

Foraging ranges of solitary bees

ACHIM GATHMANN and TEJA TSCHARNTKE

Agroecology, University of Göttingen, Waldweg 26, D-37073 Göttingen, Germany

Summary

1. Habitat requirements of solitary bees include nesting sites, food resources and nesting material. We used translocation experiments to establish foraging distances and measured foraging trip duration to analyse how solitary bees cope with the distance between nesting sites and suitable food plants in different habitat types.

2. Maximum foraging distance between nesting site and food patch was 150–600 m for the 16 bee species examined. Foraging distance was correlated positively with body length. Mean foraging trip duration, measured for seven bee species, ranged from 6 to 28 min and was also correlated with body length. In a study of the polylectic species *Osmia rufa*, we found a significant decrease in foraging trip duration with increasing number of plant species. Logistic regressions showed that the oligolectic *Megachile lapponica* nested in trap nests with a probability of 50% if the distance between trap nest and food patch was less than 250 m. The oligolectic *Chelostoma rapunculi* utilized trap nests when the distance to the nearest food patch was less than 300 m.

3. These experiments showed that solitary bees have a rather small foraging range so local habitat structure appears to be of more importance than large-scale landscape structure. All requirements for sustaining viable populations must be within this range. Therefore, it is necessary to maintain and restore a dense network of habitat patches in landscapes to ensure long-term sustainability of wild bee diversity and their ecological function as pollinators.

Key-words: body length, foraging distance, habitat structure, trap nests, translocation experiments.

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Introduction

The habitat of most animals provides resources of different types that are essential for the species' survival, but these may not necessarily be close together. Accordingly, these animals have to bridge some temporal or spatial distance to locate the essential resources such as food, nesting sites and mates. Most spectacular are the seasonal migrations of ungulates in the Serengeti to find sufficient food (McNaughton 1979). Butterflies need both food plants for the larvae and flowers for the nutrition of adults (Thomas 1996). In contrast, essential resources may be close together. For example, the distance between flowers for feeding and stems for mating and oviposition is only a few centimetres for the thistle herbivore *Urophora cardui* (Linnaeus) (Diptera; Tephritidae) (Zwölfer 1982). The

required use of spatially separated resources is related to the concept of landscape complementation, which occurs when the landscape structure permits access among multiple required resources (Dunning, Danielson & Pulliam 1992). Simulation models by Fahrig (2001) showed that information on movement rates of organisms in fragmented landscapes is critical for predicting extinction thresholds, but little is known of the dispersal ability of most groups.

For reproduction of solitary bees, a number of different resources must be located within foraging range of their nest. These resources include species-specific nest sites, specific materials for nest construction, nectar sources to maintain the activities of the adult bees and pollen as the essential component of the larval food (Westrich 1996). The paucity of above-ground-nesting bees in agricultural landscapes is often due to the lack of suitable nest sites. Populations of these bees can be enhanced by placing suitable trap nests in the habitat (Tscharntke, Gathmann & Steffan-Dewenter 1998); nest sites are probably more often a limiting factor than flowers as pollen and nectar sources.

Correspondence: Dr Achim Gathmann, Biology V, RWTH Aachen, Worringerweg 1, D-52056 Aachen, Germany. Tel. +49 241 80 26 676. Fax: +49 241 80 22 182. E-mail: gathmann@bio5.rwth-aachen.de

Data on foraging ability and foraging behaviour are therefore necessary to the understanding of population dynamics and community structure of bees as well as to develop conservation strategies. Telemetric observations have been carried out in studies of mammals, birds or large insects (White & Garrot 1990; Priede & Swift 1992; Williams, Carreck & Poppy 1996). Harmonic radar has been used to track both honey bees and bumble bees in flight to determine foraging distances and routes (Williams *et al.* 1996), but transmitters of all these methods are too large and heavy for small flying insects such as solitary wild bees. Mass release-recapture experiments with small insects are also seldom successful (Nève de Mévergnies & Baguette 1990), so we found only indirect methods to be feasible to detect foraging distances of solitary bees.

