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Foraging Behaviour of Wild Bees at Hot Pepper Flowers (*Capsicum annuum*) and its Possible Influence on Cross Pollination

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Native bees are effective pollinators of hot pepper plants, *Capsicum annuum*. In four gardens in south-central Brazil (Patos de Minas and Brasília) flowers of three cultivars received visits from 16 species of bees in eight genera: *Hylaeus* (Colletidae), *Dialictus*, *Halictus*, *Augochlora*, *Augochloropsis* and *Ceratalictus* (Halictidae), *Exomalopsis* and *Bombus* (Apidae). No other insects were observed to visit the flowers. Some species of bee occurred in more than one garden. Individual bees gathered a full pollen load from 18 to 47 flowers and visited one to eight plants on a single foraging trip. In 76 shifts between plants, the bees made nine switches between cultivars. It is suggested that small native species of bees pollinate the flowers effectively and that their small foraging areas are important in keeping the cultivars of both hot and sweet peppers genetically distinct where several cultivars are grown close together.

Key words: *Capsicum annuum*, hot pepper, native bees, fruit set, Brazil.

INTRODUCTION

The likelihood that an animal will cross pollinate a flower depends on (*a*) the distance between conspecific plants, (*b*) the distance the animal is able to travel, (*c*) the number of flowers on a plant, (*d*) the amount of food available in each flower and (*e*) the amount of food the animal collects. The emphasis in the present investigation is on this latter factor which varies greatly with the type of visitor; for example, some animals continually take small amounts of food for their own consumption, whereas others (like nesting bees) forage at many flowers to feed others. Collection of substantial amounts of food on discrete foraging trips simplifies investigation into the visiting behaviour of bees. Ideally a foraging bee visits flowers until the maximum transportable amount has been collected.

Hot pepper, *Capsicum annuum* L. (Solanaceae), was chosen for the present investigation because several varieties are often cultivated close together, convenient numbers of flowers are open on a plant at the same time and both the bee visitors and flowers are small. The purpose of the study was to make a detailed investigation of the foraging activities of wild bees on the flowers.

The flowers of *Capsicum*, like those of many cultivated Solanaceae, are pendulous and each anther is tubular, dehiscing along a lateral slit. To obtain the pollen, the visitor must grip the anther and vibrate its wing muscles. In this way the pollen grains are dislodged and fall onto the insect, an activity termed 'buzz' pollination (Buchmann, 1983). Several genera of bees are adept at this behaviour, but it is of particular relevance to the cultivation of solanaceous species (tomato—*Lycopersicon esculentum* Miller; eggplant—*Solanum melongena* L., jiló—*S. gilo* Raddi; and sweet and hot peppers) that most species of bees, including honeybees (*Apis mellifera* L.), do not possess this ability. The flower contains five separate stamens and a single stigma. Depending on the temperature, the flowers open an hour or two after sunrise. However, dehiscence of the anthers, and hence access to the pollen, might be delayed and it has been reported that anthers sometimes fail to dehisce (Murthy and Murthy, 1962). Nectar accumulates near the base of the petals (Vogel, 1998).

There has been some confusion over the identity of the hot peppers of commerce. Some authors have referred to the plants they studied as *Capsicum frutescens* L., but in the opinion of both Purseglove (1968) and Cobley (1976) all types of sweet and most hot peppers are cultivars of a single species, *C. annuum*. Purseglove (1968) cites the work of Heiser and Smith (1953) who distinguished two closely related, cultivated species: *C. annuum* bears flowers singly in the leaf axils and the many cultivars produce various types of fruits; whereas *C. frutescens* bears clusters of flowers in the leaf axils and small, red, very hot fruits.

MATERIALS AND METHODS

Three cultivars of *C. annuum* were investigated. The flowers of all three appeared identical in colour, form and size. Despite differences in the sizes of the fruits, all measured 9–10 mm across the more separated petal tips. The cultivars have local names which vary throughout Brazil and elsewhere. The mature fruits can be recognized by the following characteristics: Type A, Creamy yellow; somewhat rounded, but with a rather squashed appearance. Larger: 2 to 4 cm long and 3 to 5 cm wide. This type is known as 'pimenta-de-cheiro' in the States of Bahia and Pará in Brazil, 'cambaci' in central Brazil and as 'manzana' in other parts of Latin

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America. Type B, Bright red; long and pointed. Larger: 5 to 10 cm long and 1·5 to 2·5 cm wide. This type is known in Brazil as 'dedo-da-moça' (maiden's finger). Type C, Bright red; long and pointed. Smaller: 1·5 to 3 cm long and 0·5 to 1 cm wide. This type is known throughout Brazil as 'malagueta' and is very like 'red serrano' and 'cayenne' elsewhere.

