

# Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances

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## Abstract

Bees require suitably close foraging and nesting sites to minimize travel time and energy expenditure for brood provisioning. Knowing foraging distances in persistent ('healthy') populations is therefore crucial for assessing harmful levels of habitat fragmentation. For small bees, such distances are poorly known because of the difficulty of individual tagging and problems with mark-recapture approaches. Using apiarist's number tags and colour codes, we marked 2689 males and females of four oligolectic and two polylectic species of Osmiini bees (Megachilidae, genera *Chelostoma*, *Heriades*, *Hoplitis*, *Osmia*) with body lengths of 6 to 15 mm. The work was carried out in 21 ha-large urban garden that harbours at least 106 species of wild bees. Based on 450 re-sightings, mean female flight distances ranged from 73 to 121 m and male distances from 59 to 100 m. These foraging distances suggest that as a rule of thumb, flower strips and nesting sites for supporting small solitary bees should be no further than 150 m apart.

## Keywords

Anthophila, body size, foraging distances, individual tagging, Megachilidae, solitary bees, urban garden

## Introduction

Wild bees are pollinators of high conservation concern. One reason for this derives from the relatively small spatial and temporal scale of their life cycles, habitat ranges, and nesting behaviour (Westrich 1996; Gathmann and Tscharrntke 2002; Greenleaf et al. 2007; Franzén et al. 2009; Zurbuchen et al. 2010a; Wood et al. 2016), which makes them vulnerable to landscape fragmentation. Bees are central-place foragers, with females shuttling between foraging sites and nests to provide brood cells with pollen, nectar or oil, and the distance between these resources largely determines bees' reproductive success (Zurbuchen et al. 2010b). The further nest and food sources are apart, the higher bees' energetic and reproductive costs (Williams and Tepedino 2003; Zurbuchen et al. 2010b). Thus, in the European solitary species *Hoplitis adunca* and *Chelostoma rapunculi* (Megachilidae), the number of brood cells provisioned per time decreased by a third to almost half (31% or 46%) when foraging flight distances were experimentally increased by 200 or 500 m (Zurbuchen et al. 2010b). In the solitary *Megachile rotundata*, 74% fewer offspring were produced when flight distances increased by 150 m (Peterson and Roitberg 2006). Increased flight requirements reduce adult lifespan (Schmid-Hempel and Wolf 1988), and absences from the nest increase brood cell parasitism, as parasites enter the nest while the nest owner is away (Seidelmann 2006). Proximity of nesting and foraging sites is therefore crucial for the reproductive success of bees, and we need more data on foraging distances to predict the effects of habitat enhancements for conservation purposes (Nicholson et al. 2019).

Bee foraging distances have been investigated with a range of methods, including microsatellite DNA markers to determine to which colony a bumblebee worker belongs (Chapman et al. 2003; Knight et al. 2005), pollen analysis to check the content of pollen loads or brood cells for plants occurring at known distances (Williams and Tepedino 2003; Beil et al. 2008), and radio tracking for species large enough for carrying a transmitter (Carreck et al. 1999). The two most widely used methods are translocation experiments (e.g., Gathmann and Tscharrntke 2002) and mark-recapture studies (e.g., Osborne et al. 2008; Wolf and Moritz 2008; Franzén et al. 2009; Zurbuchen et al. 2010a). In translocation experiments, bees are removed from their nest and released at increasing distances until no more returnees are recorded at the nesting sites. This is biologically highly different from a natural foraging flight in which a bee travels from, and returns to, its nest. Mark-recapture studies instead involve marking, releasing, and recapturing bees, but not transporting them (in darkened boxes) away from their nests.

All these approaches aim to find maximal flight distances, which are key to inferring body size/distance relationships. A linear regression model that included body length and maximum flight distance in 17 European solitary bees showed that distance roughly triples as body length doubles (Gathmann and Tscharrntke 2002), with the smallest species studied being *Chelostoma florissomne* (7 to 11 mm), the largest the European carpenter bee *Xylocopa violacea* (20 to 30 mm). A non-linear regression analysis of the maximum distances of 62 species worldwide that regressed intertegular distance as a proxy for body size on distance found that larger bees had disproportionately larger foraging distances than smaller bees (Greenleaf et al. 2007).

