

Microsite conditions dominate habitat selection of the red mason bee (*Osmia bicornis*, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany

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ABSTRACT

The red mason bee (*Osmia bicornis* L.) is a common wild bee in urban environments which contributes to early-season pollination. We know only little about how any species of wild bee in cities responds to resource distribution or landscape structure and the urban habitat(s) that they prefer. We employed a citizen science approach to investigate drivers behind the spatial distribution of this solitary bee in the urban region of Leipzig (Germany). Volunteers hung trap nests at different locations and collected information on eight local, microsite conditions (such as sun exposure, attachment position, local flower availability). We derived 14 landscape factors from a digital GIS biotope data map (e.g. distance to flower sites and urban matrix properties such as size and edge length of patches). Both occurrence and abundance of *O. bicornis* were then analyzed using a combination of machine learning and multiple (logistic) regression. The results indicate that the red mason bee is ubiquitous in urban area but clearly profits from nearby floral resources. Although we expected a balanced influence of landscape factors and microsite conditions, we found that hang location of the trap nest was most important, followed by sun exposure. Cities with many fine-scaled floral resources (such as private gardens but not parks) and an open housing structure with higher sun exposure between buildings provide a good environment for cavity-nesting bees such as *O. bicornis*. In places without suitable nesting opportunities, artificial nest can support the bees.

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1. Introduction

The conservation of pollinators in urban areas is gaining scientific interest (Gaston, Smith, Thompson, & Warren, 2005; Matteson, Ascher, & Langellotto, 2008). Although honeybees and wild bees are generally associated with pollination of crops in agricultural areas, pollination services are required in cities as well. They increase seed set, fruit mass and plant reproduction of wild and ornamental plants and vegetables and thus enhance important levels in the food chain of the urban ecosystem (Osborne, Williams, & Corbet, 1991). Pollination services in cities are provided to a substantial extent by wild bees since most honeybee colonies are

located in the countryside in order to pollinate mass-flowering crops. Urbanization can limit the fulfillment of nesting and foraging requirements of wild bees and the conservation of wild bee habitats in cities is of current debate (e.g. Cane, Minckley, Kervin, Roulston, & Williams, 2006; Corbet et al., 2001).

Cities provide favorable microclimatic conditions for wild bees and can harbor a high number of species (Frankie et al., 2005; Saure, 1996). Wild bees require a combination of the right foraging resources and specific nesting resources (Westrich, 1996). Urbanization generally leads to native plant loss (Hahs et al., 2009), but cities also provide a range of successional stages at brownfield sites with a species-rich ruderal vegetation including Red Data Book listed bee-pollinated plant species (Flügel, 2005; Saure, 1996). Such sites have diverse vegetation and little disturbed seed banks (Flügel, 2005; Tommasi, Miro, Higo, & Winston, 2004). Exotic plants at sun-exposed sites in backyards, allotments, parks and even on balconies offer pollen and nectar throughout the whole season (Flügel, 2005) but their value for bees is unclear. Some believe that nectar and pollen are largely inaccessible to native pollinators or are not provided at all (Comba et al., 1999; Corbet et al., 2001;

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Tommasi et al., 2004), while others have shown that many ornamental exotic plants are used as forage (Barthell, Bromberger, Daly, & Thorp, 1998; Frankie et al., 2005; Goulson, Hughes, Derwent, & Stout, 2002). The availability of nesting resources is also altered by urbanization. Many urban soils are probably too compacted to nest in (Matteson et al., 2008), but urban gardens have higher nest densities of bumblebees than a homogeneous countryside (Osborne et al., 2008). Cavity nesting bees may fail to find enough nesting resources in urban green spaces and backyards due to frequent mowing and removal of dead stems (Matteson et al., 2008), but cities also provide a high diversity of compensating anthropogenic substrates suitable for cavity nesting bees, such as wooden fences, barns and mortar brick walls (Cane & Tepedino, 2001; Saure, 1996). Cavity nesting bees were for example more abundant in small urban habitat fragments than in natural vegetation, probably due to enhanced nesting opportunities (Cane et al., 2006).

The spatial distribution of foraging and nesting resources may play a crucial role, especially in cities where foraging patches and nesting habitat are highly fragmented (Cane & Tepedino, 2001; Matteson et al., 2008). Effects of fragmentation on bees are contradicting (Cane, 2001; Kremen & Ricketts, 2000). The abundance of bees increased with habitat connectivity in an agricultural landscape (Steffan-Dewenter, 2003), but elsewhere pollinator diversity was only predicted by vegetation cover and the same diversity was found for both small isolated and large patches (Donaldson, Nanni, Zachariades, Kemper, & Thomson, 2002). The effect of fragmentation and urbanization on bees are better understood when bees with a different nesting guild or diet breadth are analyzed as separate groups (Cane et al., 2006). Also traffic was thought to limit wild bee movement (Banaszak, 1995), but recent experiments show that they cross busy motorways (Zurbuchen, Bachofen, Muller, Hein, & Dorn, 2010). Roads probably do not separate nesting and foraging patches.

The red mason bee, *Osmia bicornis* syn. *rufa* L., is common to urban areas in Europe, along with other solitary bee species such as *Anthophora plumipes*, *Andrena flavipes*, *Andrena fulva*, *Nomada fucata* and *Melecta albifrons* (Banaszak, 1995; Flügel, 2005). *O. bicornis* is common in our study region as well and a suitable species for studying urban distribution patterns with standardized trap nests. The use of a single species has the advantage that landscape structure effects are not cancelled out by taxonomical differences (Cane et al., 2006). Solitary bees such as *O. bicornis* visit several times more flowers per day than honeybees (Teppner, 1996) and require spring flowering plants in high quantities. *O. bicornis* prefers small cavities and clay and loam as building material (Flügel, 2005). Urban features affect Hymenoptera assemblages in trap-nests, probably by affecting the biotic and abiotic microsite conditions (Zanette, Martins, & Ribeiro, 2005). Our leading questions were: Does *O. bicornis* build nests in every part of the city? Do urban areas provide enough foraging resources (pollen and nectar-rich flowers) and nesting resources (hollow tubes) and is the number of brood cells that *O. bicornis* builds affected by it? How do microsite attributes around the nest (abiotic conditions and nest site quality) affect nest distribution and number of brood cells?