To indicate the size variation among species of bees, the fore-wings were measured on three females of each.

Surveys were conducted on the species of bees that visited the flowers of *C. annuum* in two suburban gardens 1 km apart in Patos de Minas, Minas Gerais State, Brazil (18° 35′ S, 46° 30′ W) from February 1994 to October 1996 and additional observations were made in two gardens near Brasília (15° 52′ S, 48° 52′ W and 15° 55′ S, 48° 53′ W) in October 1996. The plants in Brasília were grown from seed of the plants in Patos de Minas.

Detailed observations of bees' activities were made in the two gardens in Patos de Minas. Mature plants with flowers of all three cultivars were available to the bees at both sites. The numbers of plants at site 1 were four of type A, two of type B and three of type C, and at site 2 there were, respectively, five, five and six. As the objective of the study was to investigate the foraging behaviour of the bees, the distances recorded between plants were the minimum distance between the closest open flowers of each pair of plants regardless of cultivar.

Activities of foraging bees on the plants were observed on 10 d for 30 min per day totalling 5 h per site. Data were collected between 0800 h and 1000 h because previous observations from 0700 h to 1800 h showed that after 1000 h fewer bees visited the flowers and each bee spent less time at each flower and visited greater numbers of flowers per unit time. Periods of 3 or 4 weeks passed between the collecting days so that the size of the bee populations was not depleted. To verify the determination of the species and so as not to count a visitor more than once, each bee was collected after observation of her had ceased.

For some species, the number of flowers a bee visited to obtain a full load of pollen was estimated. The flowers of *C. annuum* also produce nectar (Vogel, 1998) but, as it is not possible to ascertain the amount accumulated by foraging bees, estimates were limited to the quantities of pollen they collected. Bees which arrived at the plants without pollen on the scopa or corbicula were identified and observed until they left the vicinity of the plants and it was estimated that they carried a full pollen load. From previous observations it had proved possible to ascertain, in most instances, when a bee had finished collecting food on a foraging trip: when a bee stops foraging at a flower and immediately flies off she probably returns to her nest, although occasionally a bee flies several centimetres upwards, presumably to orient herself, before flying off. Alternatively when a bee approaches several flowers without feeding, and flies close to other plants, it is very likely that she has not accumulated a full load of food and is looking for flowers. *Bombus* and *Hylaeus* were excluded from this analysis because too few individuals were encountered. All the workers of *B. atratus* carried pollen on their arrival and none bore a full pollen load on leaving, so the number of flowers these bees visited to gather a full load could not be estimated. It was not possible to distinguish the start of a foraging trip for females of *Hylaeus tricolor* because members of this genus do not carry the pollen externally, but ingest it with the nectar (O'Toole and Raw, 1991).

RESULTS

The visitors

A total of 207 females representing 16 species and belonging to either genera of bees visited the flowers of hot pepper at the four sites. Four genera were especially well represented (*Dialictus* with 40 individuals, *Augochlora* with 35, *Augochloropsis* with 35 and *Exomalopsis* with 45) and comprised 75% of the total number of bees collected (Table 1). Male bees were not seen visiting the flowers, nor were *Apis mellifera* or other taxa of insects. These data are presented by site and not by plant because many bees visited more than one plant and some visited more than one cultivar. The lengths of the fore-wings of the bees ranged from 3·7 mm to 16 mm (Table 1), while those of the seven studied in greater detail were 3·7 to 8·9 mm (Tables 2 and 3).

The numbers of individual bees which visited the flowers at the four sites ranged from 39 to 62, and the number of species encountered at each site was ten and nine at Patos de Minas and ten and six at Brasília (Table 1). Of the 16 species collected, four were restricted to Patos de Minas and four to Brasília, while eight occurred at both localities. Six species were confined to one site, three to two sites, five to three sites, while two species were found at all four sites. In terms of the genera, members of *Augochloropsis* and *Exomalopsis* were present at all four sites, those of *Dialictus*, *Augochlora* and *Bombus* occurred at three, while *Hylaeus*, *Halictus* and *Ceratalictus* were only found at one site each. The method of percentages of similarity of Raabe (1952, cited in Southwood, 1966) was used to compare sites. The numbers of individuals of each species at a site are converted to percentages of the total at that site and the percentage of individuals of all species present at two sites are compared, summing the lowest value of each species (a species occurring at only one site having a zero value where it was absent). There was relatively little difference between sites; the proportions they had in common varied from 36 to 57% with slightly higher values between than within towns (Table 2).

