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Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee–flower relationships

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ABSTRACT

Knowledge about the quantitative pollen requirements of solitary bees is crucial for the preservation of endangered bee species and the understanding of the evolution of bee–flower relationships. We estimate the number of flowers required to rear a single larva for 41 European bee species (i) by comparing the pollen content of brood cells with the pollen quantity contained in the flowers of the bees' host plants and (ii) by deducing the pollen requirements from a regression model describing the relationship between the average bee dry body mass and the average brood cell pollen content. The flower requirements of the bee species examined vary by three orders of magnitude. Depending on both bee species and host plant, from seven to 1100 flowers or from 0.9 to 4.5 flower heads are needed to rear a single larva. As only about 40% of the pollen contained in a flower was found to be available to a single female bee, these minimal figures have to be multiplied by a factor of approximately 2.5 to obtain a realistic estimate of bee flower requirements. The amount of pollen lost from flowers for bee nutrition is surprisingly high. We hypothesize that the recent decline of many bee species may have its main cause in a food shortage provoked by a decrease in flower diversity and quantity following habitat destruction and modern agricultural practices. The substantial pollen losses to bees as documented in this study support earlier findings on floral adaptations against excessive pollen harvesting by bees.

1. Introduction

Bees (Hymenoptera, Apoidea) provide their brood cells with a mixture of pollen and nectar on which the larvae later develop. While the floral preferences are quite well known at least in the bee species of Central Europe and North America (e.g., Moldenke, 1979; Westrich, 1989), information on the quantity of pollen needed for a single brood cell, i.e., to rear one offspring, is sparse. Only few studies address the question of how many flowers are required to feed a single bee larva: an average flower head of *Helianthus annuus* (Asteraceae) produces enough pollen for three to four brood cells of the sunflower specialist *Dieunomia triangulifera* (Halictidae), a brood cell of the bee *Ptilothrix plumata* (Apidae) contains the

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pollen of 28–40 flowers of its host plant *Pavonia cancellata* (Malvaceae), and 36–79 flowers of *Campanula rapunculus* (Campanulaceae) are needed to rear one larva of *Chelostoma rapunculi* (Megachilidae), an oligolege of *Campanula* (Minckley et al., 1994; Schlindwein and Martins, 2000; Schlindwein et al., 2005).

Information on the quantitative pollen requirements of bees is urgently needed for two reasons. First, bees are a key pollinator group which has suffered a considerable decline in both local species diversity and population size during the last few decades, largely as a result of modern agricultural practices and habitat degradation (Kearns and Inouye, 1997; Kearns et al., 1998; Buchmann and Ascher, 2005). From 25% up to 65% of the species are listed on national and regional Red Data Books in Europe (Else and Spooner, 1987; Amiet, 1994; Westrich et al., 1998, 2000; Mandery et al., 2003; Burger et al., 2004), depending on the region and the location considered (e.g., Oertli et al., 2005). To conserve populations of endangered bee species, knowledge about their quantitative pollen and flower requirements is crucial. Second, the understanding of evolutionary forces which have shaped and still shape bee–flower relationships requires insights into the amount of pollen which is collected from the flowers by the female bees and which is therefore lost for plant reproduction.

The present study aims at estimating the number of flowers required to rear a single larva for a set of mostly rare or endangered Central European bee species. In six species, we directly compared the average pollen content of a brood cell with the average pollen content in the flowers of the corresponding host plants. To deduce the flower requirements of another 35 species we developed a regression model which describes the relationship between the average bee dry body mass and the average brood cell pollen content. These estimates are based on the simplified assumption that the whole pollen content of a flower is extractable by a female bee and refer therefore to the minimal number of flowers required to provision a single brood cell. To get an estimate of how much pollen is actually available to a single female bee, we quantified the extractable pollen in the flowers of five plant species under natural conditions.

Studies on quantitative aspects of bee larval provisions are often based on the mass of the brood cell content (e.g., Maddocks and Paulus, 1987; Neff and Danforth, 1991). However, results based on this method cannot be compared among different bee species as the pollen–nectar ratio of the provision mass is known to vary widely from one bee species to another (Westrich, 1989; Westerkamp, 1996). Data on caloric content after combustion of the provision mass in bomb calorimeters do not simply correspond to digestible nutrients as they include calories of poorly or undigestible parts of the pollen grains, such as the pollen wall (Roulston and Cane, 2000). In addition, the role of nectar in the provision mass of bees is still unclear. Nectar might have its primary function in facilitating pollen digestion by inducing the germination of the pollen grains rather than being a nutritional component (Dobson and Peng, 1997; Roulston and Cane, 2000). Considering these facts, we used the number and the volume of the pollen grains to quantitatively estimate the pollen requirements of bees. We thereby assumed the volume of a pollen grain to be a reliable indicator of its nutrient content. Pollen grain volume was indeed found to be positively correlated with the mass of protein (Roulston et al., 2000), which is probably the most important factor for bee larval growth (Roulston and Cane, 2002).

2. Materials and methods

2.1. *Bee parameters*

We determined the average pollen content in a brood cell for 14 European bee species broadly differing in size (Table 1). As pollen quantification was expected to be easier with only a limited number of different pollen grain shapes and sizes, oligolectic bee species were chosen which are known to exclusively collect pollen on flowers belonging to a single plant genus or to several related genera within a single plant family. *Colletes cunicularius*, which we assumed to be a strict specialist of *Salix* (Westrich, 1989) at the beginning of our study, turned out to be polylectic. For the estimation of the average pollen volume in a single brood cell based on a regression model developed in the present study, 35 additional European bee species were selected (Table 4), most of which are rare or endangered in Switzerland (Amiet, 1994). Bee nomenclature follows Schwarz et al. (1996), genus delimitation is according to Michener (2000).

To determine the average dry mass of the selected bee species, individuals from museum and private insect collections were carefully removed from their pins and weighed using an electronic scale (Mettler MT5). As many bee species show a pronounced sex dimorphism in size, we assessed the average dry body mass of males and females (with empty pollen brushes) separately. Specimens collected less than one year prior to weighing were dried at 80 °C for 48 h. To minimize a potential population bias, not more than five individuals collected at the same site and date were weighed.

Brood cells were collected in the field by opening the nests of the selected bee species. Apart from *Hoplitis mocsaryi* whose nests were dug out in southern France, brood cells of all the other species were collected in Switzerland. Brood cells of the soil-nesting species *Colletes cunicularius*, *C. daviesanus*, *C. hederae*, *Andrena ruficrus* and *A. vaga* were dug out at different places within large and dense nest aggregations. We therefore expect that the collected brood cells were mostly built by different females. In those species which arrange their brood cells linearly in insect borings, stems or empty snail shells, we processed all suitable brood cells of a single nest together. The pollen grain counts were then divided by the number of brood cells resulting in an average brood cell pollen content per nest. All nests analysed were constructed by different females. Only closed brood cells which contained an egg or a freshly hatched larva were considered. In order to avoid fungal infestation, the content of the brood cells was kept refrigerated and processed within 48 h.

