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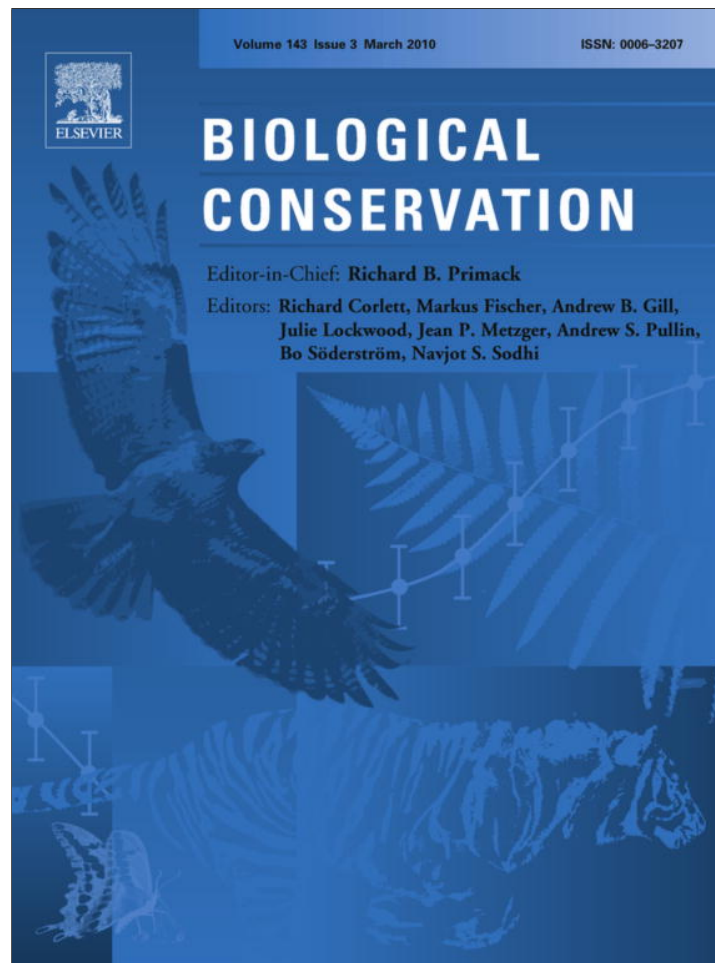
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Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances

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ABSTRACT

To preserve populations of endangered bee species, sound knowledge of their maximum foraging distance between nest and host plants is crucial. Previous investigations predicted maximum foraging distances of 100–200 m for small bee species and up to 1100 m for very large species based on mainly indirect methods. The present study applied a new and direct approach to experimentally investigate maximum foraging distances in solitary bees. One endangered and two common species of different body sizes, all of which restrict pollen foraging to a single plant genus, were established in a landscape lacking their specific host plants. Females were forced to collect pollen on potted host plants that were successively placed in increasing distance from fixed nesting stands. The maximum foraging distance recorded for the small *Hylaeus punctulatus* was 1100 m, for the medium sized *Chelostoma rapunculi* 1275 m and for the large *Hoplitis adunca* 1400 m, indicating that maximum foraging distances at species level have been underestimated. However, the capability to use resources on such a large spatial scale applied only to a small percentage of individuals as 50% of the females of *H. punctulatus* and *H. adunca* did not forage at distances longer than 100–225 m and 300 m, respectively. This finding suggests that a close neighbourhood of nesting and foraging habitat within few hundred meters is crucial to maintain populations of these species, and that threshold distances at which half of the population discontinues foraging are a more meaningful parameter for conservation practice than the species specific maximum foraging distances.

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1. Introduction

Pollinating animals provide enormous ecological and economic benefits to flowering plants, wildlife and humans (Buchmann and Ascher, 2005). Bees are among the world's most important pollinators (Allen-Wardell et al., 1998; Buchmann and Ascher, 2005; Klein et al., 2007). However, bees have suffered a substantial decline in local species diversity and population size during the last few decades (Biesmeijer et al., 2006; Grixti et al., 2009; Kearns et al., 1998; Murray et al., 2009). In Western and Central Europe, 25–65% of the bee species are listed in national and regional Red Data Books (Amiet, 1994; Burger et al., 2004; Else and Spooner, 1987; Mandery et al., 2003; Steffan-Dewenter et al., 2005; Westrich et al., 1998, 2000, 2008). Modern agricultural practices, landscape fragmentation and habitat degradation have been negatively affecting bee populations by the elimination of resources

needed for successful reproduction such as nesting sites and pollen and nectar sources (Klein et al., 2004; Westrich, 1996). Increased spatial separation of nest and plant resources may result from a decrease of both suitable nesting habitats (Klein et al., 2004; Westrich, 1996) and host plants (Larsson and Franzen, 2007; Müller et al., 2006) with increasing fragmentation and isolation of suitable habitats. Such spatial separation might adversely affect bee population dynamics, as female bees require a substantial number of foraging bouts between nest and pollen source to provision their brood cells. As the flight radius of an individual bee or a bee species is restricted due to internal (e.g. physiology, morphology) or external factors (e.g. landscape barriers), resources outside of this radius are not available rendering colonization or exploitation of otherwise suitable habitats impossible. In fact, the distance between crop fields and natural or semi-natural habitats containing suitable nesting sites was found to be negatively correlated with species richness and abundance of crop pollinators in America (Kremen et al., 2004; Ricketts et al., 2004), Asia (Klein et al., 2003) and Europe (Free, 1993). Furthermore, bees might to a certain extent be able to adjust to changes in the spatial arrangement of nest and plant resources and forage increasing distances, which might involve a substantial fitness cost however. Higher energy and time

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investments spent on longer foraging distances are assumed to negatively affect the number of progeny that can be produced during a bee's reproductive life span (Peterson and Roitberg, 2006; Zurbuchen et al., in press).