2. Methods

2.1. Study area

Leipzig is located in eastern Germany (51°20'N, 12°22' E). Climate characteristics are intermediate between temperate and continental with an average annual temperature of 8.8°C and 511 mm precipitation. Leipzig is a compact city with a population of approximately 500,000 people. The city core consists of a densely developed area with administrative and cultural facilities, little housebound green (gardens, balconies etc.) and several small

parks. The core is surrounded by a residential ring, dominated by tenement blocks from the late 19th and early 20th century with green backyards and balconies with ornamental flowers. A second residential ring is formed around Leipzig consisting of terraced and detached houses with gardens, mainly built between 1900 and 1940, as well as socialist-era prefabricated multi-storey housing estates surrounded by lawns with very few flowers, but often with flower-rich balconies. Larger parts of the eastern and western sides of the city are covered by industrial and commercial land use with little green space.

Despite being compact, Leipzig has a significant amount of green space. The city has several large parks and a large floodplain forest is running past the core city. Many small allotment garden plots are situated along railway tracks and around the city. Former lignite open-cast mines that are being turned into an artificial lake district are located to the south of the city. Otherwise, the rural surrounding is dominated by intensively used agricultural land (Fig. 1).

2.2. Bee sampling and microsite assessment

We sampled bees following a citizen-science approach. We handed out 350 trap nests to employees of the Helmholtz Centre for Environmental Research in Leipzig in March 2008. Participants were asked to hang their trap nest at or around their home and return it in June. Although this approach does not yield a perfectly balanced design, it covered the city well, reaching beyond public spaces. We gave the participants a questionnaire that enquired about microsite attributes describing nest site quality and abiotic conditions. The questionnaire included the address of the nest location, predefined categories about *trap orientation* (West, East, South, North, None), *sun exposure* (fully shaded, partly shaded, fully sunlit), *wind protection* (yes/no), *hang location* (house, garden, allotment, backyard, or specify other location), *object of attachment* (window, balcony, roof-terrace, tree/shrub, ground, wall, or specify other object), *floor* (if at a house), *flowers within 100 m* of the trap nest (yes/no) and flower types (*meadow flowers*, *ornamental flowers*; yes/no). In addition, we asked the volunteers to provide us with photographs of the trap location.

Each trap nest was constructed as a plastic tube, 20 cm long and 10.5 cm in diameter, filled with a bundle of approx. 33 bamboo tubes, each 20 cm long with a cavity diameter > 5 mm (which is the minimal diameter for *O. bicornis*: Budriene, Budrys, & Nevronytė, 2004; Ivanov, 2006).

The participants in the study returned 250 nests in June 2008 along with the questionnaires and we counted the number of cells built by *O. bicornis* (excluding the vestibule). A trap nest is a unit where multiple females nest and each female uses one or more tubes, so that individual nests cannot be identified by this method. We used the number of brood cells to estimate the response to local resources since brood cells contain pollen and nectar from floral resources. The main flight period of *O. bicornis* is from the middle of April until the end of May (Maddocks & Paulus, 1987; Teppner, 1996). We only used trap nests that hung at least between 16 April 2008 and 25 May 2008. The locations of the 239 trap nests that met this criterion are shown in Fig. 1. These exposure days are characterized by a mean daily temperature of 12.8°C and 8.1 h of sunshine and 0.6 mm of rainfall on average per day (Deutsche Wetterdienst, 2011). We included the day of nest removal (Julian day – 145), the total number of bamboo tubes per trap and the proportion of tubes with an internode (which serves as additional nest protection) as correction factors in the analysis.

2.3. Habitat suitability and landscape factors

We quantified foraging and nesting resources at the landscape level since pollinators are mobile and operate at scales larger

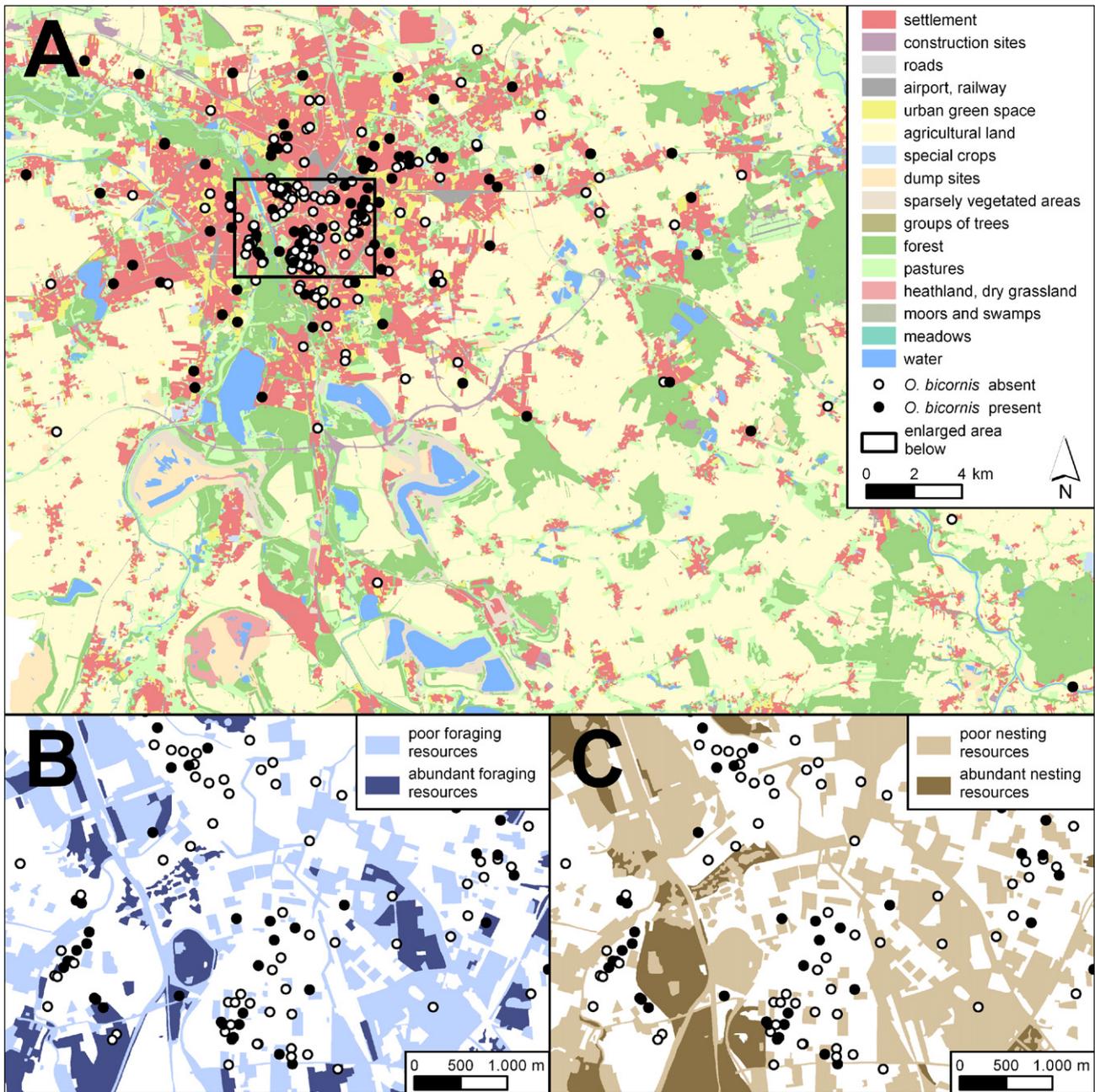


Fig. 1. This map shows the major land cover classes in and around Leipzig and the distribution of the trap nests (a). (b) shows the classification of foraging resources and (c) of the nesting resources for *O. bicornis* (moderate foraging and nesting resources omitted, white space). Note that (a)–(c) are three different reclassifications of the detailed biotope classes.

