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Checking in at bee hotels: trap-nesting occupancy and fitness of cavity-nesting bees in an urbanised biodiversity hotspot

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Abstract

With urbanisation leading to loss of nesting resources, and increasing public interest in helping bees, bee hotels (trap-nests) are becoming popularised. However, their success is relatively understudied. The influence of habitat type in determining occupancy and emergence is also poorly known. Over two years across 7 bushland remnant and 7 residential garden sites, trap-nests were installed and completed nests collected monthly over spring-summer. Bees appeared to take a month to find the trap-nests, irrespective of month they were installed. A small percentage (13% and 6% in the two years) of tubes were occupied, but this was within the range of other trap-nesting studies. Smaller 4 and 7 mm diameter nests had a higher occupancy rate than 10 mm diameter tubes. An impressive number – 24 bee species – occupied the trap-nests. Representation however was dominated by five species. The species composition (species and their relative abundances) of cavity-nesting bees differed greatly between those using the trap-nests compared with those observed in the field. Bushland remnants tended to have more bee hotels occupied, and male body size of emerged bees was larger in this habitat. Unexpectedly native and total flower diversity reduced bee hotel occupancy, whereas native flower parameters tended to positively influence bee fitness. Overall installing bee hotels can provide additional nesting resources for native bees in urbanised areas, and providing high proportions of native flora in the vicinity should enhance fitness of the bees using them.

Keywords Bees · Bee hotels · Colletidae · Megachilidae · Solitary bees · Trap-nests · Urbanisation · Wild bees

Introduction

Urbanisation is a major driver of habitat loss and fragmentation of natural habitat (Winfree et al. 2009) – a key factor implicated in threatening wild bees (Brown and Paxton 2009; Steffan-Dewenter et al. 2006; Winfree et al. 2011). Urban expansion is predicted to increase globally by 285% between 2000 and 2030 (Seto et al. 2012). There is thus an urgent need to understand how native bees respond to this leading form of land-use modification and make-science based recommendations to inform the public and policy-makers so that urbanisation can harmonise with native bee conservation (McKinney 2002).

Despite the general opinion that cities are ecological deserts, there is evidence that native bees can persist, even at higher abundances, than in other landscape types ((Prendergast et al. 2022a). Yet the relative value of different greenspace habitat types within cities has received little attention, especially with regards to comparing fragments of remnant vegetation with managed greenspaces, of which the main type is residential gardens. With urban development placing pressure on these native vegetation fragments, it is important to understand the value of these patches of native vegetation within the urban milieu, and whether residential gardens can serve as analogues, or even replacements, for the original vegetation in a now urbanised landscape. With pollinators being critical to pollination of flora (Willmer et al. 2017) – be it wildflowers in native fragments, flora in parks and gardens, urban agricultural gardens, and other greenspaces – which in turn provide key ecosystem services to humans and other urban fauna – it is vital to understand how native bees respond to urbanisation.

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Bees are central place foragers, where they travel to and from a nest site to collect provisions to stock the nest (Westrich 1996). Simply measuring bees in an area however cannot reveal whether the area is used for nesting, and rather than being part of the population, bees may be vagrants at a locality. Moreover, the true measure of fitness of a population is its reproductive output.

Trap-nests, also known as trap-nests (especially among popular media), have been successfully used to record the presence, abundance, and diversity of cavity-nesting bee taxa, but also their reproductive output, nesting biology and phenology, and other fitness-related parameters such as offspring mortality rate, sex ratio, body size or body mass, and rates of mortality from predators, parasites and kleptoparasites (Alves-dos-Santos 2003; Bosch 2008; Dainese et al. 2017; Hudewenz and Klein 2015; Loyola and Martins 2006; Paini 2004; Paini and Bailey 2002; Paini et al. 2005; Pereira-Peixoto et al. 2014; Peterson et al. 2006; Roubik and Villanueva-Gutiérrez 2009; Tscharntke et al. 1998). This includes in urban areas (Fortel et al. 2016; Makinson et al. 2016)(Everaars, 2011 #235}.

Measuring these nesting parameters can be an indicator of the quality of the habitat in which the trap-nests are installed (Holzschuh et al. 2010; Sheffield et al. 2008; Steffan-Dewenter and Schiele 2008; Tscharntke et al. 1998).

If resources are limiting – due to poor-quality of fragmented habitat, or competition from honeybees (Cane and Tepedino 2016)– it can be predicted that:

a) Females will have to spend a longer duration foraging away from the nest to obtain sufficient resources in resource-poor habitat, fragmented habitat, or if honeybees have usurped most resources. This will lead to fewer offspring per nest (Kim and Thorp 2001; Peterson and Roitberg 2006; Thomson 2004; Zurbuchen et al. 2010).
b) When there are fewer resources, pollen provisions will be smaller, leading to smaller offspring (Bosch and Vicens 2002; Radmacher and Strohm 2010); this in turn impacts fitness because smaller progeny are less likely to survive (Bosch 2008; Tepedino and Torchio 1982), and if they do survive, large individuals tend to have higher fitness (survival and reproduction) (Honěk 1993; Kim and Thorp 2001; Kim 1997).
c) Females in poorer quality habitat will produce a greater proportion of offspring of the sex requiring the least energetic investment, leading to skewed sex ratios, with potential flow-on effects in depressing populations (Bosch 2008; Cane and Tepedino 2016; Peterson et al. 2006).
d) If females have to spend longer foraging away from the nest to obtain sufficient resources, this will increase brood parasitism (Goodell 2000).

This study involved the use of trap-nests to measure the diversity, abundance, species composition, nesting biology, and fitness parameters of cavity-nesting bees in the urbanised region of southwest Western Australia (WA). Trap-nest occupancy and parameters of nesting success were used to address the following research questions:

- Does trap-nest occupancy differ between bushland remnants vs. residential gardens?
- What environmental variables influence trap-nest occupancy?
- How do parameters of nesting success and reproduction of trap-nesting bees differ between bushland remnants vs. residential gardens?
- What environmental variables are associated with parameters of nesting success and reproduction?

Methods

During November-February, and September-March, eight trap-nests per site were installed in seven residential gardens, and seven urban bushland fragments and checked monthly. Sites were > 1 km apart – above the average flight range for native bees – and sites of different habitat types were interspersed to ensure independence and prevent spatial autocorrelation. The order sites were visited to check trap-nests was roughly maintained between months, and sites of the same habitat type were typically checked on alternative surveys.

