

# Solitary Bees As Pollinators



Bettina Maccagnani and Fabio Sgolastra

## 1 Working Mothers: This Makes the Difference

What makes the difference between solitary and social bees? Every female makes her own nest, and has her own brood to rear without the assistance from other females. This means that each female collects pollen, and the need of nectar is limited to the amount required to get enough energy for individual activities plus little amounts used to mix up the pollen for the brood (Ladurner et al. 1999). This biological trait has the direct consequence that solitary bees can profit also from flowers that are not particularly rich in nectar or in its sugar concentration, while they are much more interested in the pollen rewards offered by the flowers (Nepi et al. 2005).

The pollen collecting organs of the solitary bees can be very different from the well-known structures honey bees have on the hind legs, which build up a compact pollen mass around a spine, mixing a little nectar to the pollen in order to fix it (Fig. 1a-b). In Antophoridae bees, for example, the hind legs are covered by dense and long hairs which allows them to collect huge amounts of pollen (Fig. 2a and Fig. 3a-d). Megachilidae bees collect pollen through series of special hairs in the ventral part of the abdomen Fig. 3a-b; in (Fig. 1b, Fig. 3a-b); in other species hairs are distributed both in the legs and in the ventral parts of the abdomen and of the thorax. The most important difference with the pollen mass produced by honey bees

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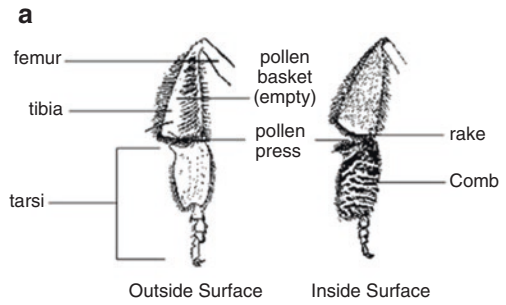
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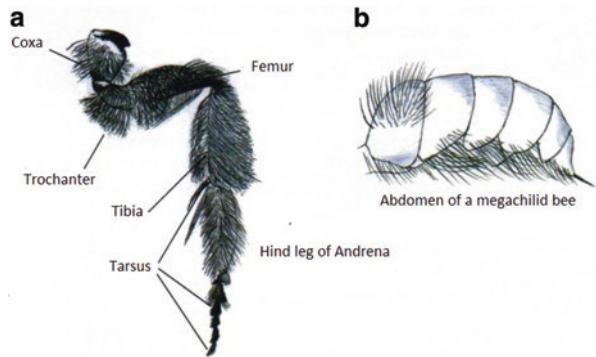
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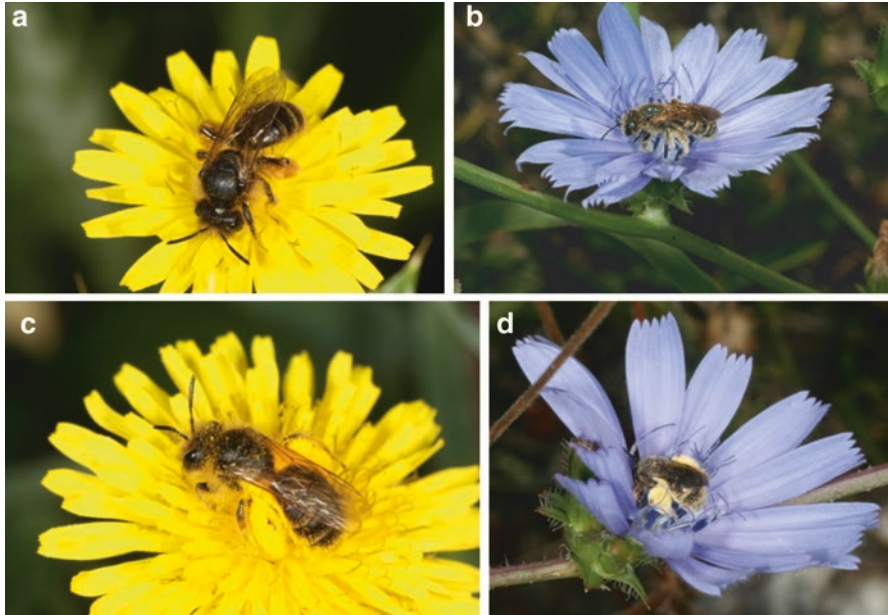
**Fig. 1** The hind leg of a honey bee (a) and a honey bee with a bi-color pollen load (b)



**Fig. 2** Pollen collecting organs in *Andrena* (a) and *Megachile* (b) (Alessandra Montanari)



and bumble bees is that the pollen remains dusty, and easily can detach from the body of the bee when passing from one flower to another. This morphological aspects plus the behavioural trait of landing on the reproductive organs in the central part of the flower (Fig. 5a-b) are present in many solitary bee species, which bring the collected pollen directly in contact with the stigmas. This increase the pollinating efficiency compared with the performance of the nectar foraging honeybees, which very often land on the petals, unless they are contemporarily collecting pollen and nectar, or in case of flower shapes that oblige them to land in the central part of the flower to reach the nectar (Fig. 6a-b) (Fig. 4).



