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Author(s): Narcís Vicens and Jordi Bosch
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Pollinating Efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' Apple

NARCÍS VICENS[1] and JORDI BOSCH[1, 2]

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ABSTRACT The foraging behavior and pollinating efficacy of *Osmia cornuta* (Latreille) and *Apis mellifera* L. were studied in an orchard of 'Delicious' apple, *Malus domestica* Borkh, in northeastern Spain. Yields after one single visit were more than five times higher in flowers visited by *O. cornuta* than in those visited by *A. mellifera* nectar gatherers. This is attributed to the lower rate of stigma contact in *A. mellifera* visits, rather than to insufficient deposition of compatible pollen when the stigmas are contacted. *A. mellifera* pollen collectors had very high rates of stigma contact, but they were very scarce (3%) on 'Delicious' flowers despite the presence of abundant brood in their hives. One single visit per flower by *O. cornuta* produced commercial fruit set (27.4%) and fruit size (>70 mm diameter). Based on cell production, average number of trips required to provision a male and a female cell, and flower visiting rates, it is estimated that a mean of 22,252 apple flower visits per female *O. cornuta* were made during the 15-d flowering period. This result indicates that 530 nesting *O. cornuta* females per hectare are enough to provide adequate apple pollination.

KEY WORDS *Apis mellifera*, *Osmia cornuta*, foraging behavior, 'Delicious' apples, pollination

Most cultivated apple, *Malus domestica* Borkh, are either self-incompatible or benefit from cross-pollination, so that commercial orchards normally include more than one variety. *Apis mellifera* L. hives are commonly introduced at bloom time to increase pollen transfer between varieties (McGregor 1976, Free 1993). In spite of these practices, the productivity of several cultivars, especially in the 'Delicious' group, is often limited by insufficient pollination (Dennis and Hoopingarner 1987). In these cultivars, nectar-collecting *A. mellifera* workers often do not contact the reproductive organs of the flowers because they reach the nectaries, located between the bases of the stamens and the style, from the petals (Roberts 1945). This side-working behavior is possible because of gaps at the base of the androecium that allow the bees to introduce their proboscis while standing on the petals (Robinson 1979). Such problems, coupled with the difficulty of obtaining enough hives adequately prepared for pollination, has prompted the study of alternative manageable orchard pollinators in several parts of the world. The best results have been obtained with species in the genus *Osmia*—*Osmia cornifrons* (Radoszkowski) in Japan (Maeta and Kitamura 1974), *Osmia lignaria* Say in the United States (Torchio 1985), and *Osmia cornuta* (Latreille) in Europe (Bosch 1994a).

Because of its foraging behavior, *O. cornuta* is, at the individual level, a more efficient pollinator of almond than *A. mellifera,* with a greater mobility between trees and a percentage legitimate visits near 100% (Bosch and Blas 1994). *O. cornuta* also has been released in apple orchards (Torchio and Asensio 1985, Krunic et al. 1989), but its pollinating efficacy on this species has not been evaluated. In this study, we analyze the foraging behavior and the pollinating efficacy of *O. cornuta* in comparison with *A. mellifera* on the apple cultivar 'Royal Red Delicious'. The results obtained on *O. cornuta* are used to determine the approximate number of bees per hectare necessary to achieve adequate pollination.

Materials and Methods

This study was undertaken in a 0.5-ha orchard at the Research Station of Mas Badia, in Canet de la Tallada (Girona, NE Spain) in 1995. The orchard was composed of 7 rows of 70 trees each, with 'Royal Red Delicious' as the main cultivar and 'Golden Delicious' as the pollinizer (rows 2 and 6). Distance between rows was 3.5 m, and distance between two adjacent trees within a row was 2 m, so that their limbs sometimes overlapped. Trees were ≈3 m high and trellised, which facilitated observations of bee foraging behavior.

A population of 800 *O. cornuta* field-trapped in Girona and Lleida the previous year was released in two nesting shelters located at the north end of the orchard. Each shelter consisted of a wooden box with the front side open, held 1.5 m above the ground on four metal fence posts, and provided with 45 wood blocks as nesting material. Each block had 25 drilled holes to accommodate a paraffin-coated paper straw (15 cm long, 8 mm inside diameter). On 6 April 1995, 300 female cocoons were individually inserted in 300

[1] Departament de Biologia Animal, Facultat de Biologia, Universitat de Barcelona, Diagonal 645, 08028 Barcelona, Spain.
[2] Bee Biology and Systematics Laboratory, USDA–ARS, Utah State University, Logan, UT 84322–5310.