Maximum flight distances can be treated as a species-level trait, i.e., the result of the averaged physiological and mechanical capacities of a species. In the present study, we *instead* focus on mean flight distances (which is not a species-level trait, but instead context-dependent), using a mark-release-re-sighting approach on large numbers of individuals of several species. Such data are needed to help conservation measures, such as the planting of flower strips or other resource stepping stones. Of 436 Central European species for which we compiled body sizes, 92% are between 4.5 and 13.5 mm long (Hofmann et al. 2019). We therefore selected six small species to quantify *average* flight distances in a flower-rich and nesting-site-rich botanic garden that harbours at least 106 species of wild bees (Hofmann et al. 2018). This provides independent data to compare to the flight distances of 150–600 m for 5.5 to 12 mm-long bees obtained in the above analysis in which bees were marked individually with ‘tip-ex’ or acrylic colour, transported to various release points, and the distance from the release site to the nest then measured (Gathmann and Tschardt 2002).

## Material and methods

### Study sites and species

The study took place in the Munich Botanic Garden during the 2017 and 2018 bee foraging seasons (March to August). The garden opened in May 1914, covers about 21 ha and borders on the 210-ha-large Nymphenburg Palace Park at 48°09'45"N, 11°30'06"E at 500 m above sea level. It is currently home to 106 bee species whose abundances were scored in 1997–1999 and again in 2016/2017 by repeated monitoring walks (Hofmann et al. 2018). Several cavity nest boxes for solitary bees are located in the garden, with the larger ones harbouring well-established populations. The botanical garden provides a flower-rich habitat with both flower beds and near-natural meadows blooming throughout the year.

We investigated six above-ground nesting species of Osmiini (Megachilidae) with different flight times (Table 1) and body lengths, namely *Chelostoma florisomne* (7.0–8.0 mm), *C. rapunculi* (8.0–10.0 mm), *Heriades truncorum* (6.0–7.0 mm), *Hoplitis adunca* (11.0–13.0 mm), *O. bicornis* (8.0–12.0 mm), and *Osmia cornuta* (11.0–13.0 mm). Species body sizes are from Amiet et al. (2004) and Scheuchl (2006). We did not ask the students who marked the 2689 bees to also measure body lengths because we wanted to keep bees alive and able to forage after having undergone the capturing and marking procedure; also, as explained in the Introduction, our study goal was not to test correlations between body size and flight distance.

Megachilidae are solitary bees, and the species we investigated are widespread in Europe, Northern Africa and Asia (Scheuchl and Willner 2016). While the two *Osmia* species are polylectic (meaning they forage for pollen on a wide taxonomic variety of plants; Cane and Sipes 2006), the others are oligolectic (they collect pollen at only a few plant families), with *Chelostoma florisomne* specialized on *Ranunculus* (Ranunculaceae), *C. rapunculi* on Campanulaceae, *Heriades truncorum* on Asteraceae,

**Table 1.** The studied species (tribe Osmiini, family Megachilidae) with their male and female body sizes, flight periods, and foraging preferences (Amiet et al. 2004; Scheuchl and Willner 2016).