After carefully cleaning the brood cell from soil or pith particles with a fine brush, the brood cell provision consisting of a mixture of pollen and nectar was placed into a

Table 1 – The 14 selected bee species, their body lengths, exclusive host plants and nesting sites

Bee species	Body length	Host plants	Nesting sites
Colletidae			
Hylaeus punctulatissimus	6–8 mm	*Allium* spec. (Liliaceae)	insect borings in dead wood, hollow stems
Hylaeus signatus	6–9 mm	*Reseda* spec. (Resedaceae)	soil cracks, insect borings in dead wood, hollow stems
Colletes cunicularius	12–14 mm	*Salix* spec. (Salicaceae) and other plants	soil
Colletes daviesanus	7–10 mm	Asteraceae	soil
Colletes hederae	10–14 mm	*Hedera* spec. (Araliaceae)	soil
Andrenidae			
Andrena ruficrus	8–11 mm	*Salix* spec. (Salicaceae)	soil
Andrena vaga	12–15 mm	*Salix* spec. (Salicaceae)	soil
Megachilidae			
Chelostoma florisomne	8–11 mm	*Ranunculus* spec. (Ranunculaceae)	insect borings in dead wood, hollow stems
Chelostoma rapunculi	8–10 mm	*Campanula* spec. (Campanulaceae)	insect borings in dead wood, hollow stems
Heriades truncorum	5–7 mm	Asteraceae	insect borings in dead wood, hollow stems
Hoplitis adunca	11–13 mm	*Echium* spec. (Boraginaceae)	insect borings in dead wood, hollow stems
Hoplitis mocsaryi	12–14 mm	*Linum* spec. (Linaceae)	soil
Hoplitis tridentata	10–12 mm	Fabaceae	pithy stems
Hoplosmia spinulosa	7–8 mm	Asteraceae	empty snail shells

centrifugation vial and rinsed with 5 ml ethanol (70%) to remove the adhesive pollenkitt. After ultrasonic treatment for 2 min with an ultrasonic bar (Vibra Cell 72446, Bioblock Scientific) at 20 kHz to loosen the pollen grains from each other, the alcohol-pollen mixture was centrifuged at 2500 rpm for 5 min. Four millilitres of the resulting supernatant was discarded and 4 ml H_2O added to elute the sugar from the nectar. This procedure was repeated once again to completely remove the ethanol. Afterwards, 0.1 ml methylene blue + azure II (5% each) was added for 1 h to stain the pollen. After thoroughly stirring to evenly dispense the pollen grains within the solution, one drop of the pollen solution was given into the chamber of a haemocytometer (Neubauer improved, Brand). The pollen grains in each of the four big corner squares were counted with a microscope (Olympus BX 50) at a magnification of 100×. This procedure was carried out three times, resulting in a sample size of 12 squares counted per brood cell. Sterile pollen grains recognizable by their small and shrivelled shape were not counted. In order to get an estimate of the total number of pollen grains in the brood cell, the twelve pollen grain counts were averaged and multiplied by 50,000, as the volume in a single corner square was equal to 1/50,000 of the entire volume of the pollen solution.

2.2. *Plant parameters*

We assessed the average pollen content in a single flower or in a single flower head (indicated by an asterisk below) for the following 16 plant species, which are the exclusive or important pollen hosts of the 41 bee species investigated in the present study: *Ranunculus acris* (Ranunculaceae), *Erysimum rhaeticum* (Brassicaceae), *Reseda lutea* (Resedaceae), *Lotus corniculatus*, *Medicago sativa* and *Onobrychis viciifolia* (all Fabaceae), *Lythrum salicaria* (Lythraceae), *Hedera helix* (Araliaceae), *Convolvulus arvensis* (Convolvulaceae), *Echium vulgare* (Boraginaceae), *Stachys recta* (Lamiaceae), *Campanula patula* and *Campanula rotundifolia* (both Campanulaceae), *Knautia arvensis** and *Succisa pratensis** (both Dipsacaceae), and *Buphthalmum salicifolium** (Asteraceae). Plant nomenclature follows Hess et al. (1967–1972).

We divided the measurable pollen content of a flower or flower head into three categories: total (P_{tot}), exposed (P_{exp}) and hidden (P_{hid}), where P_{exp} is the pollen that is momentarily extractable for a flower visitor and P_{hid} is pollen still enclosed in the anthers and therefore not yet accessible. P_{tot} is the sum of exposed pollen, hidden pollen and pollen lost (P_{off}) to previous visitors: $P_{tot} = P_{exp} + P_{hid} + P_{off}$.

To estimate the *maximal amount of pollen* (P_{tot}) supplied by a flower, we collected flowers which were either freshly opened or in the late bud stage. For each species, we randomly picked 30 flowers from 30 different plant individuals at each of two different sites situated at least 700 m apart. Due to the continuous maturation of anthers in polyandrous flowers and flower heads, calculation of P_{tot} of *Ranunculus acris*, *Knautia arvensis*, *Succisa pratensis* and *Buphthalmum salicifolium* was adjusted to the specific species as follows: for *R. acris* by assessing the average number of pollen grains in 300 anthers from 30 different plants multiplied by the average number of anthers per flower (n = 30 flowers); for *K. arvensis* and *S. pratensis* by determining the average number of pollen grains in 300 anthers from 30 different plants multiplied by 4 (= number of anthers) and the average number of flowers per flower head (n = 30 flower heads); and for *B. salicifolium* by assessing the average number of pollen grains in 30 flowers from 30 different plants multiplied by the average number of flowers per flower head (n = 30 flower heads).

The flowers or anthers were placed in 50 ml plastic tubes immediately after collection. Ten flowers or 100 anthers were processed together. They were dried in a drying chamber for 24 h at 60 °C which caused still closed anthers to open. Afterwards, 5 ml ethanol (70%) was added to remove the adhesive pollenkitt. The sample was then treated for 2 min with an ultrasonic bar at 20 kHz to free the pollen grains from the flower parts. The flower vestiges were carefully removed with tweezers before the alcohol–pollen solution was centrifuged

at 2500 rpm for 2 min. The further procedure was as described in Section 2.1.