**Fig. 3** *Andrena* sp. bees foraging on *Picris hieracioides* (a) and *Cichorium intybus* (b) before and after (c-d) pollen collection



**Fig. 4** Megachilid bees foraging on *Lotus corniculatus* before starting to collect pollen (a) and with the full pollen load (b)

Being a solitary bee species does not mean to be territorial: on the contrary, many species show gregarious nesting habits. In fact, if the site offers optimal nesting conditions, hundreds of nests of solitary bees can be established in a very restricted area. The nesting habits of solitary bee species can be very different, but three main groups can be described: species that dig nests in the soil (Fig. 7), species that nest in pre-existing cavities (Fig. 8a-b), mainly in the stem of plants or in cavities excavated by other insects (or in old house walls, in the modern age), species that excavate their nests in the wood (Fig. 9).



Fig. 5 Pollen collecting (a) and nectar collecting (b) *Ceratina* sp. on *Borrago officinalis*

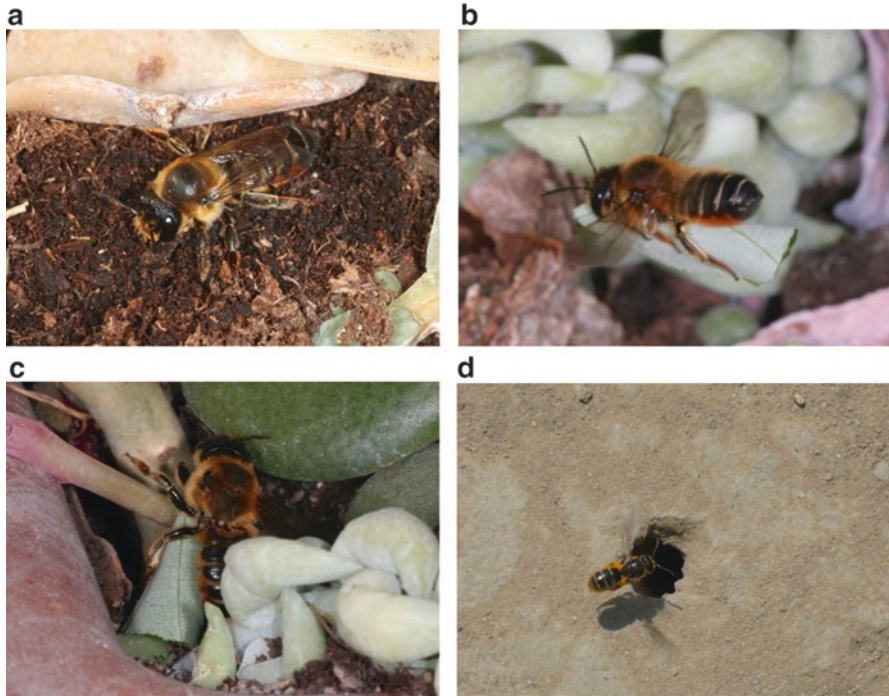


Fig. 6 Pollen collecting honey bee (a); nectar collecting honey bee (b)

## 2 Which Bee for Which Crop

Many studies have been run in recent years to find out which pollinator features are to be considered to determine which pollinator species could be candidate for improving the pollination service of a certain crop (Cane 1997; Thomson 2001; Kevan and Phillips 2001; Cane and Tepedino 2001; Bosch and Kemp 2002; James and Pitts-Singer 2008). These features consider the ecological link between plant and insect, the synchronism between foraging activity and blooming period, between flower attractiveness and exploitation modalities put into effect by the insect (McGregor 1976; Buchmann 1983; Free 1993; Benedek and Nyeki 1996; Goodell and Thomson 1998; Javorek et al. 2002) (Table 1).

The degree of effective contact between the pollinating insect and the reproductive organs of the flower depends on these modalities, and also on the ratio between the size of the insect and the size of the flower (Figs. 10; 11a-b). The relative values of pollinators to crops depend on how much pollen they remove from anthers as well as how much they deposit on stigmas. According to Goodell and Thomson (1998) in a comparison on apple pollination efficacy, *Apis* workers and *Bombus*



**Fig. 7** Megachilid leaf-cutting bee (**a-c**) and *Andrena* sp. (**d**) nesting in the soil

queens differ in both pollen deposition and removal because they frequently adopt different foraging behaviors. Nectar-collecting *Apis* removed fewer pollen grains from the anthers of cv Delicious than did nectar- and pollen-collecting *Bombus*. As these differences are part of the complex reproductive strategy of entomophilous flowered plants, they are applicable to all the other crop/pollinator species comparisons (Kendall 1973; Kendall and Solomon 1973; Harder and Thomson 1989; Harder and Wilson 1998; Thomson and Thomson 1999).

Many studies have been published on the potential pollinating efficiency of native solitary bees on several crops (Willians 2002; Shuler et al. 2005; Klein et al. 2007) which undoubtedly and essentially contribute to maintain an unwavering background ecosystem service of crop pollination. The populations of wild bees can be very abundant if sufficiently large conservation areas are preserved (Kremen et al. 2004; Potts et al. 2010; Abrol 2011).