In this study, we used translocation experiments, foraging trip duration experiments and habitat analyses for an indirect measurement of foraging range for nectar and pollen of bees to test the following hypotheses: (1) foraging distance and foraging trip duration are related positively to the bees' body size. This hypothesis is based on the conclusion of Gathmann, Greiler & Tscharniske (1994) that large bees appeared to have larger dispersal distances than small bees. (2) The response of bees to the distance between the nesting site and their specific food plants may differ between generalist, polylectic and specialist oligolectic bees, because finding the (few and distant) suitable food patches is more expensive for specialists. (3) Species-specific patterns of foraging behaviour can be expected to determine the structure of bee communities depending on habitat type. The results should give a basis to hypothesize or predict changes in the structure of bee communities with habitat disturbance.

Materials and methods

EXPERIMENTAL SITES

Experiments were performed on four sandy grasslands near Mannheim, southern Germany, in 1995, and on five habitat types near Göttingen, northern Germany, from 1995 to 1997. The sandy grasslands near Mannheim were each from 0.4 and 4 ha in size. The five habitat types near Göttingen included three crop fields with field margin strips sown with a species-rich flower mixture in 1993, three set-aside fields sown in 1993 with a grass-clover mixture, three extensively used, nutrient-rich grasslands, three nutrient-poor and dry chalk grasslands and a few observations on three orchard meadows. Field size ranged from 0.7 to 2.8 ha. The number of plant species was mapped on each field on 49 m² in June and August 1995, according to Dierschke (1994).

TRANSLOCATION EXPERIMENTS

The translocation experiments were carried out on the sandy grasslands near Mannheim in 1995 and on the

chalk grasslands near Göttingen in 1997. Nesting bees were marked individually with 'Tipp-ex' (BIC Deutschland, Art. no. 400250202) or acrylic colour (Waco Heinrich Wagner no. 5102, Zürich – Fulda, Switzerland) on the thorax. They were then transported in a darkened box to the release points. The direction of the release point was changed randomly and distance of release varied from 50 to 2000 m. The bee species used in these experiments were *Andrena barbilabris* (Kirby) (36 females), *A. flavipes* Panzer (36), *A. vaga* Panzer (42) and *Osmia rufa* (Linnaeus) (27). Additionally, an experiment with *Tetralonia salicariae* (Lepeletier) (40) (data from Molitor 1936) was reanalysed for comparison with our data. For *O. rufa* (27), the return time from release point to nest was recorded after observing bee arrival at the nests with a stop watch. Translocation experiments started at 10.00 h during the species specific main season and ended at 18.00 h on 16 sunny days in 1995 and 1997.

FORAGING TRIP DURATION

Foraging trip duration was measured for trap-nesting bees on two field margin strips, one set-aside field sown with a clover-grass mixture, two extensively managed grasslands and two chalk grasslands near Göttingen (Gathmann 1998). The nest (a reed internode, see Tscharniske *et al.* 1998) of each female was marked with acrylic colour (Waco Heinrich Wagner no. 5102, Zürich – Fulda) and the time from the female's departure from the nest and its return with food (pollen-nectar mixture) was timed with a stop watch. Species examined were *Chelostoma rapunculi* (Lepeletier) (14 females), *Heriades truncorum* (Linnaeus) (21), *Megachile versicolor* Smith (15), *Megachile lapponica* Thompson (23), *O. leaiana* (Kirby) (11), *O. parietina* Curtis (14) and *O. rufa* (41). Observations were made on 19 sunny days from 6 May to 23 July from 10.00 h and 16.00 h in 1997.

DISTANCE BETWEEN NESTING SITE AND FOOD PLANTS OF OLIGOLECTIC BEES

For the two oligolectic bees, *C. rapunculi* and *M. lapponica*, we determined the distance between food resources and nesting site. Up to 1000 m, patches of the food plant species (*Campanula* spp. for *C. rapunculi* and *Epilobium* spp. for *M. lapponica*) were recorded and related to the occurrence of these bees in trap nests. Trap nests (see Tscharniske *et al.* 1998) were placed on three field margin strips, three set-aside fields sown with a clover-grass mixture, three extensively managed grasslands, three chalk grasslands and three orchard meadows near Göttingen (Gathmann 1998).