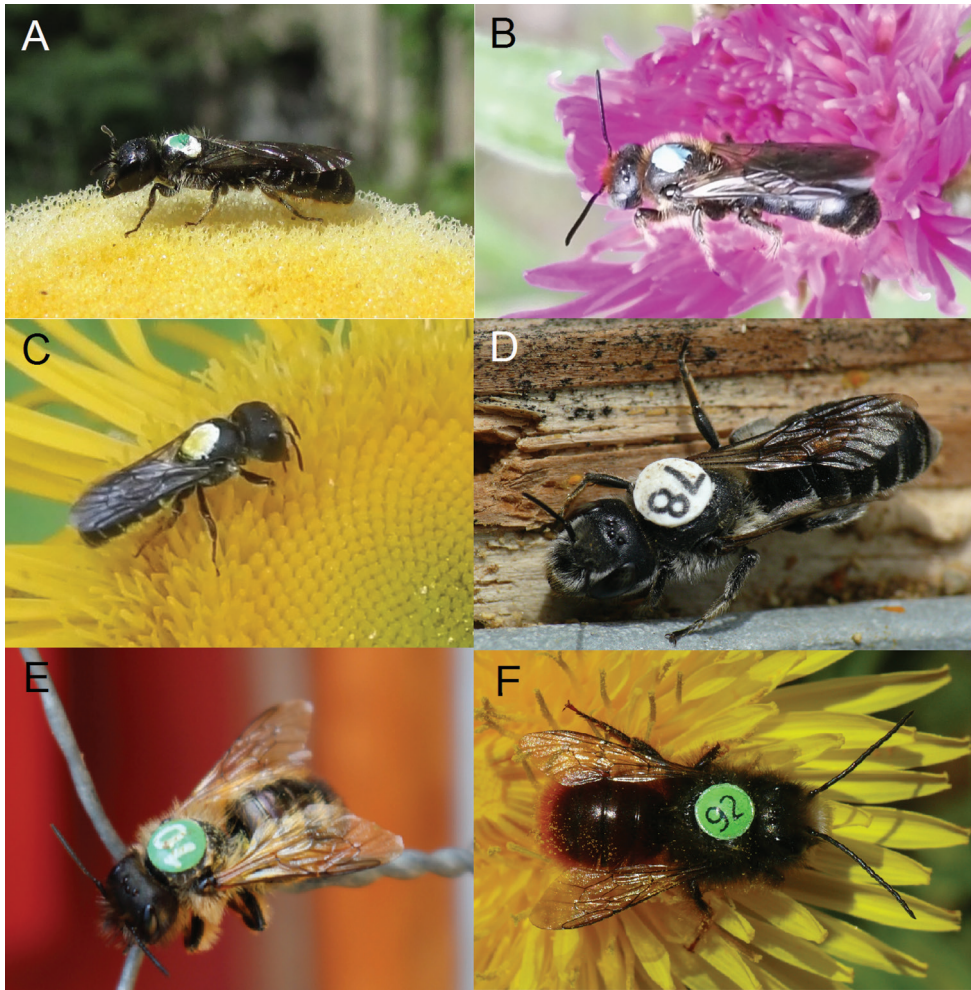
Species	Body size [mm]	Flight period	Foraging preference
<i>Chelostoma florisomne</i>	♂: 7–9 mm ♀: 7–8 mm	April–June	Oligolectic on <i>Ranunculus</i>
<i>Chelostoma rapunculi</i>	♂: 8–10 mm ♀: 8–10 mm	May–September	Oligolectic on Campanulaceae
<i>Heriades truncorum</i>	♂: 5–7 mm ♀: 6–7 mm	May–October	Oligolectic on Asteraceae
<i>Hoplitis adunca</i>	♂: 11–13 mm ♀: 11–13 mm	April–September	Oligolectic on <i>Echium</i>
<i>Osmia cornuta</i>	♂: 11–13 mm ♀: 12–15 mm	February–June	Polylectic
<i>Osmia bicornis</i>	♂: 8–12 mm ♀: 8–12 mm	March–July	Polylectic

and *Hoplitis adunca* on *Echium* (Boraginaceae). *Heriades adunca* was tagged in 2017, *Chelostoma florisomne*, *C. rapunculi*, *Heriades truncorum*, and *Osmia bicornis* in 2018, and *O. cornuta* in both 2017 and 2018.