Sound knowledge of foraging ranges is crucial in management practices to conserve populations of bees. In the last few years, maximum bee foraging ranges, which describe the maximum distance a bee species can cover between nest and host plants, have received increased attention (Table 1). However, most of these investigations applied indirect methods, which may over- or underestimate maximum foraging distances. Foraging distances deduced from translocation experiments (e.g. Abrol, 1988; Gathmann and Tschardt, 2002; Pasquet et al., 2008), which measure the percentage of bees returning to their nest from a release point, are likely to overestimate maximum foraging ranges. On the other hand, maximum foraging distances inferred from mark-recapture experiments (e.g. Abrol, 1988; Walther-Hellwig and Frankl, 2000; Wolf and Moritz, 2008; Zurbuchen et al., in press), the use of harmonic radar (e.g. Carreck et al., 1999; Osborne et al., 1999) or pollen analysis (e.g. Beil et al., 2008; Tepedino, 1983; Westrich, 2006) might represent optimized foraging distances based on local floral resource supply and distribution (Beekman and Ratnieks, 2000; Ricketts, 2001), and thereby underestimate maximum foraging distances. The same may hold true for the use of trap nest colonization (e.g. Gathmann and Tschardt, 2002) to deduce maximum foraging distances as bees are expected to optimize distances between the nesting sites and available host plant stands.

In contrast to the maximum foraging distance at the species level, the distance reached by a sizable proportion of the population (such as 50%, defined here as average distance) has received hardly any attention so far, despite its high significance for species conservation. In the present study, we used a new and direct approach to experimentally investigate both maximum and average foraging distances in solitary bees. We forced three pollen specialist bee species of different body sizes to forage on host plant patches at distinct distances from their nests in an otherwise unsuitable foraging habitat, addressing the following research question: what are maximum and average foraging distances of these three species? We discuss the implications of our findings for bee preservation.

2. Material and methods

2.1. Bee species

Hylaeus punctulatus (Smith, 1842) (Colletidae), *Chelostoma rapunculi* (Lepeletier, 1841) (Megachilidae) and *Hoplitis adunca* (Panzer, 1798) (Megachilidae) are pollen-specialist (oligolectic) solitary bee species, which exclusively collect pollen from a single plant genus (Sedivy et al., 2008; Westrich, 1990): *H. punctulatus* collects solely from *Allium* (Alliaceae), *C. rapunculi* from *Campanula* (Campanulaceae) and *H. adunca* from *Echium* (Boraginaceae). In the first species, pollen is transported back to the nest in the crop, while the latter two species transport pollen in a hair brush (scopa) on the ventral side of the abdomen. All three bee species have their reproductive period in summer (June–August). They naturally nest in beetle burrows in dead wood or hollow stems (Westrich, 1990) allowing for artificial breeding in hollow bamboo sticks or pre-drilled burrows in wooden blocks. *H. punctulatus* is a small sized species with an average dry body mass of 5.3 mg and a body length of 6–8 mm, *C. rapunculi* is medium sized with an average dry body mass of 8.6 mg and a body length of 8–10 mm, and *H. adunca* is a large species with an average dry body mass of 19.7 mg and a body length of 11–13 mm (Müller et al., 2006). Both *C. rapunculi* and *H. adunca* are

widespread and common in many regions of Central Europe, whereas *H. punctulatus* is a rare species listed in the Red Data Books of both Germany and Switzerland (Amiet, 1994; Westrich et al., 2008). For the present study, we collected nests of the three bee species at different locations in Switzerland in hollow bamboo sticks that had been offered the preceding year as artificial nesting sites. These nests were transferred to artificial nesting stands in the study area before bee emergence started.

2.2. Plant material

Host plants of the three bee species tested in this study were planted in pots (diameter: 20 cm, volume: 3520 cm³). *Allium cepa* was used as the main host plant for *H. punctulatus*, complemented later in the season by *Allium sphaerocephalon*, *Allium carinatum* and *Allium senescens*. *Campanula rapunculus* was used as host plant for *C. rapunculi* and *Echium vulgare* for *H. adunca*. To ensure a stable quantity and quality of pollen until the end of the experiments, flowering was phased by repeatedly trimming shoots before flowering (except for *Allium*) and by cooling plants in a greenhouse chamber (15 ± 2 °C, 70 ± 5% RH, 16L:8D light regime). The host plant stock was kept outdoors under an insect net to prevent flowers from being exploited by insects prior to the experiments.

2.3. Experimental agricultural landscape

The experimental area was an agricultural landscape intensively used for field crops in western Switzerland near Selzach, Solothurn (7°27'78"E, 47°11'63"N, elevation 420 m), situated in a plain devoid of potential landscape barriers such as forests or wide roads. Experiments were conducted along three straight, unpaved and parallel tracks (sites A–C) in a north–south direction. Distances between the tracks were 1780 m (A–B), 1100 m (B–C) and 2880 m (A–C). An artificial nesting stand was placed adjacent to the south end of each of the three tracks. Preliminary investigations showed that the area within a radius of 1200 m from each of the nesting stands lacked the specific host plants of the three bee species tested. To further assure that the bees had no pollen sources other than the potted plants at their disposal, we repeatedly checked the experimental landscape for plants of the genus *Allium*, *Campanula* and *Echium*, and in one case had to eliminate a small patch of *E. vulgare*.