In some cases, effective and manageable native solitary bees were identified. For example, in US, the squash bee *Peponapis pruinosa* Say is a very effective pollinator of *Cucurbita pepo* (Tepedino 1981; Artz and Nault 2011), while the southeastern blueberry bee, *Habropoda laboriosa* (Fabricius) can very well compensate for inadequate honey bee pollination the rabbiteye blueberry, *Vaccinium ashei*; on this crop, a new adaptable pollinator *Osmia ribifloris* Cockerell was successfully reared and used in captivity (Sampson and Cane 2000). Despite the high number of

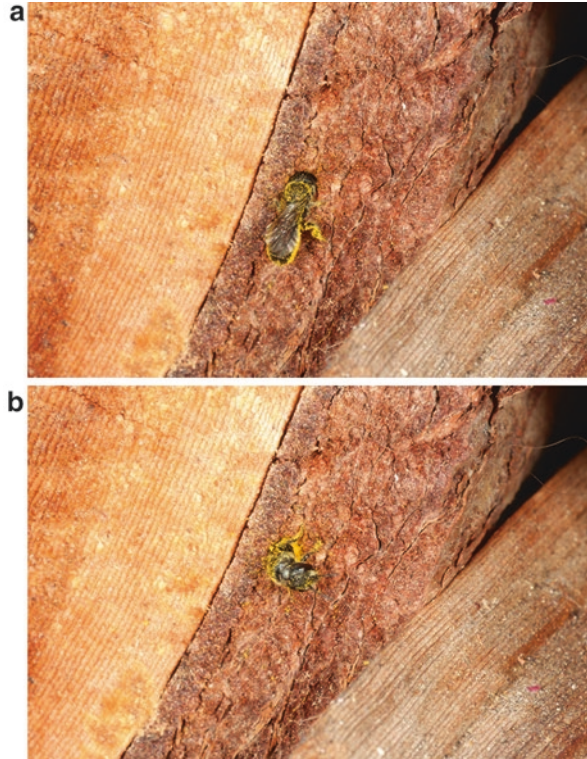
**Fig. 8** Cavity nesting species: (a) *Heriades* (top left) closed the nest with small stones kept together with resins; *Anthidium* sp. female (central) is entering her nest; on the right, a mud wall closed the nest of *Osmia cornuta*. (b) *Anthidium* sp. female resting at the nest entrance



crop-pollinator interactions studied with the aim of highlighting how effective pollinators can maximize crop yield, only few native bee species are commercially available. This discrepancy is due to some limiting factors, related to the possibility to develop a mass reared populations of pollinators: the number of reproductive cycles completed by the insect in one year, the duration of the diapause, the adaptability to artificial nesting sites, the gregariousness degree during nesting (Kevan and Phillips 2001; Cane and Tepedino 2001; Cane 2008). On the basis of these criteria, several authors give indications on how to re-establish a numerically adequate population of the pollinating insect in the cultivated area (Bosch and Kemp 2001; Kevan and Phillips 2001).

Up today among the few reared solitary bee species present in North America, the alfalfa leaf-cutter bee *Megachile rotundata* Fabricius (Pitts-Singer and Cane 2011), the blue orchard bee *Osmia lignaria* Say and the alkali bee *Nomia melanderi* Cockerell (Cane 2008) are commercially available on the large scale, or can be reared by the growers themselves. *Osmia cornifrons* (Radzowski) has been managed in Japan for apple pollination since the 1940s (McKinney and Park 2012), and is used also in Korea and China (Da-Yong and Long-Shi 2007; Lee et al. 2008); it was introduced into the United States for pollination in 1977. In Australia, a promising study on tomatoes pollination in greenhouses has been performed by rearing the blue banded bee, *Amegilla chlorocyanea* Cockerell on artificial substrates in captivity (Hoogendorn et al. 2007) ([www.beaware.org.au](http://www.beaware.org.au); <http://www.aussiebee.com.au>).

**Fig. 9** Small carpenter bee excavating her nest (a) and entering backwards with her pollen load on the abdomen (b)



**Table 1** Foraging flight duration and provision weight of *O. cornuta* populations foraging on pears

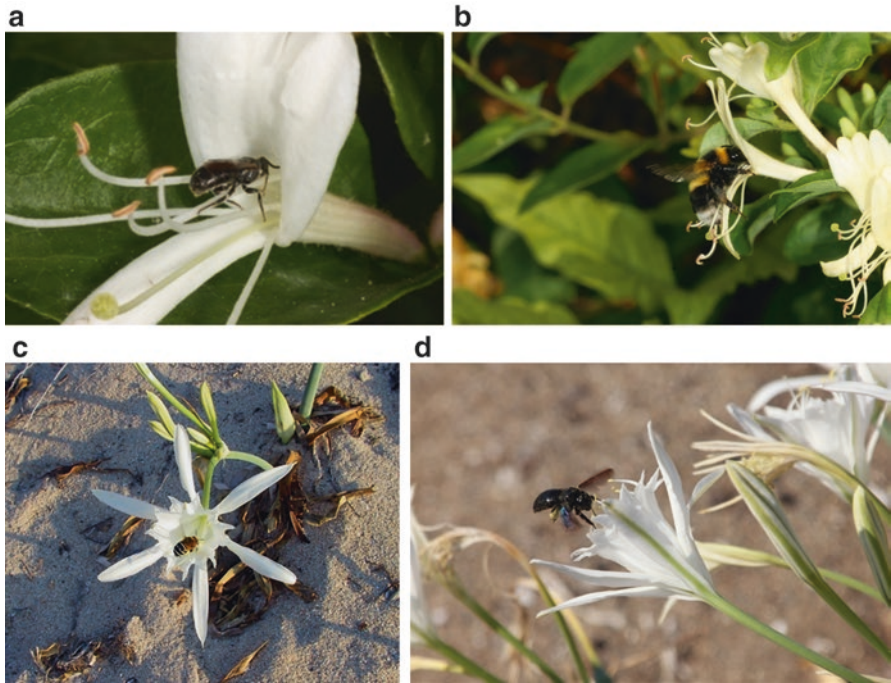
Year/Reference	Provision weight (g)
2000/Maccagnani et al. (2007)	0.509 ± 0.056 (females)
2001/Maccagnani et al. (2007)	0.591 ± 0.177 (females)
1994/Bosch (1994)	0.260 (males)
	0.451 (females)