### Bee tagging and tracking

Bees were captured with an insect net near the cavity nest boxes (shown on the garden map in Suppl. material 1: Fig. S1), and the larger species *Osmia cornuta*, *O. bicornis*, and *Hoplitis adunca* were marked using apiarist's tags (Fig. 1). Female bees were mechanically immobilized in a queen marking tube (Fig. 2); male bees were held between the experimenter's fingers such that legs and antennae were hidden from the glue and the mesonotum was freely accessible (Fig. 3). A small amount of nontoxic shellac glue (Liebert 1986) was placed on the bee's thorax with a fine metal stylus and the coloured, consecutively-numbered and slightly concave circular apiarist plastic plates (Opalith Classic from Holtermann, Brockel, Germany) were then attached. Each plate had an average weight of 1.3 mg and a diameter of 2.5 mm. For each species, several colours were used (allowing identification of sex and marking location). The same colours were used for *O. cornuta* and *H. adunca*, which had different flight times, but different colours were used for the two *Osmia* species. Each individual was identifiable by its number/colour combination.

The smaller species *Chelostoma florisomne*, *C. rapunculi* and *Heriades truncorum* with an intertegular distance < 2.5 mm were marked with paint, as apiarists' tags were too big for them. They were cold anesthetized and then marked with two dots of paint. One dot coded for the cavity nest box, one for species and sex. Bees of the same species and sex marked at the same nesting site were therefore indistinguishable in the field. Bees were released directly after being marked, which took two to three minutes per individual.



**Figure 1.** Marked individuals of **A** *Chelostoma florissomne* **B** *C. rapunculi* **C** *Heriades truncorum* **D** *Hoplitis adunca* **E** *Osmia bicornis*, and **F** *Osmia cornuta*.

We searched the garden for bees several hours per day (in both 2017 and 2018) when the weather was warm and dry, and used photography (usually by smartphone) for documenting labelled bees during floral visits. For the four oligolectic species, surveys targeted the relevant food plants. For the two polylectic species, *Osmia bicornis* and *O. cornuta*, relevant flower beds and meadows was searched, and we additionally used a citizen science approach involving garden visitors. During the outdoor season (April to October), the Munich Botanical Garden has about 2000 visitors/day. Posters near the two public entrances and on the Garden's webpage explained our project, and visitors were given three options for informing us about bee sightings: Paper forms with a gridded map of the garden available at the entrance, along with pencils and a box for dropping filled-out forms; via an email account