2.4. Bee establishment and marking

Hollow bamboo sticks and wooden nesting blocks (150 × 150 × 400 mm) with pre-drilled burrows (120 mm in length, 3–4 mm in diameter for *H. punctulatus*, 4–6 mm for *C. rapunculi* and 6–9 mm for *H. adunca*) were prepared as artificial nests and placed in a covered shelf to protect them from rain. Bees were established by transferring 100 occupied nests per species to sites A and C (*H. punctulatus* and *H. adunca*) and to site B (*C. rapunculi*). To support initiation of nesting activity by the newly emerged females, flowering host plants in pots (50 plants of *A. cepa* and *E. vulgare*, 100 plants of *C. rapunculus*) were placed at a distance of less than 1 m from the nesting stands.

Females that started to nest were caught, immobilized by placing them for 2–3 min in a cool box at 5 °C and marked individually with fast-drying enamel paint (Revell) on the thorax (1–2 positions) and the abdomen (1 position), applying colour codes with eight different colours. All females per nesting stand were marked prior to the initiation of the experiments.

Table 1

Literature data on maximum foraging distances in bees. *Foraging distance* refers to the distance between a bees' nest and the flower resources exploited for pollen and nectar. *Homing distance* refers to the distance between the location to which a bee was transferred and its nest. n.a. = not available, – = method used without testing individual bees. Within each of the four bee guilds the entries are sorted according to: (1) the method used and (2) the distances flown.

Bee species	Size (mm)	Distances flown (m)	Distance type	Method	n	References
Solitary bees/social sweat bees						
<i>Osmia adunca</i>	8–12	180	Foraging distance	Closest host plant patch	n.a.	Hembach (1993)
<i>Osmia lignaria</i>	11–12	600	Foraging distance	Closest host plant patch	n.a.	Rust (1990)
<i>Colletes hederæ</i>	7–16	1000	Foraging distance	Closest host plant patch	n.a.	Westrich (1996)
<i>Chelostoma rapunculi</i>	8–10	200	Foraging distance	Trap nest colonization, statistical modelling	n.a.	Gathmann and Tschardtke (2002)
<i>Megachile lapponica</i>	6–8	300	Foraging distance	Trap nest colonization, statistical, modelling	n.a.	Gathmann and Tschardtke (2002)
<i>Chelostoma florissomne</i>	7–11	150	Foraging distance	Mark-recapture	n.a.	Käpylä (1978)
<i>Megachile flavipes</i>	8–10	500	Foraging distance	Mark-recapture	n.a.	Abrol (1988)
<i>Chelostoma florissomne</i>	7–11	650	Foraging distance	Mark-recapture	18	Zurbuchen et al. (in press)
<i>Megachile nana</i>	8–10	750	Foraging distance	Mark-recapture	n.a.	Abrol (1988)
<i>Colletes daviesanus</i>	7–9	2225	Foraging distance	Mark-recapture	74	Esser (2005)
<i>Andrena hattorfiana</i>	13–16	130	Flying range	Mark-recapture (marked while foraging)	270	Franzen et al. (2009)
<i>Osmia maritima</i>	n.a.	150	n.a.	n.a.	n.a.	Haeseler (1982)
<i>Panurgus banksianus</i>	10–12	250	n.a.	n.a.	n.a.	Münster-Swendsen (1968)
<i>Colletes cunicularis</i>	11–14	350	n.a.	n.a.	n.a.	Weserling (1996)
<i>Colletes hederæ</i>	7–16	400	n.a.	n.a.	n.a.	Schmid-Egger et al. (1995)
<i>Andrena cineraria</i>	10–14	300	Foraging distance	Observation on host plants	n.a.	Gebhardt and Röhr (1987)
<i>Andrena clarkella</i>	11–13	300	Foraging distance	Observation on host plants	n.a.	Gebhardt and Röhr (1987)
<i>Hylaeus punctulatus</i>	6–8	1100	Foraging distance	Oligolectic bees, host plants in distinct distances	85	This study