STATISTICS

Analyses of variance and regression statistics were computed using Statgraphics software (Statgraphics

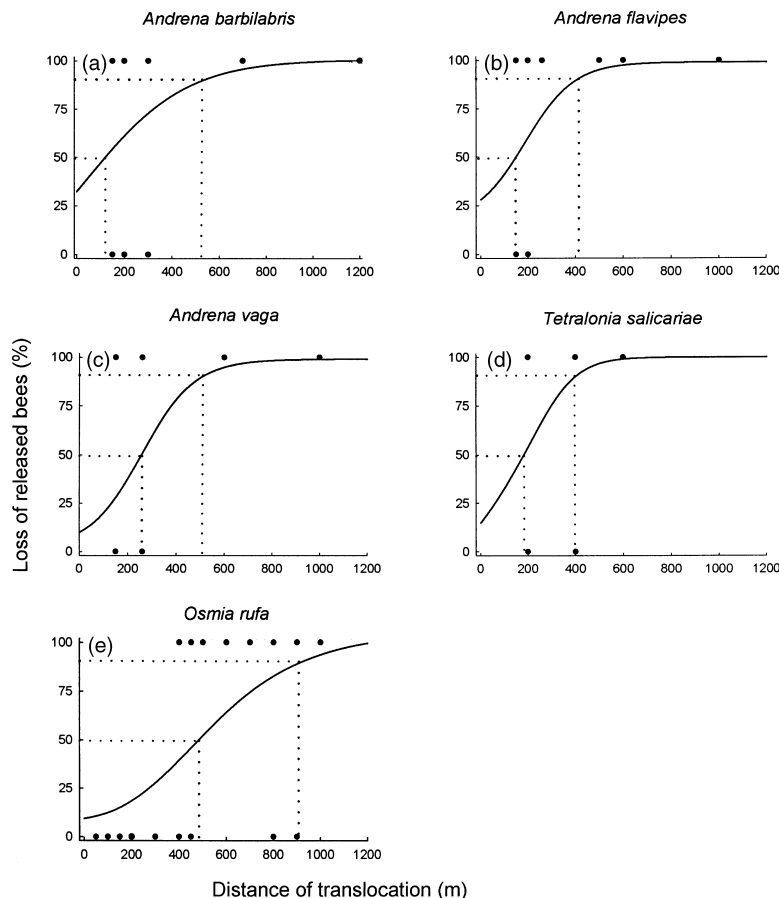


Fig. 1. Percentage loss of released female bees in relation to the distance of translocation. Logistic regression models for (a) *A. barbilabris*: $\text{logit}(y) = -0.76 + 0.006x$, $\chi^2 = 6.05$, $n = 38$, $P = 0.013$. (b) *A. flavipes*: $\text{logit}(y) = -0.87 + 0.008x$, $\chi^2 = 5.18$, $n = 36$, $P = 0.022$. (c) *A. vaga*: $\text{logit}(y) = -2.56 + 0.01x$, $\chi^2 = 13.25$, $n = 42$, $P < 0.001$. (d) *T. salicariae*: $\text{logit}(y) = -1.93 + 0.02x$, $\chi^2 = 7.17$, $n = 40$, $P = 0.007$. Data based on Molitor (1936). (e) *O. rufa*: $\text{logit}(y) = -2.96 + 0.008x$, $\chi^2 = 17.46$, $n = 25$, $P < 0.001$. Dotted lines indicate translocation distances of 50% and 90% probability of loss of released female bees.

1997). Homogeneous groups were separated using Tukey tests. Best fit regressions were generated using log-transformed and untransformed variables. Arithmetic means \pm standard errors are given.

Results

TRANSLOCATION EXPERIMENTS

Results of the translocation experiments with five bee species were analysed using logistic regressions. Fifty per cent of the females of *A. barbilabris* (Fig. 1a) and *A. flavipes* (Fig. 1b) returned to their nests from a distance of 120 and 150 m, respectively, whereas only 10% of the *A. barbilabris* females displaced more than 530 m and 10% of *A. flavipes* females displaced more than 415 m came back to the nesting sites. Similarly, 50% of the females of *A. vaga* displaced 260 m returned to the nests and only 10% of the females displaced more than 510 m found the way back (Fig. 1c). Molitor's (1937) data showed that females of *T. salicariae* did not return to their nests from release points more than 600 m away. Fifty per cent of the females returned to the nest sites if displaced by 185 m and less than 10% when displaced

by more than 400 m (Fig. 1d). *O. rufa* females have a larger foraging range than the other four species. Fifty per cent of the 500 m displaced and 10% of the females displaced 900 m were able to return to their nests (Fig. 1e).

We tested the expectation that bees need more time to return from far than from near release sites. In fact, females of *O. rufa* returned within a few minutes from near release sites, while those that had to cover more than 600 m returned after 2–4 h. Overall, time of return was correlated with distance of translocation (Fig. 2).