To estimate the *pollen content under natural conditions*, P_{exp} and P_{hid} were determined for *Ranunculus acris*, *Hedera helix*, *Convolvulus arvensis*, *Echium vulgare* and *Stachys recta* at the same two sites where P_{tot} was assessed. The selection of these five species was based on their different floral morphologies ranging from simple flowers with an open morphology and readily accessible rewards (*R. acris, H. helix*) to complex flowers which package their rewards in a way that excludes access for many potential visitors (*S. recta*). 30 open flowers from 30 different plants were randomly picked at each of the two sites on sunny days at 13.30 pm. P_{exp} and P_{hid} were assessed at the same flowers. To estimate P_{exp}, 10 flowers were dipped for 30 s in 30 ml ethanol (70%) to transfer the pollen grains into the solution. Afterwards, the pollen grains were counted with the aid of a haemocytometer (Neubauer improved, Brand). To assess P_{hid}, the same flowers were put in plastic tubes, dried for 24 h at 60 °C and processed as above.

The average number of flowers or flower heads per individual plant was determined at the same two sites, where the pollen content was assessed. Thirty individuals per species and site were randomly chosen and the number of buds, flowers and fruits counted. In the case of *Knautia arvensis*, *Succisa pratensis* and *Buphthalmum salicifolium*, the number of flowers in one randomly chosen flower head from 30 different plants at each of the two sites was counted and multiplied by the average number of flower heads per individual (n = 30 plants). In *Hedera helix*, we assessed the average number of flowers per umbel by counting the flowers of 50 inflorescences (consisting of 4–14 umbels) at two sites each.

2.3. Pollen volume of brood cells and flowers

The pollen volume of a brood cell was calculated by multiplying the number of pollen grains with their average volume. To determine pollen grain volume, a pollen sample for each brood cell was embedded in glycerine gelatine on a slide. Eighty pollen grains were measured with an ocular micrometer at a magnification of 320×. Only pollen grains whose equatorial and polar view could be identified were measured. The brood cells of *Colletes cunicularius* (polylectic, see Section 2.1), of *Heriades truncorum* and *Hoplitis tridentata* (both specialized at the level of plant family, see Table 1), and of *Hoplitis mocsaryi* (specialized at the level of plant genus) were found to contain up to four different pollen types strongly varying in size and shape. These different pollen types were weighted according to their volume and frequency. In all other bee species, the brood cells consisted of pollen grains all of the same shape and of approximately the same size. With the exception of *Colletes cunicularius, C. hederae, Andrena ruficrus* and *A. vaga*, no distinction was possible between male and female brood cells. Thus, we cannot rule out that the estimated average pollen volumes are partially sex-biased in those species which show a distinct sex dimorphism in size. However, the large number of nests and brood cells investigated (on average 18 nests and 30 cells per species) should keep the sex-bias in a reasonable scale.

The pollen volume of a flower or flower head was calculated by multiplying the average number of pollen grains per flower or flower head with the average volume of a single pollen grain. Pollen grain volume was assessed by measuring 75–150 pollen grains per species. As small- and medium-sized pollen grains of the tristylous *Lythrum salicaria* were not distinguishable, only two pollen sizes (s/m for small- and medium-sized and l for large grains) were distinguished.

Pollen shape was considered to be spherical ($V = (4/3)\pi r^3$, with r = radius) in *Ranunculus acris*, *Erysimum rhaeticum*, *Reseda lutea*, *Medicago sativa*, *Hedera helix, Stachys recta*, *Campanula patula*, *Campanula rotundifolia, Knautia arvensis*, *Succisa pratensis* and *Buphthalmum salicifolium*. The pollen grains of *Lotus corniculatus* and *Onobrychis viciifolia* were considered to be ellipsoid and the volume was calculated as $V = (4/3)\pi(e/2)(p/2)^2$, with e = equatorial diameter and p = polar diameter. The volume of the pear-shaped pollen grains of *Echium vulgare* was estimated as the sum of a hemisphere and half of an ellipsoid. The pollen shape of *Lythrum salicaria*, *Linum* and *Convolvulus arvensis* was considered to be triangular cylindric ($V = (a^2/4)\sqrt{3}\,h$, with a = base of triangle and h = height of the cylinder in equatorial view). Pollen grains of *Allium* have approximately the shape of an orange fruit segment, the volume was estimated by $V = (1/4)(4/3)\pi r^3$, with r = radius.

2.4. Estimation of minimal pollen requirements

For six of the 14 bee species listed in Table 1 a determination of the minimal flower requirements for the rearing of a single larva was possible based exclusively on pollen grain counts of brood cells and flowers (Table 3). For the other eight species exact determination of the minimal flower requirements was not possible as they either collect pollen from *Salix* catkins composed of tiny flowers (*Colletes cunicularius, Andrena ruficrus, A. vaga*), their pollen provisions were found to consist of up to four different pollen types (*Heriades truncorum, Hoplitis mocsaryi, Hoplitis tridentata*, see Section 2.3), or the pollen grains could not be safely assigned to a single plant species (*Hylaeus punctulatissimus, Colletes daviesanus*). To get the minimal number of flowers or flower heads, we divided the average pollen volume in a brood cell by the average pollen volume in a flower or a flower head of the corresponding host plant. To get the minimal number of host plant individuals needed to provision one brood cell, we divided the calculated number of flowers or flower heads by the average number of flowers or flower heads of the corresponding plant species. Due to the growth habit of *Hedera helix* as a tall liana, the number of umbels instead of the number of plant individuals was determined.

For 35 different bee species (Table 4), a regression model (see below) was used to estimate the average pollen volume in a single brood cell. Based on the calculated brood cell volumes, the minimal number of flowers or flower heads was determined as above. For the oligolectic species, we selected the exclusive or main pollen host in Central Europe, for the polylectic species we chose plant species which are often exploited in the bees' Central European distribution range.

2.5. Statistics

A regression analysis was conducted with the average brood cell pollen volume of the 14 bee species as dependent variable and their average dry body mass as independent variable. All

data were log-transformed to minimize the errors in x-direction and to fulfill the requirement of normality. To achieve equality of variances and to improve the fit of the regression line, brood cell pollen volume and dry mass were split for males and females in four species (*Colletes cunicularius, C. hederae, Andrena ruficrus* and *A. vaga*). As in these four species the males are distinctly smaller than the females, the brood cells could be reliably assigned to sex, based solely on their pollen volumes. All statistical tests used were two-tailed, the analyses were carried out with SPSS (Version 11) for Mac OS X.