<i>Chelostoma rapunculi</i>	8–10	1275	Foraging distance	Oligolectic bees, host plants in distinct distances	35	This study
<i>Hoplitis adunca</i>	8–12	1400	Foraging distance	Oligolectic bees, host plants in distinct distances	39	This study
<i>Lasioglossum marginellum</i>	n.a.	200	Foraging distance	Pollen analysis	8	Westrich (2006)
<i>Megachile rotundata</i>	6–8	500	Foraging distance	Pollen analysis, closest host plants	n.a.	Tepedino (1983)
<i>Andrena dorsata</i>	8–10	650	Foraging distance	Pollen analysis, closest host plants	1	Beil et al. (2008)
<i>Lasioglossum calceatum</i>	8–10	1000	Foraging distance	Pollen analysis, closest host plants	4	Beil et al. (2008)
<i>Andrena flavipes</i>	10–14	1150	Foraging distance	Pollen analysis, closest host plants	3	Beil et al. (2008)
<i>Andrena carbonaria</i> agg.	n.a.	1250	Foraging distance	Pollen analysis, closest host plants	1	Beil et al. (2008)
<i>Lasioglossum fulvicorne</i>	6–7	1250	Foraging distance	Pollen analysis, closest host plants	1	Beil et al. (2008)
<i>Megachile rotundata</i>	6–8	100	Foraging distance	Pollination rates within a radius from nesting site	–	Tasei and Delaude (1984)
<i>Megachile</i> spp.	6–9	1000	Foraging distance	Pollination, dispersal of pollen	–	Amand et al. (2000)
<i>Xylocopa flavorufa</i>	24–26	6040	Foraging distance	Radio-transmitter	135	Pasquet et al. (2008)
<i>Osmia anthocopoides</i>	8–11	150	Homing distance	Translocation experiment	n.a.	Molitor (1937)
<i>Megachile femorata</i>	13–14	500	Homing distance	Translocation experiment	10	Abrol (1986)
<i>Andrena vaga</i>	11–15	510	Homing distance	Translocation experiment	42	Gathmann and Tschardtke (2002)
<i>Andrena barbilabris</i>	10–12	530	Homing distance	Translocation experiment	38	Gathmann and Tschardtke (2002)
<i>Andrena flavipes</i>	10–14	530	Homing distance	Translocation experiment	36	Gathmann and Tschardtke (2002)
<i>Tetralonia salicariae</i>	9–10	600	Homing distance	Translocation experiment	40	Gathmann and Tschardtke (2002)
<i>Megachile nana</i>	n.a.	650	Homing distance	Translocation experiment	20	Abrol (1988)
<i>Megachile flavipes</i>	n.a.	800	Homing distance	Translocation experiment	20	Abrol (1988)
<i>Osmia rufa</i>	8–13	900	Homing distance	Translocation experiment	25	Gathmann and Tschardtke (2002)
<i>Osmia mustelina</i>	10–14	1000	Homing distance	Translocation experiment	n.a.	Molitor (1937)
<i>Anthidium septendentatum</i>	9–12	1200	Homing distance	Translocation experiment	n.a.	Molitor (1937)
<i>Xylocopa violacea</i>	20–23	1200	Homing distance	Translocation experiment	n.a.	Molitor (1937)
<i>Chelostoma florissomne</i>	7–11	2000	Homing distance	Translocation experiment	6	Herrmann (1999)
<i>Xylocopa flavorufa</i>	24–26	10,000	Homing distance	Translocation experiment	22	Pasquet et al. (2008)
<i>Anthophora abrupta</i>	14–17	12,500	Homing distance	Translocation experiment	66	Rau (1929)
<i>Tetralonia salicariae</i>	9–10	400	Homing distance	Translocation, logistic regression	n.a.	Weserling and Tschardtke (1995)
<i>Andrena barbilabris</i>	10–12	500	Homing distance	Translocation, logistic regression	n.a.	Weserling and Tschardtke (1995)
<i>Andrena flavipes</i>	10–14	600	Homing distance	Translocation, logistic regression	n.a.	Weserling and Tschardtke (1995)
<i>Andrena vaga</i>	11–15	600	Homing distance	Translocation, logistic regression	n.a.	Weserling and Tschardtke (1995)
<i>Osmia rufa</i>	8–13	900	Homing distance	Translocation, logistic regression	n.a.	Gathmann and Tschardtke (2002)

