

Social Organization and Pollination Efficiency in the Carpenter Bee *Xylocopa pubescens* (Hymenoptera: Apidae: Anthophorinae)

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Many agricultural greenhouse crops suffer reduced yields due to insufficient pollination. This problem can be alleviated by introducing efficient pollinating insects into the greenhouse. The bee *Xylocopa pubescens* Spinola 1838, a candidate for domestication as an agricultural pollinator, is unique in its facultative social organization. Females either nest solitarily, or together with a second female (a non-reproducing guard). Social nesting occurs when food and nest sites are limited, and carries fitness benefits and costs to the bees as compared to solitary nesting. The implications of *X. pubescens*' social organization for crop pollination were investigated.

Honeydew melons were grown as a model crop in a small greenhouse. The non-crop plants *Portulaca oleracea* L., *Solanum rantonnetii* C., *Lavandula angustifolia* Mill and *Ocimum basilicum* L. supplemented the bees' diet. Social and solitary *X. pubescens* nesters were introduced into the greenhouse in alternation. The bees' daily activity pattern, the frequency and duration of visits to each flower species, and the run-lengths of consecutive visits to each flower species were recorded. The melons' fruit set, and the fruits' mass and seed number, were determined.

Social nesters visited *P. oleracea* more frequently than solitary bees when this species was in bloom. After *P. oleracea* finished blooming, socially nesting bees visited melon more often than solitary nesters. Social bees spent a longer time at the melon patch and tended to be more flower constant than solitary nesters, but spent less time per flower than solitary individuals. Solitary and social bees did not differ in their daily activity patterns and flower visitation rates. Pollination by both types of nesters resulted in similar fruit sets, fruit mass and fruit seed numbers.

The dissimilarities in foraging behaviour may reflect differences in the dietary demands of solitary vs social nesters. The similarity in fruit sets and flower constancy suggests that both nest types provide pollination services of similar quality.

Key words: *Xylocopa pubescens* Spinola 1838 – constancy – domestication – foraging – fruit set – greenhouse – honeydew melon – sociality

קיסר ת, שדה ע, שילו מ, זיו י [מדה"ח, מכללת אחוה, ד.ג. שקמים 79800]: **ארגון חברתי ועילות האבקה בדבורת העץ *Xylocopa pubescens* (L.) (Hymenoptera: Apidae: Anthophorinae)**. Entomol Gener 29(2/4): 225–236; Stuttgart 2007-01. --- [Article]

תקציר

גידולי חממת רבים סובלים מיבול דל ולא איכותי עקב האבקה לא יעילה של הפרחים. הדבורה *Xylocopa pubescens* מועמדת לביות כמאביק חקלאי פוטנציאלי בחממות. מאביק זה ייחודי בארגון החברתי הפקולטטיבי, המשתנה בהתאם לתנאי הסביבה. בסביבה עשירה במזון ובאתרי קינון, נקבות מקננות באופן יחידאי. לעומת זאת, בתנאי מחסור במזון ובאתרי קינון,

הדבורים מקימות קינים חברתיים המכילים שתי נקבות: דומיננטית המשחרת למוון ומתרבה, ושומרת שאינה מתרבה. במחקר זה בדקנו את הקשר בין הארגון החברתי בקן לבין יעילות האבקה של *X. pubescens*.

גידלנו בחממה קטנה מלונים (*Cucumis melo*) כגידול חקלאי, וכן ארבעה צמחי מרעה נוספים (*Portulaca oleracea*, *Ocimum basil*, *Solanum Rantonnetii*, *Lavandula angustifolia*). הכנסנו לחממה, לסירוגין, קינים יחידאיים וחברתיים. לגבי כל אחד מהם, אפיינו את התנהגות הדבורים (שעות פעילות, העדפת מיני הפרחים בחממה, משך שהייה על פרח, נאמנות) וכן מדדים מצד המלון (אחוז חנטת פירות, משקלם ומספר הזרעים שבהם).

דבורים חברתיות בקרו ב *P. oleracea* בתדירות גבוהה יותר מאשר דבורים יחידאיות. לאחר תום עונת הפריחה של *P. oleracea*, ביקרו הנקבות החברתיות בשכיחות גבוהה יותר במלון בהשוואה לנקבות היחידאיות. דבורים חברתיות שהו יותר בסביבת המלון ונטו יותר לנאמנות מאשר דבורים יחידאיות, אך שהו פחות זמן על פרח של מלון לעומת יחידאיות. דבורים חברתיות ויחידאיות לא נבדלו במדדי הפעילות היומיים שלהן ובסך מספר הביקורים שלהן בפרחי המלון. האבקה על ידי דבורים משני סוגי הקינון הובילה לשיעור דומה של חנטת פירות, ללא הבדל במשקל הפרי ובמספר הזרעים.