Table 1. Percentage of legitimate visits (visits in which the stigmas were contacted), visitation time (s per flower), visitation rate (flowers per min), and flowers consecutively visited per tree in *Osmia cornuta* females and *Apis mellifera* nectar gatherers foraging on apple

Species	n	Legitimate visits %	Visitation time $\bar{x} \pm$ SE	Visitation rate		Visits/tree	
				n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE
O. cornuta	1388	97.7[a]	3.4 ± 0.35[b]	29	12.3 ± 0.45[a]	207	6.4 ± 0.50
A. mellifera	846	32.7[b]	5.3 ± 0.70[a]	20	7.9 ± 0.34[b]	124	6.4 ± 0.58

Means with different superscripts are significantly different ($P < 0.02$).

of the paper straws, and 500 male cocoons were placed in open cardboard boxes in the two shelters. *A. mellifera* from >20 hives installed in neighboring plantations were always abundant in the orchard.

Data on foraging behavior and pollinating efficacy were obtained when both cultivars were in simultaneous bloom with 30% or more of their flowers open. Data were gathered only on days with weather favorable to the activity of both bee species (Vicens 1997), between 1200 and 1500 hours. Foraging behavior was studied by following *O. cornuta* females and *A. mellifera* workers from their first flower visit to a tree until we lost sight of them. We took data on the following: (1) resources collected (nectar and/or pollen), (2) legitimacy of the visits (apple blossoms have 5 stigmas and it is difficult to ascertain how many are contacted, so we scored visits as either contacting some stigmas or none), (3) visitation times (time spent on the flower), (4) flower visitation rates (flowers visited per minute), (5) number of flowers visited per tree, and (6) distance between trees consecutively visited.

Pollinating efficacy was tested on 'Royal Red Delicious' trees in rows adjacent to the pollinizing cultivar. Because 'Delicious' flowers are most receptive on the first day of anthesis (Free 1993), limbs with flower buds were covered with fine mesh nylon bags to prevent insect visitation and inspected daily. When open flowers were available, they were unbagged and continuously watched until either a female *O. cornuta* or worker *A. mellifera* visited a flower. Visited flowers (only one visit per flower was allowed) were labeled and rebagged. Data on bee species, resources collected, and legitimacy of the visit were recorded for each flower. In early May, bags were removed and fruit set (percentage of flowers setting fruit) was evaluated, and in early June, when fruits were >30 mm in diameter, they were collected and the number of seeds and seeded carpels per fruit were recorded.

Differences between species on visit legitimacy, inter-row flight frequency, and fruit set after one visit were analyzed using the *G*-test. Differences on flower visiting time, flower visiting rate, number of visits per tree, and seed set after one visit were analyzed with the *t*-test.

Before bloom, flower buds on four branches each of five 'Royal Red Delicious' trees were counted. Every day, newly opened flowers on these branches were hand-pollinated by depositing abundant fresh 'Golden Delicious' pollen on all five stigmas with a fine paintbrush. Fruit set and seed contents were measured as explained for the pollinating efficacy experiment. Commercial fruit size (diameter) of 'Royal Red Delicious' apples is 70 mm. In September, the number of seeds and seeded carpels in 50 mature fruits measuring 70-mm were counted.

The timing of pollen-nectar foraging trips by female *O. cornuta* was recorded with the use of a video camera positioned in front of one of the nesting shelters. After petal fall, *O. cornuta* nesting materials containing developing progeny were taken to the laboratory and incubated at 25°C. In September, when progeny had reached the adult stage, nests were dissected, and the number of male and female cells were counted. To identify the pollen species in these cells, larval fecal pellets from 30 cells were mounted on fuchsin-stained gelatin slides (Beattie 1971), and 300 pollen grains per sample were examined under the microscope.

Results

Foraging Behavior. *Osmia cornuta* females systematically land on the reproductive organs of apple flowers and collect pollen and nectar simultaneously. Contact between the bee and the stigmas occurred in 97.7% of the 1,388 flower visits observed (Table 1). On most visits, the female pushed her head through the stamens from the top to reach the nectaries, while she repeatedly brushed the anthers and stigmas with her legs to pack pollen on her ventral scopa. The contact between the body of the bee and the stigmas was always clear and thorough; probably all 5 stigmas were contacted on most visits. More rarely, females introduced their proboscis from the side of the flower's reproductive column, but because their bodies were always positioned above the anthers and stigmas, these visits were also legitimate. Occasionally, females collecting only nectar were spotted. We dusted some of them with fluorescent powder to individualize them, and observed at the nesting shelters that they were either plugging a nest (and therefore collecting nectar for their own consumption) or had just laid an egg and were depositing nectar around its attachment area on the provision. Although these females were only collecting nectar, they also landed on the stigmas of the flowers, and therefore were legitimate visitors. *O. cornuta* males collect nectar only for their own consumption and have a foraging behavior similar to nectar-collecting females. Of 75 male visits observed, 96% were legitimate.