In Europe, *O. rufa* L. (syn. *O. bicornis*) and *O. cornuta* Latreille are reared and used for orchard pollination and seed productions (Pinzauti et al. 1997; Ladurner et al. 2002; Maccagnani et al. 2003a, b; Kronic et al. 2005; Gruber et al. 2011).

### 3 Solitary Bees: A Focus on *Osmia* sp.

The genus *Osmia* Panzer (Hymenoptera Megachilidae) comprises 300 species (Michener 2000). Among those already commercially available as crop pollinators, *O. cornuta*, *O. rufa* and *O. cornifrons* are Palearctic species; *O. cornuta* (Fig. 12)

**Fig. 10** The giant and the small, *Xylocopa violacea* and *Ceratina* sp. on *Cynara cardunculus*



**Fig. 11** Too small bee size (a, c); proper bee size (b, d)

occurs in Central and Southern Europe, Turkey and Northern Africa; *O. rufa* (Fig. 13) shows a more Northern distribution, while *O. cornifrons* (Fig. 14) is native from Japan. *O. lignaria* (Fig. 15), with different subspecies, is a Nearctic species, widely distributed in the U.S., where also *O. cornuta* has been introduced in the late eighties for almond and apple pollination, and is now established (Torchio and Asensio 1985; Vicens and Bosch 2000).



**Fig. 12** *Osmia cornuta* on *Pyrus malus* (apple) flower



**Fig. 13** *Osmia rufa* (syn. *bicornis*) on *Papaver rhoeas*



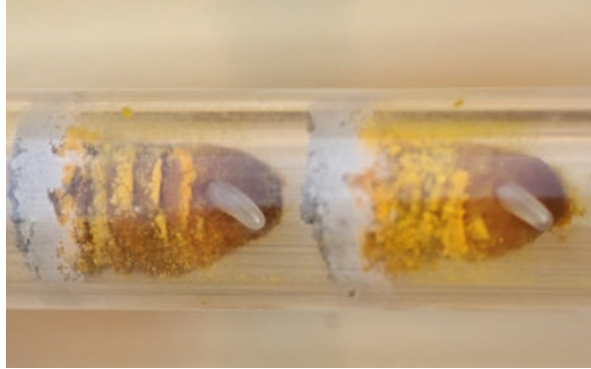
*Osmia* species show gregarious nesting behavior and build their nests in pre-existing cavities (Fig. 16), where the female produces a linear series of cells divided by mud walls (Tasei 1973; Peters 1977) (Fig. 17). This is why they are called generically “mason bees”; in each pedotrophic cell, one egg is laid on a nectar-pollen based mixture (Nepi et al. 2005) which the five larval instars will grow on.

Concerning the relationship with the plant food source exploited, *Osmia* species are oligolectic or polylectic, and for many of them the timing of the life cycle is related to the flowering of the Rosaceae botanical family (Márquez et al. 1994), whose pollen is highly preferred in comparison to others (Tasei 1973; Márquez et al. 1994; Maccagnani et al. 2003a, b). Their efficiency as pollinators, which has been compared to that one of honey bees by many authors (Bosch 1994; Monzon et al. 2004; Maccagnani et al. 2003a, b) is due to several eco-ethological traits. The most noticeable trait is that their foraging activity is mainly oriented to collect pollen, and in this aspect *Osmia* species are substantially different from honeybees. In fact, the flower visit performed by honeybees in search of nectar implies a limited contact with the reproductive parts of the flowers, as foragers land very often on petals than elongate the proboscis towards the nectaries, at the base of the stamens (Barth 1985; Free 1993, Fig. 9). Instead, mason bees are “top-foragers” and collect

**Fig. 14** *Osmia cornifrons***Fig. 15** *Osmia lignaria***Fig. 16** Nesting females at the entrance of their nests in the early morning, waiting to warm up before flying

the pollen with their ventral abdominal sets of hairs, using either the forelegs or the abdomen to scratch the anthers, according to the flower morphology (Tasei 1973). Direct observations of *O. cornuta* foraging on apple flowers showed that all visits are performed landing on the flower reproductive organs to collect pollen from the anthers, contemporarily feeding a small amount of nectar, which is possible thanks to a much longer tongue with respect to honey bees (personal observations). The dimensions, the kind of approach to the flower and the efficiency of the ventral

