



**HAL**  
open science

# Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; *Osmia*) as fruit tree pollinators

Claudio Sedivy, Silvia Dorn

► **To cite this version:**

Claudio Sedivy, Silvia Dorn. Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; *Osmia*) as fruit tree pollinators. *Apidologie*, 2013, 45 (1), pp.88-105. 10.1007/s13592-013-0231-8 . hal-01234708

**HAL Id: hal-01234708**

**<https://hal.science/hal-01234708>**

Submitted on 27 Nov 2015

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# Towards a sustainable management of bees of the subgenus *Osmia* (Megachilidae; *Osmia*) as fruit tree pollinators

Claudio SEDIVY, Silvia DORN

ETH Zurich, Institute of Agricultural Sciences, Applied Entomology, Schmelzbergstrasse 9/LFO, 8092 Zurich, Switzerland

Received 31 January 2013 – Revised 14 June 2013 – Accepted 18 July 2013

**Abstract** – The limited pollination efficiency of honeybees (Apidae; *Apis*) for certain crop plants and, more recently, their global decline fostered commercial development of further bee species to complement crop pollination in agricultural systems. In particular, a number of mason bees (Megachilidae; *Osmia*) are among the most widely used alternative pollinators, and their utilisation has been fine-tuned specifically for pollination in fruit tree orchards. A successful management system should not only aim at optimising pollination efficiency but also consider the relevant biological and ecological requirements to achieve sustainable and healthy bee populations. Here, we review the factors influencing the rate of population increase during the implementation of *Osmia* bees as orchard pollinators. These factors include nesting material, release methods, and control of antagonists as well as methods optimising management of developmental stages to synchronize bee activity with orchard bloom and to minimize developmental mortality.

**orchard pollination / alternative pollinator / *Osmia* / fruit trees**

## 1. INTRODUCTION

Solitary bees hold the potential to complement honeybees in safeguarding pollination services in both agricultural and natural environments (Klein et al. 2007; Adamson et al. 2012; Holzschuh et al. 2012; Brittain et al. 2013; Garibaldi et al. 2013). Honeybees will continue to play an important role in crop pollination and security despite the numerous hazards threatening thriving honeybee populations, which include (1) the cosmopolitan spread of the mite *Varroa destructor* Anderson & Trueman (reviewed in Dietemann et al. 2012), (2) viral, bacterial and fungal diseases (reviewed in Genersch 2010), (3) long-distance migratory bee

keeping such as practiced in the USA, (4) neonicotinoid pesticides in pollen and nectar (Henry et al. 2012), and (5) nutritional stress due to reduced quantitative and qualitative flower supply (Naug 2009); or a combination of two or more of these factors (Alaux et al. 2010). Honeybees are highly versatile pollinators comprising an incomparably broad host plant spectrum. However, because they are not specialists of any plant species, even their broad pollination spectrum has limits. For instance, honeybees do not efficiently pollinate certain crop plants such as blueberries (*Vaccinium* spec.) or tomatoes and potatoes (*Solanum* spp.) because of their inability to buzz-pollinate. Furthermore, they are unsuitable to pollinate in greenhouses where they suffer disorientation and may behave aggressively towards working staff when disturbed. To complement honeybees, alternative bee species have been

Corresponding author: C. Sedivy,  
claudio.sedivy@gmail.com  
Manuscript editor: Peter Rosenkranz

commercially developed and implemented for pollination of some crop plants. Such successfully managed pollinators include the social bumblebees (*Bombus* spp.) as well as solitary bee species such as the alfalfa leafcutter bee (*Megachile rotundata* Fabricius) and several mason bee species (*Osmia* spp.).

Mason bees (hereafter termed *Osmia* bees) are mainly used as pollinators of rosaceous fruit tree species including almond, peach, apricot, plum, cherry, apple and pear (Maeta and Kitamura 1974; Torchio 1976; Bosch et al. 2000, 2008; Bosch and Kemp 2001; Kormmilch 2010). An exception constitutes *Osmia ribifloris* Say, which has been developed successfully as an efficient pollinator of blueberries in the southern USA (Torchio 1990; Sampson and Cane 2000; Sampson et al. 2004, 2009). All *Osmia* bees other than *O. ribifloris* comprise a group of closely related species within the subgenus *Osmia* s. str. (Michener 2007; Haider et al. 2013) characterized by a pair of horn-like extensions on the clypeus in the female. The gregarious nesting behaviour of these solitary bees and their acceptance of a variety of different man-made nesting materials are important prerequisites for successful mass rearing (Torchio 1976). In their natural habitats, most *Osmia* bee species are highly generalist pollen foragers collecting pollen from between 9 and 20 plant families (Mitchell 1962; Rust 1974; Torchio 1987; Westrich 1989; Haider et al. 2013). However, their foraging behaviour often shows a relatively high pollen constancy as these bees tend to prefer certain pollen sources provided these are abundant near their nesting site (Westrich 1989; Radmacher and Strohm 2010). This trait is advantageous for commercial fruit tree pollination in orchards.

The four most intensively studied and successfully managed *Osmia* species are (1) *Osmia cornifrons* (Radoszkowski) native to eastern Asia (Yamada et al. 1971; Maeta and Kitamura 1974), (2) *Osmia lignaria* Say native to North America (Torchio 1976; Bosch and Kemp 2001), (3) *Osmia cornuta* (Latreille) native to Europe (Bosch and Kemp 2002; Kronic and Stanisavljevic 2006) and (4) *Osmia bicornis*, also native to Europe (Kronic and Stanisavljevic 2006; Kormmilch 2010; Schindler and Peters 2011). Utilisation of *O.*

*cornifrons* has been developed for apple pollination in Japan since the 1940s (Kitamura 1969), and today, this species is being used to pollinate over 75 % of Japan's apple orchards (Bosch and Kemp 2001; Sekita 2001). Utilisation of *O. lignaria* has been developed mainly for pollination of apple (Torchio 1976), almond (Torchio 1981a) and cherry (Bosch and Kemp 1999) since the mid-1970s. The development of the utilisation of the European *O. cornuta* as an orchard pollinator commenced in the mid-1980s, when a population was introduced into the USA (Torchio and Asensio 1985), and it was later continued especially in Spain with the main focus on almond pollination (Bosch et al. 2000). *O. bicornis* (formerly *O. rufa*) was developed as pollinator for fruit trees and other crops such as strawberries (*Fragaria* spp.) and oil seed rape (*Brassica napus*) since the mid-1970s (Holm 1973; Wilkaniec and Radajewska 1997; Kormmilch 2010; Gruber et al. 2011). Further, *Osmia* species, including *O. excavata*, *O. pedicornis*, *O. taurus* and *O. tersula*, showed promise for development as pollinators of fruit tree orchards (Maeta 1978; Wei et al. 2002; Sheffield et al. 2008a).