Trap-nests were made out of 20 cm deep x 15 cm high x 15 cm wide blocks of Jarrah (*Eucalyptus marginata*) wood – a dominant and endemic species to the region. 15 holes 15 cm deep were drilled, 5 each of the following diameters: 4 mm, 7 and 10 mm. Cardboard bee tubes (Custom Paper Tubes™) were inserted into the holes. During each survey, bee tubes that had been completed, evident by a cap of material (sand, resin, leaves, plant material, secretions, depending on the species) were removed and placed in plastic take-away containers labelled with site and date of collection, with five 1 mm holes in the lid for aeration, and new tubes replaced.

The containers were placed in the lab which was maintained at around 22°C.

In season one, bee tubes that had not had progeny emerged were X-rayed with a Faxitron Xray in August, and again July, to quantify the number of cells, occupied cells, and developmental stage at which progeny were at.

Bee tubes that had not had bees emerge from season one after winter and then the spring/summer period were X-rayed again in autumn (March 27th – April 2nd 2018). Those that still appeared to have viable larvae (larvae that were plump and glowed brightly white, indicating live tissue) were stored in unlit incubators at 18°C for two weeks from 3rd April 2018, and then stored at 25°C for another two weeks from 17th April 2018, then at 30°C for another two weeks starting from 1st May 2018. Every few days tubes were checked for emerged progeny. This temperature regime was designed so as to mimic a winter then spring period such that the change in temperature would break dormancy and trigger development, pupation and emergence (based on studies on temperate bees where bees were stored at cold then warm temperatures (Bosch 2008; Bosch and Kemp 2002; Bosch et al. 2000; Kemp and Bosch 2000); temperatures in this study were modified to more accurately mimic those naturally experienced in the Western Australian environment).

When progeny emerged, date of emergence, number of progeny per nest, sex of the offspring, and body size (measured as intertegular distance – the linear distance between the wing tegulae (insertion points of the wings) across the thoracic dorsum of a bee (Cane 1987)) were recorded. Tubes were dissected to quantify the number of cells, number of provisioned cells, and any progeny that failed to develop.

Emerged bees were identified with reference to the WA Museum collection and PaDIL (PaDIL). A type of each male and female specimen per year were pinned and labelled, other specimens of a given species were stored in labelled jars in 80% ethanol.

In addition to comparing bee tube occupancy and nesting success between bushland remnant and residential garden habitats, environmental variables that can be predicted to influence these parameters were evaluated for their contribution to explaining variation in bee tube occupancy and adult emergence success:

- Total floral abundance.
- Australian native floral species abundance.
- Total floral species richness.
- Species richness of Australian native flora.
- Proportion of flowers that were Australian natives.
- Proportion of flowering plant species that were Australian natives.
- Density of woody plants (shrubs and trees).
- Area of the site.
- Distance to the nearest bushland reserve (an index of connectivity with, or isolation from, "natural" habitat").
- Proportion of builtspace (roads, buildings, pavements etc.) within a 500 m radius around each site.

Floral variables were measured within a 100 m x 100 m area; for residential areas this was not a uniform quadrat shape due to the area exceeding the residential garden so verge and neighbouring front door gardens were surveyed. Native flora were identified with reference to a field guide for the region (Barrett and Tay 2016) and in consultation with K. Dixon, C. Tauss, or H. Lambers; non-native flora were identified through public garden forums and by consulting M. Tusak. Area of the site and distance to nearest bushland were measured through GoogleEarth. Proportion of builtspace was calculated by quantifying gridcells representing builtspace from a grid of 10 × 10 m on a GoogleEarth image of the site within a 500 m radius buffer. For further information refer to ((Prendergast et al. 2022b).

Statistical tests for mean values involved modelling the response variable in relation to habitat type with generalised linear mixed models (lme4 package in R), with site as a random factor, using the function 'glmer'. Count data used a Poisson error structure, continuous data a Gaussian error structure, and proportion data a Binomial error structure. Overdispersion for glmers using count data was assessed using the function 'dispersion_glmer' with the package 'blemco', where values > 1.4 indicated that overdispersion was an issue; in such cases an random observation level effect was included in the model structure.

Significance of explanatory values was determined by a log-likelihood approach, performing an ANOVA between the model with and without the explanatory variable or interactions between explanatory variables, with significance set at $p < 0.05$.

When there was a significant effect of a variable with > 2 levels, significance between levels was analysed using Tukey's tests with the 'emmeans' package in R.

Investigating the environmental variable(s) that best explained variation in bee tube occupancy, number of occupied cells, and number of progeny to emerge was analysed in R using a model averaging approach. A global model with the variables hypothesised to influence bee use was first created. Due to the vastly different ranges of the potential predictor values, which led to scaling warnings when running the initial model, and to reduce the influence of outliers, woody plant density, flower abundance, richness, and native flower richness, and builtspace, were log-transformed. A correlation matrix was used to check for multicollinearity between variables (Supplementary Information 3).

Floral abundance and native floral abundance, and area and builtspace were correlated (> 0.65), so only floral abundance and builtspace were used. For the bee nests dataset, convergence issues warnings when modelling number of provisioned cells, number of emerged offspring, mortality rate and sex ratio as the response variable indicated that the random effect of site was essentially explaining everything and leaving no variation for fixed effects or the residual variance, and so GLM models were used. The family "poisson" was used for integer responses, and "binomial" for proportional responses. Male and female body size were modelled with a lmer model. The explanatory variables that best explained variation in visitation was determined by a dredge function using the package 'MuMIn' (Barton 2009). When more than one model was selected (within 2 AICcs), model averaging was used to determine which variables best explained insect visitation using the function 'AICcmodavg' (Mazerolle 2020).

Overall assemblage composition was compared between years, habitats and cohorts with a PERMANOVA using the function "adonis" with the package "vegan". The matrix of species, based on number of nests, was fourth-root transformed, and a Bray-curtis distance matrix with 999 permutations was used. An nMDS plot was created in ggplot2 after running an nMDS with the function "metaMDS" in the package "vegan."

The proportion of all cavity-nesting species of Megachilidae and Hylaeinae that emerged from trap-nests was compared with the number of these species collected during surveys of the sites conducted on the same day trap-nests were checked, The relative representation of species in trap-nest assemblages based on number of nests per species was compared with their representation from field caught specimens. For a list of the full field caught species assemblage and methods of collection refer to (Prendergast 2020; (Prendergast et al. 2020, 2022b).

Results

Trap-nest occupancy

In year one, a total of 672 sealed bee tubes, as evidenced by caps of resin, sand, plant material, or leaves were collected during the 2016/17 survey season. This amounts to an occupancy rate of 13.3%. In year two, a total of 664 sealed bee tubes were collected, amounting to an overall occupancy of 6.34%.

