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Foraging by Male and Female Solitary Bees with Implications for Pollination

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Both male and female solitary bees visit flowers for rewards. Sex related differences in foraging efficiency may also affect their probability to act as pollinators. In some major genera of solitary bees, males can be identified from a distance enabling a comparative foraging-behavior study. We have simultaneously examined nectar foraging of males and females of three bee species on five plant species in northern Israel. Males and females harvested equal nectar amounts but males spent less time in each flower increasing their foraging efficiency at this scale. The overall average visit frequencies of females and males was 27.2 and 21.6 visits per flower per minute respectively. Females flew shorter distances increasing their visit frequency, relative foraging efficiency and their probability to pollinate. The proportion of conspecific pollen was higher on females, indicating higher floral constancy and pollination probability. The longer flights of males increase their probability to cross-pollinate. Our results indicate that female solitary bees are more efficient foragers; females seem also to be more efficient pollinators but males contribute more to long-distance pollen flow.

KEY WORDS: female; foraging; male; Mediterranean; pollination; solitary-bees.

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INTRODUCTION

Bees, whose nutrition is solely dependent on floral resources, are considered one of the most important groups of pollinators (O’Toole and Raw, 1991). The number of bee species in the world is estimated at 20,000–30,000, most of which are not social but solitary bees (Michener, 2000). Male bees forage only for themselves whilst females forage also to provision their larvae, males also perform at least two co-occurring activities, foraging and mate searching, while females concentrate mainly in foraging. Therefore, it is expected that male and female solitary bees will differ in their foraging efficiencies and their contribution to pollination.

The movement of animals is determined by many factors but mainly by foraging, predator avoidance and mate searching, separately or in combination. Female fitness depends mainly on the number and quality of their offspring, which is closely dependent on foraging efficiency, whereas male fitness is mainly affected by the number of females fertilized by each male (Bonduriansky, 2001). Such differences between male and female bees should affect their foraging behavior and their consequent efficiency to act as pollinators. Females, which are responsible for the nutrition of the young next generation, are expected to forage in a more efficient way and consequently play a more important role in pollination than males (O’Toole and Raw, 1991; Proctor and Yeo, 1973). However, this hypothesis has never been critically examined.

Optimal foraging theory states that animals forage in such a way as to maximize their fitness (Waddington, 1983; Milinski and Parker, 1991). A bee that maximizes its energy intake by collecting more nectar in a shorter time and with less energy expended increases its fitness (Pyke *et al.*, 1977; Waddington, 1983; Bertsch, 1987). Nectar foraging efficiency depends mainly on the amount and caloric value of nectar intake, the average time spent visiting a single flower, flight duration and distance between successive visits and the distance of the flowering patch from the nesting site (Harder *et al.*, 2001). It is generally accepted that bees forage in a near to optimal way (Pyke *et al.*, 1977; Waddington, 1983; Motro and Shmida, 1995). Pollen is also a very important constitute of a bee’s diet, but bees’ foraging efficiency when gathering pollen has rarely been studied.

The amount and the spatial pattern of nectar distribution within a patch vary in space and time (Pleasants and Zimmerman, 1979, 1983; Marden, 1984a, 1984b; Selten and Shmida, 1991; Shmida and Kadmon, 1991; Kadmon and Shmida, 1992). Each foraging individual visiting a flowering patch must make a decision, after each visit, whether to stay in the patch or leave for a richer one (MacArthur and Pianka, 1966). The decision to stay or leave is based mainly on the reward obtained in the last few (1–3) visited flowers (Pyke, 1982; Waddington, 1983; Cibula and Zimmerman, 1986; Kadmon and Shmida, 1992; Dukas and Real, 1993a, 1993b; Friedman and Shmida, 1995; Motro and Shmida, 1995; Keasar *et al.*, 1996; Thomson and Chittka, 2001).

Foraging bees are likely to fly short distances and change directions between successive visits in high reward patches and fly longer distances in the same direction in low reward patches (Pyke, 1978, 1979, 1982; Marden and Waddington, 1981; Waddington, 1983; Waser, 1983; Motro and Shmida, 1995; Keasar *et al.*, 1996). This type of local search behavior was termed ‘Area Restricted Search’ by Tinbergen *et al.* (1967) and ‘near-far’ strategy by Motro and Shmida (1995) and is considered an optimal foraging mode (Pyke, 1978; Waddington, 1983). When handling time and flight distances are short, energy gain is maximized (Hodges and Wolf, 1981; Kadmon and Shmida, 1992). Shmida (Motro and Shmida, 1995) demonstrated that in rich and highly rewarding patches the ‘near–far’ searching pattern is advantageous and is an evolutionarily stable strategy (ESS). Thus, ‘near–far’ foraging behavior can be used as a measure for foraging efficiency.