than the individual garden (Goddard, Dougill, & Benton, 2010). Solitary wild bees respond to landscape structure at scales up to 750 m in contrast to honeybees and bumble bees which operate at larger scales (Steffan-Dewenter, Münzenberg, Bürger, Thies, & Tschardtke, 2002). We classified the landscape based upon the most recent (2005) biotope map of Saxony (Sächsisches Landesamt für Umwelt Landwirtschaft und Geologie, 2008). The biotope map was derived from 1:10,000 color-infrared ortho-photos by manual classification into biotopes with a minimal area of 0.25 ha. Biotope definitions are detailed land-use descriptions from a biological perspective and include (semi-) natural biotopes such as different forest types and water bodies as well as agricultural biotopes such as orchards and hedgerows but also urban habitats such as roads and different building types. This biotope classification was developed in Germany as a proxy for habitats that organisms use and is a

useful and diverse classification when large areas are inaccessible for detailed plant surveys, as it is the case in urban areas where the majority of the land is private. We reclassified the land cover twice, focusing on estimated availability of foraging resources (areas with potential suitable bloom) and nesting resources respectively, based on rules given by Lonsdorf et al. (2009). *O. bicornis* forages on spring flowering vegetation (among others found at meadows with dandelion or areas having blossoming trees) and nests in cavities (found at places with dead stems). A summary of the re-classification rules is given in Table 1. We re-classified into *abundant foraging resources* and *poor foraging resources*. Biotope classes that were not clearly rich or poor in foraging resources were classified as *moderate* and not used for further analysis. We did likewise for nesting resources. Fig. 1b and c shows two enlarged areas of the re-classified map for foraging and nesting habitat respectively.

Table 1

Classification of nesting and foraging resources. The classification for *O. bicornis* into poor and abundant resources is based on the original biotope classes. Biotopes providing moderate resources were not considered.

New classification	Old classification
Abundant foraging resources	Meadow (only those providing either a rich flora or abundant dandelions), hedgerow (often contain spring flowering trees), forest edge, orchard, riparian buffer zone, botanical garden, allotment area, garden, castle/monastery/estate area, mixed rural area
Poor foraging resources	Water bodies without flowering vegetation, concrete buildings for non-living and non-public usage, industrial area, golf course, roads (all types), species-poor intensively-used grassland, coniferous forest
Abundant nesting resources	Hedgerow, shrubbery, deciduous woodland (all types without conifers), forest edge, castle/monastery/estate area, reed bed, meadow orchard
Poor nesting resources	Water bodies without reed beds, concrete buildings for non-living and non-public usage, industrial area, sewage field, golf course, road (all types), road ditch, intensively used grassland, sand plains, coniferous forest, afforestation area, agricultural fields

We determined the minimum distance between the trap nest and each of the four suitability classes as well as their proportion within a 500 m buffer radius (typical foraging area of *O. bicornis* (Gathmann & Tschardt, 2002)) around the trap nest covering flight effort and resource availability respectively. We determined landscape structure (diversity and complexity) with basic tools from ArcGIS 9.3 and the Patch Analyst 0.9.4. We calculated the following landscape metrics within each buffer radius from the original biotope classes: *number of patches*, *mean patch fractal dimension*, *total edge length*, *edge density*, *mean patch size* and *mean shape index*, giving 14 different landscape factors in total.

2.4. Statistical analysis

Before analyzing the data, we grouped hang locations by similarity. *Backyard* and *park* were joined into one class, as were *garden* and *allotment*. Likewise we grouped the attachment objects, including those that were not pre-defined: *balcony* and *roof terrace*, *carport* and *shed wall*, *window* and *stone wall*. All remaining objects except *tree* or *shrub* were grouped as *other object*. We used the statistical software R (R Development Core Team, 2009) for analysis and proceeded in the following steps. First we addressed possible collinearity by reducing the number of variables so that all bivariate correlations were below a set threshold (Pearson's $r^2 < 0.49$; the ecologically more plausible predictor was retained). The parameters that meet this criterion are listed in Table 2 and include both landscape-level variables and microsite attributes. Resource availability was incorporated into the presence-absence analysis as minimal distance to a resource patch and in the abundance analysis as the proportion within 500 m radius. We then selected the most important variables, because our study had more predictors than could be fitted in a multiple regression. We used the machine learning approach of randomForest (Breiman, 2001) to rank the variables by importance (separately for presence and abundance of *O. bicornis*). With the six top-ranked variables we performed a (generalized) linear regression model selection based on the Bayes Information Criterion (BIC). We included quadratic responses and interactions between variables in the full model.

Table 2

Selected regression models. The models for explaining presence and abundance of *O. bicornis* are based on model parameters that remained after correction for collinearity^a. Parameters describing microsite attributes are written in italics. Deviance, *p*-value and degrees of freedom (df) are given for each model.

Predictor	df	Deviance	<i>p</i> -Value
Model A: presence (1)			
Null deviance: 306.30			
<i>Object of attachment</i>	4	49.63	<0.001
<i>Sun exposure</i>	2	26.15	<0.001
Abundant foraging resources (distance)	1	8.13	0.004
Day of removal ^b	1	6.51	0.011
Model B: abundance (1)			
Null deviance: 131.05			
<i>Object of attachment</i>	4	20.44	<0.001
Proportion of tubes with internode ^b	1	8.24	0.004
Abundant nesting resources (500 m radius)	1	4.46	0.035
Model C: presence (2)			
Null deviance: 306.30			
<i>Object of attachment with hang location</i>	9	66.61	<0.001
<i>Sun exposure</i>	2	23.45	<0.001
Abundant foraging resources (distance)	1	3.75	n.s. (0.053)
Day of removal ^b	1	6.78	0.001
Model D: abundance (2)			
Null deviance: 143.71			
<i>Object of attachment with hang location</i>	9	33.63	<0.001
Proportion of tubes with internode ^b	1	9.06	0.003
Abundant nesting resources (500 m radius)	1	4.21	0.040
Model E: abundance (3)			
Null deviance 131.04			
<i>Proportion of occupied trap nests per class</i>	1	20.00	<0.001
Proportion of tubes with internode ^b	1	8.24	0.004
Abundant nesting resources (500 m radius)	1	4.96	0.026

^a Candidate predictors below bivariate correlation threshold ($r^2 < 0.49$): abundant foraging resources, abundant nesting resources, poor nesting resources, number of patches, mean shape index, *object of attachment*, *sun exposure*, *tube orientation*, *wind protection*, *presence of flowers within 100 m*, *meadow flowers*, *ornamental flowers*, *day of removal*^b, *proportion of tubes with an internode*^b, *total number of tubes*^b.