Foraging behaviour

In the study areas, individual plants of the three cultivars bore up to 62 (type A), 56 (type B) and 96 (type C) open flowers at one time. The sequence of plants and the number of flowers a bee visited on each of them were recorded for 23 females of seven species (Table 3). The bees collected pollen and nectar from 756 flowers (261 flowers of type A, 65 of type B and 259 of type C). The bees visited one to eight plants on a single foraging trip, but only three bees visited more than six. Two bees, one of *Dialictus picadensis*

TABLE 1. *Numbers of individuals of the 16 species of bees which visited flowers of hot peppers,* Capsicum annuum, *during 5 h of observation at each of four sites in central Brazil*

Bee species	Length of fore-wing (mm)	Patos de Minas		Brasíla		Total
		Site 1	Site 2	Site 3	Site 4	
Dialictus picadensis (Strand)	2·4	3	8	–	8	19
Dialictus ypirangensis (Schrottky)	2·6	11	5	–	5	21
Hylaeus tricolor Schrottky	2·6	6	–	–	–	6
Augochlora thalia Smith	2·7	–	7	7	–	14
Ceratalictus theius (Schrottky)	2·8		2	–	–	2
Augochloropsis laeta (Smith)	3·3 to 3·5	4	1	4	9	18
Halictus lanei (Moure)	3·5	4	–	–	–	4
Augochlora morrae Strand	3·5	5	8	4	–	17
Exomalopsis auropilosa Spinola	4·0	8	6	11	6	31
Exomalopsis analis Spinola	4·1	5	7	–	–	12
Augochloropsis wallacei (Cockerell)	4·4	–	–	4	–	4
Augochloropsis aurifluens (Vachal)	4·8	–	–	1	–	4
Augochloropsis heterochroa (Cockerell)	5·1	–	–	3	–	3
Augochloropsis cleopatra (Schrottky)	5·2	–	–	6	3	9
Exomalopsis fulvofasciata Smith	5·2 to 5·7	7	4	3	–	14
Bombus atratus Franklin	13 to 16	5	–	9	8	22
Totals		58	48	62	39	207

TABLE 2. *Comparison of percentages of similarity (after Raabe, 1952) of the species of bees that visited flowers of hot peppers,* Capsicum annuum, *at four sites in central Brazil*

	Site 2 (Patos de Minas)	Site 3 (Brasília)	Site 4 (Brasíia)
Site 1 (Patos de Minas)	57	37	41
Site 2 (Patos de Minas)		36	44
Site 3 (Brasília)			48

and one of *Augochlora morrae*, gathered a full pollen load from a single plant. The former visited 17 flowers on a plant which bore 47 open flowers and the latter 25 on a plant with 54 flowers. The mean number of flowers a bee visited on a plant varied among the three cultivars and averaged 6·7 on type A, 5·9 on type B and 9·6 on type C.

The 23 foraging bees made a total of 79 switches, of which 70 were to the same cultivar and nine were to different cultivars. *Dialictus ypirangensis* visited only type A, while *D. picadensis*, *Augochlora morrae*, *Augochloropsis laeta* and *Exomalopsis analis* visited types A and C, but on different foraging trips. *E. auropilosa* and *E. fulvofasciata* visited all three cultivars. Furthermore, one *E. fulvofasciata* switched between cultivars A and C during a single foraging trip. *E. auropilosa* was the least constant to a cultivar, and in 24 shifts between plants the four bees made seven switches from one cultivar to another. These were three switches from A to C, two from C to A and one each from B to C and from C to B (Table 4). As far as could be discerned, a bee did not return to a flower she had already visited on a foraging trip.

The bees made 79 switches between plants along 24 routes of which 74 were along 19 routes to adjacent plants (up to 124 cm). On only five occasions did a bee fly past a pepper plant in bloom to visit a more distant one and these routes were longer than those to an adjacent plant (125 to 272 cm). The mean (±s.d.) distances of the routes covered by the seven species ranged from 44 (±23) to 97 (±28) cm (Table 4) and the overall mean for all seven species is 81 (±43) cm.

The numbers of flowers of *C. annuum* visited by 23 bees of seven species to obtain a full pollen load were recorded. The species averaged 18·3 (±5·1) to 46·7 (±7·2) visits to flowers to gather a load and the period required for this activity varied from 2 min 18 sec (s.d. ± 24·8 sec) to 6 min 37 sec (s.d. ± 50·2 sec) (Table 5). The flowers of *C. annuum* are small for *Bombus atratus* which is much larger than any of the other species of bees encountered. Workers of *B. atratus* were seen to visit up to 53 flowers of *C. annuum* consecutively.