Phenology

Occupancy varied significantly by month in both year one (X^2 = 23.33, df = 2, p-value < 0.001) and year two (X^2 = 28.05, df = 2, p-value < 0.001). In the first year, there were significant pairwise differences between Dec and Jan and Dec and Feb (p < 0.001), but not Jan and Feb (p = 0.999), with fewer nests completed in Dec (Fig. 1a). Occupancy also varied by month in the second year (X^2 = 63.67, df = 5, p-value < 0.001). In contrast to the first year, December had the highest occupancy (Fig. 1b). Occupancy was lowest in October, increasing to peak in December, declining until February, with another increase

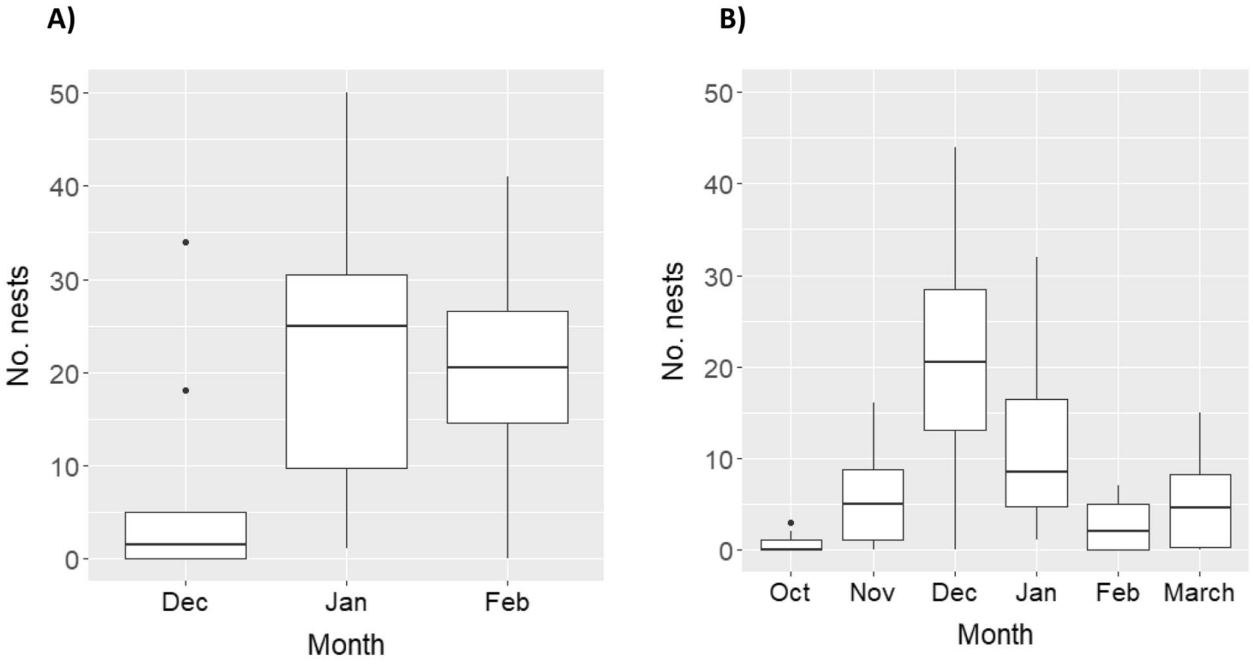


Fig. 1 Phenology of trap-nest use. (**A**) Year one, (**B**) Year two

in March (Fig. 1b). There were significant differences between all months except Dec-Jan ($p = 0.184$), Feb-March ($p = 0.542$), Nov-Feb ($p = 0.262$), Nov-Jan ($p = 0.156$), and Nov-March ($p = 0.997$).

Tube diameters

In year one, 4 mm tubes had the highest occupancy, followed by 7 mm tubes, with 10 mm tubes having the lowest occupancy rates, a statistically significant difference (X^2 = 28.05, df = 2, p-value < 0.001). Pairwise differences were significant between 4 mm vs. 10 mm ($p < 0.001$) and 7 mm vs. 10 mm ($p < 0.001$), but not 4 mm vs. 7 mm ($p = 0.696$).

In year two, occupancy of bee tubes also differed significantly between tubes of different diameters (X^2 = 48.83, df = 2, p-value < 2.2e-16). However, in the second year, with over half of the bee tubes occupied, the 7 mm bee tubes had the highest occupancy, followed by the 4 mm bee tubes. 10 mm bee tubes made up only less than 10% of occupied bee tubes. Again however pairwise difference were only significant with the 10 mm nests (both $p < 0.001$), but not between 4 mm vs. 7 mm ($p = 0.274$).

Occupancy by habitat

In year one, 429 tubes were collected in bushland, and 264 in gardens; in year two 384 were collected in bushland and 280 in gardens.

Average number of nests was greater in bushland than gardens across both years, but did not reach statistical significance at $p < 0.05$ ($X^2 = 3.28$, df = 1, $p = 0.070$). There was no interaction between years (X^2 = 0.006, df = 2, $p = 0.938$) or with tube diameter (X^2 = 0.213, df = 2, $p = 0.899$).

Variables influencing occupancy

Three models were within 2 AICcs, and the averaged model retained builtspace, floral species richness, native floral species richness, and woody plant density. Of this final model, only flower richness, and native flower richness were significant. Unexpectedly, total flower species richness (est= -0.44, se = 0.09, z = 4.71, $p < 0.001$) and native flower richness (-0.34, se = 0.08, z = 4.4, $p < 0.001$) were negatively related to bee tube occupancy.

Bee nests and emergences

X-raying of the bee tubes from which no progeny had yet emerged prior to winter revealed that surprisingly, despite being capped, there were tubes that showed no sign of provisioning. In year one, 82 of the 672 bee tubes (12.2%) were empty, with no signs of any provisioning, and of the tubes collected in year two where progeny did not emerge prior to winter, X-rays revealed that 49 bee tubes (7.7%) had no provisions.

In the majority of tubes collected that were provisioned, not all the cells were filled, with empty cells representing vestibular (an empty cell next to the entrance) or intercalary cells (empty cells within the nest between provisioned cells) (Krombein 1967). In year one, across all bee tube sizes, species, and sites, the average number of total cells was 6.27 ± 0.15, with the average number of provisioned cells being 3.89 ± 0.12, and the average proportion of cells that were provisioned was 0.615 ± 0.012. In year two, again there were vestibular and intercalary spaces between provisioned cells, andacross all bee tubes in year two, they contained an average of 6.18 ± 0.108 cells, of which 4.08 ± 0.096 were provisioned, amounting to an average proportion of 0.655 ± 0.009 being provisioned.