FORAGING RANGE OF OLIGOLECTIC WILD BEES

Oligolectic bees specialize on one family or genus of food plants, e.g. *M. lapponica* forages on *Epilobium* spp. and *C. rapunculi* on *Campanula* spp. We tested the hypothesis that such oligolectic bees would nest in trap nests only if their food plant was available within foraging range of the nest. Two oligolectic and trap-nesting bees, *M. lapponica* and *C. rapunculi*, were recorded and related to the nearest distance to food-plant patches.

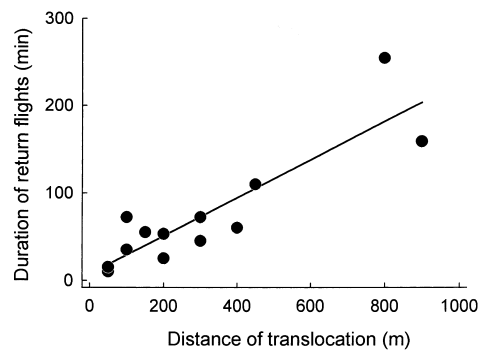


Fig. 2. Time between release of *O. rufa* females at various distances from the nest and return to their nest. Linear regression model: $y = 0.72 + 0.21x$, $F = 35.58$, $r^2 = 78\%$, $n = 13$, $P < 0.001$.

M. lapponica nested on 10 of the 15 field sites. Trap nests were colonized with a probability of 90% when the distance between nest and food plant was less than 115 m and with a probability of 50% at a distance of 256 m (Fig. 3a).

C. rapunculi used trap nests on five of the 15 field sites. The regression model predicted a 50% probability of nesting in trap nests when the distance between nest and food plant was 260 m and no successful colonization at a distance of more than 300 m (Fig. 3b).

FORAGING RANGE AND BODY LENGTH

We tested the hypothesis that the foraging range depends on body length, using maximum foraging ranges of wild bees from our own studies and from the literature (Table 1). Molitor (1937) recorded a foraging distance of 1200 m for the largest bee of our sample, *Xylocopa violacea* (Linnaeus). In his translocation experiments, Rathjen (1994) estimated the foraging range of *O. rufa*

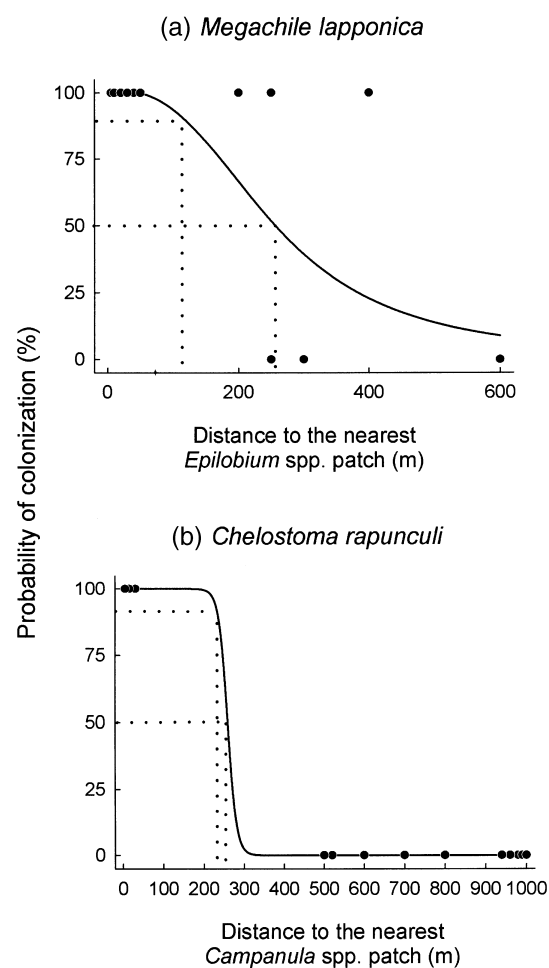


Fig. 3. Probability of trap nest colonization by two oligolectic solitary bees in relation to the nearest population of food plants. Logistic regression models for (a) *M. lapponica*: $\text{logit}(y) = 3.78 + 0.01x$, $\chi^2 = 9.32$, $n = 15$, $P = 0.002$. (b) *C. rapunculi*: $\text{logit}(y) = 32.2 + 0.12x$, $\chi^2 = 19.09$, $n = 15$, $P < 0.001$. Dotted lines indicate distances of 50% and 90% probability of trap nest colonization.