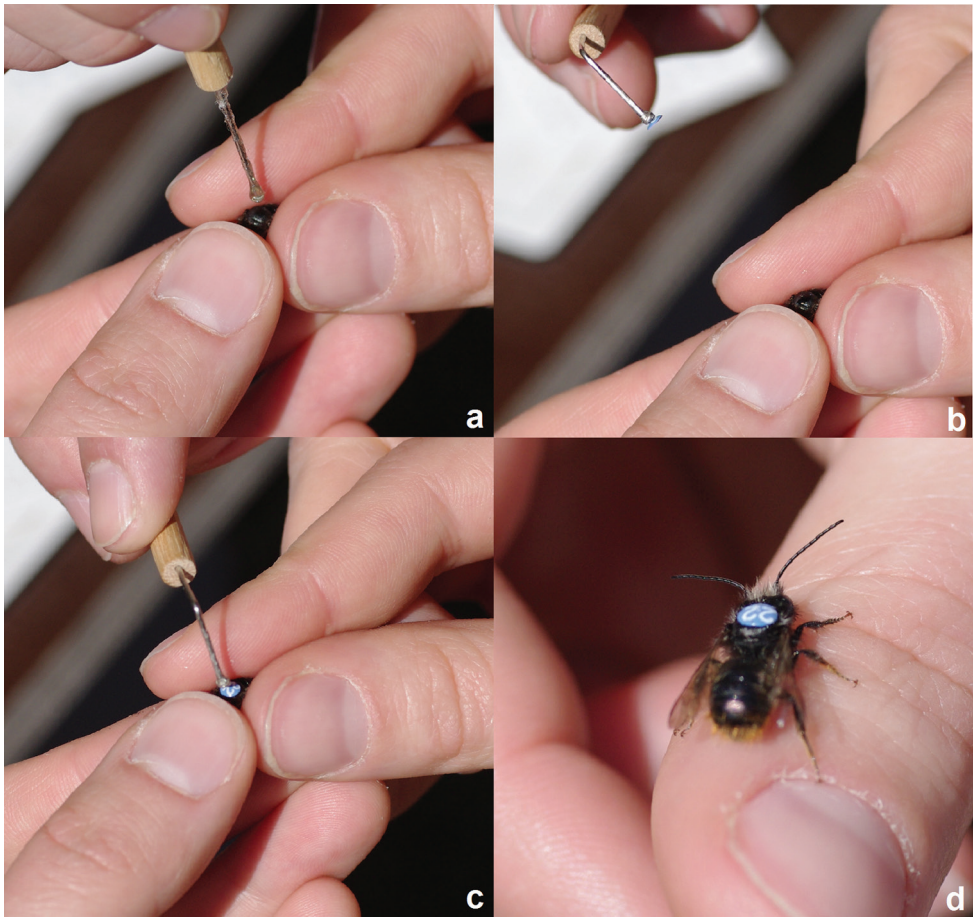




**Figure 2.** Marking of an *Osmia cornuta* female (photos: J. Kirndorfer). **a, b** A female caught with an insect net is transferred to the queen-marking tube and **c, d** pushed with the plunger to immobilize it (**e, f** a stylus is used to put glue on the mesonotum **g, h** the numbered colour plate is attached and **i** the bee released.

([wildbienen@bio.lmu.de](mailto:wildbienen@bio.lmu.de)) at which photos could be submitted; or by talking to us directly. Visitors only needed to report the colour and number of a bee's tag and where it had been seen; no special knowledge of bee species or sex was necessary for a 'successful' sighting. For smartphone pictures, GPS tracking was usually available; for oral reports, we were able to ask the visitors to show us the location directly if it was unclear; and for the reports on paper, the position of the sighted bee was directly marked on the gridded garden plan.

Since the nest locations for all individuals included in the analysis were known, we were able to measure the beeline from the respective nest box to the sites where a bee was sighted using the measuring tool of Google Earth.



**Figure 3.** Marking of an *Osmia cornuta* male (photos: J. Kirndorfer) **a** application of the glue and **b, c** attaching of the apiarists' tag **d** a labeled male ready to take off.

## Results

### Re-sighting rates and flight distances

Summed for the six species, we marked 2689 individuals, including 1808 females and 881 males (Table 2). In all, 450 of the marked individuals were re-sighted (Fig. 4 graphs all re-sightings), although individual bees could be distinguished only in the three number-tagged species (Table 1 and Suppl. material 2: Table S1). Re-sighting rates at flowers were 5.4% for *C. florissomne* females, 4% for *C. rapunculi* females, and 4.8% for *C. rapunculi* males. Of the larger species, we re-sighted 21% of *Heriades truncorum* females, 56% of *Hoplitis adunca* females, 31% of *Osmia bicornis* females, and 24 and 10% of *O. cornuta* females in 2017 in 2018, respectively (Table 2). Males were only re-sighted in *C. rapunculi*, *O. bicornis*, and *O. cornuta* (Table 2), with a 14% re-sighting rate of *O. cornuta* males in 2017 and an 11% rate in 2018. For *O. bicornis*, 24 of 37 tagged females were observed not only on flowers but also at a sand pile at

**Table 2.** Mean and maximum flight distances of tagged solitary bees in the Munich Botanical Garden in 2017 and 2018 calculated from the 450 values in Suppl. material 2: Table S1. N/A, not applicable, refers to small sample sizes. The asterisk marks a single individual found just outside the 21-ha large garden.