(continued on next page)

Table 1 (continued)

Bee species	Size (mm)	Distances flown (m)	Distance type	Method	n	References
Bumblebees						
<i>Bombus terrestris</i>	20–23	9900	Male flight distance	Density of worker- and/or drone-producing colonies	–	Kraus et al. (2009)
<i>Bombus terrestris</i>	20–23	550	Foraging distance	Harmonic radar	21	Carreck et al. (1999)
<i>Bombus terrestris</i>	20–23	630	Foraging distance	Harmonic radar	21	Osborne et al. (1999)
<i>Bombus muscorum</i>	17–19	200	Foraging distance	Mark-recapture	13	Walther-Hellwig and Frankl (2000)
<i>Bombus</i> sp.	17–23	300	Foraging distance	Mark-recapture	1	Dramstad (1996)
<i>Bombus terrestris</i>	20–23	800	Foraging distance	Mark-recapture	126	Wolf and Moritz (2008)
<i>Bombus lapidarius</i>	20–22	1500	Foraging distance	Mark-recapture	22	Walther-Hellwig and Frankl (2000)
<i>Bombus terrestris</i>	20–23	1500	Foraging distance	Mark-recapture	297	Osborne et al. (2008)
<i>Bombus terrestris</i>	20–23	1750	Foraging distance	Mark-recapture	28	Walther-Hellwig and Frankl (2000)
<i>Bombus</i> sp.	17–23	350	Flying range	Mark-recapture (marked while foraging)	36	Saville et al. (1997)
<i>Bombus pascuorum</i>	15–18	2300	Foraging distance	Model based on estimation of nest density	–	Chapman et al. (2003)
<i>Bombus terrestris</i>	20–23	2800	Foraging distance	Model based on estimation of nest density	–	Chapman et al. (2003)
<i>Bombus terrestris</i>	20–23	312.5	Foraging distance	Molecular analysis – sister-pairs	–	Darvill et al. (2004)
<i>Bombus pascuorum</i>	15–18	449	Foraging distance	Molecular analysis – sister-pairs	–	Knight et al. (2005)
<i>Bombus lapidarius</i>	20–22	450	Foraging distance	Molecular analysis – sister-pairs	–	Knight et al. (2005)
<i>Bombus pratorum</i>	15–17	674	Foraging distance	Molecular analysis – sister-pairs	–	Knight et al. (2005)
<i>Bombus terrestris</i>	20–23	758	Foraging distance	Molecular analysis – sister-pairs	–	Knight et al. (2005)
Stingless bees						
<i>Melipona mandacaia</i>	n.a.	2100	Foraging distance	Feeder training	n.a.	Kuhn-Neto et al. (2009)
<i>Nannotrigona testaceicornis</i>	n.a.	951	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Plebeia poecilochroa</i>	n.a.	951	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Scaura latitarsis</i>	n.a.	951	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Tetragonisca angustula</i>	n.a.	951	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Friesemellitta varia</i>	n.a.	1710	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Geotrigona inusitata</i>	n.a.	1710	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Partamona cupira</i>	n.a.	1710	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Scaptotrigona postica</i>	n.a.	1710	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Trigona hypogea</i>	n.a.	1710	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Trigona recurva</i>	n.a.	1710	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Melipona bicolor</i>	n.a.	2000	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Melipona scutellaris</i>	n.a.	2000	Foraging distance	Linear regression	–	Araujo et al. (2004)
<i>Plebeia droryana</i>	n.a.	540	Foraging distance	Mark-recapture	n.a.	Araujo et al. (2004)
<i>Melipona marginata</i>	n.a.	800	Foraging distance	Mark-recapture	n.a.	Araujo et al. (2004)
<i>Trigona spinipes</i>	n.a.	840	Foraging distance	Mark-recapture	n.a.	Araujo et al. (2004)
<i>Melipona quadrifasciata</i>	n.a.	2000	Foraging distance	Mark-recapture	n.a.	Araujo et al. (2004)
<i>Melipona compressipes</i>	n.a.	2470	Foraging distance	Mark-recapture	n.a.	Araujo et al. (2004)
<i>Trigona capitata</i>	n.a.	1547	Homing distance	Translocation experiment	16	Roubik and Aluja (1983)
<i>Melipona fasciata</i>	n.a.	2085	Homing distance	Translocation experiment	45	Roubik and Aluja (1983)
Honeybees						
<i>Apis florea</i>	8–10	500	Foraging distance	Mark-recapture	n.a.	Abrol (1988)
<i>Apis mellifera</i>	11–13	915	Foraging distance	Mark-recapture	131	Gary et al. (1972)
<i>Apis mellifera</i>	11–13	1100	Foraging distance	Mark-recapture	613	Gary et al. (1981)
<i>Apis mellifera</i>	11–13	1243	Foraging distance	Waggle dance	n.a.	Schneider and Hall (1997)
<i>Apis mellifera</i>	11–13	1413	Foraging distance	Waggle dance	5	Waddington et al. (1994)
<i>Apis cerana</i>	9–11	1900	Foraging distance	Waggle dance	18	Dyer and Seeley (1991)
<i>Apis mellifera</i>	11–13	7900	Foraging distance	Waggle dance	37	Dyer and Seeley (1991)
<i>Apis mellifera</i>	11–13	10,100	Foraging distance	Waggle dance	n.a.	Visscher and Seeley (1982)
<i>Apis florea</i>	8–10	11,200	Foraging distance	Waggle dance	8	Dyer and Seeley (1991)
<i>Apis dorsata</i>	12–14	12,000	Foraging distance	Waggle dance	11	Dyer and Seeley (1991)
<i>Apis mellifera</i>	11–13	13,500	Foraging distance	Waggle dance	n.a.	von Frisch (1967)
<i>Apis mellifera</i>	11–13	14,000	Foraging distance	Waggle dance	n.a.	Beekman and Ratnieks (2000)

2.5. Experimental design for *Hylaeus punctulatus* and *Hoplitis adunca*

To identify maximum foraging distances at which female bees discontinued pollen harvesting, a host plant patch consisting of 50 flowering plants, which covered an area of 2 m², was consecutively moved along the tracks to a new position in increasing distance from the fixed artificial nesting stands. Prior to data collection, bees were led to the new position of the host plant patch by a trail lined up with potted flowering host plants placed at 10 m intervals. This trail, designed to minimize the time needed by the bees to find the new position of the host plant patch, was

provided for 6 h while bees were active. Thereafter, these plants were incorporated into the previously moved host plant patch. At the same time, 10–20% of the host plants of a plant patch were replaced by new plant material from the host plant stock to assure abundant pollen and nectar supply.

The presence of marked females on the host plant patch was recorded by a first observer during 2 h. This observation period was kept constant for all distances tested. Flight duration of females to reach two subsequent positions of the plant patch (50–400 m apart from each other) was considered only marginally different. Furthermore, the probability was considered high to find any marked female during the two hour observation period, as a bee flying at a

velocity of 2 m/s needs only 8 min to reach a plant patch at a distance of 1000 m from the nest. Simultaneously with the first observer, a second observer checked the nesting stand for marked females during 3 h for *H. punctulatissimus* and during two hours for *H. adunca*. The extra hour allocated for *H. punctulatissimus* should compensate for the long absence of this species from the nest due to its long foraging time (on average 80 min per foraging bout compared to 30 min in *H. adunca*). A marked female was considered to forage at a given distance when observed both actively collecting pollen on the plant patch and provisioning brood cells at the artificial nesting stand. Individual bees that were not monitored at a given distance but were recorded to forage at a longer distance later on in the experiment were assumed to have foraged also at the shorter distance. The experiment was discontinued when marked females nesting at the artificial nesting stand could no longer be observed foraging on the plant patch during two consecutive observation periods on two different days.