ההבדלים בהתנהגות השיחור בין קינון יחידאי לחברתי עשויים להעיד על דרישות תזונתיות שונות של קינים משני הסוגים. הדמיון בכמות ובאיכות הפירות שחנטו מוביל למסקנה, כי פרטים יחידאיים וחברתיים מעניקים שירותי האבקה באיכות דומה.

מילות מפתח: ביות, חברתיות, חממה, חנטה, מלון, נאמנות, שיחור.

1 Introduction

Pollination is required for the production of many food crops, and is therefore one of the most important ecosystem services provided to agriculture. Agriculture is highly dependent on insect pollination, particularly by the honeybee, *Apis mellifera* L [CUNNINGHAM 2002]. In addition to their traditional role in pollinating field crops, honeybees have also been introduced, in recent decades, as pollinators into enclosures. This effort was initiated in the Netherlands, where honeybees (later replaced by bumblebees) were first introduced into tomato greenhouses to substitute hand pollination [DE RUITER 1999]. Honeybees were also shown to efficiently pollinate eggplant and sweet peppers in enclosures [DE RUITER et al 1991, VAN DEN EIENDE 1994]. Honeybee pollination in greenhouses is now widely practiced worldwide, but suffers several limitations: Honeybee pollination is not sufficiently effective for some crops (such as plants that require buzz pollination [BUCHMANN 1983]). Honeybees also navigate and survive poorly in enclosures. In addition, honeybee colonies are declining worldwide because of habitat loss, diseases, pesticides, and other impacts [ALLEN-WARDELL et al 1998, KREMEN et al 2002, STEFFAN-DEWENTER et al 2005], creating a demand for additional pollination services. The domestication and use of additional pollinator species is desirable as a countermeasure to these problems. A pilot experiment in Australia demonstrated the feasibility of using carpenter bees for tomato pollination in enclosures [HOGENDOORN et al 2000]. This motivated a more detailed study of the carpenter bee *Xylocopa pubescens* L as a candidate agricultural pollinator in greenhouses in Israel [SADEH 2006].

X. pubescens is a large, polylectic and thermophilic bee of Ethiopian origin [GERLING 1989, LEYS et al 2002]. In Israel, the species forms extensive populations along the Jordan Rift Valley, from the Sea of Galilee southwards [BEN MORDECHAI 1978]. The bees typically dig branched nests in decayed wood, where they hibernate in winter and rear their brood in spring and summer. Females may be reproductively active for up to 120 days, enabling them to produce 4–5 broods [GERLING et al 1981]. Ovipositing females provision each brood cell with nectar and pollen, lay a single egg in the cell, seal it and proceed to construct the next cell. The development from egg to adult takes 27–35 days. Young adults that remain in the maternal nest before dispersal are provisioned with pollen by their mother [VELTHUIS & GERLING 1983, VAN DER BLOM & VELTHUIS 1988], and obtain nectar by trophallaxis [GERLING et al 1983].

Primitive social organization, which involves unequal reproduction by two co-nesting females, has been demonstrated in eight species of large carpenter bees [GERLING et al 1989]. *X pubescens* is unique in having intra-specific plasticity in social organization. That is, the same individual may alternate between solitary and social nesting, depending on environmental conditions, within a single breeding season [GERLING et al 1981, DUNN & RICHARDS 2003]. Over-wintered females nearly always start their nest solitarily, but solitary and social nests can be found simultaneously during the major part of the breeding season [HOGENDOORN et al 1993a]. Social nests contain a reproductively dominant forager, and a non-reproductive individual that guards the nest entrance. The guard may be a related female or a formerly reproductive, unrelated female. Nest development is rather complex, because different types of females may take dominance. Firstly, a newly-matured daughter may either guard her mother's nest, or supersede her mother as the dominant female. Secondly, at a later stage the dominance may be taken over by a sister. Finally, during all stages of nest development, an unrelated intruder may invade and usurp the nest. After take-over of dominance, the formerly reproductive female may remain in the nest as a guard [VAN DER BLOM & VELTHUIS 1988]. Thus, a guard may either be a young, pre-reproductive female, or a defeated formerly reproductive female. The frequency of social nesting increases as the reproductive season progresses, and may be imposed on females by shortage in nesting sites [GERLING et al 1981, DUNN & RICHARDS 2003].