Although *A. mellifera* hives were managed to contain abundant brood as a means to enhance pollen foraging, most (97%) of the workers counted throughout the day collected only nectar. These included both side-workers and top-workers. The former landed on

Table 2. Percentage of distances (in m) moved by *Osmia cornuta* females and *Apis mellifera* nectar gatherers flying between apple trees

Species	2 m	4 m	6 m	≥8 m	Row change
O. cornuta	71.1	4.3	1.9	1.1	20.8
A. mellifera	74.4	5.6	1.1	1.1	17.8

the flower petals and introduced their proboscis between the gaps at the base of the stamens, and they touched some stigmas with only their legs when they walked across the flower to sip nectar from another petal. Instead, top-workers landed on the reproductive organs of the flower and pushed their head and part of the thorax among the stamens. In so doing, they normally contacted one or more stigmas. As a whole, 33% of nectar-gathering *A. mellifera* visits were legitimate (Table 1). Because they were so scarce, only 51 visits by pollen-gathering *A. mellifera* could be scored. Typically, they would stand with their hind legs on the petals and touch the anthers and stigmas with their head and fore legs, which they used to scrape pollen off the anthers. They rarely contacted all 5 stigmas, but most visits observed (94%) were legitimate.

Differences in visit legitimacy between *O. cornuta* and *A. mellifera* nectar gatherers are statistically significant ($G = 1227$, df = 1, $P < 0.00005$). The two pollinators also differ in other foraging behavioral traits (Table 1). *O. cornuta* spent less time per visit ($t = 2.55$, df = 48, $P = 0.014$) and visited more flowers per minute ($t = 8.00$, df = 113, $P < 0.0005$), but both species were similar in the number of flowers visited per tree ($t = 0.06$, df = 112, $P = 0.95$). In both species, most inter-tree flights (>70%) were between neighboring trees (Table 2), and differences in the frequency of flights between rows are not statistically significant ($G = 0.38$, df = 1, $P = 0.54$).

Pollinating Efficacy. Fruit set was over five times higher in flowers visited once by *O. cornuta* than in flowers visited once by *A. mellifera* nectar gatherers ($G = 17.09$, df = 1, $P < 0.0005$) (Table 3). When only legitimate visits are considered, differences between the two species are reduced and just fail significance ($G = 3.41$, df = 1, $P = 0.06$) (Table 3). The number of seeds and seeded carpels per apple in flowers visited by *O. cornuta* and *A. mellifera* also are presented in Table 3. In both cases, three or more carpels contained seed, for a total of five or more seeds per fruit. The sample size for *A. mellifera* visited flowers was very small ($n = 4$) and no statistical differences were found between the two species (seeds: $t = 0.21$, df = 20, $P = 0.84$; carpels: $t = 0.66$, df = 20, $P = 0.52$).

Of the hand-pollinated flowers ($n = 1{,}404$), 22.5% set fruit with 8.0 ± 0.09 seeds (mean ± SE) and 4.8 ± 0.03 seeded carpels per apple. The number of seeds and seeded carpels in 50 70mm mature insect-pollinated fruits was 4.3 ± 0.46 and 2.9 ± 0.28, respectively.

***Osmia cornuta* Nesting and Pollinating Potential.** Of the 300 *O. cornuta* females released, 130 nested in the two nesting shelters. Flowering in the orchard lasted 15 d, during which time 359 female and 639 male cells were produced in the nesting materials provided (2.8 females and 4.9 males per nesting female). Pollen identification revealed that 94% of the 30 cells analyzed contained 100% apple pollen. In the 6% remaining samples, 15–75% of the pollen grains were apple.