Floral constancy, or fidelity, refers to the tendency of a pollinator to restrict its visits to flowers of a single species or morph (Waser, 1986). Floral constancy may lead to higher foraging efficiency by the pollinator and to higher pollination probability of the plant (Free, 1963, 1970; Waser, 1986). Floral constancy is extremely high in honeybees (Wells and Wells, 1986), whereas bumblebees tend to visit flowers of one species at high frequency – the ‘major,’ but also forage simultaneously on some other species at low frequencies – the ‘minors’ (Heinrich, 1979).

Our study compared various parameters (bout duration, floral visitation rate, percentage of ‘near’ visits, single flower handling time and percentage of conspecific pollen) of foraging male and female solitary bees. The comparison was made by observations on male and female bees that foraged simultaneously in the same flowering patches, which makes the results more meaningful. The aims of the research were: (1) to examine the hypothesis that there is a sex dependent difference in the foraging of solitary bees; (2) using quantitative data we tested our prediction that female solitary bees are more efficient foragers, (3) to discuss the possibility that females also contribute more to pollination than males.

METHODS

Study Area and Species

The study was conducted in Mediterranean natural habitats, on Mt. Gilboa (32.2°E, 35.4°N) and Mt. Meiron (33.0°E, 35.3°N) in northern Israel during the spring of 1998 and 1999.

To test our hypotheses we selected three solitary bee species with distinctive phenotypic differences between the sexes. The males of all studied species have much longer antennae than females and a bright yellow or white patch on their forehead (Eickwort and Ginsberg, 1980), but there are no distinctive size differences between the sexes.

Anthophora plumipes (Pallas) (Anthophoridae) is widespread and common throughout Mediterranean Israel and occurs in a variety of color forms from NW Europe across central Asia as far east as temperate Japan. *Habropoda tarsta* (Anthophoridae) is widespread and common throughout Mediterranean Israel, widespread in the Mediterranean Basin and southern central Europe, and is found at least as far as the Caucasus. *Eucera nigrilabris* Lep. (Eucerindae) is common in the Mediterranean region of Israel (O' Toole, C. personal communication).

The males of most solitary bee species emerge earlier than the females and disappear early in the season after mating, whereas the females stay active longer provisioning brood cells for the next generation (O'Toole and Raw, 1991). Our observations were conducted during the overlapping activity period when both sexes were foraging.

We selected Mediterranean plant species that have conspicuous nectar producing flowers, create relatively dense flowering patches and are major nectar sources. The selected plant species have different types of inflorescence. *Symphytum palaestinum* Boiss. (Boraginaceae), *Rosmarinus officinalis* L. (Lamiaceae) and *Salvia fruticosa* Mill. (Lamiaceae) are small shrubs that have vertical inflorescences. *Trifolium clypeatum* L. (Fabaceae) is an herbaceous plant with many small flowers in heads that form a uniform carpet-like flowering. *Alkanna strigosa* Boiss. (Boraginaceae) is a dwarf shrub typical of the arid part of the Mediterranean region with many small flowers aggregated in heads (Zohary and Feinbrun-Dotan, 1966–1986; Fragman *et al.*, 1999).

Foraging Behavior

Our study compared various variables of foraging behavior by male and female solitary bees. We have observed about 270 and 290 bees during

Table I. Location, Study Plants, Their Pollinators and the Estimated Number of Flowers per Observation Patch

Location	Plant species	Pollinator species	Number of flowers per observation patch
Meiron	*Symphytum brachicalym*	*Habropoda tarsta*	20–200
Meiron	*Rosmarinus officinalis*	*Anthophora plumipes*	50–500
Meiron	*Salvia fruticosa*	*Anthophora plumipes*	50–100
Meiron	*Trifolium clypeatum*	*Anthophora plumipes*	500–1000
Gilboa	*Alkanna strigosa*	*Eucera nigrilabris*	500–2000

1998 and 1999 respectively. Detailed information on the location, plant and pollinator species and the estimated number of flowers in each observation patch is presented in Table I. The number of flowers in each observation patch were determined by our ability to observe all visiting bees.

We compared by observations on male and female bees that foraged simultaneously in the same flowering patches. This type of comparison controls for the effects of many other environmental variables that are known to affect foraging behavior, such as temperature, wind, patch size and density, co-flowering species and other co-foraging bees.

Observations on foraging behavior were made from 06:00 to 16:00. Similar numbers of male and female bees were observed on each plant. To reduce repeated observations on the same individual plants or pollinators, the distance between flower patches was more than 10 m but in most cases more than 50 m apart and each observation-patch was observed for 30 min and then switched. We defined an observation-patch as a sub-unit of the foraging area (1–5 m^2) in which we could follow the activity of all pollinators. Hence, observation-patch size was determined according to flower size and density and bee activity for each plant species (Table I).