Species	Number of tagged individuals	Number of sightings at nest box	Number of re-sightings	Mean flight distances (m)	Standard deviation	Maximum flight distance (m)
<i>Chelostoma florissomne</i>	♀: 221 ♂: 0 Total: 221	N/A	♀: 12	82 N/A	58.7 N/A	174 N/A
<i>Chelostoma rapunculi</i>	♀: 248 ♂: 103 Total: 351	N/A	♀: 10 ♂: 5	104 59	45.2 34.5	178 119
<i>Heriades truncorum</i>	♀: 534 ♂: 0 Total: 534	N/A	♀: 118	73 N/A	62.6 N/A	298 N/A
<i>Hoplitis adunca</i>	♀: 277 ♂: 92 Total: 369	♀: 100	♀: 127	112 N/A	77.3 N/A	287 N/A
<i>Osmia bicornis</i>	♀: 136 ♂: 38 Total: 174	♀: 118 ♂: 21	♀: 42 ♂: 6	121 100	44.6 40.3	250 151
<i>Osmia cornuta</i>	2017: ♀: 170 ♂: 201 Total: 371 2018: ♀: 320 ♂: 349 Total: 669	♀: 136 ♂: 135 ♀: 279 ♂: 235	♀: 40 ♂: 29 ♀: 31 ♂: 37	106 96 107 77	107.5 39.0 67.9 52.5	724* 225 226 215

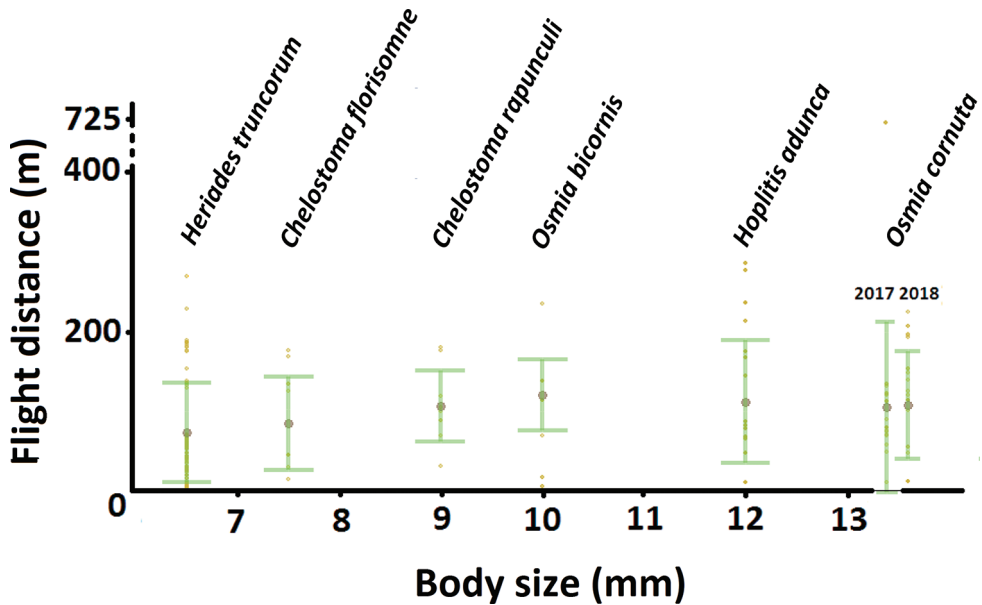
138 m distance from the nest boxes (Suppl. material 2: Table S1), where they collected earth for closing their nests.

In 2017, 77 records of individually numbered *O. cornuta* bees resulted from the citizen science approach and 72 of the 77 could be used for the distance analysis. In 2018, there were 76 records for *O. cornuta* made by citizen scientists of which 70 were usable. For *O. bicornis*, 49 records were made by garden visitors (22 on the form, 2 via email, and 25 via personal communication); all were usable.

**Comparison of male and female flight distances**

Mean female flight distances in the six species were between 73 and 121 m (Fig. 4; standard deviations and sample sizes in Tables 2 and Suppl. material 2: Tables S1). Mean male flight distances in the three species in which males could be re-sighted were between 59 and 100 m (Tables 2 and Suppl. material 2: Table S1), but sample sizes for males were low (e.g., n = 5 for *Chelostoma rapunculi* and n = 6 in *O. bicornis*).





**Figure 4.** Mean flight distances (with standard deviations) calculated from the 450 bee re-sightings shown in Suppl. material 2: Table S1, with year of observation given for *Osmia cornuta*, studied in both 2017 and 2018. All remaining data are from 2017. Species body sizes are from Amiet et al. (2004) and Scheuchl (2006). For the smaller species *Chelostoma florissomne*, *C. rapunculi*, and *Heriades truncorum*, which were colour-tagged rather than number-tagged, we cannot exclude repeated observations of the same individual.