^b Predictors used as a correction factor as explained in Section 2.

The final regression model included only significant predictor variables. The number of observations for the final model is given in the results in brackets, since it depends on the missing values in the selected parameters. We used likelihood-ratio tests to compute significance values. Explained deviance was estimated as (null deviance – residual deviance)/null deviance. For the number of brood cells we fitted a negative binomial model. Trap nests were spatially independent (model residuals spatially uncorrelated). Two correction factors remained significant after model selection (Table 2). The day of trap removal (Julian day –145) increased the probability of trap-nest occupancy from 0.3 to 0.8 ($p=0.011$) and the proportion of tubes with an internode had a slight, positive effect on the number of brood cells ($p=0.004$). For significant factorial parameters we tested pair difference significance for all combinations with a Tukey's post hoc test.

3. Results

Out of the 239 trap nests amenable to analysis, 110 were occupied by *O. bicornis* (46%). There was no obvious spatial pattern of trap-nest occupancy (Fig. 1; occupied trap nests are often close to non-occupied ones).

3.1. Presence-absence analysis

The regression model revealed the following significant parameters for the presence of *O. bicornis* (occupancy of a trap nest): the *object of attachment*, the amount of *sun exposure* and the minimal distance to *abundant foraging resources* (Table 2, model A).

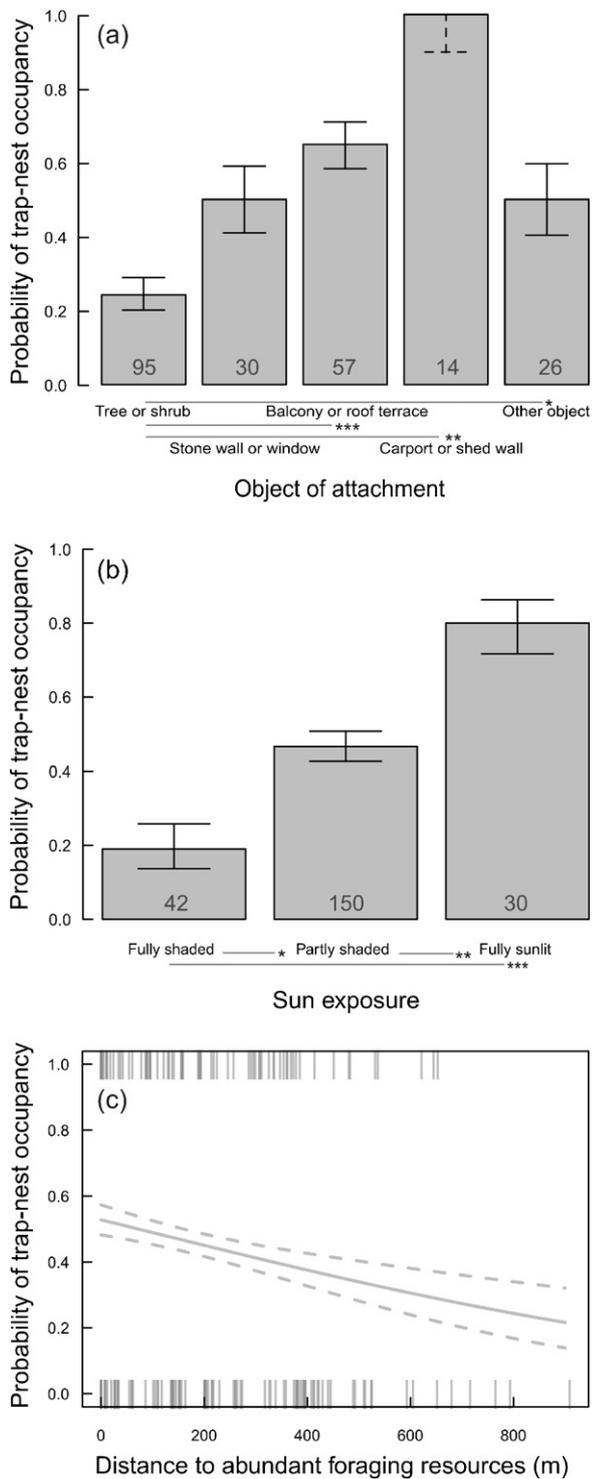


Fig. 2. Variables explaining the presence of *O. bicornis* expressed as the probability of trap-nest occupancy. Probabilities ± SE are given based on the selected model. (a) Probability of trap-nest occupancy in response to the *object of attachment*. The number on each bar represents the number of observations. All trap nests for *carport or shed wall* were occupied and hence prevented an estimation of the error. We (over-)estimated this SE with an adjusted model with one observation changed from 'present' into 'absent'. Significant differences are indicated with a grey line (significance codes: *** < 0.001, ** < 0.01, * < 0.05, significances based on the adjusted model). (b) Probability of trap-nest occupancy in response to *sun exposure*. Error bars and contrast significance are based on the original model. (c) Probability of trap-nest occupancy in response to the minimal distance between trap nests and *abundant foraging resources*. Lines indicate the model prediction ± SE and the vertical marks (at zero and one) are the original presence and absence observations.