The experiments with *H. punctulatissimus* were conducted between June and August during the two field seasons 2007 and 2008. In the first season, we tested 15 distinct distances at site A (<1 m, 50 m, 100 m, 150 m, 225 m, 300 m, 380 m, 450 m, 525 m, 600 m, 675 m, 750 m, 825 m, 900 m, 975 m) and in parallel five distances at site C (<1 m, 225 m, 525 m, 675 m, 825 m). In the second season we tested nine distances at site A (<1 m, 100 m, 200 m, 300 m, 400 m, 500 m, 600 m, 700 m, 800 m) and in parallel six distances at site C (<1 m, 380 m, 750 m, 900 m, 1100 m, 1270 m). Each distance was tested once per season and site.

The experiments with *H. adunca* were conducted between June and August 2008. Twelve distances were tested at site A (<1 m, 75 m, 200 m, 300 m, 400 m, 500 m, 600 m, 700 m, 800 m, 900 m, 1000 m, 1100 m) and in parallel seven distances at site C (<1 m, 300 m, 700 m, 1000 m, 1270 m, 1400 m, 1600 m). Each distance was tested once per site.

Weather data were recorded by a field weather station (CR10 Measurement and Control Module, Campbell Scientific Ltd., Shepshed Leicestershire, England). All observations were carried out on sunny days with maximum daily temperatures ranging from 23.2 °C to 30.7 °C between 10 am and 6 pm when bee activity was high. The prevailing wind direction was from the west, i.e. per-

pendicular to the north–south alignment of artificial nesting stand and host plant patch. Therefore, the marked females were not expected to face direct headwind nor direct downwind to reach the host plant patch. Wind was generally absent or only weak during the experiments.

2.6. Experimental design for *Chelostoma rapunculi*

Following the observation that some *C. rapunculi* females nesting at the artificial nesting stand collected yellow pollen from unknown Campanulaceae species that were not available within a radius of 1200 m from their nests, we did not apply the same experimental design for *C. rapunculi* as described above for *H. punctulatissimus* and *H. adunca*. Instead, we placed a large host plant patch of 300 *C. rapunculus* plants covering an area of 5 m² at a distance of 1000 m from the artificial nesting stand at site B. Marked females were simultaneously observed by two observers for pollen collecting activity on the host plant patch and for brood cell provisioning at the nesting stand during 2 h each on 8 days between end of June and beginning of July 2008. In addition, we identified the unknown *Campanula* species to species level by microscopic analysis of the yellow pollen, and mapped stands of *Campanula* species possessing yellow pollen outside the study area in the neighbouring villages.

3. Results

3.1. *Hylaeus punctulatissimus*

In the first year, a total of 28 females of *H. punctulatissimus* were marked (21 at site A, 7 at site C). In the second year, a total of 57 females were marked (28 at site A, 29 at site C). The observation period covered 51 days (June 30–August 19) in year 1 and 32 days (July 10–August 10) in year 2.

There was a clear decrease in the number of marked females foraging on the host plant patch with increasing foraging distance to the nest (Fig. 1). Maximum distances at which individual females were last observed to collect pollen while still provisioning

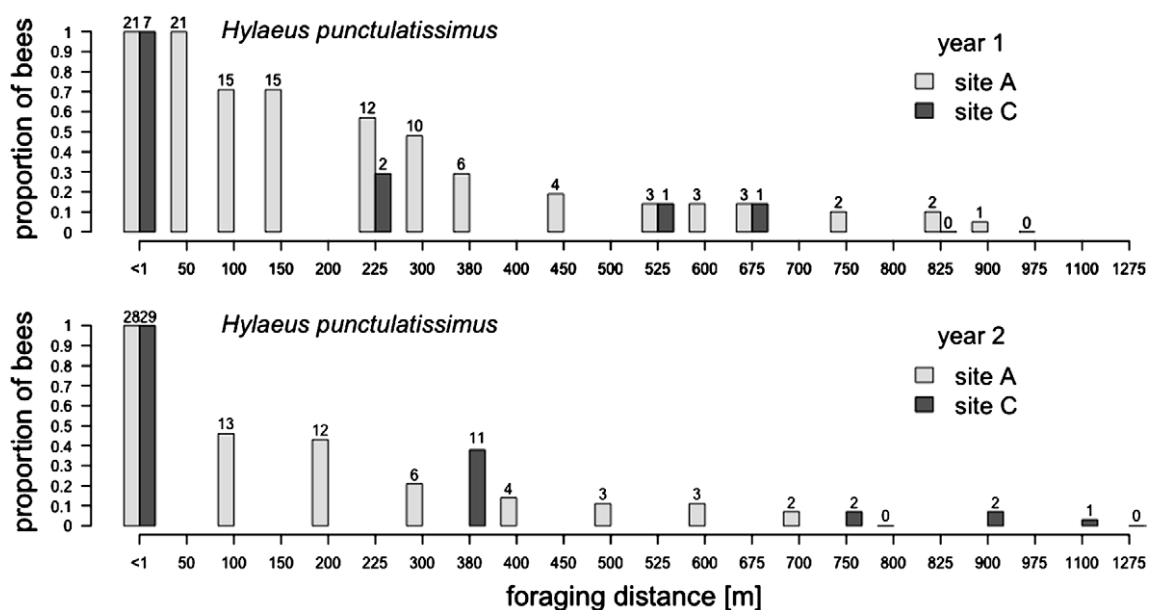


Fig. 1. Proportion of initially marked females of the small bee species *Hylaeus punctulatissimus* observed on potted host plants that were successively placed in increasing distances from a fixed nesting stand. In year 1, 15 distinct distances were tested at site A and five at site C; in year 2, nine distances were tested at site A and six at site C. Experiments were performed during a time period of 51 days in year 1 and 32 days in year 2. Numbers above bars indicate the number of females observed.