In each observation session (30 min) we followed each visiting bee, determined its species and sex and measured the total time of the forage bout between its arrival at the observation-patch and its departure from it (or our losing sight of it). For each individual visitor we calculated the visit frequency (number of visits per flower per minute) calculated from the number of visits during a single bout. The handling time of a single flower was directly measured for 25 males and 25 females of two bee species (*A. plumipes* and *E. nigrilabris*) on three plant species (*T. clypeatum*, *S. fruticosa* and *A. strigosa*).

For each individual visitor we monitored the number of ‘near’ and ‘far’ flights between two successive visits and calculated the proportion of ‘near’ flights out of the total number of flights. For each plant species we defined ‘near’ or ‘far’ flights according to the distance of successive visits. For *A.*

strigosa and *T. clypeatum* 'near' was a visit on the same flowering head and 'far' was to another flowering head. For *R. officinalis* and *S. fruticosa* 'near' was a visit on the same vertical inflorescence, or another one up to a distance of 5 cm and 'far' was to a distant inflorescence (>10 cm). For *S. palaestinum* 'near' was a visit on the same inflorescence or the one next to it and 'far' was on a distant inflorescence (>20 cm). In most cases 'far' flight resulted in landing on another individual.

Nectar

Nectar was collected and measured by means of 1 μl and 1–5 μl calibrated micro-pipettes (Vitrex – Modulom – I/S – Denmark). To examine whether visiting bees consumed all the nectar in a flower on a single visit, plants of *T. clypeatum*, *S. fruticosa* and *A. strigosa* were covered with fine cloth nets overnight to prevent insect access. The next morning nectar volume was measured in 10 covered flowers that had not been visited; then the net was removed and bees were allowed to visit previously bagged flowers; the remaining nectar volume was measured in 10 flowers immediately after the visit of a bee. Because of the small nectar amount left in visited flowers, we removed the flower immediately after a visit and collected the nectar in a destructive way from the back of the flower.

Pollen Analysis

First we prepared a reference collection of methylene-blue stained pollen for the study plants and the co-flowering plants. For pollen load analyses we caught 10 males and 10 females on each of the study plants. Pollen was washed from the bees with 5 ml of 70% alcohol and stained with methylene blue. The mixed stained pollen suspension was sampled and examined under a light microscope counting conspecific pollen grains (of the study plant on which the bee was captured) and all other pollen grains in the microscope field. The average proportion of conspecific pollen, as a measure of floral constancy, was calculated as an average of three different microscopic fields (Ne'eman and Dafni, 1999). *T. clypeatum* was the only species with pollen that could not be separated from that of other close *Trifolium* species, so the proportion of congeneric pollen was not calculated for this genus.

Data Analyses

To compare two or more averages among groups, we used t-test or ANOVA respectively. To obtain a normal distribution, proportions were arcsine(square root(P)) transformed before the statistical analyses. Statistical analyses were performed with SYSTAT 8.0 (SPSS Inc. 1998).

RESULTS

Flower handling time by males was about one third of that by females and the differences in all examined cases were significant (Fig. 1). Two-way ANOVA explained 84% of the variation with significant effects of bee sex and plant species on flower handling time with no interaction between them (Table II). The average (± SD, $n = 20$) nectar volume in overnight covered flowers of *T. clypeatum*, in *S. fruticosa* and *A. strigosa* was 6.5 ± 0.5 μl, 3.04 ± 0.2 μl, and 0.9 ± 0.2 μl respectively. After any single visit of a male or female bee of any species to a previously unvisited nectar full flower, no nectar could be extracted with a micro-pipette.

In 1998 visit frequency by male and female bees in the flowers was not different; but in most cases in 1999 females visited flowers significantly more