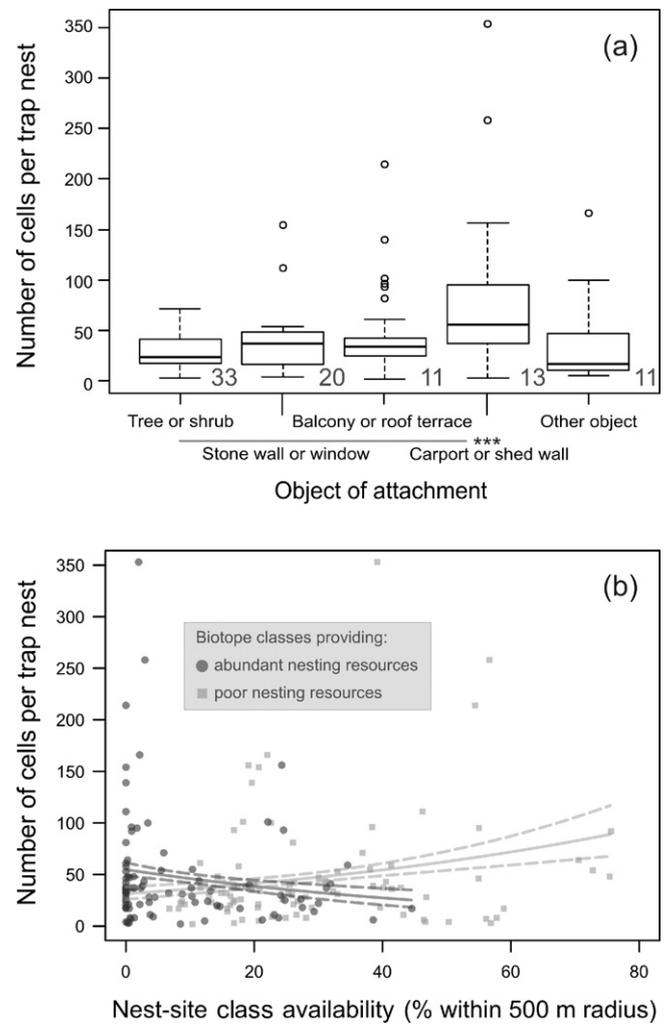


Fig. 3. Variables explaining the number of *O. bicornis* brood cells per occupied trap nest. (a) Number of brood cells in response to the *object of attachment*. The number to the lower-right from each box represents the number of observations. Significant differences are indicated with a grey line (significance codes: *** < 0.001). (b) Number of brood cells in response to the amount of nesting resources. Lines indicate the model prediction ± SE. Each trap nest is represented twice (two of three nest site classes).

Nests that were attached to *tree or shrub* showed a lower probability of trap-nest occupancy than those on balconies, at carports and other objects (Fig. 2a). Nests placed in the full sun were also more often occupied than nests located in the full shade (Fig. 2b). Trap nests located closer to abundant foraging resources were more likely to be occupied (Fig. 2c). The linear regression model ($n = 222$) explained about 30% of the deviance. A post hoc analysis revealed that all three shade-groups were significantly different (Fig. 2b). The hang location *tree or shrub* differed significantly from *balcony or roof terrace* ($p < 0.001$), from *carport or shed wall* ($p < 0.01$) and *other object* ($p < 0.05$).

3.2. Abundance analysis

Abundance of *O. bicornis* refers to the number of brood cells within the 110 occupied nests. As for presence-absence data, the *object of attachment* had the largest impact. Nests that were attached to *tree or shrub* or *other object* showed a low abundance per nest and those to *carport or shed wall* a high abundance (Fig. 3a). In addition, there was a small but significant effect of surrounding nesting resources. An increase of the proportion of

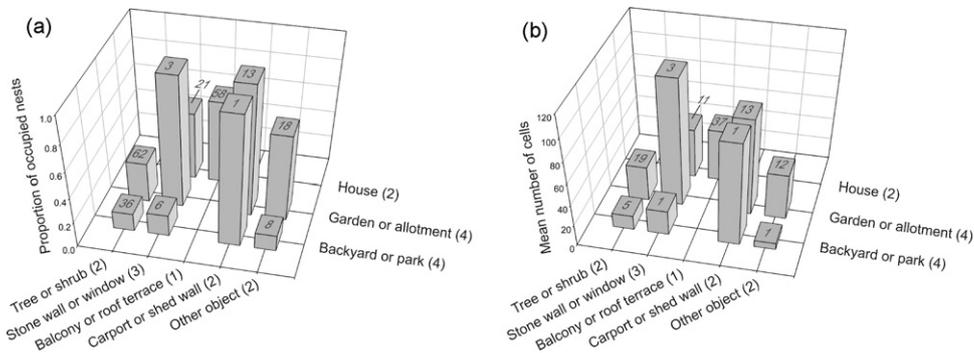


Fig. 4. Effect of *object of attachment* and *hang location*. The number of bars in each row is given in brackets. The number on top of each bar represents the number of observations in each group. (a) Proportion of occupied trap nests within each group. (b) Mean number of brood cells per trap nest in each group for occupied nests only.

abundant nesting resources within 500 m lead to fewer cells and opposing to that, an increase in poor foraging resources lead to more cells in the trap nest (Fig. 3b). Both had a significant effect by themselves, but not when taken together, since they provided similar information (despite a low correlation: Pearson's $r = -0.24$, $p < 0.05$, log-transformed data). We therefore used *abundant nesting resources* (and excluded *poor nesting resources*) in the regression model (Table 2, model B, $n = 90$), which explained 25% of the deviance. A post hoc analysis revealed that the hang location *tree or shrub* differed significantly from *carport or shed wall* ($p < 0.001$).

3.3. Interaction between the object of attachment and hang location

We initially assessed the hang location additionally to the object of attachment, but this was excluded from the final analysis due to collinearity, caused by the fact that balconies can only appear on houses while trees cannot. To reveal additional information, we separated each attachment class according to hang location (Fig. 4). We plotted the proportion of occupied nests within each class for each of the ten new classes (Fig. 4a) and the mean number of cells for each class (un-occupied nests excluded) (Fig. 4b). Both show a similar pattern. *Garden or allotment* increased the probability of trap-nest occupancy and the number of cells in comparison to *backyard or park* as long as the trap nest was attached to a *tree or shrub*, a *stone wall or window* or *other object*. In both linear regression models we replaced *object of attachment* (five classes) by these ten classes (Table 2, models C and D), increasing the explained deviance from 30% to 33% and from 25% to 33% for presence and abundance respectively. To test whether the visual similarity between Fig. 4a and b is statistically verifiable, we replaced the *object of attachment* in the regression model for abundance with the proportion of occupied nests within a class as new explaining variable for the number of cells (Table 2, model E). This regression model explained 25% of the deviance.

4. Discussion

Our citizen-science approach revealed a dominance of microsite nest conditions over foraging resource distributions at larger scales. Sun-exposed and wall-mounted nests in private gardens were particularly attractive for bees.