*Osmia* bees, which are strictly univoltine, are among the earliest emerging bees in spring (Westrich 1989). Males emerge earlier than females (protandry), and some days after mating, females start to forage for pollen–nectar provisions from suitable flowering plants, bring them back to their nest, and fly back and forth dozens of times to provision a single brood cell, into which they deposit an egg (Zurbuchen et al. 2010). The egg is either fertilized, yielding a female, or unfertilized, yielding a male (Elias et al. 2010). After hatching from the egg, the larva feeds on the pollen–nectar diet (Table I). Upon completion of larval development, the larva spins a cocoon. Then, the bee passes through a prepupal and pupal stage and finally ecloses as an adult while remaining within the intact cocoon. In this cocoon, the adult stays for the pre-wintering phase before temperature drops, and for the subsequent wintering at low temperatures (Bosch et al. 2008; Table I).

*Osmia* bees are outstanding fruit tree pollinators and often outmatch honeybees in several

**Table I.** Definitions used for major developmental stages and crucial phases in the annual cycle of *Osmia* bees.

Major develop. stage/crucial phase	Definition
Larval development	Development from larval hatching to cocoon spinning
Cocoon spinning	The larva discontinues feeding and spins an intransparent, tough cocoon before entering the prepupal stage
Prepupal stage	The summer diapause period
Pupation	Following the prepupal stage, bees enter the pupal stage before eclosing as adults
Adult eclosion	Fully developed adults eclose from the pupae and remain within cocoons
Pre-wintering	A highly susceptible stage between adult eclosion and wintering
Wintering	A quiescent stage entered by bees in cocoons exposed to low temperatures
Incubation	A process to terminate the wintering stage by exposing bees to warm temperatures, after which adult bees start to chew open their cocoon and emerge
Emergence	Bees leaving their cocoon
Pre-emerging time	Duration from start of incubation to emergence of the first bee
Emerging period	Duration from the first to the last bee to emerge after incubation

important factors. They contact the flowers stigmas during virtually every single visit (Bosch and Blas 1994b; Vicens and Bosch 2000b; Monzon et al. 2004), they visit a large number of flowers per unit time (Calzoni and Speranza 1998; Vicens and Bosch 2000b; Monzon et al. 2004) and they readily switch between trees and between rows of trees within the orchard, which is particularly important because many fruit tree cultivars are self incompatible and require cross fertilisation (Free 1993; Bosch and Blas 1994a; Vicens and Bosch 2000b; Ladurner et al. 2004). Single visit experiments revealed very high fruit and seed set rates (Kuhn and Ambrose 1984). Their limited flight radius (Hermann 2010) and their preference for Rosaceae pollen leads to distinct fruit tree flower fidelity in orchard environments (Torchio 1976; Marquez et al. 1994; Bosch et al. 2000; Sheffield et al. 2008b; Schindler and Peters 2011). Moreover, *Osmia* bees forage at lower temperatures and less favourable weather conditions, and therefore for a longer period of time per day than honeybees (Vicens and Bosch 2000c), a highly preferable trait for pollination of early blooming fruit tree species such as almond and cherry. Therefore, *Osmia* pollinated orchards may not

only produce enhanced yields in favourable years but also safeguard a yield in years that would otherwise be devoid of any yield (Bosch and Kemp 1999; Bosch et al. 2006). However, comprehensive and sustainable management system should not only aim at optimising pollination efficiency but also at achieving the bases for stable and sustainably managed bee populations in an orchard environment.

The present review article summarizes and interprets the main factors influencing the increase in *Osmia* bee populations under management conditions. The first part focuses on factors influencing *Osmia* bee reproduction in the orchard such as the provided nesting shelters, release methods, favourable bee densities, dislocation of nesting shelters as well as minimising the impact of natural enemies.

The second part focuses on factors influencing the optimisation of *Osmia* bee performance and synchronisation of their emergence with orchard bloom. All crucial developmental stages are discussed and insights are provided into suitable approaches for optimal management of *Osmia* bees to foster synchronisation while limiting developmental mortality.

## 2. FACTORS INFLUENCING THE RATE OF POPULATION INCREASE OF *OSMIA* BEES DURING THEIR NESTING ACTIVITY IN THE FRUIT TREE ORCHARD

Various abiotic and biotic factors influence the successful multiplication of *Osmia* bees in the field. While some important factors can be influenced by management practices, others are beyond human control such as weather conditions and the duration of orchard bloom. In contrast to optimal greenhouse conditions, under which *Osmia* females can produce as many as 30 offspring during a 4-week flight season (Torchio et al. 1987), uncontrollable abiotic field conditions will not allow such high reproduction rates, or might even threaten population increase. For example, low temperatures as well as windy and rainy weather can interrupt nesting activities of *Osmia* females for days (C. Sedivy, personal observation). Furthermore, low temperatures resulting in long lasting winter seasons delay orchard bloom, which in turn may lead to a foreshortened flowering period (Torchio 1981b).

A key biotic factor, which can be influenced by management practices to enhance offspring populations, is the large body size of female *Osmia* bees. Large females usually suffer less winter mortality, are more likely to establish a nest, forage more efficiently, produce more eggs and live longer (Seidelmann et al. 2010, and references therein; Tepedino and Torchio 1982a; Bosch and Kemp 2004; Bosch and Vicens 2006; Bosch 2008; but see Sheffield et al. 2008a). Furthermore, large females are less likely to exhibit pre-nesting dispersal (Steffan-Dewenter and Schiele 2004). The fact that they have attained a high body weight indicates that the habitat in the preceding season has been suitable, which may promote a conservative strategy of abiding by the maternal nesting site (Steffan-Dewenter and Schiele 2004). Large females also produce a less male biased brood, and, most importantly, they again produce larger females (Bosch and Vicens 2006; Seidelmann et al. 2010). However, heritability of size among females is very low, indicating that selective breeding to increase body size in these bees would

be unprofitable (Tepedino et al. 1984). Instead, body size largely correlates with both the quantity and the quality of pollen provisions allocated to the offspring by the female bee (Bosch and Vicens 2006; Radmacher and Strohm 2010; Sedivy et al. 2011).

Under natural conditions, *Osmia* populations are usually male biased. Since only females contribute to nesting activities, and hence account for most of the pollination service, bee management should aim to decrease the ratio of male to female progeny towards an unbiased sex ratio. Typically, *Osmia* bees produce energetically more costly females when circumstances are favourable and tend to shift towards the production of energetically cheaper males when circumstances deteriorate. The probability for a nesting mother to assign a brood cell to a daughter rather than a son increases when the mother is still young (Torchio and Tepedino 1980; Tepedino and Torchio 1982a, b; Bosch and Vicens 2005), is large (Steffan-Dewenter and Schiele 2004; Seidelmann et al. 2010), pollen–nectar resources are abundant (Tepedino and Torchio 1982a; Steffan-Dewenter and Schiele 2004), both the material and dimensions of the nesting cavity are optimized (see Sections 2.1.1. and 2.1.2.), and females are mated in time (Sampson et al. 2009). In fact, unmated females have a lower chance to successfully found a nest. They start nesting late or attempt to usurp nests of other, mated females. In case such unmated females manage to reproduce, they produce exclusively male progeny. These findings underline the necessity to ensure mating of the females by supplying sufficient males (Sampson et al. 2009).