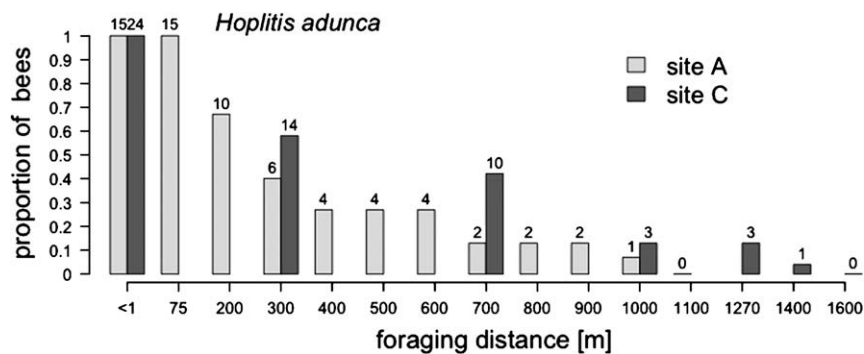


Fig. 2. Proportion of initially marked females of the large bee species *Hoplitis adunca* observed on potted host plants that were successively placed in increasing distances from a fixed nesting stand. Twelve distances were tested at site A and seven distances at site C. Experiments were performed during a time period of 45 days in year 2, overlapping with that of *H. punctulatus*. Numbers above bars indicate the number of females observed.

brood cells at the artificial nesting stand ranged from <50 m up to 900 m in year 1 and from <100 m to 1100 m in year 2. When data from sites A and C were pooled, 50% of the marked females had discontinued foraging at 225 m in year 1 and at <100 m in year 2, and 75% had discontinued foraging at 380 m in year 1 and at 400 m in year 2.

3.2. *Hoplitis adunca*

A total of 39 females of *H. adunca* were marked (15 at site A, 24 at site C). The observation period covered 45 days (June 27–August 10) in year 2.

There was a clear decrease in the number of marked females foraging on the host plant patch with increasing distance (Fig. 2). Maximum foraging distances of individual females ranged from 75 m to 1400 m. When data from sites A and C were pooled, 50% of the marked females had discontinued foraging at a distance of 300 m and 75% had discontinued foraging at a distance of 700 m.

3.3. *Chelostoma rapunculi*

Seven out of 35 marked females were recorded to collect pollen on the *C. rapunculus* patch, set at a distance of 1000 m from the artificial nesting stand. Two of these females were observed on the plant patch on five out of eight observation days, two were recorded on 3 days and another two on 2 days. These six females provisioned brood cells at the artificial nesting stand with white pollen over a time period of at least 14 days (June 26–July 7) until the end of the experiment. One marked female was observed to collect pollen on the plant patch and to provision brood cells at the nesting stand on 1 day only and then apparently left its initial nest but continued to forage on the patch.

The remaining 28 marked females were never observed on the *C. rapunculus* patch. However, 24 of them repeatedly arrived at the nesting stand carrying full loads of yellow pollen, identified microscopically as originating from *Campanula medium* and *Platycodon grandiflorum*. Both of these Campanulaceae species are exclusively grown in home gardens and parks. The closest stands of Campanulaceae with yellow pollen were found in a home garden at a distance of 1275 m from the nesting stand.

4. Discussion

Our direct approach investigating bee foraging distances revealed that all three bee species tested flew substantially longer maximum foraging distances at the species level than would have been expected from a regression model based on bee body size (Gathmann and Tscharrntke, 2002). We observed that the small

bee species *H. punctulatus* collected pollen at a maximum distance of 1100 m from the nest, whereas its expected maximum foraging distance was only 100–250 m. The medium sized *C. rapunculi* regularly foraged at a maximum distance of 1275 m, which is substantially longer than the expected 300–400 m. Finally, the large *H. adunca*, of which the maximum foraging distance was expected to be in the range of 400–600 m, exploited host plant patches at a maximum distance of 1400 m from the nest. We do not assume that these observed long distance flights are an artefact due to our experimental design, which forced the bees to fly long distances. Instead, we expect these same females to have covered similarly long distances under more natural conditions, if for example all meadows containing the specific pollen hosts had been mowed in a radius of several hundred meters around the nests. The trail of flowers that guided our bees to the new position of the host plant patch might have resulted in a decrease of time and energy spent to locate the floral resources. Thus, we can not exclude that the capability of individual bees to reach distant host plant patches would be lowered if they had to randomly search the landscape for suitable host plants.