Social nesters spend more time foraging outside their nests as compared with solitary individuals, perhaps because the presence of the guard in the nest reduces the risk associated with prolonged foraging [HOGENDOORN et al 1993a]. Social nesters also suffer fewer nest takeovers by intruders than solitary nesters, providing a possible benefit for social nesting when competition for nests is high. The guards, in turn, may benefit from increased indirect fitness (if related to the reproductive), and increase their chances of eventually taking over the nest [HOGENDOORN et al 1993b]. Thus, social organization can affect the fitness of *X pubescens* females. This begs the question whether social organization could also affect the bees' efficiency as pollinators, i.e. the fitness of their food plants. The present study aims to test the hypothesis that social nesters are more effective pollinators than solitary ones, since their foraging durations are longer, and the dietary requirements of their nests may be higher. This hypothesis was tested by comparing several parameters of foraging behaviour and pollination success between the two types of nesters. This comparison formed part of a larger effort to evaluate *X pubescens*' pollination efficiency in greenhouses [SADEH 2006].

2 Material and methods

2.1 The greenhouse and study plants

The study was conducted in an 8×4×4 m climate-controlled greenhouse. The temperature in the greenhouse ranged from 19–41 °C, relative humidity ranged from 26–86% and radiation ranged from 4–184 lux during the period of the study. 150 honeydew melon plants (*Cucumis melo* L var *Gallia*) constituted the research crop. The non-crop plants *Ocimum basilicum* L, *Portulaca oleracea* L, *Lavandula angustifolia* Mill, and *Solanum rantonnetii* C were also maintained in the greenhouse. *P. oleracea* and *S. rantonnetii* supplemented the bees' diet with pollen (preliminary observations showed that no pollen was collected from melon flowers). *O. basilicum* and *L. angustifolia* provided an additional nectar supply when melon blooming was insufficient.

Honeydew melons have several attractive characteristics as model crop plants: Plants carry male and hermaphroditic flowers, which can be easily distinguished morphologically. Hermaphrodite flowers have receptive ovaries and viable pollen, but self pollination does not occur spontaneously [ORR 1985]. This feature ensures that all developing fruit in the study were due to *X pubescens* pollination.

Flowers open in early morning, and bloom for 24 hours [SADEH 2006]. This characteristic enabled alternation between days of observations on solitary and social nests in the same greenhouse, and discrimination between flowers pollinated by different bee types.

To this end, all open hermaphrodite flowers were tagged on each observation day. Yellow and orange tags were used to mark flowers that bloomed during observations on solitary and social nests, respectively. This procedure allowed recognition of fruit arising from pollination by the two nest types. The alternation of observations on both nest types in a single greenhouse reduced pseudo-replication, because social and solitary bees were observed under very similar a-biotic conditions. Different individual bees and flowers were studied on each observation day. Therefore, each observation day was treated as a replicate.

2.2 Bees

Palm branches containing nesting *X pubescens* were collected from four locations in Israel. They were housed outside the greenhouse when not observed, and the bees were allowed to exit and reenter the nests without restriction. Nests were introduced into the greenhouse for observation periods of 2–3 days. They were checked for foraging activity one day before they were introduced into the greenhouse. Social nests were identified by the presence of the guard at the entrance after the forager exited the nest. Nests were moved into- and out of the greenhouse at night only, to minimize interference with bee activity. Solitary nesters were observed on 27 days and social nesters were observed on 12 days during July–September 2005. Ten solitary nests were introduced into the greenhouse on each observation day. Social nests were much less abundant, so that only 1–2 social nests were available on each day of observation. These nests were introduced into the greenhouse. To correct for the differences in the number of foragers observed on different days, the various behavioural measures were calculated per foraging bee, as detailed below.

2.3 Data collection

2.3.1 General flight activity

The bees' daily activity pattern was assessed by counting the number of active bees outside the nest at ten haphazardly determined time points every hour. The data were collected from 6 am till 6 pm (four observation days for solitary nests, five observations days for social nests). The proportion of activity records per hour out of the total number of activity records was calculated, for each observation day separately. This procedure corrected for the differences between observations in the number of foragers, and produced a separate activity histogram for each observation day. The activity histograms of solitary nesters vs social nesters were then averaged.