Of bee tubes with progeny, a total of 297 bee tubes were collected from bushland sites, and 118 bee tubes from residential sites, and in year two, a total of 377 bee tubes were collected from bushland remnants, and 244 from residential gardens.

Overall, from 2522 provisioned cells, 1832 progeny emerged. This represents a mortality rate overall of 27.5%. The average number of provisioned cells per nest was 3.89 ± 0.10, and average number of progeny to emerge was 2.87 ± 0.09. Sex ratio i.e. the number of females relative to males was on average 0.54 ± 0.01.

Across both years and cohorts, there was no significant difference between habitats in both number of provisioned cells ($X^2 = 0.36$, df = 1, $p = 0.551$) number of progeny to emerge ($X^2 = 2.09$, df = 1, $p = 0.417$), mortality rate (X^2 = 0.14, df = 1, $p = 0.710$), or sex ratio ($X^2 = 0.15$, df = 1, $p = 0.703$).

Male body size differed by habitat (X^2 = 10.19, df = 1, $p = 0.001$), being larger in bushland remnants than in residential gardens (bushland remnant: 3.07 ± 0.05 vs. residential gardens: 2.65 ± 0.04). Female body size however was not significantly different (X^2 = 0.52, df = 1, $p = 0.474$; bushland remnant: 3.37 ± 0.05 vs. residential gardens: 3.24 ± 0.04). Average development duration was 75.3 ± 3.43 days (approximately 2.5 months), and did not vary between habitats (X^2 = 0.73, df = 1, $p = 0.392$).

Variables influencing number of provisioned cells, number of emerged offspring, mortality rate, sex ratio, and male and female body size.

Nine models were within 2 AICs for the environmental variable(s) associated with number of provisioned cells, and retained all variables. Model averaged coefficients indicated that only density of woody plants was negatively associated with number of provisioned cells (est = -0.20, se = 0.05, z = 3.8, p = 0.0001), whereas proportion of native flora was positively associated (est = 0.29, se = 0.09, z = 3.4, p = 0.0007).

Eleven models were within 2 AICs for the environmental variable(s) associated with number of offspring to emerge, and retained all variables. Model averaged coefficients indicated that only species richness of native flora was marginally significant, being positively associated (est = 0.25, se = 0.13, z = 1.9, p = 0.059).

Eight models were within 2 AICs for the environmental variable(s) associated with mortality rate, and retained all variables. Model averaged coefficients indicated that only greater native flower species richness was negatively associated with mortality rate (est = -0.51, se = 0.15, z = 3.3, p = 0.001), positively associated with increasing distances from native vegetation reserves (est = 0.15, se = 0.04, z = 3.5, p = 0.0004), and counterintuitively, mortality rate was negatively associated with proportion of impervious surfaces (builtspace) in a 500 m radius (est = -0.15, se = 0.06, z = 2.5, p = 0.011).

Thirteen models were within 2 AICcs for environmental variable(s) associated with sex ratio, and included all explanatory variables except woody plant density. Model averaged coefficients indicated that only greater proportions of native flower abundances were positively associated with higher proportions of female offspring per nest (est = 0.36, se = 0.17, z = 2.1, p = 0.033).

Five models were within 2 AICcs for explaining variation in male body size and included proportion of native flower species, native flower species richness, proportion of builtspace at a 500 m radius, and woody plant density. Model averaged coefficients found that native flower species richness and woody plant density were positively associated with larger emerged males (native flower species richness: est = 0.26, se = 0.09, z = 2.8, p = 0.006; woody plant density: est = 0.27, se = 0.12, z = 2.1, p = 0.032), greater builtspace was marginally associated with smaller male body size (est = -0.15, se = 0.08, z = 1.8, p = 0.065); proportion of native flower species was non-significant (p = 0.183).

For female body-size, only a single model was found to explain this variable (> 2AICs below all other models) and included native flower species richness, which was positively related to female body size (est = 0.23, se = 0.06, t = 3.6, p = 0.011).

Parasitism

Excluding parasitism by *Mellitobia* which spread through trap-nests in the lab, a total of 142 nests were parasitised in the field. Parasites were predominantly predator-inquiline wasps in the family Gasteruptiidae (Prendergast & Parslow, in prep.) with the remainder being Bombyliid flies. This amounts to about one fifth of trap-nests where progeny emerged being parasitised. Parasitism rates did not differ by habitat (X^2 = 1.24, p = 0.266), nor did the number of nests parasitised (X^2 = 0.01, p = 0.923).

Species composition

A total of 24 species used the trap-nests belong to two families and four genera (Megachilidae: *Megachile* and *Rozenapis*, and Colletidae: *Hylaeus* and *Meroglossa*) (Table 1). No cleptoparasitic bees emerged. There were 70 above-ground cavity nesting bees collected in the field, and therefore the number of species that were recorded using trap-nests was only 34.3% of bees that could have occupied the hotels.

A novel observation was that one nest from Piney Lakes collected in December had both a *Hylaeus (Euprospis) violaceus*, as well as a *Megachile (Hackeriapis) oblonga*. Three female *Megachile* emerged, and one female *Hylaeus*.

There was a high skew in species representation in terms of number of nests (Fig. 2). *Megachile erythropyga* comprised 32.8% of nests. Four other species comprised about 10% of nests (*M. oblonga, M. canifrons, R. ignita*, and *M. fabricata*). Just five species therefore comprised almost three-quarters of all nests collected.

In year one in the pre-winter cohort, twelve species emerged. Both habitats had eight species each, with four species exclusive to each habitat type. In the year two cohort, fifteen species emerged, with 13 from bushland sites and nine from the residential gardens, and seven species found in both habitats. In year two, fourteen species emerged prior to winter; twelve from bushland sites and eleven from residential garden nests, with three species only emerging from bushland nests, and two only from residential garden nests. In the postwinter emergences in year two, eleven species emerged; ten were from bushland sites, and seven from residential gardens, with four exclusive to bushland sites and one to residential gardens. Hence in general bushland remnants had a slightly higher number of species to emerge than residential gardens.

Certain species were exclusive to one habitat, or only occurred in one year, and the relative representation of species present in each habitat or year also differed (Table 1). However, a PERMANOVA did not find statistically significant differences in community composition by habitat (F = 0.567, p = 0.691) or year (F = 1.25, p = 0.257) (Fig. 3a). There were however significant differences in species composition by cohort (F = 4.71, p = 0.01) (Fig. 3b).

