete may thus escape its spread. This species is native to eastern Asia and is spreading rapidly around the world to the detriment of native species (in France since 2008, Vereecken and Barbier 2009). It then became very common in artificial nest boxes made of wood or reeds in anthropized areas (Geslin et al. 2020). Because of its large body size (19–22 mm for males and 21–25 mm for females), it uses cavities with a large diameter, usually between 10 and 12 mm or more if available. It may therefore compete for nesting with large bees such as those of *Xylocopa* and *Anthidium* genera in wooden nest boxes (Geslin et al. 2020; Straffon-Díaz et al. 2021).

## Perspectives: concrete nest boxes as tools for urban agriculture?

Concrete nest boxes may be useful tools to help maintain local bee populations for urban agriculture purposes, by providing them with perennial nesting opportunities. Owing to their resistance and durability, concrete nest boxes may be integrated to biomimetic buildings, i.e. novel construction or restoration approaches designed to promote local ecosystem services (Blanco et al. 2021). Further studies are, however, needed beforehand to fully apprehend the species-specific reproductive success of bees in this specific nesting substrate. In particular, we recommend to document three main issues that could not be fully addressed in the present study:

1. *Refining the focus scale at the nest level, from colonization success to reproductive success.* The current study was caried out at the level of nest boxes as a whole, returning broad indicators of colonization or emergence success at the community level. This, however, precluded fine descriptions of species-specific preferences of nesting females for particular hole characteristics. High-resolution monitoring on the basis of individual nests would be certainly possible in a more advanced study, e.g. using videorecording, leading to thorough measurements of reproductive success *sensu stricto* (i.e. offspring size per nest or per nesting female).
2. *Comparing the attractivity of nest boxes made up of different materials.* Thorough comparisons with other nesting substrates would be advisable, including wood and other types of mineral materials. Although concrete nest boxes successfully attracted cavity-nesting females, it is still unclear whether wooden alternatives would perform better or attract different bee species. This should be coupled with simultaneous assessments of thermal properties of holes with regard to the physiological tolerance of adult bees and brood.
3. *Evaluating predators and parasitic loads.* Wooden nest boxes may promote local concentrations of brood parasites and predators. It would be advisable to assess whether a similar risk arises in concrete nest boxes. Monitoring the prevalence of pathogens on larvae is admittedly not straightforward in concrete cavities. One may place rolled paper inside holes prior to nesting, in order to subsequently remove nest contents without damaging the brood. Meanwhile, regardless the material, further studies should assess the possibility to dilute the risks of parasitism by varying nest box availability, accessibility, and distribution in the neighborhood.

Subject to clarification of these points, concrete nest boxes have the potential to promote local populations of some cavity-nesting solitary bees, with positive implications for urban agriculture as well as public outreach in urban areas. Interestingly a large European meta-analysis of urban bee surveys (Fauviau et al. 2022) revealed that *O. bicornis*, *O. cornuta*, *A. manicatum*, and *A. florentinum* were amongst the most frequently reported species in cities. Those species were also reported from our emergence survey, suggesting promising applications for concrete nest boxes in urban agriculture plots like green roofs or community gardens where wild bees are noticeably diversified (Hofmann and Renner 2018; Kratschmer et al. 2018; Baldock et al. 2019). Also these polylectic bees may contribute to the pollination of a wide range of entomophilous cultivated plants.

Urban bee communities are not random samples of wild bee communities found in surrounding natural areas. Cities act as an ‘ecological filter’, being less unfavorable to above-ground cavity nesting bee species than to below-ground ones (Fauviau et al. 2022). Artificial nests in remote urban agricultural plots such as green roofs may contribute to promote local above-ground wild bee populations, particularly when green spaces are more abundant in the surrounding areas (MacIvor 2016). This would be in line with a more global approach of biomimetic urban planning at the neighborhood scale (Blanco et al. 2021). A network of concrete nest boxes may be embedded in biomimetic building projects, which are to date mostly designed to promote vegetation-based ecosystem services, but may also consider fauna and habitat management schemes in the future (Blanco et al. 2022).

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**Author Contributions** All authors contributed to the study conception and design. Material preparation and data collection were performed by MH, BEV and LG. Data analysis was performed by MH, PJB and SB The first draft of the manuscript was written by MH and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Data Availability** All the relevant data is provided in the Electronic Supplementary Information. More detailed information can be provided upon request from the corresponding author.

## Declarations

**Competing interests** The authors declare no competing interests.

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