### 2.1. Nesting sites

*Osmia* bees accept a variety of artificial nesting sites. An ever-growing number of companies offer different designs made of various materials (Bosch and Kemp 2001, and references therein; <http://www.pollinatorparadise.com> for North America). Basically, economic aspects encompassing production cost, manageability, durability and handling of nesting sites should be balanced with ecological

aspects such as attractiveness for *Osmia* females, suitability for larval development, and constrained accessibility to parasites. Most widely used nesting materials are solid wooden or styrofoam blocks with drilled cavities and inserted paper straws; hollow boxes with a wooden front through which paper straws are inserted and sealed at the back (milk carton nesting units); stacked grooved boards; reed and bamboo segments (Bosch and Kemp 2001; Kronic and Stanislavljjevic 2006).

### 2.1.1. Attractiveness versus suitability of different nesting material

Most studies that compared attractiveness of different nesting materials to *Osmia* females revealed that wood blocks with drilled cavities were most attractive (Torchio 1981a, 1982a, b, 1984a; Bosch 1994b, 1995), followed by grooved wooden boards, reed segments and milk cartons (Bohart 1972; Bosch 1995). *Osmia* females also favoured wood over styrofoam (Torchio 1981a, 1982a, b, 1984a) even when attempts were made to camouflage the true material by placing a wooden cover with cavities over the nest entrances (Torchio 1982b). *Osmia bicornis* L., however, preferred reed sections to drilled cavities in wood (Wilkaniec and Giejdasz 2003) although wooden nests allowed for best developmental and winter survival. Therefore, attractiveness of a given nesting material should always be balanced with its suitability for successful bee development to the adult stage.

Sometimes, *Osmia* females prefer their natal nests over newly provided nesting cavities (Torchio 1981b, 1984a, but see Tepedino and Torchio 1982a; Bosch 1994a). The reason for this behaviour may lay in the attraction of *Osmia* females to chemical cues emitted by the female cocoon (Pitts-Singer 2007). In fact, when the newly provided nesting material is less attractive than the material of their natal nest, bees seem to prefer their natal nest. Conversely, when it is more attractive, new cavities tend to be favoured (Bosch 1994b). However, nesting in natal nests harbours the risk of accumulating and spreading parasites (e.g. *Chaetodactylus* mites) and infectious dis-

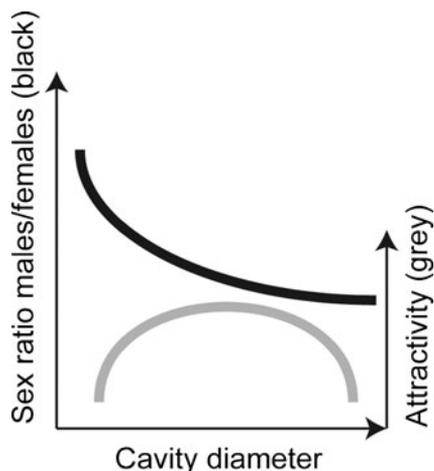
eases (foul brood), which may jeopardise successful larval development (Bosch and Kemp 2001; Kormmilch 2010).

*Osmia* bees exhibit a gregarious nesting behaviour and are therefore attracted to nesting cavities close to those already occupied by conspecifics (Kronic et al. 2001). Hence, a simple way to increase attractiveness of the nesting material provided is to take a limited number of bees into the orchard about 10 days before the release of the main bee population. By then, some of these prematurely released females will already have established at the nesting sites provided, and will hence represent a strong attractor for bees released later (Kronic et al. 2001). This method, however, is only applicable if the orchard environment provides some alternative floral resources before orchard bloom (see Section 2.4.).

### 2.1.2. Nesting cavity dimensions

Regardless of the nesting material chosen, the cavity dimensions, in particular the cavity diameter, are of utmost importance for the successful propagation of *Osmia* bees (Bosch and Kemp 2001). In general, longer and wider cavities lead to (1) a higher percentage of females, (2) a lower offspring mortality, (3) larger progeny and (4) more offspring per nest (Maeta 1978; Torchio and Tepedino 1980; Bosch 1994a, b; Figure 1). However, if cavities are too wide, they may lose some of their attractiveness (Maddocks and Paulus 1987; Bosch and Kemp 2001; Bosch 1994a).

For instance, the percentage of female *O. cornuta* offspring produced in 15-cm long cavities increased dramatically from as little as 15 % at a diameter of 7 mm to 29 % at a diameter of 8 mm, and to 37 % at a diameter of 9 mm. Furthermore, mortality decreased from 34 % (7 mm), to 26 % (8 mm) and to 20 % (9 mm). However, the 9-mm cavities were significantly less attractive to the nesting females (23 % used) compared to 7 mm (48 %) and 8 mm (53 %) cavities (Bosch 1994a). In *O. bicornis*, nesting cavities of 15 cm or longer resulted in a higher percentage of female offspring than cavities shorter than 15 cm (Gruber et al. 2011). In *O. lignaria*, however, nesting cavity



**Figure 1.** Qualitative relationship between cavity diameter, attractiveness to female *Osmia* bees and the resulting sex ratio (proportion of males to females) of the progeny.

dimensions seem to be less important than the attractiveness of the nesting material, which correlated with a higher percentage of female offspring (Torchio 1982a).

### 2.1.3. Nesting shelter and mud source for nest construction

A practically designed nesting shelter that combines optimal handling and functionality with low costs has recently been described by Cane (2006). It meets in particular the requirements for protection from rain and from predators, as discussed below.

To maximise the daily duration of bee activity, nesting shelters should be oriented in a way that nesting material is exposed to the morning sun (Bosch and Kemp 2001). Under cool temperature conditions, optimally, the opening of the nesting shelter should face in an eastern to south-eastern direction and should not be shaded in the morning (Torchio 1982a, b, c, 1985; Torchio and Asensio 1985). Shaded locations exhibit a lower ambient temperature, which results in delayed initiation of flight, and ultimately in shorter daily flight periods. This in turn leads to the reduction of the average number of cells constructed per day (Torchio

1981b). Moreover, north facing nesting shelters were found to be little attractive (Torchio 1981a). In addition, nesting material needs to be protected not only from wind and rain but also from direct sunlight when temperatures are very high, e.g. during the hottest time of the day. Moreover, nesting material should be placed above ground to protect it from humid microclimate and to allow for an effective protection from ants (Bosch and Kemp 2001; Kronic and Stanisavljevic 2006; Kormmilch 2010).

Some bird species such as tits or woodpeckers, with free access to the nesting material may cause havoc among the *Osmia* population (Bosch et al. 2006). A simple but effective way to exclude these predators is the installation of a coarse wire netting over the opening of the nesting shelter (Bosch and Kemp 2001).