In general, smaller species worked more quickly than larger ones. The quickest was *Dialictus ypirangensis* which averaged 5·8 s per flower, while *Augochlora morrae*, *Exomalopsis fulvofasciata* and *E. auropilosa* were slowest (7·7 to 8·1 s). To an extent, the differences in the speed at which the seven species visited the flowers was a result of the time they spent flying between flowers and plants.

DISCUSSION

The visitors

Although other insects have been recorded pollinating sweet pepper (Jarlan *et al.*, 1997), only females of native species of bees were seen to visit the flowers of hot pepper. Neither the genera nor the species of bees that visited the flowers of *Capsicum annuum* differed substantially over distances of 1 km or 400 km. This result is evident in the comparison of percentages of similarity and in half of the genera accounting for 75% of the total number of bees collected.

TABLE 3. *Sequence of hot pepper plants,* Capsicum annuum *and the numbers of their flowers which 23 female bees of seven species visited*

Number of foraging trip	Bee species	Number of flowers and sequence of plants									Number of flowers visited per trip
1	*Dialictus picadensis*	A3	A9	A9							21
2	*Dialictus picadensis*	C17									17
3	*Dialictus picadensis*	A9	A5	A6							20
4	*Dialictus ypirangensis*	A*7	A#10	A*5	A#2						24
5	*Dialictus ypirangensis*	A5	A8	A4							17
6	*Dialictus ypirangensis*	A8	A6								14
7	*Augochloroposis laeta*	A*10	A6	A*5	A3	A8					32
8	*Augochloroposis laeta*	A9	A5	A12	A10						36
9	*Augochloroposis laeta*	C6	C8	C*10	C4	C*11					39
10	*Augochloroposis laeta*	C11	C14	C5	C12						42
11	*Augochlora morrae*	A*10	A#7	A5	A#6	A*8					36
12	*Augochlora morrae*	C25									25
13	*Augochlora morrae*	A4	A7	A2	A8						21
14	*Exomalopsis auropilosa*	A8	A5	A*8	A6	A*7	C7	C6			47
15	*Exomalopsis auropilosa*	A3	A9	A*7	C#8	A*6	C#7				40
16	*Exomalopsis auropilosa*	B5	B#8	B*4	C8	C8	C4	C5	B*3	B#6	51
17	*Exomalopsis auropilosa*	C10	C5	A7	A8	A6	A2				38
18	*Exomalopsis analis*	C25	C11								36
19	*Exomalopsis analis*	C9	C7	C12							28
20	*Exomalopsis analis*	A8	A2	A2	A15	A5					32
21	*Exomalopsis fulvofasciata*	A7	A*8	C5	C9	C11	A*6	A4	A5		55
22	*Exomalopsis fulvofasciata*	B13	B8	B8	B*7	B3	B*4				43
23	*Exomalopsis fulvofasciata*	C5	C9	C7	C12	C2	C7				42

Each line represents a foraging trip and each combination of letter and number represents a plant; letters are the cultivars (types A, B and C) followed by the number of flowers the bee visited on that plant before moving on. When a bee visited the same plant twice on a single foraging trip that plant is indicated by a pair of the same marks (either two * or two # on a single line). For example, the first bee visited two plants of type A, returned to the first plant and then moved back to the second.

TABLE 4. *The switches between hot pepper plants,* Capsicum annuum*, which 23 foraging bees of seven species made*

Bee species (cm)	Number of plants visited	Number of shifts between plants	Number of shifts between cultivars	Mean distance between plants visited (s.d.)
Dialictus picadensis	3	2	0	
Dialictus picadensis	1	0	0	
Dialictus picadensis	3	2	0	
Total	7	4	0	97 (28)
Dialictus ypirangensis	2	3	0	
Dialictus ypirangensis	3	2	0	
Dialictus ypirangensis	2	1	0	
Total	7	6	0	75 (19)
Augochloropsis laeta	4	4	0	
Augochloropsis laeta	4	3	0	
Augochloropsis laeta	4	4	0	
Augochloropsis laeta	4	3	0	
Total	16	14	0	67 (40)
Augochlora morrae	3	4	0	
Augochlora morrae	1	0	0	
Augochlora morrae	4	3	0	
Total	8	7	0	90 (21)
Exomalopsis auropilosa	6	6	1	
Exomalopsis auropilosa	6	5	3	
Exomalopsis auropilosa	8	8	2	
Exomalopsis auropilosa	6	5	1	
Total	26	24	7	95 (54)
Exomalopsis analis	2	1	0	
Exomalopsis analis	3	2	0	
Exomalopsis analis	5	4	0	
Total	10	7	0	44 (23)
Exomalopsis fulvofasciata	7	7	2	
Exomalopsis fulvofasciata	5	5	0	
Exomalopsis fulvofasciata	6	5	0	
Total	18	17	2	98 (68)

The sequence in which the individual bees are presented follows that of Table 3.