2.3.2 Visits to melon flowers

The frequency of foraging visits to melon flowers was measured by counting all visits directed to a sample of 100 flowers in a ten-minute observation period. Counts were conducted at 6 am, 8 am, 10 am and noon during five days of observation on solitary nests and five days of observations of social nests. Each count was divided by the number of active bees at the time of observation to obtain a measure of activity per forager (thereby correcting for the differences in number of nests between observations). Average daily frequency distributions of visits to melon flowers by solitary and social foragers were produced as described in section 2.3.1.

The duration of each of ten visits to melon flowers by 11 solitary individuals on five observation days was measured. Similarly, the durations of ten visits by each of 22 social bees was measured on eight observation days. Consecutive visits by the same individuals are not independent measurements. The mean visit durations on each observation day was therefore treated as a single data point. The Mann-Whitney U-test was used to compare between visit durations of solitary and social bees.

2.3.3 Nectar measurements

Preliminary observations indicated that the bees collected only nectar from the melon flowers. The correspondence between the bee's schedule of foraging activity and the plant's daily pattern of nectar secretion was assessed. For nectar production measurements, 40 randomly selected flowers of nectar were depleted (using 1 μ l pipettes) and covered with a fine mesh net before the start of bee foraging (6 am). The nectar content of one third of the initial sample (i.e. 13–14 flowers per sample) was determined at 9 am, 12 pm and 3 pm. Nectar volumes were measured using 1 μ l capillaries, and concentrations were determined using a Bellingham-Stanley hand-held refractometer [CORBET 2003]. Data from male and hermaphrodite flowers were combined, since they did not differ in their nectar production rates and were indiscriminately visited by the bees [SADEH 2006].

While foraging, bees consume and deplete some of the nectar produced by the flowers. The residual volume, termed nectar yield, is a combined function of nectar production and consumption rates. Nectar production rates do not depend upon the type of nest (social or solitary) introduced into the greenhouse. Therefore nectar yields are expected to provide a comparative measure of foraging intensity of social vs. solitary nesters. For example, lower yields for one of the nest types would indicate more intense foraging by its occupants. To determine yield, *X pubescens* nests were left in the greenhouse after recording of flower visitation rates for 24 additional hours. Nectar yields were sampled on the second day, to avoid interference with recording of the bees' activity. Nectar volumes were measured in 20 randomly selected flowers, using 1 μ l pipettes. The same flowers were non-destructively sampled at 6, 8, 10 and 12 am. The flowers that were used for activity recording were not longer in bloom on the next day. Different samples of flower were therefore used for behavioural observations and for nectar yield determination. Nectar was sampled on seven days for solitary nests, and on five days for social nests.

2.3.4 Choice of forage plants and constancy

The proportion of visits directed to each plant species that bloomed in greenhouse on each observation day was determined (on seven and five days for solitary and social nests, respectively). The proportions of open flowers per species out of the total number of open flowers in the greenhouse were determined as well. The proportions of visits to flower species are expected to equal their relative abundance in the greenhouse, if bees choose their forage plants randomly. To test this prediction, the distribution of flowers was compared with the distribution of visits. Data from each observation day were tested separately, using chi-square tests. The dependence of the distributions of visits on nest type was then tested, using G-tests of independence. For this purpose, all records collected on solitary bees during *P oleracea*'s blooming period were pooled and compared to data collected on social bees during the same period. The distribution of visits to forage plants between solitary and social foragers after *P oleracea*'s flowering period was compared in a similar manner.

Constancy is a pollinator's tendency to visit flowers of the same species in succession. This measure allows testing whether the insect's probability for staying on the same plant species is higher than random [JONES 1997]. Constant foraging increases an insect's pollination efficiency, because it ensures that the pollinator transports conspecific pollen between successively visited flowers [GOULSON 2003]. The run-lengths of consecutive visits to melon, the bees' main forage plant, were recorded during 27 observation days on solitary nesters and during 12 observation days on social nesters. The duration of each run of consecutive visits was also recorded. The mean number of visits per run, and the mean run duration in each plant species, were compared between social and solitary nesters.

2.3.5 Crop yield

Fruit mass and seed number were determined as measures of pollination efficiency, when the melons turned yellow [MCGREGOR 1976]. Fruit set was calculated as the proportion of flowers, available for pollination by solitary vs social bees that developed into mature fruit.