*Osmia* bees require a source of muddy soil in the vicinity of their nesting shelter to construct the cell partitions and the nest plugs. If not naturally accessible, such a mud source must be artificially supplied and kept moisturised (Bosch and Kemp 2001; Kronic and Stanisavljevic 2006)

### 2.1.4. Distribution of nesting material in the orchard

When bees are released in the orchard, some females will disperse and establish nests elsewhere. An effective way to promote these bees to stay in the orchard is to provide so-called drift nests. For example Torchio (1981a, b, 1982c) showed that small trap nests attached individually to fruit trees were readily accepted and retrieved a similarly high number of progeny per provided cavity as the main nesting shelter. In general, a large number of smaller nesting shelters evenly distributed across the orchard not only leads to higher establishment rates (Torchio 1984a, b; Bosch and Blas 1994b), but also to more even pollination levels (Yamada et al. 1971; Artz et al. 2013). The average foraging range of *Osmia* bees is much smaller than that of honeybees (Hermann 2008; Zurbuchen et al. 2010), especially in an orchard environment where pollen and nectar resources are present at a particularly high density.

It amounts to approximately 50–150 m (Hermann 2010). Nesting shelters should therefore be evenly distributed throughout the orchard at a distance of 50–100 m (Kronic and Stanisavljevic 2006).

## 2.2. Release methods

*Osmia* bees can be released either from their individual natal nests, or they can be mass-released. Bees hatching from their native nests have a high establishment rate at the releasing site, usually around 60–75 % (Torchio 1982a, 1984a, b; Bosch 1994b; Bosch et al. 2000; Bosch and Kemp 2002; Monzon et al. 2004). As mentioned above, *Osmia* females exhibit a pronounced attraction to the nesting cavities from which they emerged, but also to cavities in their close proximity. The major problem with this release method is that it does not allow for efficient control of parasites or infectious diseases such as chalkbrood (Bosch and Kemp 2001; Kronic et al. 2005). When *Osmia* bees are reared in high densities, these parasites and diseases can thrive, quickly multiply and cause severe losses (Bosch 1992; see Section 2.6.).

Therefore, the great advantage of the mass release method is the opportunity to sex the cocoons (larger cocoons are usually females, whereas small cocoons are males) and to actively exclude various parasites visible outside the cocoon, such as mites or larvae of the drosophilid fly *Cacoxenus indagator* (Bosch and Kemp 2001). In addition, the cocoons can be stored more economically and can be better managed. When released, however, high pre-nesting female dispersal must be expected, with the highest pre-nesting dispersal (usually exceeding 50 %) when bees are released as already emerged adults (Torchio 1982a, b, c, 1984b; Torchio and Asensio 1985; Maccagnani et al. 2003; Monzon et al. 2004), probably because they will lack any association with the provided nesting sites (C. Sedivy, personal observation).

To overcome this problem, bees should be placed in the orchard while still inside the cocoon. The female cocoons can be inserted individually into the bottom of the nesting cavities (Monzon et al. 2004). Despite being highly labour intensive,

this seeding method has the advantage of mimicking hatching from the natal nest, sometimes resulting in a favourably low pre-nesting dispersal of around 20 % in *O. cornuta* (Bosch 1994a).

## 2.3. Bee densities

*Osmia* bees are highly efficient orchard pollinators (Bosch and Blas 1994b; Vicens and Bosch 2000b; Hermann 2010). Depending on the crop plant (apple, cherry, almond, etc.) and tree size (number of flowers per tree), as few as 350–750 nesting females per hectare are required for optimal pollination (Maeta and Kitamura 1974; Torchio 1985, 1991a; Maeta 1990; Bosch 1994c; Vicens and Bosch 2000b; Bosch and Kemp 2001, 2004; Ladurner et al. 2004). To achieve optimal population growth, these numbers should not be increased exceedingly (Bosch and Blas 1994a; Vicens and Bosch 2000b; Bosch and Kemp 2004). High bee densities might not only lead to increased pre-nesting dispersal (Torchio 1985) but also to strong competition for pollen and nectar, which may trigger a domino effect on other factors influencing bee population growth (Torchio 1985). Facing a pollen–nectar shortage, bees respond by provisioning their cells with smaller pollen–nectar provisions and by producing mainly male offspring. Furthermore, they produce not only fewer but also smaller females that eventually suffer highly increased developmental mortality (Torchio and Tepedino 1980; Tepedino and Torchio 1982b). A shortage in nectar also prevents the females from firmly anchoring their eggs to the pollen provisions, which leads to pre-hatching egg collapse. Freshly hatched larvae may fail to ingest the dry cell provision. The accumulation of these negative effects triggered by only one factor (too many bees released in the orchard) is a formidable example for the complex and sometimes counter-intuitive reactions of *Osmia* populations to mismanagement (Torchio 1985).

## 2.4. Alternative pollen–nectar resources

A valuable supplement to the precise timing of bee emergence with bloom of the fruit trees is

to provide alternative pollen–nectar resources (Bosch and Kemp 2001; Sheffield et al. 2008b). Since all *Osmia* bees used as pollinators in fruit tree orchards are broad pollen generalists (Westrich 1989; Mitchell 1962; Haider et al. 2013), a range of different plant species can be used. In particular, plants that flower before orchard bloom can be planted within the orchard, thus allowing for an early bee establishment. The great advantage of this method is that females are already in full nesting activity and at the peak of their pollination efficiency by the time orchard bloom starts. This method also allows for more flexibility regarding the timing of bee release and towards unfavourable weather development. Once the orchard is in bloom, these alternative pollen–nectar resources usually do not compete with the highly abundant and often favoured fruit trees for pollination (Bosch and Kemp 2001).

Such alternative plants (1) should start flowering at least 1 week before the onset of orchard bloom, (2) should be located in proximity to the nesting shelters, (3) should be sufficiently attractive and resourceful to *Osmia* bees to promote nest establishment, (4) should not compromise crop production, and (4) should be easily and cheaply manageable. Promising candidates include certain Brassicaceae species such as *B. napus* L. (Maccagnani et al. 2007), *B. alba* L. (Abel and Wilson 1998; Maccagnani et al. 2004) and *Sinapis arvensis* L. (Sedivy et al. 2011; Haider et al. 2012) for *O. bicornis*, *O. cornifrons* and *O. cornuta* as well as *Lupinus* spec. (Sheffield et al. 2008b) and *Limnanthes alba* Benthham (Bosch and Kemp 2001) for *O. lignaria*. Optimally, sufficient alternative pollen–nectar sources are naturally available in close proximity such as various weeds in organic farms (Bosch and Kemp 2001), early flowering hedges (Maccagnani et al. 2007) or neighbouring orchards with early blooming species or cultivars (Krunic et al. 2001; Bosch et al. 2006). Despite the fact that *Osmia* females are less fecund and produce mainly males towards the end of their flight season (Seidelmann et al. 2010), alternative pollen–nectar sources that outlast orchard bloom may contribute to increased female reproductive

rate (Bosch et al. 2006; Maccagnani et al. 2007). Hence, inclusion of carefully selected flowering plants into the orchard can effectively enhance both orchard pollination and bee population increase.