Based on the number of foraging trips required to produce average male and female cells, and on the number of flowers visited per foraging trip, the approximate number of flowers visited per nesting female can be estimated. In a previous study on almonds, the mean number of pollen-nectar foraging trips necessary to make a provision was 26.8 for female cells and 16.8 for male cells (Bosch 1994a). Foraging trips in the Canet orchard lasted 17 min 50 s ± 6 min 57 mean ± SD s; $n = 55$). It was not possible to measure the time used by bees to fly from their nests to the first tree visited in a foraging trip, and from the last tree visited back to their nest. However, our observations indicate that these activities take only a very small fraction of the total foraging time. To be very conservative in our estimations, we can assume that only two-thirds (11 min 53 s) of the foraging times are spent flying between and visiting flowers. Because *O. cornuta* females visited 12.35 flowers per minute (Table 1), at least 146 flowers were visited in an average foraging trip. The provisioning of average female and male cells would then require 3,911 and 2,447 flower visits, respectively. Taking into account only those cells that contained 100% apple pollen, the females that nested in the nesting shelters in Canet in 1995 would have made an average of 22,252 visits to apple flowers. These estimates do not include flowers visited during nectar-collecting visits by females, and they ignore all visits by males.

Discussion

The percentage of legitimate visits to flowers of fruit trees is as high in *O. cornuta* (apple: 97.7%; almond,

Table 3. Fruit set in apple flowers visited once by *Osmia cornuta* females and *Apis mellifera* nectar foragers

Species	Visits n	Fruits n	% fruit set[a]	Seeded carpels/fruit $\bar{x}$ ± SE	Seeds/fruit $\bar{x}$ ± SE	Legitimate visits n	% fruit set of legitimate visits
O. cornuta	84	23	27.4	3.7 ± 2.4	5.3 ± 0.7	84	27.4
A. mellifera	83	4	4.8	3.0 ± 1.0	5.0 ± 2.0	33	12.1

[a] Significantly different between species ($P < 0.0005$).

Prunus amygdalus Batsch: 98.7%) (Bosch and Blas 1994) as in *O. cornifrons* (apple: 96.7%) (Yamada et al. 1971), and *O. lignaria* (almond: near 100%) (Torchio 1981). This high rate of stigma contact results from the behavior of the bee to land on the reproductive column of the flower, even when only nectar is collected. In *A. mellifera,* stigma contact rate is more dependent on the resources collected, being much higher for pollen gatherers (Kendall 1973, Robinson 1979, Bosch and Blas 1994). As already mentioned, the morphology of 'Delicious' flowers does not favor pollen deposition by *A. mellifera* nectar gatherers. Because stamens and pistils are straight and relatively rigid, it is difficult for top-workers to reach the nectaries, whereas side-workers can easily introduce their proboscis through the gaps at the base of the crown of stamens (Roberts 1945, Free 1960, Robinson 1979). Side-workers are able to collect nectar three times faster than top-workers (Robinson 1981), and the number of side-workers increases throughout the flowering period, as workers learn the most efficient behavior (DeGrandi-Hoffman et al. 1985). In contrast, pollen foragers have very high rates of stigma contact (86–100%) (Robinson 1979, this study).

The percentage of *A. mellifera* collecting pollen was very low (3%). This appears to be a phenomenon common to cultivars of the 'Delicious' group. In a 1997 study, six strong hives with abundant brood were installed in a nearby orchard planted with 'Oregon Spur' (also in the 'Delicious' group). Only 1% of the workers observed collected pollen, whereas up to 55% did so in other apple cultivars and, especially, on pear (N.V., unpublished data). The proportion of pollen gatherers increases with the quantity of brood in the colony, and hives managed for pollination should contain abundant uncapped brood (Free 1993). Nevertheless, 'Delicious' flowers do not appear to be a preferred pollen source for *A. mellifera.*

In self-incompatible crops, the deposition of compatible pollen is favored by the mobility of the pollinators and their tendency to move between varieties. Contrary to results obtained on almond, where *O. cornuta* showed a greater mobility than *A. mellifera* (Bosch and Blas 1994), in this study the two species behaved similarly in the number of flowers visited per tree and their tendency to change rows. The trellised growth and the overlapping of branches of adjacent trees may have contributed to an overall lower rate of flights between rows than in previous studies (Bosch and Blas 1994). Both the mean time spent visiting a flower and the mean time spent flying between two flowers are shorter in *O. cornuta* than in *A. mellifera* nectar collectors, so that the former has a higher flower visiting rate (12.3 flowers per minute). Results obtained for *A. mellifera* (7.9 flowers per minute) are within the range reported in other studies (7–11 flowers per minute) (Free 1960, Free and Spencer-Booth 1964, Anasiewicz 1972, Wilkaniec 1987).