3 Results

3.1 Bee daily activity in relation to nectar availability

Both types of nesters were active in the greenhouse from 6 am to 6 pm (**Fig 1**). The daily activity distributions of the two types of nesters did not differ significantly (Kolmogorov-Smirnov, $Z = 0.392$, $p = 0.998$, $n = 26$). Visit frequency to melon peaked at 10 am for both types of nesters, but the peak was narrower for social nesters than for solitary ones (**Fig 2**). The temporal distribution of the visits to melon flowers differed significantly between social and solitary nesters (Kolmogorov-Smirnov, $Z = 2.041$, $p < 0.001$, $n = 40$). The number of visits to melon flowers also differed significantly between observation hours for social bees (One way ANOVA, $F_{3, 16} = 6.972$, $p = 0.003$), but not for solitary bees (One way ANOVA, $F_{3, 16} = 1.612$, $p = 0.226$). This difference supports the observation that social bees tended to concentrate their activity to a narrower time window than solitary bees.

Nectar production rates in melon flowers were maximal in early morning, and gradually decreased during the day (**Fig 3**). Nectar production rates did not correlate with the daily distribution of foraging visits to melon flowers by solitary bees (Pearson correlation = -0.028 , $p = 0.907$, $n = 20$) or social bees (Pearson correlation = -0.063 , $p = 0.792$, $n = 20$).

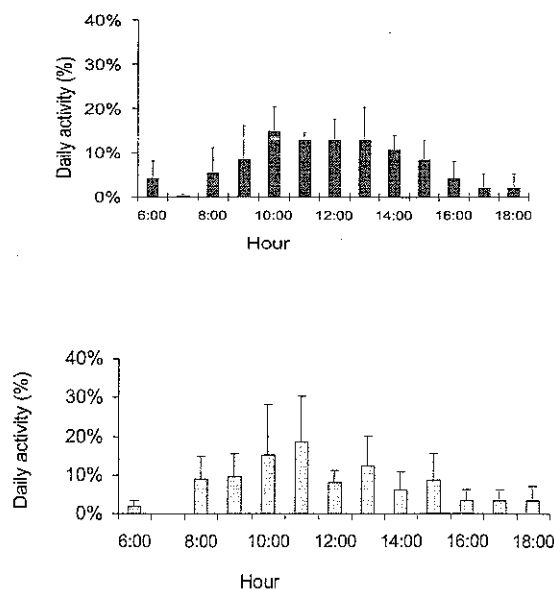


Fig 1: Daily activity distribution of social (black bars, top) and solitary (grey bars, bottom) nesters (Hymenoptera: Apidae: Anthophoridae: *Xylocopa pubescens* Spinola 1838). The proportions of activity records per hour, out of the total number of activity records, were first calculated for each observation day, then averaged over all observation days. Error bars are one standard deviation.

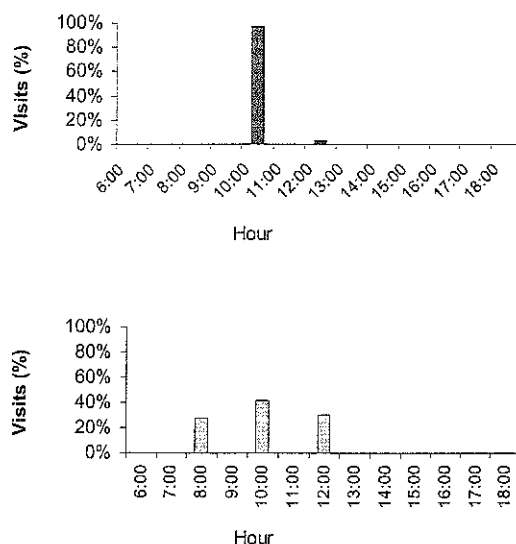


Fig 2: Visits frequency (%) of melon flowers (*Cucumis melo* L var Gallia) during morning hours, of social (black bars, top) and solitary (grey bars, bottom) nesters (Hymenoptera: Apidae: Anthophoridae: *Xylocopa pubescens* Spinola 1838). The proportions of visits per hour, out of the total number of visits, were first calculated for each observation day, then averaged over all observation days. Error bars are one standard deviation.

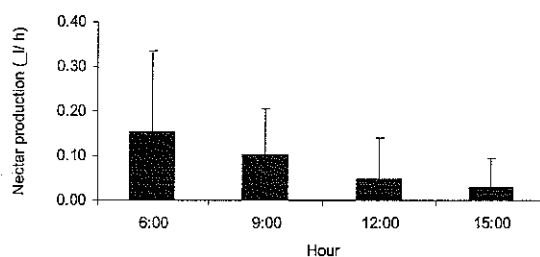


Fig 3: Mean hourly nectar production rates of melon flowers (*Cucumis melo* L var Gallia) during the study period. Data for male and hermaphrodite flowers were pooled. Error bars are one standard deviation.