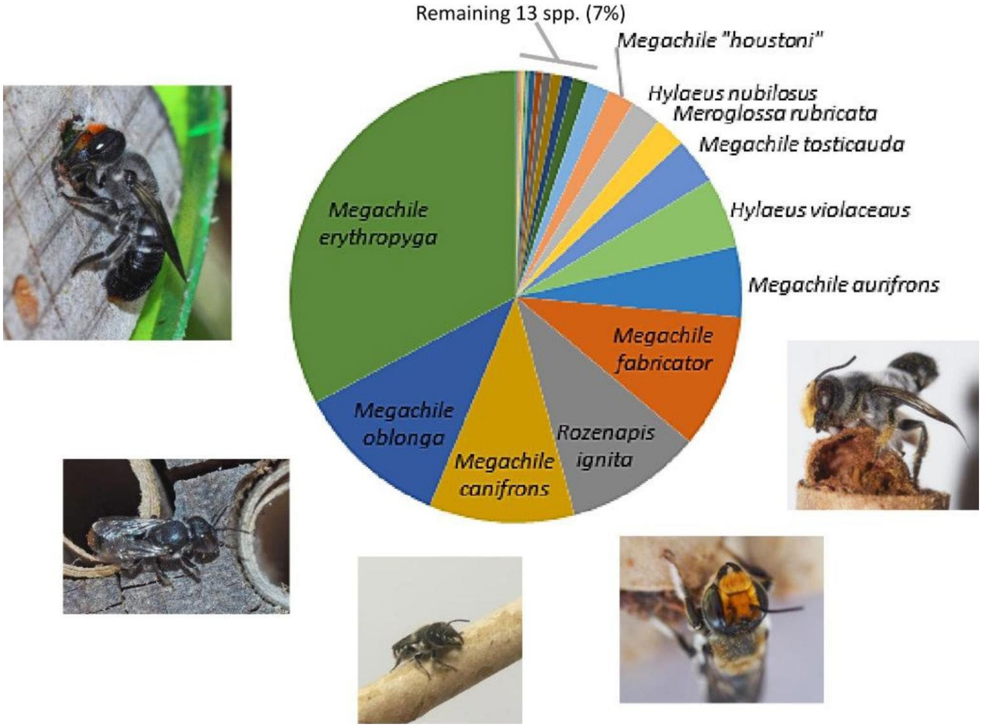
Trap-nest use vs. in the field

There was a stark difference often in the representation of a species based on its use of trap-nests compared with its

Table 1 Species of native bees that emerged from trap-nests, and the number of nests per species by year, cohort, and their representation in the two habitat types

Species	Year	Cohort	Nests occupied	
			Bushland remnant	Residential garden
Hylaeus (Euprosopis) violaceaus	one	prewinter1	9	6
Hylaeus (Gnathoprosopis) amiculus	one	prewinter1	1	
Hylaeus (Gnathoprosopis) euxanthus	one	prewinter1		1
Meroglossa rubricata	one	prewinter1		3
Megachile (Eutricharaeae) obtusa	one	prewinter1		3
Megachile (Mitchellapis) fabricator	one	prewinter1	30	8
Megachile aurifrons	one	prewinter1	2	4
Megachile erythropyga	one	prewinter1	18	67
Megachile fultoni	one	prewinter1	1	
Megachile "houstoni"	one	prewinter1	1	
Megachile (Hackeriapis) oblonga	one	prewinter1		2
Rozenapis (syn. Megachile) ignita	one	prewinter1	4	
Hylaeus (Euprosopis) ruficeps kalamundae	one	postwinter1	2	1
Hylaeus (Euprosopis) violaceaus	one	postwinter1	1	1
Megachile "houstoni"	one	postwinter1	8	
Megachile "paramaculae"	one	postwinter1		1
Megachile (Hackeriapis) horatii	one	postwinter1	10	
Megachile (Hackeriapis) oblonga	one	postwinter1	34	22
Megachile (Hackeriapis) speluncarum	one	postwinter1	6	1
Megachile (Hackeriapis) tosticauda	one	postwinter1	7	11
Megachile (Mitchellapis) fabricator	one	postwinter1	10	1
Megachile (Schizomegachile) monstrosa	one	postwinter1	1	
Megachile sp.57	one	postwinter1	1	
Megachile aurifrons	one	postwinter1		3
Megachile canifrons	one	postwinter1	1	
Megachile erythropyga	one	postwinter1	2	8
Rozenapis (syn. Megachile) ignita	one	postwinter1	3	
Hylaeus (Hylaeorhiza) nubilosus	two	prewinter2	2	12
Hylaeus (Gnathoprosopis) euxanthus	two	prewinter2		2
Hylaeus (Euprosopoides) ruficeps kalamundae	two	prewinter2	2	
Hylaeus (Euprosopis) violaceus	two	prewinter2	8	6
Meroglossa rubricata	two	prewinter2	6	5
Megachile sp. 27	two	prewinter2	2	1
Megachile erythropyga	two	prewinter2	42	69
Megachile aurifrons	two	prewinter2	10	10
Megachile (Mitchellapis) fabricator	two	prewinter2	4	8
Megachile (Hackeriapis) oblonga	two	prewinter2	1	
Megachile (Hackeriapis) canifrons	two	prewinter2	47	10
Megachile (Hackeriapis) "parimaculae"	two	prewinter2		3
Megachile "houstoni"	two	prewinter2	1	
Rozenapis (syn. Megachile) ignita	two	prewinter2	42	10
Hylaeus (Euprosopis) violaceus	two	postwinter2		1
Megachile (Hackeriapis) tosticauda	two	postwinter3	2	1
Megachile "houstoni"	two	postwinter4	2	
Megachile (Hackeriapis) canifrons	two	postwinter5	5	3
Megachile sp. 27	two	postwinter6	2	
Megachile aurifrons	two	postwinter7	2	1
Megachile sp. 30	two	postwinter8	1	
Megachile (Hackeriapis) oblonga	two	postwinter9	4	7
Megachile (Austrochile) resinfera	two	postwinter10	1	
Rozenapis (syn. Megachile) ignita	two	postwinter11	2	1
Megachile erythropyga	two	postwinter12	1	1