3. Results

3.1. Relationship between dry body mass and cell provision volume

Brood cell pollen volumes did not significantly deviate from normality (Kolmogorov–Smirnov, $0.36 < Z < 0.87$, $0.44 < p < 0.99$) and the variances were homogenous (Levene statistic = 1.46, df1 = 17, df2 = 230, $p = 0.113$). Due to the visual assessment of the residuals, a linear relationship is assumed between the log-transformed values of the average dry body mass and the average cell provision volume. This relationship is described by $\log y = 8.868 \log x + 0.433$ with $p < 0.001$ (linear regression, $F = 45.49$, df = 17) and $R^2 = 0.74$ (Table 2, Fig. 1). *Hylaeus punctulatissimus* shows a conspicuous deviation from the calculated regression line.

3.2. Minimal pollen requirements

The minimal number of flowers required to rear a single larva varies by three orders of magnitude depending on both the body size of the bee species and the pollen content of the host plant (Tables 3 and 4). To rear one larva of the tiny *Chelostoma campanularum* the pollen content of seven flowers of *Campanula rotundifolia* is required and 10 flowers of the polyandrous *Ranunculus acris* are needed for the middle-sized *Chelostoma florisomne*. At the other end, the two large species *Anthidium manicatum* and *Megachile parietina* require more than 1000 flowers of their corresponding host plants to provision one brood cell. The bee species which collect pollen from dense inflorescences need between one (*Andrena marginata* on *Succisa pratensis*) and five flower heads (*Hoplitis dalmatica* on *Knautia arvensis*). The minimal number of plant individuals required to rear a single larva varies from 0.1 to 17 (Tables 3 and 4).

The average total pollen volume per flower or flower head (Appendix A), the average number of flowers per plant (Appendix B) and the average number of flower heads per plant (Appendix C) were found to vary widely between the

Table 2 – Average brood cell pollen volume and average dry body mass of the 14 bee species examined

Bee species	Average pollen volume per brood cell				Average dry body mass						
					Females			Males			Species
	[mm³]	*sd*	*N*	*n*	[mg]	*sd*	*n*	[mg]	*sd*	*n*	[mg]
Hylaeus punctulatissimus	**4.30**	0.93	16	20	**5.9**	1.4	20	**4.6**	1.1	20	**5.3**
Hylaeus signatus	**11.58**	3.39	2	2	**8.0**	2.5	20	**5.6**	1.3	20	**6.8**
Colletes cunicularius	**61.86**	15.27	15	15	**43.1**	13.1	20	**25.0**	9.7	20	**34.1**
Female	68.61	10.80	11	11							
Male	43.30	8.56	4	4							
Colletes daviesanus	**29.43**	6.09	10	10	**11.1**	2.2	20	**6.6**	1.0	20	**8.9**
Colletes hederae	**42.44**	13.41	30	30	**33.3**	5.9	20	**13.6**	2.9	10	**23.8**
Female	58.72	5.17	11	11							
Male	33.02	4.40	19	19							
Andrena ruficrus	**15.92**	5.12	15	15	**12.0**	2.8	20	**5.0**	1.1	20	**8.5**
Female	20.42	3.59	7	7							
Male	11.97	1.79	8	8							
Andrena vaga	**47.60**	14.11	15	15	**37.5**	8.5	20	**17.6**	4.4	20	**27.6**
Female	56.00	7.60	10	10							
Male	30.80	6.11	5	5							
Chelostoma florisomne	**34.55**	7.58	28	98	**13.4**	4.1	20	**11.5**	3.6	20	**12.5**
Chelostoma rapunculi	**24.40**	3.42	30	67	**8.7**	1.7	20	**8.5**	2.4	20	**8.6**
Heriades truncorum	**15.23**	3.43	30	45	**7.2**	2.4	20	**3.7**	0.8	20	**5.5**
Hoplitis adunca	**21.14**	4.71	30	43	**22.6**	3.0	20	**16.7**	4.2	20	**19.7**
Hoplitis mocsaryi	**41.95**	8.13	10	23	**25.1**	1.2	8	**19.5**	1.6	8	**22.3**
Hoplitis tridentata	**50.80**	9.66	7	8	**29.0**	4.6	20	**21.4**	4.2	15	**25.2**
Hoplosmia spinulosa	**27.94**	2.39	10	17	**9.4**	2.0	20	**9.0**	1.5	20	**9.2**

In four species characterized by a distinct sex dimorphism in size, the average brood cell pollen volume is given separately for females and males. sd, standard deviation; *N* = number of different nests; *n* = total number of brood cells and number of specimens weighed, respectively.

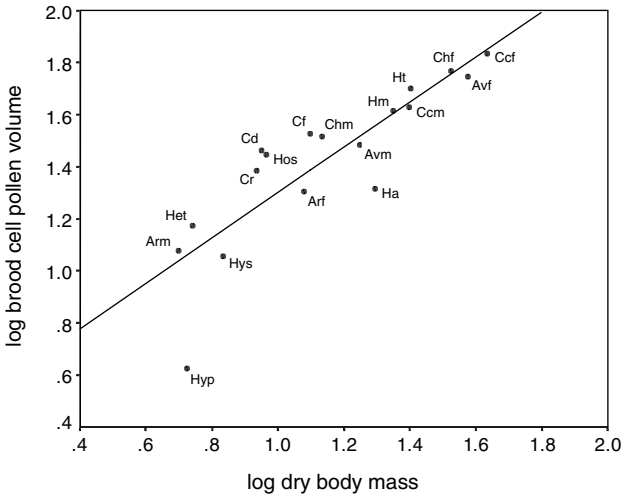

Fig. 1 – Relationship between the average brood cell pollen volume and the average dry body mass of the 14 bee species examined. Linear regression $\log y = 0.868 \log x + 0.433$ ($F = 45.49$, df = 17, $p < 0.001$, $R^2 = 0.74$). Arf, *Andrena ruficrus* (female); Arm, *Andrena ruficrus* (male); Avf, *Andrena vaga* (female); Avm, *Andrena vaga* (male); Ccf, *Colletes cunicularius* (female); Ccm, *Colletes cunicularius* (male); Cd, *Colletes daviesanus*; Chf, *Colletes hederae* (female); Chm, *Colletes hederae* (male); Cf, *Chelostoma florisomne*; Cr, *Chelostoma rapunculi*; Ha, *Hoplitis adunca*; Hm, *Hoplitis mocsaryi*; Ht, *Hoplitis tridentata*; Het, *Heriades truncorum*; Hos, *Hoplosmia spinulosa*; Hyp, *Hylaeus punctulatissimus*; Hys, *Hylaeus signatus*.

two sites in most of the plant species examined. Although closely related, *Campanula patula* and *C. rotundifolia* differ in their average pollen content by almost 60% (Appendix A).