Neither did the daily distribution of visits correlate with nectar sugar concentration (Social: Pearson Correlation = 0.230, $p = 0.391$, $n = 16$, Solitary: Pearson Correlation = 0.200, $p = 0.457$, $n = 16$).

Nectar yields measured during observations of solitary and social bees did not differ significantly (**Fig 4**, One way ANOVA, $F_{1,958} = 1.312$, $p = 0.252$). They were also not significantly affected by sampling hour (One way ANOVA, $F_{3,36} = 2.230$, $p = 0.101$).

3.2 Foraging visits to melon flowers

Solitary nesters visited 5.677 ± 3.21 (SD) melon flowers/min, while social nesters visited melon flowers at a rate of 5.114 ± 3.24 flowers/min. Nest type did not significantly affect flower visitation rates ($U = 15$, $n_1 = 7$, $n_2 = 5$, $p = 0.685$).

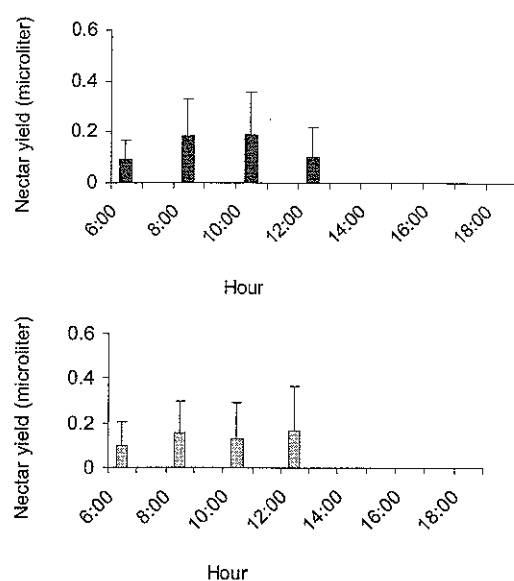


Fig 4: Average nectar yields (μl) in melon flowers (*Cucumis melo* L var Gallia), recorded during the activity of social (black bars, top) and solitary (grey bars, bottom) bees (Hymenoptera: Apidae: Anthophoridae: *Xylocopa pubescens* Spinola 1838). Error bars are one standard deviation.

However, solitary bees stayed longer on each melon flower than social bees ((Mean \pm SD visit duration for solitary bees: 7.429 ± 8.306 seconds; for social bees: 5.221 ± 5.514 seconds; One way ANOVA, $F_{1, 421} = 10.765$, $P = 0.001$).

3.3 Choices of forage plants and constancy

The distribution of the bees' visits to the plant species differed significantly from the distribution of available flowers on all observation days, and for both nest types (Chi-square tests, $df = 3$, $P < 0.001$ for all tests). The choice proportions of solitary and social bees differed significantly both when *P. oleracea* was in bloom ($G_3 = 171.696$, $p < 0.001$), and after this species ceased blooming ($G_3 = 214.176$, $p < 0.001$). Social nesters visited *P. oleracea* more frequently than solitary nesters during the blooming period of this species, and visited melon more frequently than solitary nesters after the end of *P. oleracea*'s bloom (**Fig 5**).

The mean (\pm SD) number of consecutive visits to melon flowers per run was 25.61 ± 35.53 for solitary nesters and 40.77 ± 62.72 for social nesters. These means did not differ significantly (square-root transformed data, $t_{49} = 1.17$, $p = 0.12$, power = 0.31). The large difference between the means, and the low power of the test, suggest that non-significance may be due to small sample sizes. In agreement with this possibility, the average duration of runs of consecutive visits to melon differed significantly between solitary and social foragers (4.82 ± 6.67 minutes for solitary foragers, 9.55 ± 10.02 for social foragers; $t_{45} = 2.354$, $p = 0.011$).

3.4 Crop yield

Melons that developed following pollination by solitary nesters had a mean (\pm SD) mass of 179.06 ± 58.33 g and a mean seed number of 101.15 ± 52.29 ($n = 13$). Mean fruit mass and seed number were 161.56 ± 89.42 and 81.20 ± 52.58 for melons arising from pollination by social nesters ($n = 8$).