4.1. Landscape effects and resource limitations

We expected that low levels of foraging resources at the landscape scale would have a negative effect on presence and abundance of *O. bicornis*. The probability of trap-nest occupancy decreased indeed slightly in response to the distance from abundant foraging resources (Fig. 2c), but foraging resources did not

affect the number of cells. We believe that foraging resources (floral abundance) are not a major limitation in the urban area of Leipzig. There were always *abundant foraging resources* within the maximum foraging distance (900 m for *O. bicornis*; Gathmann & Tscharntke, 2002, see Fig. 2c). Additionally, bees may have foraged on flowers in areas that we classified as *moderate foraging resources* (Fig. 1b). Note that most of the participants (97%) affirmed there were flowers within 100 m, strengthening the idea that abundance was affected by more local floral resources.

Nesting resources around the trap nests affected abundance. The most straight-forward hypothesis is that areas poor in nesting resources have lower population densities and affect abundance negatively. We found the opposite: the number of cells increased with decreasing *abundant nesting resources* (Fig. 3b), probably due to a concentration effect. Bees are observed in high concentrations on flower patches in flower-poor areas (Veddeleer, Klein, & Tscharntke, 2006; Williams & Osborne, 2009). A similar inversely proportional relationship between observed bees and availability of bloom is becoming clear for flower-mimicking colored pan traps (Cane, Minckley, & Kervin, 2000; McIntyre & Hostetler, 2001; Roulston, Smith, & Brewster, 2007). Our results suggest that the same concentration effect applies to trap nests placed in nesting-resource-poor areas. We also found indication for an accumulation effect: a trap nest discovered sooner probably allows for more cells to be built and more bee individuals to use it ($p < 0.001$, Table 2, model E). Nest-site rather than flower availability is probably limiting *O. bicornis* in German cities as well as in the German agricultural landscape (Steffan-Dewenter & Schiele, 2008).

Landscape features explained little compared to microsite attributes and none of the structural metrics had a significant influence. Our food estimation and scale of assessment were rather rough, leading to a sub-optimal resource definition for *O. bicornis*. Although the rules for land-use classification were quite specific for *O. bicornis*, we did not have detailed floral resource descriptions. Allotment areas also could have been dominated by lawns instead of abundant flowers and for exotic mass blooming shrubs such as *Forsythia × intermedia* we knew neither location nor suitability for *O. bicornis*. In some environments *O. bicornis* uses large amounts of oak (*Quercus robur*) pollen (Raw, 1974), whereas we focused more on Ranunculaceae and Rosaceae as well as dandelion-rich parks as preferred urban foraging resource (Tommasi et al., 2004). Despite these concerns we think that a resource based land-use classification is a meaningful approach. Too many land-use classes lead to zero-inflated variables when it comes to land cover around the trap nest. In a preliminary analysis, 52 urban land-cover classes were used instead of habitat suitability and none of these single classes affected *O. bicornis* significantly. As an improvement for the current method we recommend the analysis of collected pollen in the studied region so that the classification of wild bee foraging habitat can be validated or else specific plant surveys can be performed.

4.2. Importance of microsite attributes

Fully sun-exposed trap nest had a higher probability of being occupied than shaded trap nests. The preference of sun exposed sites is known for many solitary bees (Osborne et al., 1991; Tschardt & Brandl, 2004) and now clearly shown experimentally (Fig. 2b). Sun exposure reduces the thermal constraints of bees (Willmer & Stone, 2004) and may be an important criterion for nest-site selection. *O. bicornis* has a higher warm-up rate than expected (based on body mass) as adaptation to the cooler temperatures in early spring (Stone & Willmer, 1989). Sun exposure may therefore be more important for *O. bicornis* than for other solitary bees, explaining the strength of this microsite attribute for the probability of trap-nest occupancy.

The importance of the object of attachment for both the probability of trap-nest occupancy and the number of cells indicates a strong preference of *O. bicornis* for certain objects. Although a preference for a micro-habitat makes sense, we can only speculate about the mechanisms that make carpports, shed walls and balconies more attractive than trees or shrubs (Fig. 2a). Dead wood (found in carpports and shed walls) may resemble natural nest sites of *O. bicornis*. The closely related mason bee *Osmia cornuta* also prefers dead wood for nesting (Bosch, 1995), but dead wood alone does not guarantee a high occupancy (Gaston et al., 2005). Balconies may represent an attractive habitat where searching for nesting places is profitable. Solitary bees can find many nesting cavities at balconies such as in reed mats, chairs, flower pots and nail holes. *O. bicornis* may even nest in key holes and a folded table-cloth (Flügel, 2005; Linsley, 1958). It is remarkable that trap nests at the location *house* (mainly balconies) had a much higher probability of occupancy than in *backyard or park* (Fig. 4a), although balconies hang in Leipzig just above backyards. Microsite characteristics seem to be more important than adjacent foraging resources. Trap nests in trees and shrubs are naturally shaded by the canopy, which may explain the low occupancy. Trees (subset *tree or shrub*, $n=98$) had less fully sunlit trap nests than overall (8% compared to 16%), but there was no significant interaction between *object of attachment* and *sun exposure*. Trap nests in *tree or shrub in garden or allotment* had a higher probability of occupancy than those in *backyard or park* (Fig. 4a). The young and healthy trees common to urban areas (opposed to old and dead trees with cavities) may explain the negative effect of attachment to a tree *per se*. Another experiment with *O. bicornis* also showed a low acceptance (3.4–35%) for trap nests hung in trees (Free & Williams, 1970). This is not the case when trap nests are hung in commercial orchard trees (Bosch, 1992; Steffan-Dewenter & Schiele, 2008). An explanation is that bees have no alternative nesting sites in orchards leading to a stronger concentration effect of bees than in urban areas (marginally present, Fig. 3b).

In order to find better explanations for the strong differences at the level of *object of attachment*, we thought of several other factors influencing trap-nest attractiveness, distributed a second questionnaire and analyzed received photographs. We asked about *visibility* of the trap nest (from all directions, from most directions, from few directions, almost covered), *exposure to rain* (yes/no), *tree type* according to foraging resource availability (apple or pear, other *Rocaceae*, other tree) and *height within the tree* (below 2 m or higher). We tested these new explaining factors for trap nests in *tree or shrub* (largest class, $n=98$) but none of these had a significant effect on the probability of trap-nest occupancy or number of cells. For trap nests on balconies (second largest class), we used height (*floor*) from the first questionnaire to see whether it requires more energy investment. *O. bicornis* was more or less equally distributed over different floors both in presence and abundance (*floor* had no effect) which may not be surprising since even smaller solitary bees can overcome a height difference of 130 m (Zurbuchen et al., 2010). Other suggestions include that cavity-nesting bees use scent (dead

wood) rather than vision for nest-site selection, or that they may avoid nests with birds in their vicinities.