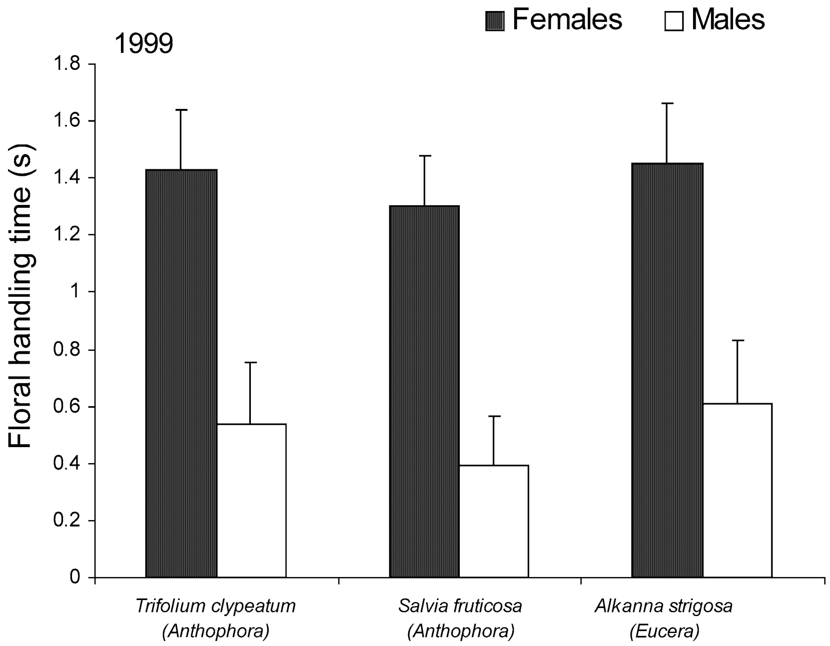

Fig. 1. Average floral handling time by male and female solitary bees (X axis in parentheses) foraging on various plant species (X axis) during 1999 ($n = 156$). Error bars represent S.D.

Table II. Effect of Bee Sex, Plant Species and Their Interaction on Floral Handling Time by Male and Female Solitary Bees in 1999, Tested by Two-way ANOVA

Variable	Sum of squares	*df*	F	*P*	r^2
Sex	30.312	1	739.194	<0.001	0.835
Plant	0.936	2	11.410	<0.001	
Sex × Plant	0.036	2	0.435	0.648	
Error	6.151	150			

frequently (Fig. 2). Plant species significantly affected floral visit frequency in both years, while bee sex and the interaction were significant only in 1999 (Two-way ANOVA, Table III).

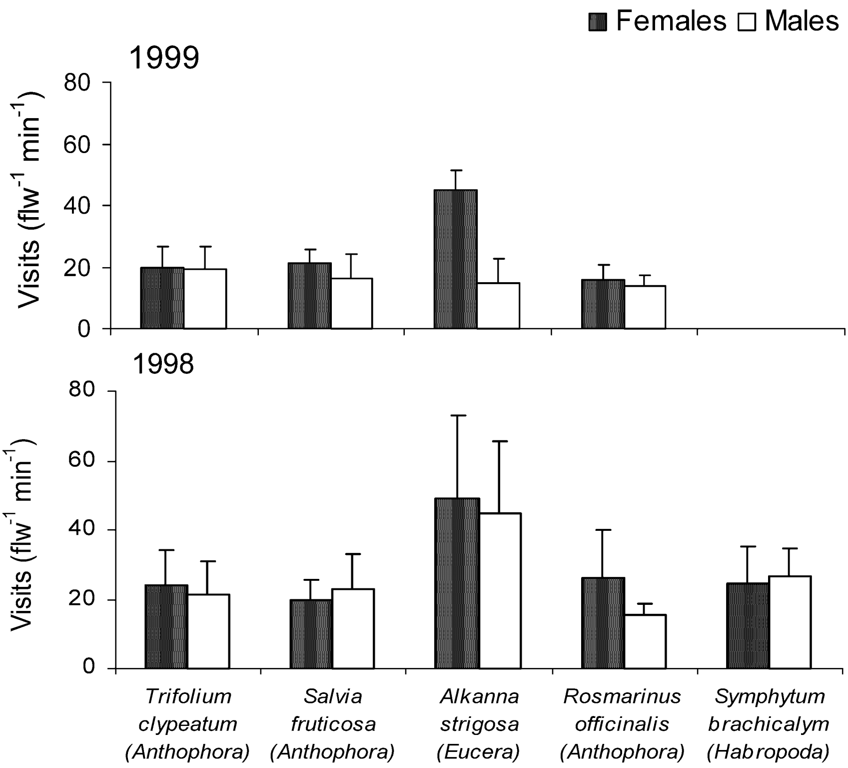

Fig. 2. Average floral visit frequencies by male and female solitary bees (X axis in parentheses) foraging on various plant species (X axis) during 1998 ($n = 279$) and 1999 ($n = 296$). X labels are identical for both years. Error bars represent S.D.

Table III. Effect of Bee Sex, Plant Species, and Their Interaction on Visit Frequencies by Male and Female Solitary Bees, Tested by Two-way ANOVA

Year	Variable	Sum of squares	*df*	*F*	*P*	r^2
1998	Sex	174.093	1	0.671	0.413	0.359
	Plant	38226.038	4	36.852	>0.001	
	Sex × Plant	790.261	4	0.762	0.551	
	Error	69756.645	269			
1999	Sex	3085.037	1	10.778	0.001	0.350
	Plant	11174.066	3	13.013	>0.001	
	Sex × Plant	18208.193	3	21.204	>0.001	
	Error	82434.908	288			

The proportion of ‘near’ visits, out of the total number of visits, by females was double that by males and all differences were significant (Fig. 3). Bee sex had a significant effect on the proportion of ‘near’ visits in 1998 and 1999. Plant species and its interaction with bee sex had a significant effect only in 1999 (Two-way ANOVA, Table IV).