**Fig. 17** Portion of an *Osmia cornuta* nest within a transparent plastic tube. Two mud walls are clearly visible. Two pollen provisions, made up by adding pollen and secretions, show the succession of dry pollen and wet components. One egg is visible on each provision



scopa allow *Osmia* species to collect the pollen with quick and effective movements, ensuring, at the same time, very fast flower handling and high pollinating efficiency, thus reaching also 100% flower pollination (Bosch and Blas 1994; Maeta 1978; Vicens and Bosch 2000). In fact, the number of pollen granules transferred to the stigma by mason bees is much higher with respect to the honeybees, which transport the collected pollen with the hindlegs, a modality that prevent any direct contact between the collected granules and the reproductive flower organs (Harder and Wilson 1998). Pinzauti (2001) demonstrated in *Osmia* that the pollen germination potential is conserved until the deposition of the mass in the larval cell. In fact, only in this moment the female adds to the discharged pollen little drop of stomodeal content, composed by nectar with the addition of glandular secretions that, somehow, reduces the pollen viability (Nepi et al. 2005).

*Osmia* species have been assessed for crop pollination in different countries, both in open field on fruit trees like almond, apricot and apple (Bosch 1994; Bosch and Blas 1994; Kronic et al. 1995; Pinzauti et al. 1997) and in confined environments (Ladurner et al. 2002; Felicioli and Pinzauti 2008). Excellent results were obtained using *O. cornuta* for pear pollination (Maccagnani et al. 2003a, b, 2007; Monzon et al. 2004). Vicens and Bosch (2000) found that this species is a more efficient pollinator on almond and apple flowers than *A. mellifera*, because of its higher rate of stigma contact. Mason bees move from tree to tree more readily than honey bees, are less prone to orient along rows, thus enhancing cross pollination. Moreover, *O. cornuta* can adapt to a number of artificial nesting materials: another important aspect for the development of a pollinator management system (Kronic et al. 1995; Bosch 1995; Bosch and Kemp 2002).

#### 4 *Osmia cornuta*

*Osmia cornuta* is an obligate monovoltine species distributed in the South-Central Europe and in Northern Africa, and is a highly gregarious nesting species.

Females emerge from cocoons in March (some variations depend on the latitude), and the nesting period is concluded within 1 month. In natural environments, nests are constructed in broken giant cane stems (*Arundo donax* L.), but females easily accept many different substrates if dimensions are appropriated (8–10 mm diameter). Visual stimuli are very important for the females to orient their choice during the search for a suitable place to nest. *Osmia cornuta* shows no difference in visual perception and colour discrimination ability when compared to honey bees (Menzel et al. 1988). Thus, every dark point visible from the distance is explored. In its lifetime, the female lays around 30 eggs, producing, on average, one cell per day (Tasei 1973; Kronic et al. 2005). The pollen is collected and transported on the abdomen, thanks to a ventral hairy structure named scopa (Fig. 8). Upon return to her nest from a foraging flight, the female compacts the pollen discharged during the previous flight by using the head and the frontlegs, and while doing this, she deposits drops of stomodeal content on the pollen mass. Then, she turns back within the nest and discharges the new pollen load. When the diameter is too small, the female gets out, turns back at the nest entrance, and reaches the provision walking backwards.

Nepi et al. (2005) hypothesized that adding stomodeal regurgitation (plus glandular secretions?) to the pollen, to prepare the provision the larva will feed on, may serve to initiate germination or pseudo-germination. Pollen grains are probably the most difficult food from which nutrients can be obtained, because the pollen walls are among the hardest structures in the biological world. Thus, pollen feeding animals have evolved different and complicated mechanisms to obtain the nutrients and the energy stored in the pollen cytoplasm (Roulston and Cane 2000; Nepi et al. 2005). The morphological and biochemical changes occurring in *O. cornuta* pollen provisions might be necessary for “activating” the pollen grains for the digestive process. Other active substances could play a role in the pollen digestion process in the solitary bee larvae, such as mother-derived secretions produced by the female and added to the provision (Ladurner et al. 1999; Heroin-Delauney 1966).

It is worthwhile to point out that solitary bee larvae feed directly on the mother provision, and this makes a big difference with respect to the social species like *Bombus terrestris*, in which adult workers contribute to larval nutrition pre-digesting the pollen (Ribeiro et al. 1999; Pereboom 2000), and *A. mellifera*, in which nurse bees feed the larvae with a glandular secretion after having themselves eaten and digested the pollen (Roulston and Cane 2000). The possible role of commensalistic microbial fauna of the larval cell in inducing biochemical changes in pollen-nectar provision remains to be investigated.

The energetic investment in the two sexes is quite different, as female cocoons weigh, on average, around 0.4–0.5 g while male cocoons only 0.2 g (Bosch 1994; Maccagnani et al. 2007). As a result, a sex-dependent dimorphism is considerably high in *O. cornuta*, and implies a much stronger foraging effort to produce female cell provisions than to produce males. Coherently, the female progeny originated from fertilized (diploid) eggs is produced at the beginning of the nesting period, when the mother female is at her maximum efficiency, while males are produced at the end, from unfertilized eggs. The pre-imaginal development lasts several weeks,

and go through five moults, the first occurring within the egg. The first larva that can be observed feeding on cell provision is the second stage larva,; the following larval stages consume the provision in a few weeks. Than the fifth instar larva spin its cocoons, overpass the summer, and undergo the methamorphosis into adult before Autumn. Overwintering occurs as adult in the cocoon.