## 2.5. Moving occupied nesting sites

Once a female *Osmia* bee has selected a nesting cavity and started nest provisioning, it becomes strongly conditioned to both its nesting site and adjacent visual landmarks (Vicens and Bosch 2000a). In general, nesting shelters with actively nesting *Osmia* bees should not be moved because females are easily disturbed and tend to abandon their nests (Bosch and Kemp 2001). Furthermore, vibrations during transportation may cause eggs and young larvae to detach from their pollen provisions and die (Kornmilch 2010). However, moving nesting shelters may be taken into consideration under certain circumstances, for example to avoid exposure to an insecticide application, or to provide sufficient pollen supply when orchard bloom ended early.

The first option, moving nesting shelters and reinstalling them in the original site after completion of insecticide intervention may be recommendable, and is possibly linked to only moderate losses, as suggested by the following experiment with *O. cornuta*. Good results with only 10–30 % nest abandoning were achieved when nesting units were collected from the field at night (when the females were asleep inside their nests), stored in a cooling chamber for four days and reinstalled at the original location in the orchard (Vicens and Bosch 2000a; Maccagnani et al. 2004, 2007). To the females, this procedure mimics an often naturally occurring cold spell that they endure inside their nest.

The second option, moving nests to a new location for continued pollen–nectar supply, may be more problematic, as it can cause major losses depending on the *Osmia* species and/or the size of the relocated population. Maccagnani et al. (2007) moved nesting shelters of *O. cornuta* from one pear orchard to another after the shelters had been brought for one night into a cold room, resulting

in as much as 30–65 % nest abandoning. When the nesting shelters were moved from one cropping system to another (from an orchard to a rapeseed field), providing plenty of suitable pollen–nectar resources, nest abandoning even amounted to as much as 90 %, probably due to the lack of similar visual cues to those of the original nesting site (Maccagnani et al. 2007). The chances for a successful nest site dislocation seem to differ strongly between *Osmia* species (Vicens and Bosch 2000a). Nesting females of *O. lignaria* were incapable of finding their nests and eventually abandoned them when their small nesting unit was simply moved from one side of a tree trunk to the other (Torchio 1991b). In strong contrast, studies involving large nest shelters on trailers produced contrary results: 87 % of *O. lignaria* females continued nesting activities at the new site. These bees can use large nesting shelters or associated visual signals such as a chucked canvas as medium range landmarks for nest location (Torchio 1991b).

## 2.6. Parasites, parasitoids, predators and pathogens

A variety of different cleptoparasites (e.g. Coleoptera; Acari; Hymenoptera), parasitoids (e.g. Hymenoptera; Diptera), predators (e.g. ants; birds; rodents) and pathogens (e.g. chalkbrood: *Ascosphaera* spp.) threaten the successful multiplication of commercially managed *Osmia* bees (Youssef et al. 1985; Torchio 1989; Rust and Torchio 1991, 1992; Bosch and Kemp 2001, 2002; Kronic et al. 2001, 2005; Bosch 1992, 2008; Seidelmann et al. 2010). Since commercially managed *Osmia* bees occur in unnaturally high densities, antagonist populations can thrive at an enhanced rate and cause substantial damage if left uncontrolled. Due to the similarity and extensive overlap of the antagonists associated with the different *Osmia* species, a large proportion of the proposed measures can be applied in the management of all *Osmia* bees. Important conclusions can be drawn from the comprehensive overviews on natural enemies of *Osmia* bees and suitable countermeasures, provided for *O. lignaria* by

Bosch and Kemp (2001), for *O. bicornis* and *O. cornuta* by Kronic et al. (2005), and for *O. bicornis* by Kommilch (2010):

Cleptoparasites, such as the drosophilid fly *C. indagator*, consume the pollen–nectar provision within the bee cell reducing the provisions for the larvae and, thus, their size and fitness, thereby often killing the bee progeny. Other cleptoparasites that may cause serious problems in mass reared *Osmia* population are *Chaetodactylus* mites (Park et al. 2009; Sampson et al. 2009). Opening of bee nests and removal of bee cocoons in late summer effectively allows for detection and removal of cleptoparasites. Chemical treatments, if applicable, and disinfection of the nesting material, for instance by heating it, are both effective treatments against this common cleptoparasite.

Some parasitoids, such as chalcid wasps *Monodontomerus* spp., are hard to detect because their larvae develop within the bee offspring inside the bee cocoon. They produce two to four generations per year and are able to parasitize *Osmia* bees within their cocoons by piercing the bee cocoon with their ovipositor. Loose cocoons may therefore suffer heavy mortality unless protected. Covering cocoons in sawdust and attracting and killing adult wasps with black light traps may drastically reduce losses to this dangerous *Osmia* bee pest.

Chalkbrood includes a number of pathogenic fungi species of the genus *Ascosphaera* that lethally infest developing *Osmia* bee larvae (Rust and Torchio 1991, 1992; Torchio 1992). To reduce chalkbrood levels, development temperature should be as high as to guarantee fast larval development (see Section 3.1.), infested larvae should be removed and nesting material should be replaced or thoroughly sanitized before reuse to prevent reinfestation by the persistent spores.

Several species of birds as well as some rodents such as mice and squirrels prey on both adult *Osmia* bees and their nests. Placing chicken wire in front of the nest entrances represents an effective protection against these dangerous enemies. Sticky barriers on the posts of

the nesting shelter effectively protect bees from attacks by ants.

### 3. OPTIMISING *OSMIA* BEE POPULATION PERFORMANCE AND SYNCHRONISATION OF THEIR EMERGENCE WITH ORCHARD BLOOM

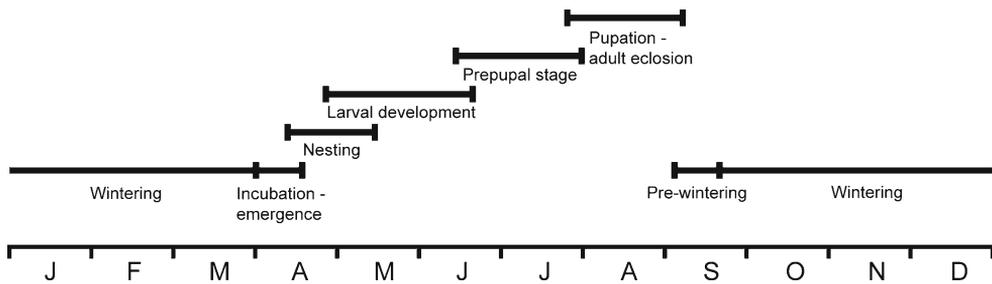
Optimal timing of bee emergence (Table I) in commercial orchards in relation to tree bloom is crucial for both bee reproduction and fruit tree pollination (Bosch and Blas 1994a; Bosch et al. 2000; Bosch and Kemp 2000, 2004). If bees emerge before bloom has started, many will leave the orchard in search of more resourceful habitats. If bees emerge after the initial phase of bloom has passed, the valuable early flowers (king blossoms in apple) will not be properly pollinated (Bosch and Kemp 2001). Furthermore, most fruit tree orchards that contain a single fruit species only bloom for a short period of time, often substantially shorter than the natural nesting activity of an *Osmia* female, which typically lasts for more than a month (Bosch and Kemp 2001). Therefore, delayed bee release after the onset of flowering may further shorten the period of optimal pollen–nectar supply and hence decrease bee reproduction.