Fruit set in flowers visited only once is similar in *O. cornuta* (apple: 27.4% [this study]; almond: 22–30% [Bosch and Blas 1994]), and *O. lignaria* (apple: 29% [Kuhn and Ambrose 1984]). Fruit set in hand-pollinated flowers in Canet (22.5%) indicates that probably all flowers visited by *O. cornuta* in the pollinating efficacy experiment were adequately pollinated. One of every four flowers visited by *O. cornuta* set fruit, while only one of every 21 flowers visited by *A. mellifera* nectar foragers did so. When only legitimate visits are considered, one in every eight *A. mellifera* visits was successful. This indicates that the main difference between the two pollinators lies in their stigma contact rates rather than in the deposition of compatible pollen when contact occurs. This is in agreement with results obtained on almond (Bosch and Blas 1994) and questions the usefulness of pollen dispensers at the hive entrance to increase the pollinating efficacy of *A. mellifera* on fruit trees (Free 1993).

The size of a mature apple depends on, among other factors, its number of seeds and the number of fruits produced by the tree. Mean numbers of seeds and seeded carpels in fruits obtained after a single *O. cornuta* visit are higher (5.3 and 3.4, respectively), than those in fruits of minimum commercial size (70 mm) obtained from open pollination (4.3 and 2.9, respectively). In another apple orchard, trees adjacent to *O. lignaria* and *O. cornifrons* nesting shelters produced fruits with more seeds and seeded carpels (5.5–7 and 3.5–4.5, respectively) than trees adjacent to *A. mellifera* hives (3–4.5 and 2–3, respectively) (Kuhn and Ambrose 1984). In our study, the few fruits (n = 4) produced from single *A. mellifera* visits had a high number of seeds and seeded carpels (5 and 3, respectively) indicating, once more, an adequate deposition of compatible pollen when flower visits are legitimate.

Results obtained with *O. cornuta* demonstrate the high pollinating potential of this species on apple. Although most parameters used in our estimation of the number of flowers visited per female will vary between years and orchards, our results can be considered representative. Thus, the cell production obtained in this study (2.8 females and 4.9 males per nesting female) is similar to or lower than those obtained in other orchard releases (up to 6 females and 14 males per nesting female) (Bosch 1994b, 1994c; unpublished data). The potential competition of other plants blooming in synchrony with apple is negligible because *O. cornuta* shows a clear preference to collect on Rosaceae. Cells from nests build in other apple orchards also contained very high percentages of apple pollen (80–94%) (Torchio and Asensio 1985, Márquez et al. 1994). As for the number of flower visits necessary per provision, Maeta and Kitamura (1974) estimated 1,620 visits for *O. cornifrons* foraging on apple. Although this parameter undoubtedly depends on pollen-nectar standing crops (affected by flower visitor populations in the orchard, among other factors), our results (male provisions: 2,446 visits; female provisions: 3,911 visits) agree with the larger body size of *O. cornuta,* about twice larger than *O. cornifrons* (Maeta et al. 1993, Bosch 1994a, Vicens 1997).

In the Girona area, an average apple tree produces some 2,000 flowers (J. Carbó, personal communication). Because a single *O. cornuta* visit results in a commercially acceptable fruit set and fruit size, 1 female nesting at the Canet orchard in 1995 could potentially pollinate 11 trees. This estimate assumes that all flowers have the same probability of being visited, which is unlikely, because trees nearer to nesting shelters tend to be visited more often than those farther away (unpublished data). This is partially compensated by the tendency of *O. cornuta* females to expand their foraging areas based on the amount of flowers (and probably pollen and nectar) available in the vicinity of their nesting site. Thus, in 2 almond orchards with profuse bloom in Murcia, 90% of *O. cornuta* females foraged within a 100-m radius from their nesting shelters (A. Lacasa, J.B., and N. V.; unpublished data), whereas in Canet, with many fewer flowers per tree, foraging areas extended up to 200 m (N.V., unpublished data). Smaller and more numerous nesting shelters spread across the orchard may help reduce foraging area overlap. In a more realistic estimate based on 2–3 visits per flower, a single female could adequately pollinate 3.5–5.5 trees.

In Girona, 1 ha of apples typically contains ≈2,000 trees (Carbó et al. 1999), which means that at 2–3 visits per flower, 355–530 nesting *O. cornuta* females would provide adequate pollination for 1 ha. In Japan, 500–600 nesting *O. cornifrons* females per hectare are recommended (Maeta and Kitamura 1974, Maeta 1990) and in the United States, a maximum of 625 *O. lignaria* females per hectare (Torchio 1985). Even when large populations of efficient pollinators are available, apple pollination may be limited by inclement weather. A parallel study in the Canet orchard (Vicens 1997) demonstrates that *O. cornuta* has lower temperature and solar radiation thresholds for foraging activity than other bees occurring in the orchard, including *A. mellifera.* In conjunction with its very high pollinating efficacy, this result increases the value of *O. cornuta* as a commercial orchard pollinator.

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