The average duration of a forage bout was longer for female than for male bees in all examined combinations of plant and bee species. In all plant species except *T. calypeatum* the difference was significant (Fig. 4). Bee sex and plant species had a significant effect on the duration of forage bouts in 1998 and 1999 (Two-way ANOVA, Table V). The results indicate that females forage in a more local and restricted area than males, which forage in more distant patches. However, the relatively low explained variation (r^2 in Table V) indicates that there are additional factors affecting duration of forage bouts besides bee sex and plant species.

The proportion of conspecific pollen grains (the pollen of the foraged plant) out of the total number of pollen grains on bees’ bodies was in all cases more than double on females than on males and all differences were significant (Fig. 5). Bee sex had a significant effect on the proportion of conspecific pollen, but there was no effect of plant species on the proportion of conspecific pollen and there was no interaction between the factors (Two-way ANOVA, Table VI).

DISCUSSION

Foraging

The results demonstrate a clear difference in floral handling time between males and females; females stayed three times longer in each flower

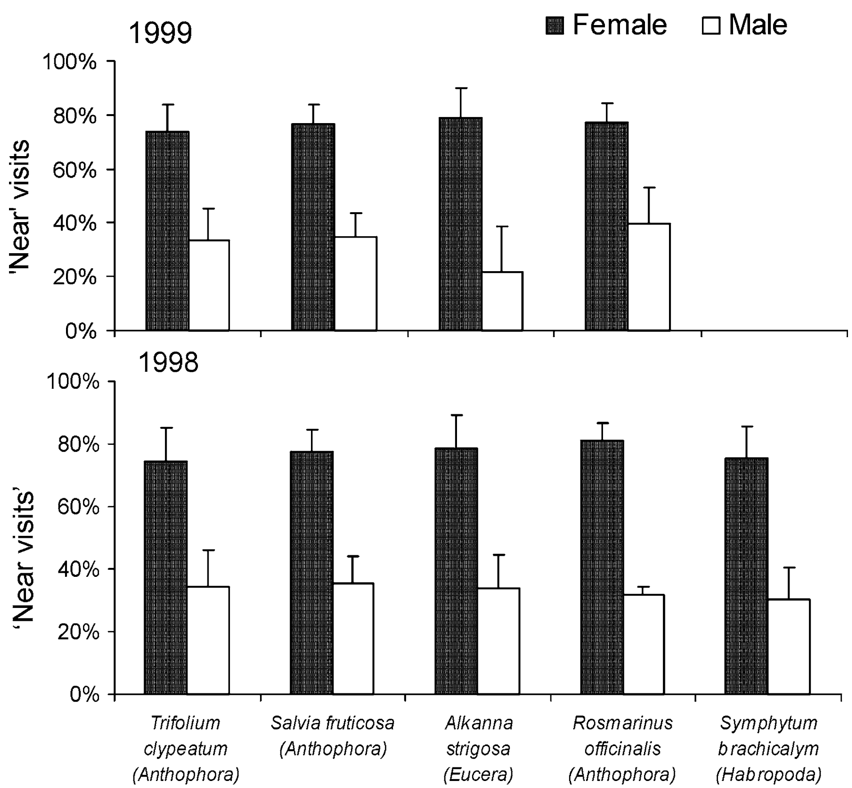

Fig. 3. Average proportion of 'near' visits by male and female solitary bees (X axis in parentheses) foraging on various plant species (X axis) during 1998 ($n = 279$) and 1999 ($n = 296$). X labels are identical for both years. Error bars represent S.D.

Table IV. Effect of Bee Sex, Plant Species, and Their Interaction on the Proportion (Arcsin Square Root Transformed) of 'Near' Visits Out of the Total Number of Visits by Male and Female Solitary Bees, Tested by Two-way ANOVA

Year	Variable	Sum of squares	*df*	*F*	*P*	r^2
1998	Sex	6.630	1	478.602	>0.001	0.805
	Plant	0.076	4	1.372	0.244	
	Sex × Plant	0.051	4	0.919	0.454	
	Error	3.726	269			
1999	Sex	13.984	1	677.668	>0.001	0.787
	Plant	0.390	3	6.303	>0.001	
	Sex × Plant	0.886	3	14.317	>0.001	
	Error	5.943	288			