3.3. *Pollen content of flowers under natural conditions*

The figures in Tables 3 and 4 refer to the minimal number of flowers required to provision one brood cell assuming that the whole pollen content of a flower is available for a female bee. To get an estimate of the pollen quantity which is extractable by a single female, P_{exp}, P_{hid} and P_{off} are given for five different plant species in Fig. 2 as a percentage of P_{tot}. Depending on the species, exposed pollen which can immediately be collected by a flower visitor represents 16.3–37.2% (on average 27.3%) of the total pollen content, pollen still enclosed in the anthers 14.4–58.6% (on average 30.1%) and pollen already lost to previous visitors 17.1–54.0% (on average 42.6%). Therefore, a pollen-harvesting female bee has on average 27.3% + (30.1% × 0.426) = 40.1% of the whole pollen content of a flower at her disposal.

4. Discussion

Though highly variable depending on both host plant and bee species, the quantitative flower requirements of bees were found to be surprisingly high. In 85% of the 41 bee species examined, the whole pollen content of more than 30 flowers is required to rear a single larva. The estimates of the number of flowers presented in our study, however, do not refer to the natural conditions. As only about 40% of the pollen contained in a flower was found to be available to a single female bee, these estimates have to be multiplied by a factor of about 2.5 to correct for pollen that has already been removed and for pollen that will later be removed by other flower visitors. Given the high variability in pollen availability among the five plant species investigated and the small sample size, this factor is only a rough approximation not deserving universal validity, however. In addition, female bees do not only provision one brood cell during their flight period, they usually construct from 10 to maximally 30 brood cells under suitable weather conditions (Müller, 1994; Müller et al., 1997). The large amount of pollen that is withdrawn from the flowers by the female bees has consequences both for the decline and conservation of endangered bee species as well as for our understanding of the evolution of bee–flower relationships.

4.1. *Implications for bee conservation*

The large pollen quantities needed for reproduction are probably an important reason for the decline of many bee species during the last few decades. Habitat destruction and modern agricultural practices led to a notable decrease in the diversity of plant species and in the quantity of flowers in many regions of the world. As soon as the pollen quantity of the host

Table 3 – Flower and plant requirements for provisioning of a single brood cell of six bee species based on pollen grain counts of brood cells and flowers

Bee species	Host plant species	Minimal number of flowers resp. flower heads* required	Minimal number of plants resp. umbels* required
Hylaeus signatus (Colletidae)	*Reseda lutea* (Resedaceae)	18.3	–
Colletes hederae (Colletidae)	*Hedera helix* (Araliaceae)	109.9	7.3*
Chelostoma florisomne (Megachilidae)	*Ranunculus acris* (Ranunculaceae)	9.9	2.0
Chelostoma rapunculi (Megachilidae)	*Campanula patula* (Campanulaceae)	22.1	1.4
	Campanula rotundifolia (Campanulaceae)	36.9	9.2
Hoplitis adunca (Megachilidae)	*Echium vulgare* (Boraginaceae)	140.0	0.4
Hoplosmia spinulosa (Megachilidae)	*Buphthalmum salicifolium* (Asteraceae)	3.9*	0.5

The estimates of the minimal number of flowers and plants are based on the data given in Table 2 (average pollen volume per brood cell), Appendix A (average total pollen volume per flower or flower head), Appendix B (average number of flowers per plant) and Appendix C (average number of flower heads per plant).

Table 4 – Host plants, body lengths and extrapolated pollen, flower and plant requirements for provisioning of a single brood cell of 35 bee species

Exclusive or important host plant species	Bee species	Body length	Extrapolated pollen requirement (mm^3)	Minimal number of flowers resp. flower heads* required	Minimal number of plants required
Erysimum rhaeticum (Brassicaceae)	*Andrena probata* (Andrenidae)	13–15 mm	45.99	87.4	4.0
	Osmia brevicornis (Megachilidae)	8–11 mm	34.59	65.8	3.0
Lotus corniculatus (Fabaceae)	*Anthidium punctatum* (Megachilidae)	8–10 mm	34.59	224.6	8.6
	Hoplitis loti (Megachilidae)	8–11 mm	26.78	173.9	6.7
	Hoplitis ravouxi (Megachilidae)	8–10 mm	21.21	137.7	5.3
	Hoplitis tridentata (Megachilidae)	10–12 mm	44.61	289.7	11.1
	Osmia caerulescens (Megachilidae)	8–10 mm	22.24	144.4	5.6
Medicago sativa (Fabaceae)	*Melitturga clavicornis* (Andrenidae)	13–15 mm	67.20	420.0	0.4
	Rhophitoides canus (Halictidae)	7–8 mm	12.09	75.6	0.1
	Melitta leporina (Melittidae)	11–13 mm	36.02	225.1	0.2
Onobrychis viciifolia (Fabaceae)	*Melitta dimidiata* (Melittidae)	11–13 mm	53.84	618.9	2.3
	Megachile parietina (Megachilidae)	14–18 mm	99.09	1139.0	4.3
Lythrum salicaria (Lythraceae)	*Melitta nigricans* (Melittidae)	10–12 mm	30.24	245.9	0.2
	Tetraloniella salicariae (Apidae)	9–11 mm	28.60	232.5	0.2
Convolvulus arvensis (Convolvulaceae)	*Systropha curvicornis* (Halictidae)	8–10 mm	25.62	33.9	2.1
	Systropha planidens (Halictidae)	10–11 mm	39.96	52.9	3.3
Echium vulgare (Boraginaceae)	*Hoplitis anthocopoides* (Megachilidae)	8–11 mm	24.78	164.1	0.5
	Hoplitis lepeletieri (Megachilidae)	12–13 mm	42.91	284.2	0.8
	Anthophora balneorum (Apidae)	11–14 mm	75.49	499.9	1.5
Stachys recta (Lamiaceae)	*Rophites algirus* (Halictidae)	8–10 mm	24.10	349.3	1.8
	Lasioglossum clypeare (Halictidae)	6–7 mm	9.61	139.3	0.7
	Anthidium manicatum (Megachilidae)	11–17 mm	69.36	1005.2	5.3
	Osmia andrenoides (Megachilidae)	6–8 mm	17.54	254.2	1.3
Campanula patula (Campanulaceae)	*Andrena curvungula* (Andrenidae)	11–14 mm	38.71	35.0	2.2
	Andrena pandellei (Andrenidae)	9–12 mm	30.24	27.4	1.7
Campanula rotundifolia (Campanulaceae)	*Dufourea dentiventris* (Halictidae)	7–8 mm	11.90	18.0	4.5
	Lasioglossum costulatum (Halictidae)	9–10 mm	23.26	35.2	8.8
	Melitta haemorrhoidalis (Melittidae)	11–13 mm	43.84	66.3	16.6
	Chelostoma campanularum (Megachilidae)	4–6 mm	4.51	6.8	1.7
	Hoplitis mitis (Megachilidae)	7–9 mm	27.44	41.5	10.4
Knautia arvensis (Dipsacaceae)	*Andrena hattorfiana* (Andrenidae)	13–16 mm	49.79	3.2*	0.5
	Chelostoma grande (Megachilidae)	12–15 mm	50.09	3.2*	0.5
	Hoplitis dalmatica (Megachilidae)	11–14 mm	70.07	4.5*	0.8
Succisa pratensis (Dipsacaceae)	*Andrena marginata* (Andrenidae)	9–10 mm	17.19	0.9*	0.2
Buphthalmum salicifolium (Asteraceae)	*Heriades truncorum* (Megachilidae)	5–7 mm	11.90	1.7*	0.2