In the sister species *O. lignaria*, Sgolastra et al. (2011, 2012) found that adult eclosion follows the end of the summer diapause occurred during the prepupal stage; few weeks later, the adults lower their respiration rates (to  $\sim 0.1$  ml/g h) and undergo the winter diapause, that lasts until February–March, depending on the latitude. Winter diapause development in *Osmia* spp. occur in two phases. In the first phase, cold temperatures are required to increase the respiration response, which reaches a plateau in mid-winter. In the second phase, the respiration response follows an exponential increase, and when it has reached 0.45 ml/g/h the adult emerge promptly when exposed to 20°C, indicating diapause completion (Sgolastra et al. 2010).

In *O. bicornis*, a study by Wasielewski et al. (2013) found a complex dynamic of different energetic resources and enzymes that could explain the changes in the respiratory trends.

As each female can occupy simultaneously more cavities, and female eggs are layed at the beginning of the nesting period, female cocoons are generally found at the bottom of the cavity, while male cocoons occupy the front part of it. This behaviour has the biological significance of inducing a pronounced proterandry, resulting in the activation of males some days before females (likely related to the warmer temperatures in the front portion of the nesting tunnels, and to a higher oxigen diffusion, in comparison to the adults overwintering in the bottom portion), and to protect the female progeny (half of the male progeny, sex-ratio ff:mm 1:2) by rearing females in the most protected part of the nest.

In the perspective of the use of solitary bees to enhance pollination, it has to be considered the time needed for adult diapause termination in early spring. This duration depends on overwintering conditions and on early spring weather conditions, mainly the mean daily temperature.

If the release of *O. cornuta* populations occurs at the beginning of crop flowering, females might not be “ready” for an efficient pollination service before the end of the flowering period. Early flowering crops with short flowering periods would profit from a good landscape management with the introduction of ecological infrastructures with nectariferous/polliniferous botanical species can support the bee population prior and after the blooming period of the target crop, thus enhancing both crop pollination and bee reproduction (Maccagnani et al. 2007).

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## References

- Abrol DP (2011) *Pollination biology: biodiversity conservation and agricultural production*. Springer Science & Business Media, ISBN 978-94-007-1942-2
- Artz DR, Nault BA (2011) Performance of *Apis mellifera*, *Bombus impatiens* and *Peponapis pruinosa* (Hymenoptera: Apidae) as pollinators of pumpkin. *J Econ Entomol* 104(4):1153–1161
- Barth FG (1985) *Insects and flowers: the biology of a partnership*. Allen & Unwin, ISBN 0045740291, 9780045740291
- Benedek P, Nyeki J (1996) Pollinating efficiency of honeybees on apple cultivars as affected by their flower characteristics. *Hortic Sci* 28:40–47
- Bosch J (1994) The nesting behaviour of the mason bee *Osmia cornuta* (Latr.) with special reference to its pollinating potential (Hymenoptera, Megachilidae). *Apidologie* 25:84–93
- Bosch J (1995) Comparison of nesting materials for the orchard pollinator *Osmia cornuta* (Hymenoptera: Megachilidae). *Entomologia Generalis* 19:285–289
- Bosch J, Blas M (1994) Effect of overwintering and incubation temperatures on adult emergence in *Osmia cornuta* Latr (Hymenoptera, Megachilidae). *Apidologie* 25(3):265–277. <https://doi.org/10.1051/apido:19940301>
- Bosch J, Kemp WP (2001) *How to manage the blue orchard bee*, USDA-SARE, sustainable agriculture network, handbook series, book 5, Washington, DC
- Bosch J, Kemp WP (2002) Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *Bull Entomol Res* 92:3–16
- Buchmann S (1983) Buzz pollination in angiosperms. In: Jones CE, Little RJ (eds) *Handbook of experimental pollination biology*. Scientific and Academic Press, New York
- Cane JH (1997) Ground nesting bees: the neglected pollinator resource for agriculture. *Acta Horti* (437):309–324
- Cane JH (2008) A native ground-nesting bee (*Nomia melanderi*) sustainably managed to pollinate alfalfa across an intensively agricultural landscape. *Apidologie* 39(3):315–323
- Cane JH, Tepedino VJ (2001) Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conserv Ecol* 5(1): 1. [online] URL: <http://www.consecol.org/vol5/iss1/art1/>
- Da-Yong J, Long-Shi L (2007) The activity of wild and orchard *Osmia cornifrons*. *Chin Bull Entomol* 44:275–276
- Felicioli A, Pinzauti M (2008) Pollination by *Osmia* Bees (Hymenoptera: Megachilidae) encyclopedia of entomology. [https://doi.org/10.1007/978-1-4020-6359-6\\_3029978-1-4020-6359-6](https://doi.org/10.1007/978-1-4020-6359-6_3029978-1-4020-6359-6)
- Free JB (1993) *Insect pollination of crops*. Academic, San Diego
- Goodell K, Thomson JD (1998) Comparisons of pollen removal and deposition by honeybees and bumblebees visiting apple. *Acta Horti* 437:103–107. <https://doi.org/10.17660/ActaHortic.1997.437.8>
- Gruber B, Eckel K, Everaars J, Dormann CF (2011) On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie* 42:564–576. <https://doi.org/10.1007/s13592-011-0059-z>
- Harder LD, Thomson JD (1989) Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *Am Nat* 133:323–344. <http://www.jstor.org/stable/2462124>
- Harder LD, Wilson WG (1998) Theoretical consequences of heterogeneous transport conditions for pollen dispersal by animals. *Ecology* 79:2789–2807. [https://doi.org/10.1890/0012-9658\(1998\)079\[2789:TCOHTC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2789:TCOHTC]2.0.CO;2)
- Heroin-Delauney Y (1966) Etude des constructions d'*Osmia cornuta* (Hym. Apoidea) après injections de produits marqués. *Comptes rendus des Séances de la Société de Biologie et de ses filiales*. 160: 2027–2030
- Hoogendorn K, Steven C, Keller MA (2007) Foraging behaviour of a blue banded bee, *Amegilla chlorocyanea* in greenhouses: implications for use as tomato pollinators. *Apidologie* 38:86–92. <https://doi.org/10.1051/apido:2006060>