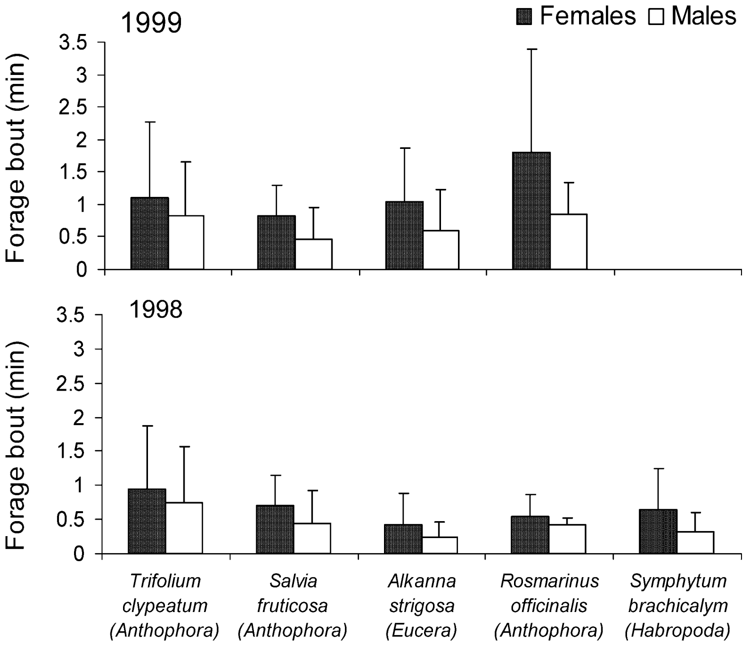

Fig. 4. Average duration of forage bouts by male and female solitary bees (X axis in parentheses) on various plant species (X axis) during 1998 ($n = 279$) and 1999 ($n = 296$). X labels are identical for both years. Error bars represent S.D.

than males. Flower handling time has been shown to be correlated this with the amount of nectar reward in flowers (Marden, 1984a, 1984b; Real and Rathcke, 1988; Shmida and Kadmon, 1991; Kadmon and Shmida, 1992). However, the shorter handling time of females cannot be explained by

Table V Effects of Bee Sex, Plant Species, and Their Interaction on the Duration of Forage Bouts Within an Observation Patch by Male and Female Solitary Bees, Tested by Two-way ANOVA

Year	Variable	Sum of squares	*df*	*F*	*P*	r^2
1998	Sex	1.347	1	4.774	0.030	0.148
	Plant	9.533	4	8.447	>0.001	
	Sex × Plant	0.279	4	0.247	0.911	
	Error	75.891	269			
1999	Sex	2.060	1	2.908	>0.001	0.145
	Plant	13.620	3	6.410	>0.001	
	Sex × Plant	16.111	3	7.583	>0.001	
	Error	203.973	288			

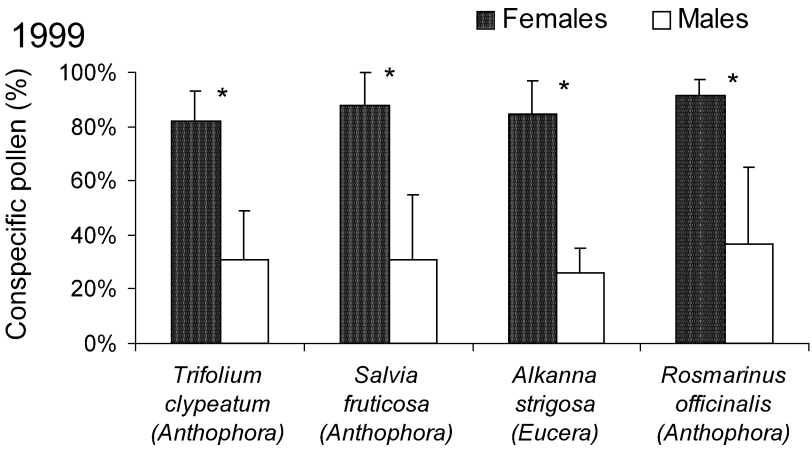

Fig. 5. Average proportion of conspecific pollen grains out of the total number of pollen grains on male and female solitary bees (X axis in parentheses) foraging on various plant species (X axis) during 1999 ($n = 80$). Error bars represent S.D. * indicates significant difference (T-test, $P < 0.05$).

differences in the collected nectar volume because we measured handling time of females and males simultaneously in the same flowering patch. Therefore, only if males visited a higher proportion of empty flowers than females, which is hard to believe because female and males were observed simultaneously in the same patch of flowers, would nectar amount have explained the differences in handling time. Differences in handling time among bee species when the nectar amounts were equal, have been described earlier (Thomson *et al.*, 1982; Bertsch, 1987), as have differences among individuals of the same species (Marden, 1984b). One explanation for the differences between sexes in the present study could be that the females collected nectar and pollen simultaneously from each flower, but