Fig. 2 Overall species representation by nest occupancy



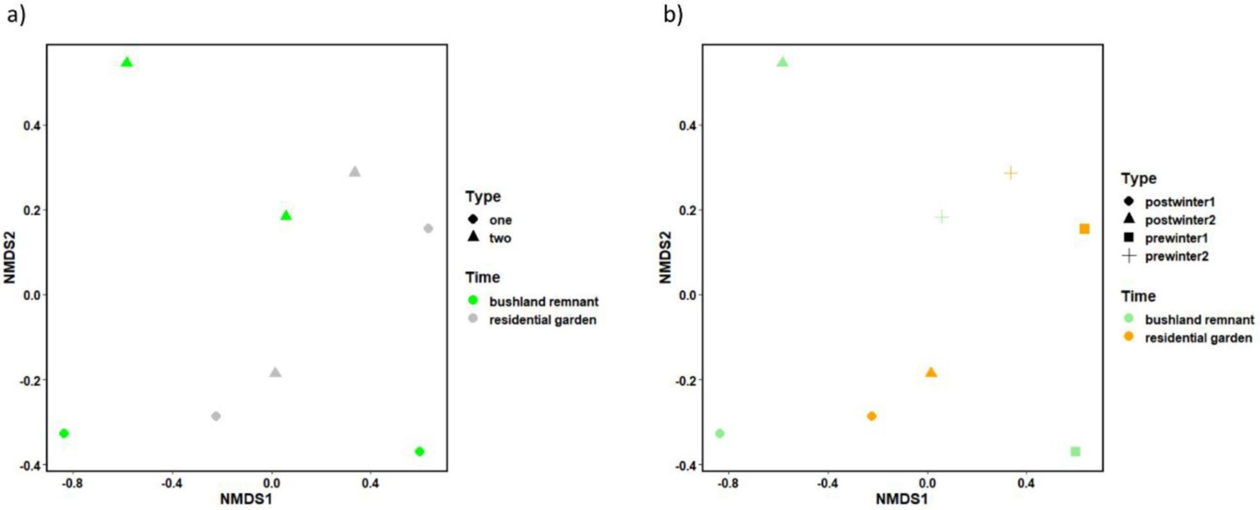


Fig. 3 NMDS plots of the assemblage composition based on the number of nests per species that emerged by (a) habitat and year, and (b) habitat and cohort

representation in the field (Table 2). Moreover, the species that used the trap-nests were only a subset (21.9%) of all cavity-nesting species observed. In addition, two species were recorded from the trap-nests, but were not collected in the field (Table 2).

Discussion

Over the 10 months of surveys, a total of 1,886 bees belonging to 24 species emerged from the trap-nests. Despite being just a fraction of the total number of cavity-nesting species observed during visual surveys (Prendergast 2020), this diversity nevertheless is relatively high compared with other trap-nesting studies in urban areas in Australia. Another study in urbanised southern New South Wales, Australia, across 28 sites with four trap-nests per site but only over

Table 2 Relative representation of bee species in terms of number of nests occupied vs. number of individuals collected in the field

Species	Nests	Proportion	%nests	FieldN	Proportion	%FieldN
Hylaeus (Euprosopoides) ruficeps kalamundae	5	0.007874	0.787402	14	0.011129	1.112878
Hylaeus (Gnathoprosopis) amiculus	1	0.001575	0.15748	24	0.019078	1.90779
Hylaeus (Gnathoprosopis) euxanthus	3	0.004724	0.472441	32	0.025437	2.54372
Hylaeus nubilosus	14	0.022047	2.204724	6	0.004769	0.476948
Hylaeus violaceaus	32	0.050394	5.03937	29	0.023052	2.305246
Megachile "houstoni"	12	0.018898	1.889764	311	0.247218	24.72178
Megachile "paramaculae"	4	0.006299	0.629921	35	0.027822	2.782194
Megachile (Austrochile) resinfera	1	0.001575	0.15748	1	0.000795	0.079491
Megachile (Eutricharaeae) obtusa	3	0.004724	0.472441	115	0.091415	9.141494
Megachile (Hackeriapis) horatii	10	0.015748	1.574803	33	0.026232	2.623211
Megachile (Hackeriapis) speluncarum	7	0.011024	1.102362	253	0.201113	20.11129
Megachile (Schizomegachile) monstrosa	1	0.001575	0.15748	4	0.00318	0.317965
Megachile aurifrons	32	0.050394	5.03937	48	0.038156	3.81558
Megachile canifrons	66	0.103937	10.3937	36	0.028617	2.861685
Megachile erythropyga	208	0.327559	32.75591	10	0.007949	0.794913
Megachile fabricator	61	0.096063	9.606299	11	0.008744	0.874404
Megachile fultoni	1	0.001575	0.15748	38	0.030207	3.020668
Megachile oblonga	70	0.110236	11.02362	28	0.022258	2.225755
Megachile sp. 27	5	0.007874	0.787402	16	0.012719	1.27186
Megachile sp. 30	1	0.001575	0.15748	0	0	0
Megachile sp.57	1	0.001575	0.15748	0	0	0
Megachile tosticauda	21	0.033071	3.307087	16	0.012719	1.27186
Meroglossa rubricata	14	0.022047	2.204724	53	0.04213	4.213037
Rozenapis ignita	62	0.097638	9.76378	145	0.115262	11.52623

one season recorded just 165 bees to emerge from nine native bee species, and one introduced bee species (Makinson et al. 2016). The reason for this discrepancy warrants further investigation. The reduced numbers in Makinson et al. (2016) may be due to the type of habitat type sampled – community gardens. As the current study revealed, it appears that residential, managed greenspaces may represent inferior habitat for native bees, with fewer nests and therefore total offspring emerging overall compared with urban natural vegetation remnants. The biogeographic region itself may also cause these differences: this study, whilst also being urbanised, was conducted in an internationally recognised biodiversity hotspot (Hopper and Gioia 2004). Other studies across the globe have reported fewer species using trap-nests: a recent study found conducted around the city of Freiburb, Southern Germany, reported that just eight species of native bees colonised trap nests (von Königslöw et al. 2019); a study conducted over three years on trap-nests on greenroofs recorded just 11 species (MacIvor 2015); a trap-nesting study conducted over three years in urban gardens in Sheffield, UK, recorded just two native bee species (Gaston et al. 2005) and a thesis project involving 20 sites recorded that just seven sites had bees emerge, belonging to eight species (Horn 2010; Pereira-Peixoto et al. 2014)'s study that, like the current study, had eight trap-nests per site across fourteen sites recorded 20 species, again fewer than the current study. My results underscore the value of Perth and the surrounding suburbs in southwest Western Australia as a biodiverse regions for native bees, despite having undergone urbanisation.