The estimates of pollen requirements are deduced from the regression equation $\log y = 8.868 \log x + 0.433$ with x as the average dry body mass (Appendix D), the estimates of the minimal number of flowers and plants are based on the pollen and flower data in Appendix A–C.

plants falls below a certain threshold within the flight range of the female bees, which is assumed to be in the range of maximally 150–600 m from their nests (Gathmann and Tscharntke, 2002), bee species may face the risk of local extinction. *Megachile* (*Chalicodoma*) *parietina*, for example, a large and conspicuous bee, which builds exposed mud cells on rock surfaces, has suffered a dramatic decline in Central Europe for reasons which are not yet fully understood (Westrich, 1989; Westrich et al., 2000; Amiet et al., 2004). Prior to 1950, *M. parietina* was quite common and widely distributed in Central Europe. Its distribution range extended northwards up to central Germany. Today, the species has disappeared from most of its former Central European range with only a few small and scattered populations remaining north of the Alps. Although polylectic (Westrich, 1989), *M. parietina* prefers the flowers of *Onobrychis viciifolia* as pollen source in Central Europe (Müller et al., 1997; M. Herrmann, personal communication). *O. viciifolia* was extensively cultivated as a forage crop and as an intercrop in the former three-field system until the middle of the last century (Kummer, 1953). Today it grows on

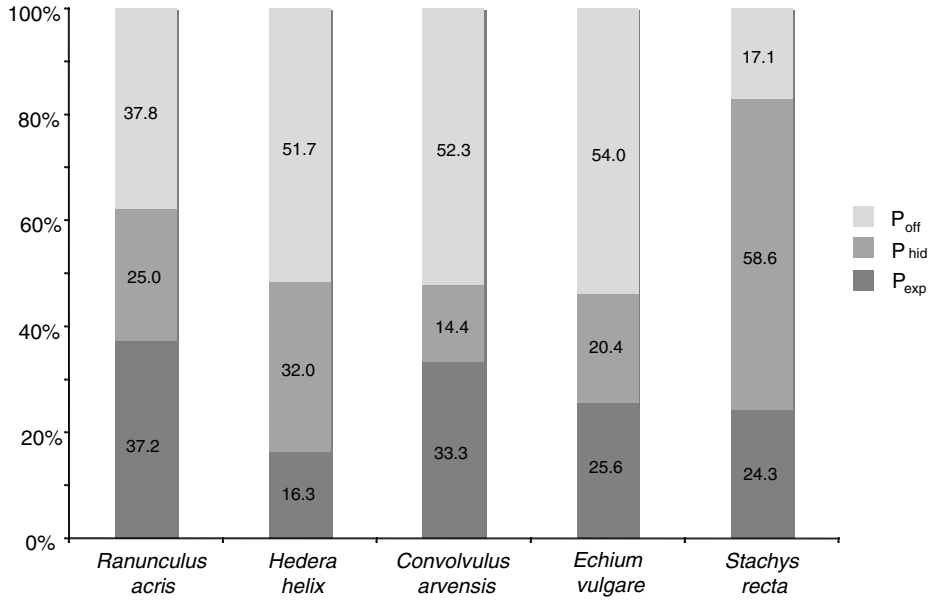

Fig. 2 – Pollen content in the flowers of five plant species under natural conditions. P_{exp}, exposed pollen which is momentarily accessible to a flower visitor; P_{hid}, hidden pollen which is still enclosed in the anthers; P_{off}, pollen already lost to previous visitors.

nutrient-poor meadows and ruderal sites. According to the results presented in this study, a female of *M. parietina* needs on average the whole pollen content of 1139 *Onobrychis* flowers or 4.3 *Onobrychis* plants to rear one offspring. By assuming that only an estimated 40% of the total pollen content is in fact available for pollen-harvesting females due to the concurrence of other flower visitors and that a female builds ten brood cells during her entire life, the quantity of pollen needed increases to 28,475 flowers or 107 plants which must occur within the flight range of a single female. When, moreover, the pollen requirement of a whole population is taken into account, flower density may soon fall below a threshold for maintaining a viable population. The main reason for the dramatic decline of *M. parietina* in Central Europe may thus lie in a shortage of *Onobrychis* plants due to the recent abandonment of their cultivation and the decrease in nutrient-poor meadows (Tamis et al., 2005).

We hypothesize that the considerable decline of many other bee species during the last few decades may have its main cause in a food shortage as well. Owing to their higher pollen requirements, large bee species are expected to be more prone to local extinction than smaller species. Indeed, proneness of extinction was found to correlate with average body mass of bees and large-bodied bees tended to be most extinction-prone (Larsen et al., 2005). Similarly, the delayed flowering of critical bee floral resources in northwestern Costa Rica during El Nino and La Nina years resulted in a reduction of large anthophrid bee species while smaller bee taxa remained about the same in abundance (Frankie et al., 2005).

4.2. *Implications for bee–flower relationships*

As shown in this study, plants lose considerable amounts of pollen to the bees. In a pioneering study, Schlindwein et al. (2005) found that 95.5% of the pollen produced by flowers of *Campanula rapunculus* were withdrawn for bee reproduction while only 3.7% contributed to pollination. Consequently, a strong competition for pollen exists between flowers and bees. Flowers are thus expected to minimize pollen loss to bees by restricting access to pollen. Several flower traits can actually be interpreted as adaptations against excessive pollen harvesting by bees. Heteranthery, where showy anthers provide fodder pollen while pollen for fertilization is produced by unconspicuous anthers, occurs in a number of mainly tropical plant taxa (Vogel, 1993). Flowers of several taxa hide their anthers in a position which prevents most bees from efficiently collecting pollen (Westerkamp, 1996, 1997): (i) Nototribic flowers of e.g., the Lamiaceae and Scrophulariaceae, where the anthers are in a raised position below the upper lip, can only be exploited by bees possessing either specialized pollen-harvesting bristles on head and thorax or behavioural adaptations (Müller, 1996; Houston, 2000; Thorp, 2000). (ii) In the flowers of e.g., many Boraginaceae, Primulaceae and of *Muscari* (Hyacinthaceae), the anthers are concealed within narrow tubes. Again, bees known to collect pollen from these flowers are equipped with modified bristles on proboscis or forelegs (Thorp, 1979, 2000; Parker and Tepedino, 1982; Müller, 1995; Müller and Kuhlmann, 2003; Neff, 2004; Müller, in press). (iii) The successful exploitation of the keel flowers of the Fabaceae, in which the anthers are completely hidden within the two lowermost petals, is restricted to bees capable of bringing the pollen or the pollen-bearing structures to extrude from the tip of the keel by actively lowering the wing–keel-complex with their legs (Westerkamp, 1997). (iv) Finally, pollen is concealed within poricide anthers in members of at least 72 angiosperm families from where it can only be harvested by those bees which are capable of vibrating the flowers by buzzing (Buchmann, 1983). In all these cases, the

concealement of the anthers restricts pollen harvesting to only a small subset of a local bee fauna.