4.3. Citizen science with trap nests

Our study provides a good example of volunteers (the 239 participants that returned their trap-nest and questionnaire) collecting a considerable amount of ecological data and encourages the use of the citizen-science approach for future ecological research. This approach gave us valuable information about the ecology of *O. bicornis* that we could not retrieve from coarse-scale land-use data. The citizen-science approach has its limits, too. Conversations taught us that people were often unable to reliably identify the occupancy status of a nest by *O. bicornis* and assessing response variables must be quality-checked by researchers. Only few participants were able to identify more than the plant species on their own balcony. As a consequence, we had to lump plant species into very large and vague groups (*meadow flowers*, *ornamental flowers*), which proved not useful for explaining bee habitat preferences. Among the participants the higher educated people (and therewith some of the parameters) may have been overrepresented (campaigning at a scientific institute) although many volunteers of the supporting staff (from secretaries to construction workers) participated and we sampled a high diversity of housing types and hang locations and covered most areas of Leipzig.

The information requests afterwards demonstrated that the collaboration with volunteers was fruitful for raising public awareness of wild bees. The participants were afterwards notably better informed about the biology of wild bees, their endangerment and the importance of pollination. Overall, we think this approach was efficient and, through a good level of standardization of nests and questionnaires, scientifically rewarding.

Trap nests are a widely used and valuable research tool but our results suggest that increased standardization can benefit the clarity of results. The dominant impact of *object of attachment* and *sun exposure* resulted in a spatial pattern with occupied trap nests nearby unused ones (Fig. 1), which complicates disentanglement of local presence of an *O. bicornis* population and nest-site attractiveness. Attaching trap nests to wooden poles as proposed by Westphal et al. (2008) and placing them at sun-exposed sites would be the best way of standardizing trap-nests' sampling effort. Trap-unit factors concerning the tubes (such as the *proportion of tubes with an internode*) can be valuable as correction factor.

4.4. Implications for conservation

O. bicornis was present in all city regions (Fig. 1) and does not seem to be isolated or particularly negatively affected by urban landscape features. Microsite effects were stronger than resource effects at the landscape scale. In urban environments not only wild bees but also beetles (Niemela et al., 2002), grasshoppers (Strauss & Biedermann, 2006) and birds (Evans, Newson, & Gaston, 2009) respond more to microsite attributes than to landscape level features or urbanization gradients. In cities there is enough habitat heterogeneity to allow some species to survive even in cities centers. Changes in cities can work out negatively on bees when urban waste land is reclaimed or buildings are renovated (Flügel, 2005), which may be true especially in formerly socialist cities such as Leipzig (Saure, 1996). Similar experiments as ours in other cities could give further hints to which specific features of cities are relevant for bees.

Wild bees can be promoted in cities in different ways. Planting flowers with abundant nectar and pollen and maintaining open, sun-exposed sites seems to be a universal result supported by other studies. In our study the amount of foraging resources, being present in substantial amounts, played only a marginal role in occu-

pancy of trap nests. Therefore more attention could be given to microsite attributes such as sun exposure and ways to enhance nesting opportunities in cities, rather than to conservation and restoration of foraging resources alone. Bee communities can be supported by artificial nests at places where nesting conditions are poor. Some hang locations such as trees and parks are apparently inefficient, since bees such as *O. bicornis* will probably not use these places for nesting. Projects with wild bees can additionally help to raise public awareness of pollination issues and biodiversity conservation (Frankie et al., 2005; Matteson et al., 2008).

4.5. Final conclusions

This study demonstrates the benefit that a citizen science approach can bring to descriptive science. It shows that *O. bicornis* is ubiquitous in the city of Leipzig and is positively affected by nearby urban foraging resources and sun exposed nesting sites. Microsite attributes clearly dominate nest-site selection by *O. bicornis* in urban areas. Artificial nests can promote reproduction in regions with poor nesting resources.