Ideally, females should emerge in synchronisation with the very first fruit tree bloom in the orchard (Bosch and Kemp 2001). This requires monitoring of flower bud development in conjunction with weather forecast to predict onset of bloom as accurately as possible. In addition, bee development from egg to emerging adult should be managed and monitored in such a way as to be able to control synchronized emergence and to optimize the general performance of the bee population (Bosch and Blas 1994a). Throughout the development of *Osmia* bees, a number of crucial developmental stages can be differentiated. They can to some extent be controlled in order to achieve optimal emergence timing in conjunction with low developmental mortality (Figure 2). The following sections focus each on a crucial development phase and present, where applicable, suitable management options.

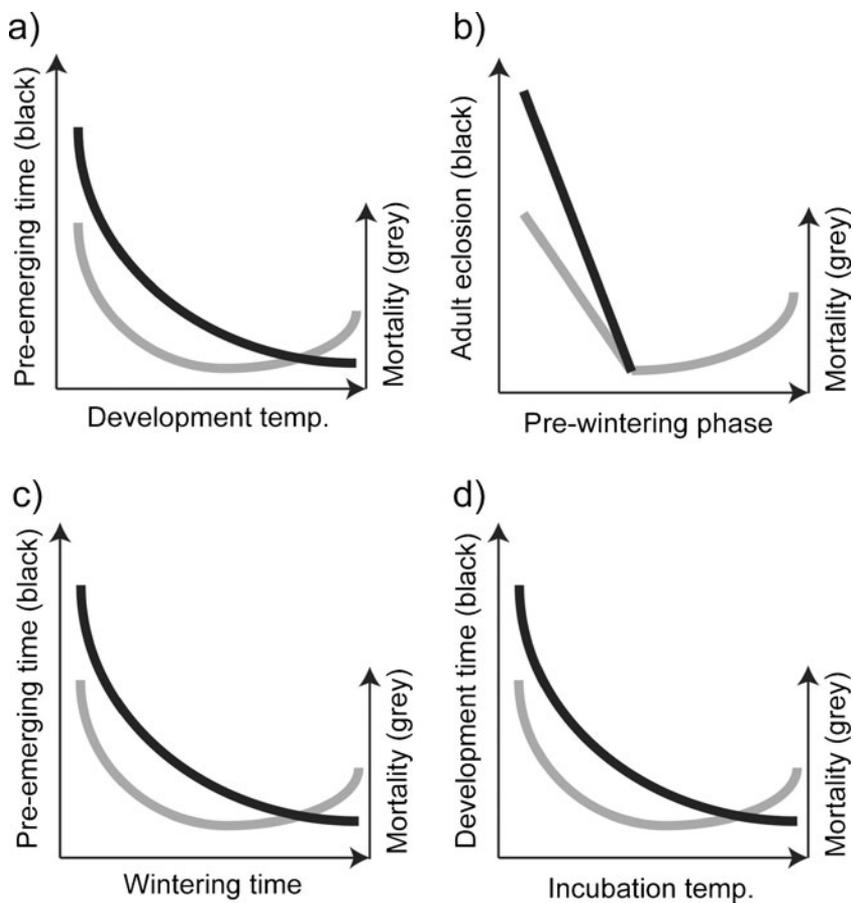
#### 3.1. Larval development, prepupal stage, pupation and adult eclosion

*Osmia* bees differ from many other solitary and univoltine bee species insofar as they undergo their whole developmental cycle from egg to fully developed adult bee before winter (Figure 2); a derived trait within the Megachilidae (Bosch et al. 2001). In contrast, many other bee species overwinter in the prepupal stage and complete development in spring (Westrich 1989). The main factor determining developmental time in *Osmia* bees is the temperature regime during bee development (Figure 3a), which also has a great impact on developmental mortality (Radmacher and Strohm 2011). For instance, in *O. lignaria*, both developmental time and developmental mortality decrease with increasing constant temperature, and best conditions for rapid development and high survival are provided by temperatures between 26 and 29 °C (Bosch and Kemp 2000). Even higher temperatures lead to increased mortality. Interestingly, under fluctuating temperatures (14 °C for 8 h and 27 °C for 16 h; average, 22.7 °C), developmental time was found to be considerably shorter than under a constant temperature of 22 °C (69 days compared to 87 days) while developmental mortality was very low (Bosch and Kemp 2000). This reduction in developmental time could mainly be attributed to a reduced length of the prepupal stage.

In the prepupal stage, *Osmia* bees undergo a dormancy that seems to correspond to a summer diapause (Sgolastra et al. 2012; Table I). It is also the stage with the lowest susceptibility to high temperatures (Radmacher and Strohm 2011). Its duration strongly varies between populations originating from different climatic regions, even when these bees are reared under identical conditions (Sgolastra et al. 2012). Whereas it lasted as long as 2.5 months for a population of *O. lignaria* adapted to the oceanic climate of California exhibiting a relatively long growing season, it lasted only 1 month for a population of the same species adapted to the more extreme continental climate of Utah exhibiting a much shorter growing season. Sgolastra et al. (2011) demonstrated that oxygen consumption during



**Figure 2.** Schematic illustration of the annual cycle (from January to December) including all major developmental stages and crucial phases of *Osmia* bee development. Based on and modified from Bosch and Kemp (2001).



**Figure 3.** Qualitative impact of **a** development temperature on developmental time and mortality of *Osmia* bees, **b** duration of the pre-wintering phase on mortality, **c** wintering time on pre-emerging time and mortality and **d** incubation temperature on pre-emerging time and mortality.

this stage was strongly reduced compared to both the larval and the pupal stages. They concluded that prepupal summer dormancy was probably adaptive accounting for the main mechanism through which *Osmia* populations synchronize adult eclosion with the onset of wintering, thus avoiding the negative effects of both abbreviated and prolonged pre-wintering periods (see Section 3.2.). Howsoever long the prepupal summer dormancy lasts, it is important that adult eclosion is terminated before wintering because specimens wintered as pupae do not develop into healthy adults (Bosch 1994a; Vicens and Bosch 2000a; Bosch and Kemp 2001; Bosch et al. 2006).

The *Osmia* species commercially used as orchard pollinators come from a wide geographic range, often spanning several climate zones. For instance, *O. cornuta* subsp. *cornuta* ranges from Portugal to Russia, and from Poland to Tunisia (Müller 2013). It is therefore to be expected that a specific temperature regime will result in greatly different developmental times for populations of the same species adapted to different climates. This finding also suggests that transfer of bees from one area to another should be avoided not only to simplify bee management but also to avoid ecologically unfavourable mass release of ill-adapted genotypes into wild local populations.