If there is a strong competition for pollen between bees and flowers, pollen is not expected to contain extra protein for the bees. In an extensive study, Roulston et al. (2000) found indeed no difference between the pollen protein content of zoophilous and anemophilous plants. Moreover, pollen collected by bees did not contain more protein than pollen not reported to be collected by bees. The authors conclude that the need for growing pollen tubes probably plays a more important role in determining pollen protein content than rewarding pollinators. In line with this, the available evidence suggests that bees cannot discriminate between pollen of high and low protein content (Roulston and Cane, 2002).

In addition, our study demonstrates that typical bee flowers do not have higher pollen contents than flowers which are also visited by other insects. Four of the six species with the lowest total pollen volume per flower examined in this study are typical bee flowers: *Stachys recta* (Lamiaceae), *Onobrychis viciifolia, Lotus corniculatus* and *Medicago sativa* (all Fabaceae).

In summary, the high pollen requirements of bees as documented in this study are further evidence of the recently stated postulate that the relationship of bees and flowers is best described as a balanced mutual exploitation (Westerkamp, 1996) where specialized bee flowers are faced with the constant dilemma to attract specialized bees for pollination on the one hand and to restrict pollen removal on the other hand.

4.3. *Use and reliability of the regression model*

We consider the regression model presented in this study a helpful means for conservation practice. It provides a rough estimate of the quantitative pollen requirements of any given bee species for which the average dry body mass is known. It can be applied both for oligolectic and polylectic bees as plant genera hosting pollen specialist bees do not produce pollen richer in protein than those genera not hosting pollen specialists (Roulston et al., 2000). Provided that, in addition to the average dry body mass, the average pollen volume in the flowers of the exclusive or of a preferred host plant is known, the number of flowers required to rear a single larva can easily be calculated for any bee species with the aid of the regression equation. As the considerably differing average pollen content in the flowers of the two *Campanula* species investigated clearly indicates, however, such extrapolations only work on species level. Similarly, the average pollen content per flower as well as the average number of flowers or flower heads per plant were found to vary considerably between the two different sites. These parameters, therefore, have to be assessed separately for each host plant population.

The regression model is an approximation that takes neither varying protein content in the pollen grains of the plant species examined nor different digestion efficacies of the bee species into account. Protein content was actually found to range from 2.5% to 61% in the pollen of 377 plant species from 93 families and from 15% to 61% in pollen collected by bees (Roulston et al., 2000). Bee species differ in their capability to digest lipids and to assimilate nitrogen (Dobson and Peng, 1997; Roulston and Cane, 2000). *Megachile rotundata* assimilated 87.2% of the ingested nitrogen while *Osmia lignaria* retained only 35–50% of dietary nitrogen in adult body tissue (Levin and Haydak, 1957; Wightman and Rogers, 1978). Though pollen quality and digestion efficiency were ignored in the present study, we believe that the solidity of the regression model rests on the very wide range of brood cell pollen volumes and bee body sizes. Because the latter vary much more than pollen nutrients, variation in pollen quality would have the effect of only putting individual data points slightly above or below the regression line.

The determination of pollen grain volume might be another source of inaccuracy as the precision of the measurements and the evaluation of the grain shape is limited and small deviations in pollen grain size results in large deviations in pollen provision volume. The remarkable deviation of *Hylaeus punctulatissimus* from the calculated regression line in Fig. 1 is possibly explained either by an unusually protein-rich pollen of its host plant *Allium* or by an inaccurate estimation of the pollen grain volume. Compared to the pollen grains of the other host plant species examined, the determination of the volume of the irregularly shaped *Allium* grain proved indeed to be difficult and an underestimation of its volume by up to a factor two is possible.

To test the reliability of the regression model we used data provided by Minckley et al. (1994) and Buchmann and O'Rourke (1991) to calculate the brood cell pollen volume for the sunflower specialist *Dieunomia triangulifera* and to compare the result with the estimated pollen volume deduced from the regression formula. The calculated brood cell pollen volume amounts to 4.35 (average number of pollen collecting trips per brood cell) × 672'537 (average number of pollen grains in a scopal load) × $9.74\,10^{-6}$ mm^3 (pollen grain volume of *Helianthus annuus*) = 28.5 mm^3. To determine the average dry body mass of *D. triangulifera*, we weighed five males and five females and correspondingly adjusted the mass given by Minckley et al. (1994) which only refers to the female sex. By inserting 19.4 mg as the average species mass into the regression formula, a brood cell pollen provision volume of 35.5 mm^3 results which is slightly higher than the volume calculated above. The regression model presented in this study is thus expected to provide satisfactory estimates of the pollen requirements of solitary bees.

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Appendix A

Pollen grain volume and average total pollen volume per flower resp. flower head of the plant species examined