Table 1. Maximum foraging distances of European solitary bees and mean body size based on own experiments and literature data

Species	Body length (mm)	Foraging distance (m)	Reference
<i>Andrena barbilabris</i> (Kirby)	11.5	500 300	Witt (1992), Wesslerling (1996)
<i>Andrena cineraria</i> (Linnaeus)	14	300	Gebhardt & Röhr (1987)
<i>Andrena clarkella</i> (Kirby)	13	300	Gebhardt & Röhr (1987)
<i>Andrena flavipes</i> Panzer	12	260	Wesslerling (1996)
<i>Andrena vaga</i> Panzer	14	260	Wesslerling (1996)
<i>Chelostoma florissomme</i> (Linnaeus)	5.5	150	Kapyla (1978)
<i>Chelostoma rapunculi</i> (Lepeletier)	8.5	200	Gathmann (1998)
<i>Colletes cunicularis</i> (Linnaeus)	13.5	350	Wesslerling (1996)
<i>Megachile lapponica</i> Thompson	11	600	Wesslerling (1996)
<i>Megachile rotundata</i> (Fabricius)	8.5	500 100	Tepedino (1983), Tasei & Delaude (1984)
<i>Osmia anthocopoides</i> Schenk	9.5	150	Molitor (1937)
<i>Osmia maritima</i> Friese	11.5	150	Haeseler (1982)
<i>Osmia mustelina</i> Gerstaecker	13.5	1 000	Molitor (1937)
<i>Osmia rufa</i> (Linnaeus)	11	600	Gathmann (1998)
<i>Pangurus banksianus</i> (Kirby)	11	250	Münster-Swendsen (1968)
<i>Tetralonia salicariae</i> (Lepeletier)	10.5	400	Molitor (1936)
<i>Xylocopa violacea</i> (Linnaeus)	24	1 200	Molitor (1937)

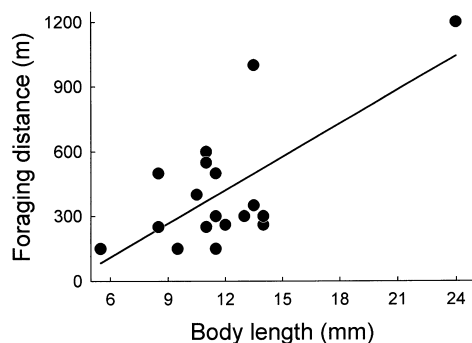


Fig. 4. Maximum foraging distance for pollen and nectar in relation to the body length of different solitary bee species. Data from Table 1 were used for the linear regression model: $y = -232.28 + 54.69x$, $F = 10.13$, $r^2 = 47\%$, $n = 21$, $P < 0.001$.

to be about 550 m Witt (1992) established a maximum foraging range of 400 m for *A. barbilabris* in his experiments. The distance between trap nests colonized by *M. lapponica* and *C. rapunculi* and their host plants (see above) led to the conclusion that their maximum foraging range was 400 m and 200 m, respectively. Colonization of trap nests by *M. lapponica* was also observed by Jung (1995): four of six trap nests that were used by *M. lapponica* were close to food plant patches. For the species *C. florissomme* (Linnaeus) a foraging range of 150 m was recorded by Kapyla (1978). Our

estimation of the foraging range of *O. rufa* was based on the fact that they needed more than 1 h to return to their nests from distant release points (> 600 m) (Fig. 2) and probably found their way back only accidentally. The interspecific comparisons confirmed our expectation that the foraging distances increased significantly with body length (Fig. 4).

FORAGING TRIP DURATION

Foraging trip duration of eight bee species was measured to study interspecific variability. Intraspecific variability could be shown with the many data from *O. rufa*. On seven different sites, 41 nesting females of *O. rufa* were observed and foraging trip duration was measured. Foraging trip duration was significantly less on chalk grassland than on set-aside fields (Fig. 5a), with intermediate values for extensive grassland and field margin strips. These differences between field types were correlated with the number of plant species (Fig. 5b). In a regression using data of eight bee species, mean foraging trip duration depended on the mean body length (Fig. 5c). The small bees *H. truncorum*, *C. rapunculi* and *O. parietina* needed only a short time for one foraging trip. Medium-sized bees such as *O. leaiana* and *O. rufa* needed more time than these small bees, but less than the large bees *M. lapponica* and *M. versicolor* (Fig. 5d).