## Discussion

To our knowledge, this is the largest tagging study of flight distances in solitary small bees in a flower-rich setting. The successful tracking of number and colour-coded tiny bees achieved in this study – ‘tracking’ because marked bees were not recaptured and hence not accidentally damaged or killed – was achieved through numerous search hours put in by students and citizen scientists in the botanical garden. In this way, we obtained 450 flight distances for six species of body lengths between 6 and 15 mm. These bees flew average distances of 75 to 125 m between their nests and their visited resources, with maximum distances up to seven times larger than mean distances (Table 2), supporting findings in other studies (Gathmann and Tschardtke 2002; Zurbuchen et al. 2010a, b) that did not use individual tagging but instead translocation experiments (e.g., Gathmann and Tschardtke 2002) or mark-recapture studies. Narrow foraging ranges thus appear to be the norm in solitary European bees, and even in the primitively eusocial *Bombus terrestris*, 40% of workers forage within a radius of 100 m around their nests (Wolf and Moritz 2008).

Bee foraging is highly context-dependent (e.g., Osborne et al. 2008; Pope and Jha 2018). For example, most *Hoplitis adunca*, a species in which both sexes prefer

*Echium* flowers as pollen and nectar sources, were observed on exactly the various *Echium* plants in the garden. Given the context-dependence of bee foraging, a limitation of our study is that it is confined to one site. For the colour-tagged (rather than number-tagged) species, our flight distances also may be pseudo-replicated because the same bee could have been seen several times. Moreover, different plants in the garden are grouped in beds or by topic (Suppl. material 1: Figure S1), which must have influenced bee foraging patterns (but so would any resource distribution anywhere). *Osmia cornuta* is the only species investigated here with different-sized males and females, but the difference is small: Tables 1 and Suppl. material 2: Table S1.

Regardless of these limitations, our results support the correlation between body size and flight distance found with different methods in previous studies (Gathmann and Tschardt 2002: 16 Central European species; Greenleaf et al. 2007: 62 species worldwide). This correlation implies that females of Central European bees, most of which are between 4.5 and 13.5 mm long (Hofmann et al. 2019), usually may not forage further than 125 to 150 meters from the nest (Gathmann and Tschardt 2002: 150 to 600 m; our Table 2: 100 m). Despite the six or seven times larger distances that these bees are able to fly when forced to do so (Gathmann and Tschardt 2002; Zurbuchen et al. 2010a, b), long flights between nests and floral resources have fitness costs in terms of lower offspring number and increased brood parasitism (Peterson and Roitberg 2006; Seidelmann 2006; Zurbuchen et al. 2010b). The persistence of populations therefore requires flower patches and nesting sites at suitable distances, for which we propose a rule-of-thumb of 150 m. This rule of thumb could be used by conservation practitioners planning urban greening measures. Implementing such simple habitat enhancements as flower strips with the appropriate spatial distribution, can greatly increase the connectivity of foraging sites and help bee conservation (Hofmann and Renner 2020).

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## Supplementary material I

### Figure S1. Map showing the garden lay-out and location of the nest boxes at which bees were tagged

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Data type: occurrence

Explanation note: Source: [http://www.botmuc.de/en/garden/garden\\_map.html](http://www.botmuc.de/en/garden/garden_map.html).

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Link: <https://doi.org/10.3897/jhr.77.51182.suppl1>



## Supplementary material 2

### Table S1

Authors: Michaela M. Hofmann, Andreas Fleischmann, Susanne S. Renner

Data type: species data

Explanation note: Flight distances of 450 males and females from six species (tribe Osmiini, family Megachilidae) re-sighted at flowers or, in the case of *Osmia cornuta* females, also at a sand pile 138 m from the nest, with year of observation given for *Osmia cornuta*, which was studied in both 2017 and 2018.

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