- James R, Pitts-Singer T (2008) Bee pollination of agricultural ecosystems (eds) Print ISBN -13: 9780195316957. Oxford Scholarship Online Sept. <https://doi.org/10.1093/acprof:oso/9780195316957.001.0001>
- Javorek SK, Mackenzie KE, Vander Kloet SP (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Ann Entomol Soc Am* 95(3):345–351
- Kendall DA (1973) Viability and compatibility of pollen on insects visiting apple blossom. *J Appl Ecol* 10:847–853
- Kendall DA, Solomon ME (1973) Quantities of pollen on bodies of insects visiting apple blossom. *J Appl Ecol* 10:627–634
- Kevan PG and Phillips TP (2001) The economic impacts of pollinator declines: an approach to assessing the consequences. *Conserv Ecol* 5(1): 8. [online] URL: <http://www.consecol.org/vol5/iss1/art8/>
- Klein MA, Vaissière BE, James HCI, Cunningham SA, Kremen C, Scharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proc R Soc B* 274:303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Kremen C, Williams NM, Bugg RL, Fay JP, Thorp RW (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol Lett* 7:1109–1119
- Krunić M, Pinzauti M, Felicioli A, Stanisavljević LJ (1995) Further observations on *Osmia cornuta* Latr. and *O. rufa* L. as alternative fruit pollinators, domestication and utilization. *Arch Biol Sci Belgrade* 47:59–66
- Krunić M, Stanisavljević L, Pinzauti M, Felicioli A (2005) The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. *Bull Insectol* 58(2):141–152
- Ladurner E, Maccagnani B, Tesoriero D, Nepi M, Felicioli A (1999) Laboratory rearing of *Osmia cornuta* (Latreille) (Hymenoptera Megachilidae) on artificial diet. – *Bollettino dell' Istituto di entomologia "G. Grandi"*. Università di Bologna 53:133–146
- Ladurner E, Santi F, Maccagnani B, Maini S (2002) Pollination of caged hybrid seed red rape, *Brassica oleracea* (Brassicaceae), with *Osmia cornuta* (Latr.) and *Apis mellifera* L. (Hymenoptera, Megachilidae and Apidae). *Bull Insectol* 55(1/2):9–11
- Lee S-B, Seo D-K, Choi K-H (2008) The visited insects on apple flowers, and the characteristics on pollinating activity of pollinators released for pollination of apple orchards. *Korean J Apic* 23(4):275–282
- Maccagnani B, Ladurner E, Santi F, Burgio G (2003a) *Osmia cornuta* (Hymenoptera Megachilidae) as a pollinator of pear (*Pyrus communis*): fruit- and seed- set. *Apidologie* 34:207–216
- Maccagnani B, Ladurner E, Tesoriero D, Sgolastra F, Burgio G (2003b) The use of *Osmia cornuta* (Latreille) (Hymenoptera Megachilidae) for pear pollination: a reason to adopt low impact farming system in a landscape management perspective. *IOBC WPRS Bull* 26(4):101–106
- Maccagnani B, Burgio G, Stanisavljević LŽ, Maini S (2007) *Osmia cornuta* management in pear orchards. *Bull Insectol* 60(1):77–82
- Maeta Y (1978) Comparative studies on the biology of the bees of the genus *Osmia* of Japan, with special reference to their managements for pollinations of crops (Hymenoptera: Megachilidae). *Bull Tohoku Nat Agric Exp Stn* 57:1–221
- Márquez J, Bosch J, Vicens N (1994) Pollens collected by wild and managed populations of the potential orchard pollinator *Osmia cornuta* (Latr.) (Hym., Megachilidae). *J Appl Entomol* 117(1–5):353–359. <https://doi.org/10.1111/j.1439-0418.1994.tb00746.x>
- McGregor SE (1976) Insect pollination of cultivated crop plants. *Agricultural handbook No. 496*. USDA, Agricultural Research Service, Washington
- McKinney MI, Yong-Lak Park (2012) Nesting activity and behavior of *Osmia cornifrons* (Hymenoptera: Megachilidae) elucidated using videography. *Psyche* ID 814097, <https://doi.org/10.1155/2012/814097> 1–7
- Menzel R, Steinmann E, De Souza J, Backhaus W (1988) Spectral sensitivity of photoreceptors and colour vision in the solitary bee, *Osmia rufa*. *J Exp Biol* 136:35–52