TABLE 5. *The numbers of flowers of hot peppers,* Capsicum annuum*, which seven species of bees visited to obtain a full pollen load*

Bee species	Number of bees recorded	Mean number (s.d.) of flowers visited per bee	Mean length of time (s.d.) observed at flowers (s)	Mean period per flower (s) based on two previous columns
Dialictus picadensis	3	19·3 (2·1)	134 (9·6)	7·1
Dialictus ypirangensis	3	18·3 (5·1)	138 (24·8)	5·8
Augochloropsis laeta	4	37·3 (4·3)	265 (20·9)	7·0
Augochlora morrae	3	27·3 (7·7)	234 (49·9)	7·7
Exomalopsis auropilosa	4	44 (6·1)	342 (40·7)	7·8
Exomalopsis analis	3	32 (4·0)	284 (18·0)	7·2
Exomalopsis fulvofasciata	3	46·7 (7·2)	397 (50·2)	8·1

Comments on outcrossing

The two contrasting requirements of fruit production in self-fertile annual plants are that self pollination can reduce genetic contamination of the cultivar, but cross pollination can substantially increase fruit set (Bateman, 1947). Both self and cross pollination of hot and sweet peppers, *C. annuum*, have been reported (Martin and Crawford, 1951; Murthy and Murthy, 1962). Erwin (1932) demonstrated that 71% of crossed flowers developed into fruits, whereas only 46% of selfed flowers did so. Moreover, Sampson (1936 in Free, 1970) reported that only 20% of bagged flowers set fruits.

C. annuum may be similar to tomato, which is self-fertile, but the flowers require disturbance to effect pollination (Rick, 1950). In order to shed light on this question, preliminary observations were made on fruit set of *C. annuum* under different conditions. Six similar plants of type C were grown behind glass. Their flowers did not receive insect visitors, nor were they subject to wind. After 7 d, the stems of three plants were shaken sharply three or four times each morning for 4 d; the undisturbed plants were controls. After

22 d none of the three control plants had set fruit, whereas the three plants that were shaken set 7, 11 and 12 fruits. This suggests that wind or the mechanical action of a non-specialist visitor enables self pollination of some flowers of *C. annuum*. A similar situation occurs in some varieties of strawberry and tomato (Rick, 1950; Allen and Gaede, 1963). This may explain the pollination of sweet pepper in glasshouses by *Eristalis tenax* (Jarlan *et al.*, 1997) where visits by hover-flies increased fruit set, but the authors state that the study did not discriminate between the mechanical action of the fly and transfer of pollen between flowers. It might also explain the report that ants pollinate the flowers of *C. annuum* (Purseglove, 1968; Cobley, 1976).

Two aspects of the foraging activity of bees are relevant to the question of outcrossing between cultivars; the number of flowers a bee visits on a foraging trip and the distance between cultivars. A small bee which gathers a full pollen load from 20 to 50 flowers of *C. annuum* is likely to visit very few plants on a foraging trip. Larger bees are able to carry larger loads over longer distances than smaller bees do (Raw, 1976; pers. obs.).

Clearly the distances between cultivars will also affect the degree of outcrossing. Apparently the first detailed investigation into this question was that of Cane and Mather (1943) who found that outcrossing between two radish varieties visited by honeybees was $>30\%$ when grown 20 cm apart, but was 1% at 4·5 m apart. The distances the bees traversed between flowering plants of *C. annuum* were short and, where several plants of the same cultivar were grown together, presumably the possibility of crossing between cultivars was small. This was illustrated at one of the sites near Brasília where less than 1 m separated plants of the three cultivars of *C. annuum*. The bees passed from one cultivar to another and the owners of the garden remarked that the peppers did not breed 'true'. At other sites outcrossing was not noticeable at a distance of 9 m.

The present work suggests that several small, native species of bees pollinate the flowers of *C. annuum* effectively. With their small foraging areas these bees may be especially important in maintaining the various cultivars of both hot and sweet peppers genetically distinct where the plants are grown relatively close together. The minimum distances required between cultivars to maintain their genetic identity is shorter when small species visit the flowers compared to plants whose flowers are visited by larger species, e.g. *Bombus* and *Apis*, which visit many more flowers to obtain a full load of food. Furthermore, this aspect of the behaviour of foraging bees has important implications for outcrossing and, therefore, for the maintenance of varieties of crops.

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