The results of our study indicate that maximum bee foraging distances at the species level might have been underestimated so far. This conclusion is in line with an increasing number of observations of long maximum foraging distances in solitary bees (including social sweat bees), bumblebees, stingless bees and honeybees (Table 1). Single individuals of small to medium sized species of the genera *Andrena*, *Chelostoma*, *Lasioglossum* and *Megachile* were found to forage at maximum distances of 500 m up to 1250 m from their nests as revealed indirectly by pollen analyses and mark-recapture experiments (Beil et al., 2008). The closest host plant stand of the large pollen specialist species *Colletes hederarum* was located at a distance of 1000 m from a nest aggregation (Wes-trich, 1996). The maximum foraging distance documented for a female of the medium sized species *Colletes daviesanus* was 2225 m (Esser, 2005) and one female of the giant *Xylocopa flavorufa* was radio-tracked at a distance of 6040 m from its nest (Pasquet et al., 2008). Bumblebees were shown to forage at maximum distances of 800–1750 m from their nest in mark-recapture experiments (Osborne et al., 2008; Walther-Hellwig and Frankl, 2000) and were calculated to fly 2300–2800 m based on models of nest densities (Chapman et al., 2003). Similarly, stingless bees were repeatedly found to forage at distances of 1000–2500 m from their hive (Araujo et al., 2004; Kuhn-Neto et al., 2009; Roubik and Aluja, 1983), and analysis of waggle dances of the honeybee revealed foraging distances ranging from 1250 m to 14,000 m (Beekman and Ratnieks, 2000; Dyer and Seeley, 1991; Visscher and Seeley, 1982; von Frisch, 1967; Waddington et al., 1994).

The unexpectedly long maximum foraging distances in *H. punctulatus* and *H. adunca* concerned only single females. In fact,

the number of nesting females decreased rapidly with increasing foraging distance in both species. Only 50% of the females of the small *H. punctulatissimus* and the large *H. adunca* foraged at distances longer than 100–225 m and 300 m, respectively, and 75% had discontinued foraging at a distance of 380–400 m and 700 m, respectively, which is still considerably less than the maximum foraging distance recorded for the small and the large species (1100 m and 1400 m, respectively). For the medium sized species *C. rapunculi*, as many as 90% of the marked females were foraging at distances of 1000 m or more. This comparatively high proportion of females foraging long distances might have resulted in part from a relatively short observation period (14 days) at the beginning of the nesting season compared to much longer observation periods (32–51 days) in the other two bee species. As longer distances were tested relatively late in the nesting season of both *H. punctulatissimus* and *H. adunca*, increased natural mortality might also have contributed to the rapid decrease of foraging females with increasing distance. Thus, we can not exclude that more individuals of these two species would have managed to forage long distances if tested early in the nesting season. However, mortality alone can not fully explain the rapid decrease of foraging individuals. In fact, many females of both species discontinued foraging but were still present at the original nesting stand. Other females might have dispersed by routine movement (Van Dyck and Baguette, 2005) to alternative nesting habitats outside the radius of the host plant free space. Both behaviours are expected to be a consequence of increasing foraging costs with increasing distances.

Studies in the context of dispersal showed that individual insects within a population may vary in their capacity for long flights (Keil et al., 2001). The proportion of individuals that successfully reaches distant resources is in many cases relatively low (Dorn et al., 1999; Gu et al., 2006; Pasquet et al., 2008), whereas a relatively high proportion of individuals can successfully cover short distances (Hughes and Dorn, 2002; Keil et al., 2001; Sarvary et al., 2008). This is in line with our finding that only few individuals of *H. punctulatissimus* and *H. adunca* foraged at a distance of more than 1000 m, which indicates that populations of these bee species are negatively affected by increasing foraging distance already at a considerably smaller spatial scale than maximum foraging distances would suggest.

The finding that threshold distances at which 50% of the females discontinued foraging were substantially shorter than the species specific maximum foraging distances indicate that a close neighbourhood of suitable nesting sites and flower rich foraging habitats may be crucial for maintaining populations of bees. In the two bee species investigated, only half of the tested individuals managed to overcome distances of more than 100–225 m and 300 m, respectively, suggesting that a spatial separation of nesting and foraging habitat of less than few hundred meters might be fundamental for population persistence in these two species. In addition to threshold and maximum foraging distances, conservation strategies for endangered bee species also have to consider the costs of foraging flights. Indeed, there are indications that foraging flights may impose high costs on solitary bees. Females of *Osmia lignaria* produced enough offspring to guarantee population maintenance when their nesting site was surrounded by natural habitat offering suitable flower resources, whereas the number of offspring generated by females nesting at sites more distant from natural habitats was too low for population persistence (Williams and Kremen, 2007). Similarly, the mean number of brood cells completed during one season was 75% lower in females of *Megachile rotundata*, which foraged in plant patches 150 m away from their nests, compared to females foraging at plant patches directly adjacent to the nests (Peterson and Roitberg, 2006).

In conclusion, the maximum foraging distances of solitary bees at the species level appear to have been underestimated so far.

However, the capability to use resources on a larger spatial scale might only apply to a small proportion of individuals within a population. Consequently, for the conservation of bee populations knowledge of threshold distances at which for example 50% of females discontinue their foraging activity is supposed to be more important than the mere knowledge of species specific maximum foraging distances covered only by a small proportion of individuals. Such threshold distances may be substantially shorter than maximum foraging distances as shown in the present study, indicating that a close neighbourhood of nesting and foraging habitats within few hundred meters is crucial to preserve populations of bees.

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