### 3.2. Pre-wintering

The developmental phase most sensitive to survival is the pre-wintering phase. During this time, in which adult eclosion is completed (Table 1), metabolic rates increase unless bees are chilled (Bosch and Kemp 2001; Monzon et al. 2004). On the one hand, if pre-wintering adults are kept for an excessively long period of time at high temperatures, their fat body reserves are depleted. This leads to higher wintering mortality and to adults that are unable to chew their way out of the cocoon or that are not vigorous enough to fly (Bosch 1994a; Bosch and Blas 1994b; Bosch et al. 2000, 2010; Bosch and Kemp 2004; Monzon et al. 2004; Radmacher and Strohm 2011; Sgolastra et al. 2011). On the other hand, the pre-wintering period must not be too short

since the bees seem to require some time to lower their respiration rates to an appropriate level for wintering (Bosch et al. 2010; Radmacher and Strohm 2011). Ideally, *Osmia* bees should be cooled 2–4 weeks after eclosion of the first individuals (Bosch and Kemp 2001, 2004), because not all individuals in a population reach adulthood simultaneously (Bosch and Kemp 2000; Bosch et al. 2000). During this crucial phase, development should be carefully monitored (by either X-raying or dissection of cocoon samples) to keep pre-wintering time short and to avoid wintering individuals still in the pupal phase (Bosch and Kemp 2001, 2002; Figure 3b). Finally, short pre-wintering periods will also allow for prolonged wintering periods, which in turn leads to faster pre-emerging time and shorter emerging periods (see Section 3.4.). The latter are important traits that greatly facilitate optimal timing of bee release (Bosch and Kemp 2004).

### 3.3. Wintering

Both duration of wintering and ambient temperature directly affect pre-emerging time, emerging period (Table 1) as well as bee survival. In analogy to developmental patterns of different *Osmia* populations, optimal wintering regimes should be adjusted to the specific characteristics of the local bee population and its respective adaptation to the local climate (Bosch and Blas 1994a). In general, longer wintering periods lead to shorter pre-emerging time and reduced emerging periods, which facilitates synchronisation of bee emergence to orchard bloom (Bosch et al. 2000; Bosch and Kemp 2000, 2001). Conversely, short wintering leads to protracted pre-emerging time and extended emerging periods (Bosch 1995; Bosch et al. 2000; Bosch and Kemp 2004). For instance, in *O. lignaria*, wintering period could be artificially prolonged to up to 220 days (Bosch and Kemp 2000) and even 270 days (Bosch and Kemp 2003) with no or only little effect on bee survival and fitness. However, artificially shortened wintering to <90 days led to a dramatic decrease in bee survival and vigour (Bosch 1995; Bosch and Kemp 2004; Kemp et al. 2004) and should therefore be avoided (Figure 3c).

Wintering temperature directly affects pre-emerging time. Bee populations native to the area, in which they are managed as orchard pollinators, or native to a region with a similar climate, can be wintered under natural temperature conditions if protected from moisture and predators. However, optimal management of pre-wintering and wintering phases and, thus, the timing of bee emergence in synchronisation with the onset of orchard bloom can be achieved only when cocoons are transferred to a controlled cold climate.

When wintered at warmer temperatures, bees emerge faster (Bosch et al. 2000; Bosch and Kemp 2001, 2004; but see Bosch and Kemp 2003). For instance, *O. lignaria* bees wintered at 7 °C emerged in half the time than bees wintered at 4 °C (Bosch et al. 2000). However, bees exposed to milder wintering temperatures tend to express higher mortality and lower reproductive success (Bosch and Blas 1994a). Furthermore, the risk of premature male emergence (males emerging within the cooler before the onset of incubation) increases under a high wintering temperature regime (Bosch and Kemp 2001). Excessively high wintering temperatures should therefore be avoided, especially since the length of the wintering period is more important than the wintering temperature for timing of adult emergence (Bosch and Blas 1994a). Controlled conditions for wintering offer the advantages of predictable climate and of controlled synchrony of emergence with crop flowering. For cases without climate chamber facilities, Sheffield et al. (2008a) reported promising results for *O. lignaria* wintered under ambient outside, albeit sheltered conditions in Nova Scotia, Canada. Natural emergence coincided favourably with apple flowering, and survival exceeded 95 %.

### 3.4. Incubation

Under natural conditions, *Osmia* bees emerge in spring when ambient temperature rises. However, for the precise and optimal synchronisation of bee emergence with the bloom of the respective crop, artificial incubation might be useful to reduce pre-emerging time (Bosch and Kemp 2001; White et al. 2009). Pre-emerging time

should be minimized not only to synchronize bee emergence with orchard bloom but also to increase bee nesting success (Sgolastra 2007). In general, the higher the incubation temperature, the more bee emergence can be accelerated. However, if incubation temperature is too high (30 °C and above for *O. lignaria*), some bees may fail to emerge (Bosch and Kemp 2001; Figure 3d). Moreover, if the *Osmia* population is well managed, male emergence, which significantly precedes female emergence, may begin within hours after bee transfer to incubation temperatures. Since incubation for only a short period of time was shown to have no significant effect on pre-emerging time (Bosch and Blas 1994a), bees should be incubated only if male pre-emerging time under room temperature exceeds about two days. A simple but effective way to evaluate the need for incubation of bee populations is to transfer a representative sample of male cocoons to room temperature about 2 weeks prior to orchard bloom. Provided these males do not emerge within the expected short period of time, artificial incubation might be advisable (Bosch and Kemp 2001).

Even when well managed, *Osmia* bees express prolonged pre-emerging time if ambient temperatures in the orchard are low (Bosch and Kemp 2001). If temperatures are expected to be too low to allow for prompt bee emergence, but high enough for the continuation of fruit tree flower development, bee incubation is highly advantageous. Bosch and Kemp (2001) describe an indoor incubation box that allows for laborious yet very precise synchronisation of bee emergence with orchard bloom initiation. Pitts-Singer et al. (2008) describe an elaborate in-field incubation box that uses electric power to raise the nest temperature thus accelerating bee emergence.

## 4. CONCLUSIONS

A successful management system for *Osmia* bees as fruit tree pollinators will strive not only for enhancing pollination efficiency, but in particular also for optimising rearing management to obtain sustainable and healthy bee populations. This

requires especially considering opportunities to enhance female body size and thereby population fitness. In view of the unnaturally high population densities given by females nesting at the same nesting shelter, protection from natural enemies and repeated active suppression of parasites are mandatory for maintaining thriving bee populations. Thoughtful choice and positioning of nesting shelters, which are optimally constructed with favourable material, are equally important as proper synchronisation of bee emergence with orchard bloom, which is approachable with suitable measures. Crucial developmental stages such as pre-wintering and pre-emergence time can be monitored and managed to minimize developmental mortality and to further increase bee fitness.

## ACKNOWLEDGEMENTS

We thank Andreas Müller, Kathrin Tschudi, and the two anonymous reviewers for helpful comments on the manuscript.