- Michener CD (2000) *The Bees of the World*. Baltimore and London. The John Hopkins University Press. ISBN 0-8018-6133-0
- Monzon VH, Bosch J, Retana J (2004) Foraging behaviour and pollinating effectiveness of *Osmia cornuta* (Hymenoptera: Megachilidae) and *Apis mellifera* (Hymenoptera: Apidae) on 'Comice' pear. *Apidologie* 35:575–585
- Nepi M, Cresti L, Maccagnani B, Ladurner E, Pacini E (2005) From the anther to the proctodeum: pear (*Pyrus communis*) pollen digestion in *Osmia cornuta* larvae. *J Insect Physiol* 51(7):749–757. <https://doi.org/10.1016/j.jinsphys.2005.03.003>
- Pereboom JM (2000) The composition of larval food and the significance of exocrine secretions in the bumblebee *Bombus terrestris*. *Insect Soc* 47:11–20
- Peters DS (1977) Systematik und Zoogeographie der west-paläarktischen Arten von *Osmia* sstr. *Monosmia* und *Orientosmia*. *Senckenberg Biol* 58:287–346
- Pinzauti M (2001) Investigation on the germinating potential of pollen transported by some bees. IX Convegno Nazionale Associazione Nazionale Studio Artropodi Sociali e Presociali. Parma –6–8 giugno 2001
- Pinzauti M, Lazzarini D, Felicioli A, Richards KW (1997) Preliminary investigations of *Osmia cornuta* Latr. (Hymenoptera, Megachilidae) as a potential pollinator for blackberry (*Rubus fruticosus* L.) under confined environment. *Proceedings of the 7th International Symposium on Pollination*, Lethbridge, Alberta, June 23–28 1996, pp. 329–333
- Pitts-Singer TL, Cane JH (2011) The alfalfa leafcutting bee, *Megachile rotundata*: the world's most intensively managed solitary bee. *Annu Rev Entomol* 56:221–237. <https://doi.org/10.1146/annurev-ento-120709-144836>
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25(6):345–353
- Ribeiro MF, Velthuis HHW, Duchateau MJ, van der Twee I (1999) Feeding frequency and caste differentiation in *Bombus terrestris* larvae. *Insect Soc* 46(4):306–314
- Roulston TH, Cane JH (2000) Pollen nutritional content and digestibility for animals. *Plant Syst Evol* 222(1–4):189–209
- Sampson BJ, Cane JH (2000) Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. *J Econ Entomol* 93(6):1726–1731
- Sgolastra F, Bosch J, Molowny-Horas R, Maini S, Kemp WP (2010) Effect of temperature regime on diapause intensity in an adult-wintering Hymenopteran with obligate diapauses. *J Insect Physiol* 56(2):185–194. <https://doi.org/10.1016/j.jinsphys.2009.10.001>
- Sgolastra F, Kemp WP, Buckner JS, Pitts-Singer TL, Maini S, Bosch J (2011) The long summer: pre-wintering temperatures affect metabolic expenditure and winter survival in a solitary bee. *J Insect Physiol* 57(12):1651–1659
- Sgolastra F, Kemp WP, Maini S, Bosch J (2012) Duration of prepupal summer dormancy regulates synchronization of adult diapause with winter temperatures in bees of the genus *Osmia*. *J Insect Physiol* 58:924–933
- Shuler RE, Roulston TH, Farris GE (2005) Farming practices influence wild pollinator populations on squash and pumpkin. *J Econ Entomol* 98(3):790–795
- Tasei JN (1973) Le comportement de nidification chez *Osmia* (*Osmia*) *cornuta* Latr. et *Osmia* (*Osmia*) *rufa* L. (Hymenoptera Megachilidae). *Apidologie* 4(3):195–225
- Tepedino VJ (1981) The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honeybee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). *J Kansas Entomol Soc* 54:359–377
- Thomson JD (2001) How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia* 126:386–394. <https://doi.org/10.1007/s004420000531>
- Thomson BA, Thomson JD (1999) BeeVisit. In: Jungck J (ed) Bioquest library. Academic, San Diego, pp 64–65
- Torchio PF, Asensio E (1985) The introduction of the European bee, *Osmia cornuta* Latr., into the U.S. as a potential pollinator of orchard crops, and a comparison of its manageability with *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae). *J Kansas Entomol Soc* 58(1):42–52



- Vicens N, Bosch J (2000) Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on 'Red Delicious' apple. *Environ Entomol* 29:235–240
- Wasielewski O, Wojciechowicz T, Giejdasz K, Krishnan N (2013) Overwintering strategies in the red mason solitary bee—physiological correlates of midgut metabolic activity and turnover of nutrient reserves in females of *Osmia bicornis*. *Apidologie* 44:642–656. <https://doi.org/10.1007/s13592-013-0213-x>
- Willians I (2002) Insect pollination and crop production: a European perspective. In: Kevan P, Imperatriz Fonseca VL (eds) *Pollinating bees: the conservation link between agriculture and nature*. Ministry of Environment, Brasília, pp 59–65