Table VI. Effect of Bee Sex, Plant Species, and Their Interaction on the Transformed (Arcsin(Square Root(P)) Proportion of Conspecific Pollen Grains on the Bodies of Male and Female Solitary Bees in 1999, Tested by Two-way ANOVA

Variable	Sum of squares	*df*	*F*	*P*	r^2
Sex	8.744	1	178.152	>0.001	0.717
Plant	0.164	3	1.115	0.349	
Sex × Plant	0.041	3	0.276	0.843	
Error	3.534	72			

we did not observe such behavior on the study plants. Another explanation could be that females were stricter in consuming all the nectar from each flower (Schmid-Hempel and Schmid-Hempel, 1987), whereas the males, which need no provisions for their brood, did not consume it completely (Hodges and Wolf, 1981). However, as mentioned, we could extract no nectar after a visit of either a female or a male. Another possible explanation is that because males hatch about a week earlier than females, they have more experience in manipulating flowers, which consequently is reflected in their shorter floral handling time. It is well known that floral handling time is a consequence of learning and therefore is negatively correlated with learning time (Gegear and Laverty, 2001), at least for naive animals at the beginning of the season. The fact that males and females consumed all available nectar in the visited flowers, but females spent a longer time in each flower, indicates that males are more efficient foragers than females at the local flower scale, may be because differences in the tongue length and width.

The frequency of floral visits is an important component of foraging efficiency. When foragers consume all the available nectar in visited flowers, as was the case for males and females in our study, energy intake is correlated with floral visit frequency. We found that visit frequencies were higher for females in 3 out of 9 cases (Fig. 2, Table III), indicating a tendency for a higher frequency in females. The fact that the amount of nectar extracted from each flower was similar for males and females, but visit frequencies were somewhat higher for females, indicate a small advantage in energy intake rate for females at the patch scale.

However, equal energy intake rate does not necessarily result in equal foraging efficiency, which also depends on energy expenditure. We had three indications that males spent more time and flew longer distances in their inter-floral flights than females. First, the proportion of ‘near’ visits was twice higher for females (Fig. 3, Table IV), indicating that males performed more ‘far’ flights than females. Consequently, males flew longer inter-floral distances than females. Second, because there was no pronounced difference in visit frequency between males and females and floral handling time was shorter for males (Fig. 4, Table V), we can deduce that males tended to spend more time on inter-floral flights than females. Third, the threefold shorter forage bouts of males (Fig. 4, Table V), namely the time they were observed within an observation-patch, also indicates that they flew longer than females. Therefore, the energy expended by males during foraging activity must have been higher than that of females, indicating a lower foraging efficiency of males.

To summarize, males and females extracted similar amounts of nectar in a single visit but males did so in a shorter time, indicating higher foraging efficiency at the flower scale. Because visit frequency was a little higher for females, energy intake rate for females tended to be higher at the patch scale. However, males spent less time on floral visits and generally flew longer distances between them. Therefore, their energy expended for gaining equal energy was higher. In all, it can be stated that male solitary bees are less efficient foragers than females, probably because of their mating-related activities which are performed simultaneously to foraging (O'Toole and Raw, 1991).

Pollination

Bees visit flowers for reward and plants benefit by being pollinated. The main sex-based difference between bees concerning pollination is that females collect pollen for their brood but males do not. Most of the pollen collected by females serves as supplies for their brood and only about 1% of plants' pollen production reaches stigmas (Harder *et al.*, 2001). All the study plants were nectariferous, offering mainly nectar as reward and produced only small amounts of pollen. Consequently all male and female bees were observed to forage only for nectar. Under this assumption let us compare the possible role and probabilities of male and female solitary bees to act as pollinators.

Not all visits to a flower result in successful pollination; pollination occurs only if viable compatible pollen is deposited on the receptive part of the stigma (Dafni, 1992). The receptive part of the stigma is relatively small and pollen is usually released in small portions; therefore, the probability of pollen carryover and deposition are correlated with visit duration and number of visits to a flower (Thomson and Plowright, 1980; Galen and Plowright, 1985; Thomson, 1985). Harder (1990) found that in six species, pollen removal increased with visit duration, but it did not additionally depend on the number of visits involved. By contrast, Mitchell and Waser (1992) manipulated the length and frequency of hummingbirds' visits to *Ipomopsis* and found that both male and female reproductive successes were correlated with the number of visits but not with visit duration. In our study floral handling time was 2–3 times longer for female than for male bees and visit frequency also tended to be slightly higher for female bees. Therefore, at the local flower scale females have a higher probability of contributing to pollination than males.