There have been no trap-nesting studies in "pristine" native vegetation in the southwest Western Australian biodiversity hotspot, however a study across 48 sites comprising remnant Wandoo woodland in the wheatbelt region recorded only 12 species (Murphy 2015). A study in another biodiversity hotspot in Queensland, Australia, across land-use types conducted for 23 months at seven sites also recorded fewer species (13) (Wilson et al. 2020).

It therefore appears that despite being subjected to urbanisation, the Perth region of southwest Western Australian biodiversity hotspot is a hotspot for cavity-nesting bees as well.

Occupancy patterns

Using a range of trap-nest designs, von Königslöw et al. (2019) found that total nest occupancy was 14.7%, and Gaston et al. (2005) likewise found low occupancy of 1–20%. This compares with 13.3% in season one and 6.34% in season two. The values reported here are thus within the range reported for other trap-nesting studies in urban areas. There was however high variation among nesting diameters, sites, and months. Interestingly, a large scale trap-nesting study in Toronto found that wasps occupied three-quarters of the trap-nests, whereas in this study wasps were rare, and mainly occupied the large-diameter tubes at only a subset of sites (Prendergast 2017).

Comparing the patterns in monthly occupancy over the two years, it appears that it takes bees in an area a while to adopt trap-nests after they are first installed, irrespective of month, explaining how in both seasons, despite being different months, the first month of collection had the lowest occupancy.

My results suggest that for optimal occupancy, trap-nests should include more 4 and 7 mm diameter nesting holes, but still have some larger nesting holes to cater for the larger bees which are excluded from the narrower diameters. Certainly, a range of hole diameters is recommended over a single diameter (von Königslöw et al. 2019).

Of studies that have looked at mortality rates of trap-nesting bees in urban areas, Loyola and Martins (2006) reported a mortality rate of 24.36%, and Alves-dos-Santos (2003) reported a mortality rate of less than 20% (prior to *Melittobia* infestation). Mortality rates reported here were therefore relatively high, however much of the mortality was associated with the year two postwinter cohort which suffered *Melittobia* infestation.

Bushland remnants versus residential gardens

Bushland remnants had a higher number of occupied nests, nests with progeny, and overall more offspring to emerge than residential gardens, although when averaged across sites, there was not always statistically significant differences. Male body size was also higher. Such findings suggest that bushland remnants provide superior habitat compared with residential gardens for native bees ((Prendergast et al. 2022a, b; Prendergast and Ollerton 2021). No previous trap-nesting studies have explicitly compared urban native vegetation remnants with residential gardens, however a thesis found that gardens with higher areas of greenspace in the landscape supported a greater abundance and generic-richness of bees in trap-nests (Pellkofer 2011), and another thesis reported that more filled trap-nest tubes in “greenspaces” (which included not just natural areas of open and wooded green spaces and conservation areas, but also golf courses and city parks) than in residential areas (both new and old)(Horn 2010), but only in one year.

The lack of a difference in average numbers of offspring to emerge between the habitats may relate to how in bushland remnants there are more natural resources, and females can distribute their offspring over a greater number of nests as a bet-hedging strategy (Hopper 1999), resulting in few offspring per nest, but potentially a greater number of offspring to emerge overall. This hypothesis is supported by a study on factors influencing trap-nest occupancy by *Osmia bicornis* in the city of Leipzig, Germany, where it was found that cell numbers were negatively associated with the abundance of natural nesting resources in the flight range of the species (Everaars et al. 2011). Future studies tagging individual females may help to elucidate whether this hypothesis has merit.

Male body size was on average greater from bees emerging from bushland remnant nests compared with residential gardens. As is typical of most bees (Helms 1994), for the majority of species, sexual dimorphism was apparent with females being the larger sex (Prendergast, in prep.). It may be that female bees invest first in producing daughters, given that females are a more “limiting” resource than males, and then if additional resources are available, invest in males, whereby the larger sons may be healthier or sire more offspring – such a situation would mean females tend to be fairly uniform in body size, but in habitats where there are additional resources, females can then invest in larger males. Again, this suggests bushland habitats are of superior quality than residential gardens for native bee fitness (Veller et al. 2016).

Variables influencing hotel occupancy and emergence parameters

Analysing the different fitness components revealed that different environmental variables were influential for the different components, or even the same variables were significantly associated, but in opposite directions.

Although there is generally a positive relationship between connectivity and abundance (Bennett 1999; Braaker et al. 2014), isolation could cause individuals increase in density (Biella et al.), generating the positive relationship between trap nest occupancy and isolation from native vegetation.

Unexpectedly, total and native flower species richness were negatively associated with number of completed nests per survey. This contrasts with conventional wisdom, as well as numerous studies finding that native flora, and floral diversity, tend to be positively associated with bee abundance and diversity (Biesmeijer et al. 2006; Kremen et al. 2004; Potts et al. 2003) and studies reporting positive relationships with of plant diversity on bee reproductive success (Ebeling et al. 2012; Orford, Murray, Vaughan, & Memmott, 2016). However it is not unique, for other studies have found negative correlations between plant diversity and bees (Horn 2010; Geslin et al. 2016; (Prendergast et al. 2022b), including for cavity-nesting bees (Ebeling et al. 2012; Sheffield et al. 2008), and that reproductive output of solitary bee species declines under higher plant diversity (Dorado and Vázquez 2016). This may be due to how higher numbers of flower species within an area means a lower proportion of preferred flowers, especially for specialists, and may make foraging more challenging; thus the identity of the flower species, not total flower species, may be important. It is likely that "not all flowers are equal" and with a greater diversity of flower resources, native bees may find it harder to locate patches of rewarding, quality flora ((Prendergast et al. 2022b). Greater flower diversity may also give introduced European honeybees a competitive edge (Prendergast et al. 2021).

Woody plant density was negatively associated with the number of provisioned cells. This may be due to how if there are more suitable natural nesting resources, females will "bet hedge" and put fewer cells per nest and spread them over a greater number of nests.

In addition to native flowers, mortality rate increased with isolation from reserves, but unexpectedly decreased with greater impervious surfaces. Further investigation is required into the mechanism behind these patterns. Sites isolated from reserves may mean females have to forage on inferior pollen resources as they have a restricted ability to move through the landscape; greater inbreeding depression due to lack of migration between habitat patches under fragmentation; or greater exposure to toxins in pollen or nectar.