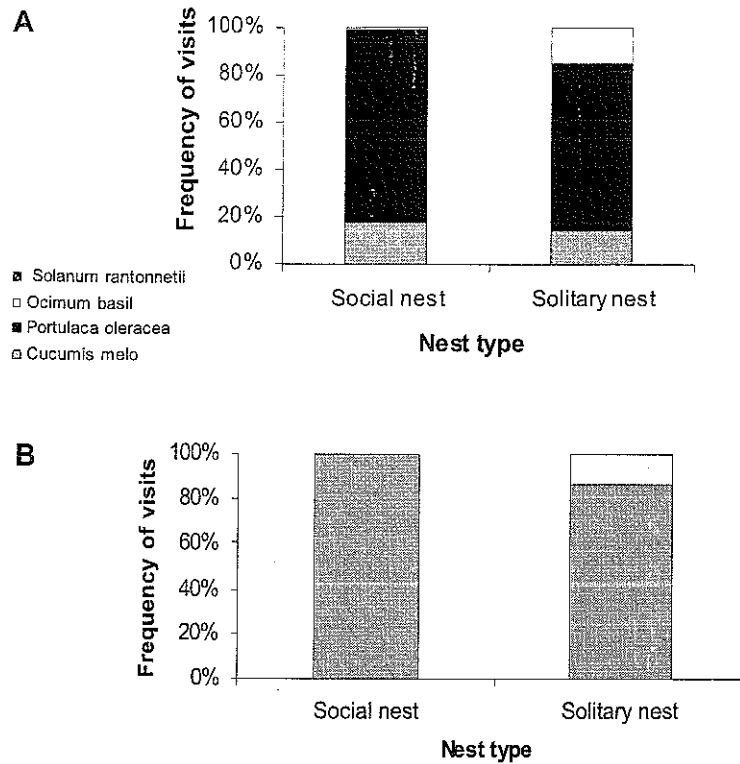


Fig 5: Frequency of visits to the various flowering plants in the greenhouse by solitary vs social nesters (Hymenoptera: Apidae: Anthophoridae: *Xylocopa pubescens* Spinola 1838). **A** – During *P. oleracea*'s blooming period; **B** – after *P. oleracea*'s blooming period.

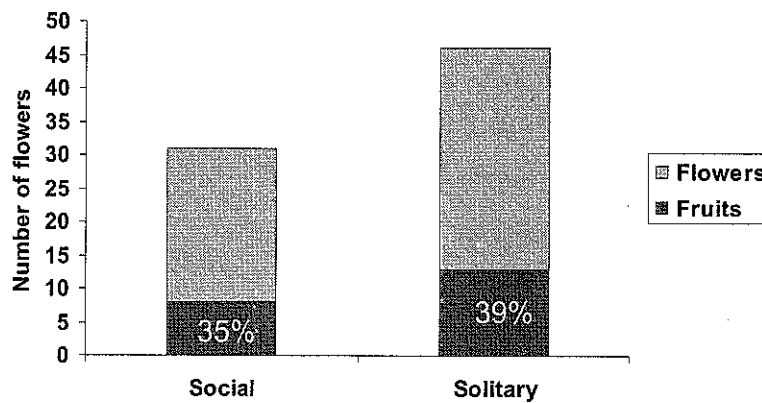


Fig 6: Fruit set arising from pollination by social vs. solitary nesters (Hymenoptera: Apidae: Anthophoridae: *Xylocopa pubescens* Spinola 1838), calculated as the number of mature melons (dark bars) divided by the flowers available in the greenhouse (grey bars). Data of 27 observation days on solitary nesters, and 12 observation days on social nesters were pooled.

Fruit mass and seed number were not significantly affected by pollinator type (Fig 6, $t_{19} = -0.447$, $p = 0.660$, power = 0.112 for weight, and $t_{19} = 0.042$, $p = 0.967$, power = 0.201 for seeds). The fruit set that resulted from pollination by solitary bees was not significantly higher than the fruit set arising from pollination by social bees (Fig 6, $\chi^2_{(1)} = 0.0768$, $p = 0.781$).