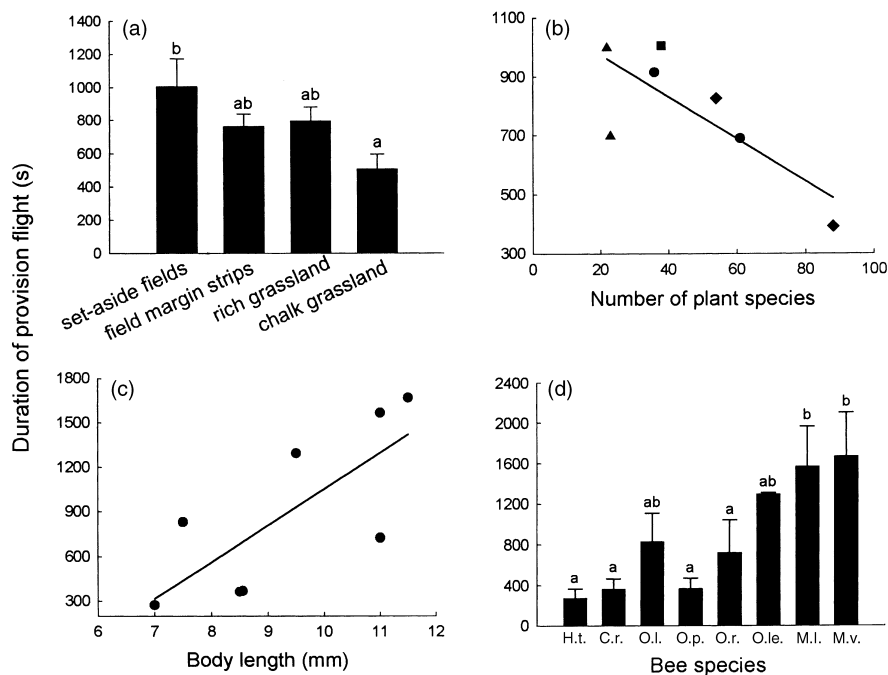


Fig. 5. Relation between habitat structure and mean body length of bee species and the mean foraging trip duration: (a) Foraging trip duration of *O. rufa* in different habitat types ANOVA: $F = 2.89$, $n = 41$, $P = 0.048$. (b) Foraging trip duration of *O. rufa* in relation to the number of plant species. Linear regression model: $y = 1118 - 7.14x$, $F = 9.88$, $r^2 = 59\%$, $n = 7$, $P = 0.026$. Field type symbols: set-aside fields sown with grass-clover mixture, ● field margin strips, π extensively used grassland, ◆ chalk grassland. (c) Foraging trip duration in relation to the mean body length of eight solitary bee species. Linear regression model: $y = -1395 + 244.8x$, $r^2 = 56\%$, $F = 7.77$, $n = 7$, $P = 0.032$. (d) Foraging trip duration for different solitary bee species. Species on the x-axis were sorted by their mean body length (left small, right large). ANOVA: $F = 18.1$, $n = 72$, $P < 0.001$. Species abbreviations: H.t., *H. truncorum*; C.r., *C. rapunculi*; O.l., *O. leucomelana*; O.p., *O. parietina*; O.r., *O. rufa*; O.le., *O. leaiana*; M.l., *M. lapponica*; M.v., *M. versicolor*. In Fig. 5a and d, arithmetic means and standard errors are given. Identical letters show homogeneous groups (Tukey test).

Discussion

Habitats of wild bees frequently have spatially separated nest sites and food plants. The ability of the bees to bridge the distance between these different habitat requirements is of vital importance for successful reproduction. Our results showed that solitary wild bees have a maximum foraging range between 150 and 600 m. The duration of provision flights depended on the habitat-specific food availability and the body length of the bees. Over long distances flying Hymenoptera use celestial orientation and landmarks to guide them (Gewecke 1995). Hymenoptera have a visual memory with a great ability to learn (Collet 1993; Dyer 1994). Orientation via landmarks is restricted to the trajectories which were used by bees to fly between different habitat parts (Wehner 1981). Translocated *Philanthus triangulum* Fabricius came back to their nest with a higher probability if they were released in their hunting ground (Tinbergen & van der Linde 1938). The results of our translocation experiments showed that 50% of the females were able to return to their nests from translocation distances between 160 and 480 m.