The positive association with the proportion of builtspace land-cover around a site and bee emergence success is unexpected and hard to explain, given that impervious surface cover tends to negative impact native bees in the cities (Ahrné 2008; Ahrne et al. 2009; Geslin et al. 2016; (Prendergast et al. 2022a), and (MacIvor 2015) reported that abundance and species richness of trap-nesting bees significantly declines with decreasing proportions of greenspace at 600 m radii. However there has also been studies that like this one, have found builtspace cover has a positive effect on bees (Lowenstein et al. 2014; Makinson et al. 2016; Rajbhandari et al. 2023). In a study modelling trap-nest occupancy of solitary bees in urbanised USA, although the proportion of builtspace in the surroundings was a significant predictor of occupancy values, the direction (positive or negative) differed depending on the species of bee and the metric of occupancy (MacIvor and Packer 2016). Greater proportions of builtspace in the surrounding landscape may reduce mortality by providing a more suitable microclimate (Geppert et al. 2022). This unexpected negative association between greater impervious surfaces and mortality rate however may also be due to the negative correlation between proportion of builtspace around a site and total area of the site (see Supplementary Information 3). As this two explanatory variables co-varied, only builtspace was used in the analyses, however this would mean that greater area of a habitat would be associated with reduced mortality rate. Such an association makes greater ecological sense, as larger areas of habitat would mean reduced fragmentation such that females may be better able to forage effectively and provision nests with adequate nutrition (da Rocha-Filho et al. 2020).

Native flower species richness, or proportions of native flora, had a positive impact on emergence fitness parameters. This can be explained by how many native bees, including the megachilids and Hylaeinae, are relatively specialised, preferring, or being oligolectic on, native Myrtaceae and Fabaceae (Houston 2000, 2018). This specialisation is unsurprising given that the southwest Western Australian biodiversity hotspot is located in an old, climatically-buffered landscape, where specialised interactions have evolved (Hopper 2009, 2021; Lambers 2014).

Greater isolation from nature reserves being negatively correlated with emergence success is more in line with expectations based on findings in agricultural landscapes that connectivity or proximity to natural habitat enhances bees (Gemmill-Herren and Ochieng 2008; Holzschuh et al. 2007; Kim et al. 2006; Landaverde-González et al. 2017; Williams and Kremen 2007), including cavity-nesting bees (Krewenka et al. 2011), whereas isolation from natural habitat results in significant reductions in reproduction of cavity nesting bees (Krewenka et al. 2011; Peterson et al. 2006). The importance of connectivity (and conversely, the detrimental effect of fragmentation and isolation from natural habitats) has primarily been evaluated in agricultural settings, but a recent study by (Banaszak-Cibicka et al. 2016) confirmed that distance from large green spaces was influential for bees in urban areas.

Other factors that were not recorded during this study may also be influential, including solar insolation (Everaars et al. 2011), substrate to which the hotel was attached (Everaars et al. 2011), wind exposure, and availability of other nesting resources (resin, leaves, other plant materials) (Hingston and Potts 2005; (Prendergast 2018b). Whilst flowering resources were measured in terms of diversity and abundance of all and native plants at the site-level, this does not take into account foraging resources outside the area surveyed but still within the flight range of bees, nor the specific flower requirements of each species.

Whilst habitat and environmental variables were found to be significant in influencing a number of bee hotel occupancy and native bee fitness parameters, some hypothesised relationships were not found to be significant. This may relate to the complexity of the models here, whereby there was insufficient power to detect significant results (Underwood and Chapman 2003; Visentin et al. 2020), as may have been the case for the multivariate models involving the floral and site attributes.

Assemblage composition

For both seasons, there was a huge discrepancy between representation in trap-nests and representation in insects collected in the field. As field collection only occurred for three hours once a month, it is unlikely to have contributed to have resulted in the difference in species composition between the species that emerged from the trap-nests, which were present throughout the month. Moreover, despite some euryglossine bees being cavity-nesters (*Euryglossula, Euryglossina* and *Pachyprosopis* (Almeida 2008), including species observed to be nesting in tiny holes in trees and wood during surveys ((Prendergast 2018a), none used the trap-nests. It may be that the diameters were too large, given the tiny size of euryglossines; however, even another study on trap-nesting hymenoptera in the wheatbelt that employed 3 mm diameter bee tubes failed to have any become occupied by Euryglossinae (Murphy 2015; Taxonomy Australia, 2020), so it may be that this group avoids using artificial nesting substrates.

Even for species that were present in both field and trap-nests, their representation was very different. My results suggest it is inappropriate to combine results from field based surveys and trap-nesting surveys (e.g. Makinson et al. (2016)), for it is likely that different factors affect the probability of a bee being observed in a given location vs. the probability it nests in a given location. These results support other research indicating that using multiple methods is appropriate due to biases associated with a given method for monitoring bee assemblages, and methods should be selected based on the question of interest (Prendergast and Hogendoorn 2021; Prendergast et al. 2020).

The nesting assemblages were consistently highly skewed, being dominated by just a few species that comprised the majority of nests. Such findings of just a few common species accounting for the majority of occupied nests appears to be common in studies on trap-nesting bees in urban areas. For example, (von Königslöw et al. 2019) found that five species accounted for 77.4% of occupied nests, (Loyola and Martins 2006) reported that two species occupied 29.41% and 23.53% of nests, respectively, MacIvor (2015) reported the introduced *Megachile rotunda* occupied 27.6% sites, and comprised 48.6% of all brood; Pereira-Peixoto et al. (2014) found that *Osmia rufa* comprised 70% of bees, and Fortel et al. (2016) reported that two *Osmia* species dominated the community, comprising over 87% of data. This pattern however does not appear to be exclusive to urban areas: a study in the wheatbelt of Western Australia reported that three megachilids (*Megachile tosticauda* (3,821 cells), *M. oblonga* (1,382), and *M.* sp. 2 (1,145), together accounted for 78.4% of constructed bee cells (Murphy 2015). Interestingly, many of the species recorded in the study by (Murphy 2015) was also recorded in the present study, but their relative representation differed: *M. tosticauda* was a much more dominant component of the assemblage in Murphy (2015), whereas *M. erythropyga* was only a minor component, in contrast to the patterns observed in the current study for the pre-winter emergences.

The assemblage of species showed variation between both the pre and post-winter emergences, and between the years. It appear that certain species have different strategies or cues for their development and emergence. These results caution against conducting trap-nesting studies for a single season (e.g. (Makinson et al. 2016), and funding bodies should invest into conducting trap-nest monitoring studies that span more than one year.

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Author contributions K.P. devised the project, conducted the fieldwork, data analysis, writing of the manuscript, editing of the manuscript, and preparation of the figures.

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Declarations

Conflict of interest none to disclose.

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