Pollinator movement pattern affects the effective distance over which pollen is dispersed (Waddington, 1981; Schulke and Waser, 2001), which consequently affects gene flow, reproductive success and brood quality (Handel, 1983; Waser and Piece, 1991). Short-range pollen dispersal, as performed by 'near' visits in our study, is usually associated with high visit frequency and high pollination probability. However, 'near' visits may increase self-pollination, geitonogamy, inbreeding and consequently low quality of brood in self-compatible plants (Darwin, 1876; Waser and Price, 1991; DeJong *et al.*, 1993). In self-incompatible plants 'near' visits may decrease fruit set and seed production by clogging the stigma with non-compatible pollen. By contrast, 'far' floral visits are usually associated with lower frequency, hence with low pollination efficiency. The longer range of pollen flow produced by 'far' visits enhances out-crossing and high quality of brood. However, in extreme situations 'far' visits may also cause outcrossing depression by reducing fertilization rate of spatially and genetically distant individuals (Waser and Price, 1991). The proportion of 'far' visits was 0.3 for females and 0.7 for males, namely males performed more than double the number of 'far' visits than females. Accordingly, males might contribute more to longer distance pollen flow and outcrossing while females might be involved more in short distance pollen flow, associated with drawbacks of geitonogamy and failure of seed production in self-incompatible plants.

Floral constancy is the selective visit of an individual pollinator to certain flower species, while bypassing other equally rewarding floral resources in the same habitat (Waser, 1986). Some scientists argue that constancy is adaptive by increasing foraging efficiency, while others argue that it is a result of limited memory capacity of the insects (see review by Chittka *et al.*, 1999). However, the advantage for the plants was recognized long ago (see in Chittka *et al.*, 1999), mainly by increasing the probability of conspecific pollen transfer among flowers (Waser, 1986; Chittka *et al.*, 1999; Gegear and Laverty, 2001). Constancy can be directly determined by behavioral observations or indirectly estimated by pollen load analyses (Ne'eman and Dafni, 1999). We observed no pollen collection by females on our study plants; therefore we could use the proportion of conspecific pollen on the bees' bodies as a reliable indicator for constancy. The proportion of conspecific pollen, pollen of a target plant on which a bee was caught adhering to the bee's body, was 2–3 times higher for female than for male bees (Fig. 5, Table VI). This is a good indication of the higher probability of females transferring pollen to conspecific stigmas. Field studies with bumblebee foragers (Chittka *et al.*, 1997; Gegear and Laverty, 2001) suggest that whether a bee is constant or switches to a different flower type may depend partly on the time and distance between a bee's departing a particular flower and encountering another flower of the same type. Assuming that learning flower-handling skills is similar in males and females and considering the longer inter-floral flights of the male bees, the 'search image hypothesis' could account for the observed differences in floral constancy because of the longer

Table VII. Comparison of Overall Foraging Behavior of Male (M) and Female (F) Solitary Bees

Utilization of a single flower	$F = M$
Flower handling time	$F > M$
Visit frequency	$F \geq M$
Proportion of 'near' visits	$F > M$
Duration of forage bout	$F < M$
Length of inter-visit flights	$F < M$
Proportion of conspecific pollen	$F > M$

time between successive visits (Gegear and Laverty, 2001). An alternative explanation is sensitivity of a bee's short-term memory to interference when learning a new flower model, or the difference in the time needed to use an active image in short-term memory or retrieve it from long-term memory (Chittka *et al.*, 1999). Both theories may explain the fact that males spend more time in flight between successive visits to flowers and that they are also less constant.

CONCLUSIONS

The results of our study allow a comparison of some major aspects of foraging behavior by male and female solitary bees, as summarized in Table VII. Both males and females harvested equal amounts of nectar from a single flower, but males spent less time in each flower, which makes them more efficient foragers at this scale, but decreases their probability of acting as pollinators. Flower visit frequencies tended to be higher for females, indicating somewhat higher energy intake efficiency and higher probability of females to act as pollinators. Females flew shorter distances between successive visits than males; consequently, females' energy expenditure during foraging was lower than males,' which increased females' relative foraging efficiency.

The higher proportion of 'near' visits increases the foraging efficiency of females and may compensate for their longer handling time. The longer flight distances may increase the probability of cross-pollination by males, which is important for seed-set in self-incompatible plants and increasing offspring quality in self-compatible plants. The higher proportion of conspecific pollen on females indicates a higher degree of floral constancy and of pollination probability. To conclude, our results indicate that female solitary bees are more efficient foragers; females seem also to be more efficient pollinators but males contribute more to long-distance pollen flow.

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