Oligolectic bees may be expected to bridge larger foraging distances than polylectic bees because they have to find few and distant food patches. However, our results showed no differences between the foraging range of oligolectic and polylectic bees. The oligolectic species *A. vaga*, *T. salicaria* and *M. lapponica* showed foraging ranges similar to those of polylectic species *O. rufa*, *A. barbilabris* and *A. flavipes*. The oligolectic species *C. rapunculi* had an even smaller foraging range, but this appeared to be due to its small body size. Our experiments and the literature data showed that the best prediction of the foraging range of solitary bees is their body size, not the food plant specialization. These results supported the general hypothesis that dispersal range of insects is correlated with body length, for example, with respect to carabid beetles and butterflies (den Boer 1990; Steffan-Dewenter & Tscharniske 1997). Due to the large foraging distance of large individuals, bee communities in disturbed habitats should be dominated by large species of solitary bees. In addition, social bees can be expected in such habitats due to their well-known high dispersal ability and their generally large size in temperate regions. In fact, Gathmann *et al.* (1994) found that very young set-aside fields were colonized immediately by large trap-nesting bees, whereas in old fields many small bees were found. Steffan-Dewenter & Tscharniske (1999) found that with isolation of flowering patches the mean body length of flower-visiting species increased. The proportion of bumble bees was significantly greater in fallows and intensively used grasslands than in extensively used, plant-species-rich grasslands (Gathmann 1998). In our current study, trip duration was greater in plant-species-poor than in plant-species-rich habitats (Fig. 5). As small bees may not be able to collect sufficient food

resources in plant-species-poor habitats during their short foraging trips, such habitat should expose a selection pressure against small bees.

We tested this hypothesis, that foraging trip duration reflects habitat quality, by comparing foraging trip duration of *O. rufa* in different habitat types and we found differences. On plant-species-poor set-aside fields, average foraging trip duration was 50% longer than on plant-species-rich chalk grasslands. The foraging trip duration was generally correlated with the number of plant species, and sites with a high number of plant species had also a higher cover of flowering plants (Gathmann 1998). Accordingly, foraging trip duration appeared to decline with an increase in abundance and diversity of food resources. Similarly, foraging flights of *O. caerulea* (Linnaeus) and *M. versicolor* took twice as long on plant-species-poor and young set-aside fields as on plant-species-rich and old orchard meadows (Gathmann *et al.* 1994). Rathjen (1994) found also a correlation between foraging trip duration and distance between nest and food plants of *O. rufa*. Short foraging trip durations of 10 min were observed for *Megachile rotundata* (Fabricius) only when they foraged close to their nests (Dorn & Weber 1988).

Do these data permit conclusions on whether habitat fragmentation affects bees more or less than other insect species? Our results show contradictory evidence. On one hand, bees differ from insects such as many gall makers (Tscharniske 1994) in that suitable nesting places and nutritious food resources may be separated spatially, so their flight range should be great enough to bridge such distances. On the other hand, solitary bees are known to be very conservative with respect to dispersal and to stay at the same nesting places over decades (Westrich 1989); furthermore, they have maximum foraging distances of only 150–600 m and do not exploit nectar–pollen resources distant from their nesting sites (Fig. 2, Steffan-Dewenter & Tscharniske 1999).

In any case, large and plant-species-rich habitats will provide solitary wild bees with both nesting places and food resources and protect bee diversity and their ecological function as pollinators. Destruction, deterioration and fragmentation of habitats in agricultural landscapes may disrupt the interactions between wild bees and their resources (Day 1991; O'Toole 1994). The resulting reduction of species diversity and abundance may affect ecosystem functions such as pollination and seed set (Naeem *et al.* 1995; Kearns, Inouye & Waser 1998; Steffan-Dewenter & Tscharniske 1999). Pollination success for many self-incompatible plants depends on the availability of wild bees, which play a prominent role as pollinators. Effective pollination increases the yield of many crops (Corbet 1987; Torchio 1991; Williams 1996) and contributes to the conservation of many endangered wild flowers (Kwak, Velterop & Boerrigter 1996). Size and spatial arrangement of each habitat requirement and the permeability of the

surrounding, unrewarding habitat matrix should determine the resulting structure of bee communities, but there is a need for more experimental evidence.

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