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References

- Banaszak, J. (1995). Natural resources of wild bees in Poland and an attempt at estimation of their changes. In J. Banaszak (Ed.), *Changes in fauna of wild bees in Europe* (pp. 9–25). Bydgoszcz, Poland: Pedagogical University.
- Barthell, J. F., Bromberger, D. M., Daly, H. V., & Thorp, R. W. (1998). Nesting biology of the solitary digger bee *Habropoda depressa* (Hymenoptera: Anthophoridae) in urban and island environments. *Journal of the Kansas Entomological Society*, 71(2), 116–136.
- Bosch, J. (1992). Parasitism in wild and managed populations of the almond pollinator *Osmia cornuta* Latr (Hymenoptera, Megachilidae). *Journal of Apicultural Research*, 31(2), 77–82.
- Bosch, J. (1995). Comparison of nesting materials for the orchard pollinator *Osmia cornuta* (Hymenoptera: Megachilidae). *Entomologia Generalis*, 19, 285–289.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45(1), 5–32.
- Budriene, A., Budrys, E., & Nevronytė, Z. (2004). Solitary Hymenoptera Aculeata inhabiting trap-nests in Lithuania: Nesting cavity choice and niche overlap. *Latvijas Entomologs*, 41, 19–31.
- Cane, J. H. (2001). Habitat fragmentation and native bees: A premature verdict? *Conservation Ecology*, 5(1). Available from: <http://www.consecol.org/vol5/iss1/art3>
- Cane, J. H., Minckley, R. L., & Kervin, L. J. (2000). Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal of the Kansas Entomological Society*, 73(4), 225–231.
- Cane, J. H., Minckley, R. L., Kervin, L. J., Roulston, T. H., & Williams, N. M. (2006). Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*, 16(2), 632–644.
- Cane, J. H., & Tepedino, V. J. (2001). Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences. *Conservation Ecology*, 5(1). Available from: <http://www.consecol.org/vol5/iss1/art1>
- Comba, L., Corbet, S. A., Barron, A., Bird, A., Collinge, S., Miyazaki, N., et al. (1999). Garden flowers: Insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany*, 83(1), 73–86.
- Corbet, S. A., Bee, J., Dasmahapatra, K., Gale, S., Gorringer, E., La Ferla, B., et al. (2001). Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. *Annals of Botany*, 87(2), 219–232.
- Donaldson, J., Nanni, I., Zachariades, C., Kemper, J., & Thomson, J. D. (2002). Effects of habitat fragmentation on pollinator diversity and plant reproductive success in Renosterveld shrublands of South Africa. *Conservation Biology*, 16(5), 1267–1276.
- Evans, K. L., Newson, S. E., & Gaston, K. J. (2009). Habitat influences on urban avian assemblages. *IBIS*, 151(1), 19–39.
- Flügel, H. (2005). Bienen in der Großstadt (Bees in the city). *Insecta*, 9, 21–26 [in German].
- Frankie, G. W., Thorp, R. W., Schindler, M., Hernandez, J. L., Ertter, B., & Rizzardi, M. A. (2005). Ecological patterns of bees and their host ornamental flowers in two northern California cities. *Journal of the Kansas Entomological Society*, 78(3), 227–246.
- Free, J. B., & Williams, I. H. (1970). Preliminary investigations on occupation of artificial nests by *Osmia rufa* L (Hymenoptera, Megachilidae). *Journal of Applied Ecology*, 7(3), 559–566.
- Gaston, K. J., Smith, R. M., Thompson, K., & Warren, P. H. (2005). Urban domestic gardens (II): Experimental tests of methods for increasing biodiversity. *Biodiversity and Conservation*, 14(2), 395–413.
- Gathmann, A., & Tschamtkke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*, 71(5), 757–764.
- Goddard, M. A., Dougill, A. J., & Benton, T. G. (2010). Scaling up from gardens: Biodiversity conservation in urban environments. *Trends in Ecology & Evolution*, 25(2), 90–98.
- Goulson, D., Hughes, W. O. H., Derwent, L. C., & Stout, J. C. (2002). Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia*, 130(2), 267–273.
- Hahs, A. K., McDonnell, M. J., McCarthy, M. A., Vesik, P. A., Corlett, R. T., Norton, B. A., et al. (2009). A global synthesis of plant extinction rates in urban areas. *Ecology Letters*, 12(11), 1165–1173.
- Ivanov, S. (2006). The nesting of *Osmia rufa* (L.) (Hymenoptera, Megachilidae) in the Crimea: Structure and composition of nests. *Entomological Review*, 86(5), 524–533.
- Kremen, C., & Ricketts, T. H. (2000). Global perspectives on pollination disruptions. *Conservation Biology*, 14(5), 1226–1228.
- Linsley, E. G. (1958). The ecology of solitary bees. *Hilgardia*, 27(19), 543–599.
- Lonsdorf, E., Kremen, C., Ricketts, T. H., Winfree, R., Williams, N. M., & Greenleaf, S. S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, 103(9), 1589–1600.
- Maddocks, R., & Paulus, H. F. (1987). Quantitative Aspekte der Brutbiologie von *Osmia rufa* L. und *Osmia cornuta* Latr. (Hymenoptera: Megachilidae): Eine vergleichende Untersuchung zu Mechanismen der Konkurrenzverminderung zweier nahverwandter Bienenarten (Quantitative aspects of the breeding biology of *Osmia rufa* L. and *Osmia cornuta* Latr. (Hymenoptera, Megachilidae): A comparative study of competition reducing mechanisms in two near related bee species). *Zoologische Jahrbücher, Abt. f. Systematik, Ökologie und Geographie der Tiere*, 114, 15–44 [in German].
- Matteson, K. C., Ascher, J. S., & Langellotto, G. A. (2008). Bee richness and abundance in New York city urban gardens. *Annals of the Entomological Society of America*, 101(1), 140–150.
- McIntyre, N. E., & Hostetler, M. E. (2001). Effects of urban land use on pollinator (Hymenoptera: Apoidea) communities in a desert metropolis. *Basic and Applied Ecology*, 2(3), 209–218.
- Niemela, J., Kotze, D. J., Venn, S., Penev, L., Stoyanov, I., Spence, J., et al. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: An international comparison. *Landscape Ecology*, 17(5), 387–401.
- Osborne, J. L., Martin, A. P., Shortall, C. R., Todd, A. D., Goulson, D., Knight, M. E., et al. (2008). Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*, 45(3), 784–792.
- Osborne, J. L., Williams, I. H., & Corbet, S. A. (1991). Bees, pollination and habitat change in the European community. *Bee World*, 72(3), 99–116.
- R Development Core Team. (2009). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raw, A. (1974). Pollen preferences of three *Osmia* species (Hymenoptera). *Oikos*, 25(1), 54–60.
- Roulston, T. H., Smith, S. A., & Brewster, A. L. (2007). A comparison of pan trap and intensive net sampling techniques for documenting a bee fauna. *Journal of the Kansas Entomological Society*, 80, 179–181.
- Sächsisches Landesamt für Umwelt Landwirtschaft und Geologie. (2008). CIR-Biotopentypen- und Landnutzungskartierung Sachsen 2005 (CIR-biotopentypen und land use mapping Saxony 2005) [in German].
- Saure, C. (1996). Urban habitats for bees: The example of the city of Berlin. In A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, & I. H. Williams (Eds.), *The conservation of bees* (pp. 47–54). London: Academic Press.
- Steffan-Dewenter, I. (2003). Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology*, 17(4), 1036–1044.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C., & Tschamtkke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83(5), 1421–1432.
- Steffan-Dewenter, I., & Schiele, S. (2008). Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology*, 89(5), 1375–1387.
- Stone, G. N., & Willmer, P. G. (1989). Warm-up rates and body temperatures in bees: The importance of body size, thermal regime and phylogeny. *Journal of Experimental Biology*, 147(1), 303–328.

- Strauss, B., & Biedermann, R. (2006). Urban brownfields as temporary habitats: Driving forces for the diversity of phytophagous insects. *Ecography*, 29(6), 928–940.
- Teppner, H. (1996). Bienen und Obstbaum-Bestäubung [Bees and fruit pollination]. *Obst, Wein, Garten*, 65(5), 3–7 [in German].
- Tommasi, D., Miro, A., Higo, H. A., & Winston, M. L. (2004). Bee diversity and abundance in an urban setting. *Canadian Entomologist*, 136(6), 851–869.
- Tscharntke, T., & Brandl, R. (2004). Plant–insect interactions in fragmented landscapes. *Annual Review of Entomology*, 49, 405–430.
- Veddeler, D., Klein, A. M., & Tscharntke, T. (2006). Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos*, 112(3), 594–601.
- Westphal, C., Bommarco, R., Carre, G., Lamborn, E., Morison, N., Petanidou, T., et al. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, 78(4), 653–671.
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, & I. H. Williams (Eds.), *The conservation of bees* (pp. 1–16). London: Academic Press.
- Williams, P. H., & Osborne, J. L. (2009). Bumblebee vulnerability and conservation world-wide. *Apidologie*, 40(3), 367–387.
- Willmer, P. G., & Stone, G. N. (2004). Behavioral, ecological, and physiological determinants of the activity patterns of bees. *Advances in the Study of Behavior*, 34, 347–466.
- Zanette, L. R. S., Martins, R. P., & Ribeiro, S. P. (2005). Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape and Urban Planning*, 71(2–4), 105–121.
- Zurbuchen, A., Bachofen, C., Muller, A., Hein, S., & Dorn, S. (2010). Are landscape structures insurmountable barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species. *Apidologie*, 41(4), 497–508.