Plant species	Pollen grain volume ($mm^3\ 10^{-6}$)			Average total pollen volume (P_{tot}) per flower resp. flower head* (mm^3)		
	Mean	*sd*	*n*	Site 1	Site 2	Site 1 + 2
				Mean	Mean	Mean
Ranunculus acris	**13.98**	6.75	80	4.058	2.920	**3.489**
Erysimum rhaeticum	**8.17**	1.53	110	0.526	–	**0.526**
Reseda lutea	**9.08**	1.53	90	0.759	0.505	**0.632**
Lotus corniculatus	**1.73**	0.26	80	0.120	0.187	**0.154**
Medicago sativa	**21.09**	3.82	80	0.176	0.144	**0.160**
Onobrychis viciifolia	**7.56**	1.31	90	0.085	0.088	**0.087**
Lythrum salicaria	**13.33 (l) resp. 3.67 (s/m)**	1.91 resp. 0.50	80 resp. 75	0.167	0.078	**0.123**
Hedera helix	**8.25**	2.24	90	0.359	0.412	**0.386**
Convolvulus arvensis	**61.30**	7.14	75	0.752	0.758	**0.755**
Echium vulgare	**1.53**	0.24	80	0.113	0.189	**0.151**
Stachys recta	**11.04**	1.14	80	0.050	0.087	**0.069**
Campanula patula	**13.50**	3.33	150	1.187	1.023	**1.105**
Campanula rotundifolia	**17.85**	4.70	150	0.758	0.563	**0.661**
Knautia arvensis	**456.45**	120.34	90	18.199*	12.643*	**15.421***
Succisa pratensis	**306.17**	69.04	90	18.762*	21.667*	**20.215***
Buphthalmum salicifolium	**8.79**	1.72	90	6.060*	8.362*	**7.211***
Linum campanulatum	**68.07**	9.18	80	–	–	–
Linum narbonense	**29.31**	3.54	80	–	–	–
Allium spec.	**4.70**	0.79	80	–	–	–

sd, standard deviation.
Average total pollen volume is given separately for each of two different sites as well as for both sites together.

Appendix B

Range and average number of flowers per plant of 11 plant species

Plant species	Number of flowers per plant				
	Site 1		Site 2		Site 1 + 2
	Range	Mean	Range	Mean	Mean
Ranunculus acris	2–14	5.5	1–16	4.4	**5**
Erysimum rhaeticum	5–85	21.7	–	–	**22**
Lotus corniculatus	4–40	17.1	15–68	34.8	**26**
Medicago sativa	512–2604	1246.2	448–1843	1080.7	**1163**
Onobrychis viciifolia	153–491	293.9	77–368	236.6	**265**
Lythrum salicaria	315–3300	1003.7	125–3880	1367.6	**1186**
Convolvulus arvensis	7–37	19.0	4–25	13.0	**16**
Echium vulgare	120–1166	397.1	90–598	287.7	**342**
Stachys recta	52–526	158.6	55–492	223.2	**191**
Campanula patula	4–41	13.4	4–45	19.3	**16**
Campanula rotundifolia	1–11	4.8	1–9	3.9	**4**

Figures are given separately for each of two different sites as well as for both sites together.

Appendix C

Range and average number of flowers per flower head resp. flower heads per plant of four plant species

Plant species	Number of flowers per flower head resp. umbel*					Number of flower heads per plant				
	Site 1		Site 2		Site 1 + 2	Site 1		Site 2		Site 1 + 2
	Range	Mean	Range	Mean	Mean	Range	Mean	Range	Mean	Mean
Hedera helix	3–34*	14.6*	3–27*	15.5*	**15***	–	–		–	–
Knautia arvensis	39–90	63.8	35–87	55.4	**60**	1–13	5.9	3–11	6.0	**6**
Succisa pratensis	21–101	47.4	18–126	51.2	**49**	1–8	3.95	1–13	5.4	**5**
Buphthalmum salicifolium	85–207	167.2	83–281	166.9	**167**	2–9	4.7	2–24	10.5	**8**

Figures are given separately for each of two different sites as well as for both sites together.

Appendix D

Average dry body mass of the 35 bee species selected for extrapolating their minimal pollen requirements from the regression model

Bee species	Average dry body mass						
	Females			Males			Species
	(mg)	*sd*	*n*	(mg)	*sd*	*n*	(mg)
Andrena curvungula	**28.1**	7.2	10	**14.7**	1.9	10	**21.4**
Andrena hattorfiana	**36.5**	4.9	10	**20.7**	3.1	10	**28.6**
Andrena marginata	**11.5**	3.4	10	**5.2**	1.4	10	**8.4**
Andrena pandellei	**21.5**	3.2	10	**10.6**	2.1	10	**16.1**
Andrena probata	**30.5**	3.1	10	**21.7**	5.1	10	**26.1**
Melitturga clavicornis	**45.1**	7.5	10	**35.6**	7.0	10	**40.4**
Dufourea dentiventris	**6.6**	3.0	10	**4.3**	0.6	10	**5.5**
Rhophitoides canus	**7.2**	1.9	7	**4.0**	0.6	10	**5.6**
Rophites algirus	**14.8**	2.3	10	**9.9**	1.6	10	**12.4**
Systropha curvicornis	**12.3**	1.7	10	**14.2**	3.1	10	**13.3**
Systropha planidens	**18.9**	4.1	5	**25.5**	3.3	10	**22.2**
Lasioglossum clypeare	**5.1**	0.9	10	**3.5**	0.1	2	**4.3**
Lasioglossum costulatum	**15.5**	3.8	10	**8.2**	1.7	10	**11.9**
Melitta dimidiata	**37.7**	4.3	5	**24.8**	3.2	10	**31.3**
Melitta haemorrhoidalis	**32.6**	5.1	10	**16.8**	3.9	10	**24.7**
Melitta leporina	**22.1**	3.7	10	**17.2**	3.5	10	**19.7**
Melitta nigricans	**20.2**	2.2	5	**12.0**	2.4	10	**16.1**
Anthidium manicatum	**32.0**	6.6	10	**51.7**	13.9	10	**41.9**
Anthidium punctatum	**18.9**	2.8	10	**18.7**	1.9	10	**18.8**
Megachile parietina	**80.2**	10.1	10	**46.1**	11.1	10	**63.2**
Chelostoma campanularum	**1.9**	1.1	10	**1.6**	0.4	10	**1.8**
Chelostoma grande	**32.2**	11.4	10	**25.3**	6.8	5	**28.8**
Hoplitis anthocopoides	**13.3**	2.4	10	**12.3**	2.0	10	**12.8**
Hoplitis dalmatica	**46.4**	4.8	10	**38.3**	4.1	10	**42.4**
Hoplitis lepeletieri	**22.5**	3.9	10	**25.7**	4.6	10	**24.1**
Hoplitis loti	**16.3**	3.4	10	**11.6**	3.0	10	**14.0**
Hoplitis mitis	**15.1**	2.2	10	**13.7**	2.6	10	**14.4**
Hoplitis ravouxi	**12.2**	2.6	10	**9.1**	2.3	10	**10.7**
Osmia andrenoides	**8.9**	2.2	10	**8.3**	2.9	10	**8.6**
Osmia brevicornis	**23.4**	4.5	10	**14.1**	5.4	10	**18.8**
Osmia caerulescens	**15.5**	3.0	10	**7.1**	2.1	10	**11.3**
Anthophora balneorum	**58.7**	7.9	10	**33.6**	5.1	10	**46.2**
Tetraloniella salicariae	**18.3**	3.0	10	**11.8**	2.6	10	**15.1**

sd, standard deviation.

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