4 Discussion

The intraspecific plasticity in the social organization of *X pubescens* offers an exciting opportunity for the study of insect sociality. Research on the evolution of sociality has traditionally taken a comparative approach, trying to identify common characteristics of groups of species with similar social organization [CHOE & CRESPI 1997]. The difficulty in this approach lies in the many evolutionary and ecological factors that differ among such species, and which complicate between-species comparisons. Intraspecific comparisons between solitary and social individuals (as in *X pubescens*) are much easier, because these individuals share the same phylogeny and life history. Comparisons between solitary and social nesters of *X pubescens* have already yielded interesting insights as to the costs and benefits of social living. These studies suggest that the costs entail the probability that the guard would usurp the nest. The most important benefits are the protection that a guard provides against pollen robbery by conspecifics, and the longer foraging time available to a forager when her nest is protected. During certain periods of intense competition for pollen or nests, the benefits clearly outweigh the costs [HOGENDOORN et al 1993a, b, DUNN & RICHARDS 2003]. The present study takes the comparison between social and solitary nesters one step further, by studying the ramifications of bee sociality for the plants that depend on their pollination services.

The results show similarities between solitary and social females in several foraging parameters that may affect pollination efficiency, including daily activity range, and flower visitation rates. Other foraging parameters differed between solitary and social bees. However, the differences do not suggest a clear-cut advantage to one of the bee types as pollinator: social individuals spent a shorter time on each melon flower, reducing their chances of pollen transfer. On the other hand, they directed a larger proportion of their visits to melon flowers, and tended to be more flower-constant (thereby increasing the flowers' pollination prospects). In line with these equivocal results on foraging behaviour, no effect of pollinator type on the quality or quantity of melon fruit was detected. This finding suggests that solitary and social nesters provide pollination services of similar quality. The results allow rejection of the initial hypothesis, which predicted better pollination performance by social foragers.

The results may have been confounded, to some degree, by the different number of nests introduced into the greenhouse on different days of observations. Although the reported behavioural parameters were calculated per forager, it is possible that competitive interactions between individuals may have affected foraging behaviour. The strength of these interactions may have been affected by the density of foragers in the greenhouse. Further studies should control for this possibility by observing a constant number of individuals in all observation sessions.

An interesting difference in foraging behaviour between solitary and social bees was found in the temporal distribution of visits to melon. The time of peak activity was at 10 am for both types of nests, but this peak was significantly more pronounced for social nesters than for solitary ones. The temporal distribution of visits did not correlate with the flowers' nectar yield patterns for both types of nests, suggesting that the bees' activity pattern was not affected by the temporal pattern of food available to them. Possibly, the bees' activity pattern is affected by abiotic factors, such as temperature, humidity and light intensity [GOTTLIEB et al 2005]. However, preliminary observations revealed no significant correlation between any of the abiotic measures and visit duration in flowers or frequency of activity in the greenhouse [KALISH et al 2006a]. An additional possibility is that different intrinsic biologic clocks cause the difference between the foraging schedules of social and solitary bees. The existence of intra-specific variability in circadian rhythms has been demonstrated in the honeybee [BLOCH et al 2001]. Similar differences may possibly exist between solitary and social *X pubescens*.

Social and solitary nesters also significantly differed in their choices of forage plant species. Social nesters visited *P. oleracea* more than solitary nesters while this species was in bloom. After *P. oleracea* finished blooming, socially-nesting bees visited melon flowers significantly more often, and *O. basilicum* less often, than solitary nesters. The higher attraction of social nesters to *P. oleracea* may reflect differences in the dietary demands of the two bee types. *P. oleracea* produces only pollen, which is mainly consumed by bee larvae, as food reward. The social bees may have been attracted to this species because they reared more larvae, or because they also needed to feed the guard in their nest. The differences in choices of melon and basil (both nectariferous plants) between the two nest types still require explanation.

The results show that social nesting does not dramatically affect foraging behaviour in *X. pubescens* females under greenhouse conditions, and therefore has little influence on their capabilities as agricultural pollinators. This is an advantage from an agricultural point of view, since both types of nests can be used indiscriminately for pollination. Moreover, pollination efficiency is predicted to be unaffected by changes in the social composition of nests, which regularly occur during the season. The next important task, from an agricultural point of view, is to evaluate the crop pollination efficiency of *X. pubescens* (whether social or solitary) in comparison with other species of agricultural pollinators. Honeybees and bumblebees are widely used for agricultural pollination in greenhouses. Bumblebees are highly effective pollinators in cool climates, and for crops that require buzz pollination. Honeybees are more heat-resistant, and are the standard pollinators for crops that do not require buzzing, such as the honeydew melon. It is therefore interesting to compare the pollination efficiency of *Xylocopa* in honeydew melons with honeybees. This evaluation is in progress [KALISH et al 2006a, b].

5 References

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