**Vers une gestion durable des abeilles du sous-genre *Osmia* (Megachilidae; *Osmia*) comme pollinisateurs d'arbres fruitiers**

**Arbres fruitiers / verger / pollinisation / pollinisateur alternatif / nid artificiel / abeille maçonne**

**Nachhaltiges Management von Bienen der Untergattung *Osmia* (Megachilidae; *Osmia*) als Bestäuber von Obstbäumen**

**Obstbestäubung / alternative Bestäuber / *Osmia* / Obstbäume**

## REFERENCES

- Abel, C.A., Wilson, R.L. (1998) The use of diverse plant species for increasing *Osmia cornifrons* (Hymenoptera: Megachilidae) in field cages. *J. Kansas Entomol. Soc.* **71**(1), 23–28
- Adamson, N.L., Roulston, T.H., Fell, R.D., Mullins, D.E. (2012) From April to August-wild bees pollinating crops through the growing season in Virginia. USA. *Environ. Entomol.* **41**(4), 813–821
- Alaux, C., Brunet, J.-L., Dussaubat, C., Mondet, F., Tchamitchan, S., Cousin, M., Brillard, J., Baldy, A., Belzunces, L.P., Le Conte, Y. (2010) Interactions between *Nosema microspores* and a neonicotinoid weaken honeybees (*Apis mellifera*). *Environ. Microbiol.* **12**(3), 774–782
- Artz, D.R., Allan, M.J., Wardell, G.I., Pitts-Singer, T.L. (2013) Nesting site density and distribution affects *Osmia lignaria* (Hymenoptera: Megachilidae) reproductive success and almond yield in a commercial orchard. *Insect Conserv. Diver.* doi:10.1111/icad.12026
- Bohart, G.E. (1972) Management of wild bees for pollination of crops. *Annu. Rev. Entomol.* **17**, 287–312
- Bosch, J. (1992) Parasitism in wild and managed populations of the almond pollinator *Osmia cornuta* Latr (Hymenoptera, Megachilidae). *J. Apic. Res.* **31**(2), 77–82
- Bosch, J. (1994a) Improvement of field management of *Osmia cornuta* (Latreille) (Hymenoptera, Megachilidae) to pollinate almond. *Apidologie* **25**(1), 71–83
- Bosch, J. (1994b) *Osmia cornuta* Latr (Hym, Megachilidae) as a potential pollinator in almond orchards—releasing methods and nest-hole length. *J. Appl. Entomol.* **117**(2), 151–157
- Bosch, J. (1994c) The nesting-behavior of the mason bee *Osmia cornuta* (Latr) with special reference to its pollinating potential (Hymenoptera, Megachilidae). *Apidologie* **25**(1), 84–93
- Bosch, J. (1995) Comparison of nesting materials for the orchard pollinator *Osmia cornuta* (Hymenoptera, Megachilidae). *Entomol. Gen.* **19**(4), 285–289
- Bosch, J. (2008) Production of undersized offspring in a solitary bee. *Anim. Behav.* **75**, 809–816
- Bosch, J., Blas, M. (1994a) Effect of over-wintering and incubation temperatures on adult emergence in *Osmia cornuta* Latr (Hymenoptera, Megachilidae). *Apidologie* **25**(3), 265–277
- Bosch, J., Blas, M. (1994b) Foraging behavior and pollinating efficiency of *Osmia cornuta* and *Apis mellifera* on almond (Hymenoptera, Megachilidae and Apidae). *Appl. Entomol. Zool.* **29**(1), 1–9
- Bosch, J., Kemp, W.P. (1999) Exceptional cherry production in an orchard pollinated with blue orchard bees. *Bee World* **80**(4), 163–173
- Bosch, J., Kemp, W.P. (2000) Development and emergence of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environ. Entomol.* **29**(1), 8–13
- Bosch, J., Kemp, W.P. (2001) How to manage the blue orchard bee, *Osmia lignaria*, as an orchard pollinator. Sustainable Agriculture Network, Washington DC
- Bosch, J., Kemp, W.P. (2002) Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. *B Entomol Res* **92**(1), 3–16
- Bosch, J., Kemp, W.P. (2003) Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environ. Entomol.* **32**(4), 711–716

- Bosch, J., Kemp, W.P. (2004) Effect of pre-wintering and wintering temperature regimes on weight loss, survival, and emergence time in the mason bee *Osmia cornuta* (Hymenoptera: Megachilidae). *Apidologie* **35**(5), 469–479
- Bosch, J., Vicens, N. (2005) Sex allocation in the solitary bee *Osmia cornuta*: do females behave in agreement with Fisher's theory? *Behav. Ecol. Sociobiol.* **59**(1), 124–132
- Bosch, J., Vicens, N. (2006) Relationship between body size, provisioning rate, longevity and reproductive success in females of the solitary bee *Osmia cornuta*. *Behav. Ecol. Sociobiol.* **60**(1), 26–33
- Bosch, J., Kemp, W.P., Peterson, S.S. (2000) Management of *Osmia lignaria* (Hymenoptera: Megachilidae) populations for almond pollination: methods to advance bee emergence. *Environ. Entomol.* **29**(5), 874–883
- Bosch, J., Maeta, Y., Rust, R. (2001) A phylogenetic analysis of nesting behavior in the genus *Osmia* (Hymenoptera: Megachilidae). *Ann. Entomol. Soc. Am.* **94**(4), 617–627
- Bosch, J., Kemp, W.P., Trostle, G.E. (2006) Bee population returns and cherry yields in an orchard pollinated with *Osmia lignaria* (Hymenoptera: Megachilidae). *J. Econ. Entomol.* **99**(2), 408–413
- Bosch, J., Sgolastra, F., Kemp, W. (2008) Life cycle ecophysiology of *Osmia* mason bees used as crop pollinators. In: James, R., Pitts-Singer, T.L. (eds.) *Bee pollination in agricultural ecosystems*, pp. 1–19. Oxford University Press, Oxford
- Bosch, J., Sgolastra, F., Kemp, W.P. (2010) Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. *J. Insect Physiol.* **56**(12), 1949–1957
- Brittain, C., Williams, N., Kremen, C., Klein, A.M. (2013) Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proc. R. Soc. B-Biol. Sci.* **280**(1754), 1–7
- Calzoni, G.L., Speranza, A. (1998) Insect controlled pollination in Japanese plum (*Prunus salicina* Lindl.). *Sci. Hortic Amsterdam* **72**(3–4), 227–237
- Cane, J.H. (2006) The Logan beemail shelter: a practical, portable unit for managing cavity-nesting agricultural pollinators. *Am. Bee J.* **146**(7), 611–613
- Dietemann, V., Pflugfelder, J., Anderson, D., Charriere, J.D., Chejanovsky, N., et al. (2012) *Varroa destructor*: research avenues towards sustainable control. *J. Apic. Res.* **51**(1), 125–132
- Elias, J., Dorn, S., Mazzi, D. (2010) Inbreeding in a natural population of the gregarious parasitoid wasp *Cotesia glomerata*. *Mol. Ecol.* **19**(11), 2336–2345
- Free, J.B. (1993) *Insect pollination in crops*. Academic, London
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**(6127), 1608–1611
- Genersch, E. (2010) Honey bee pathology: current threats to honey bees and beekeeping. *Appl. Microbiol. Biotechnol* **87**(1), 87–97
- Gruber, B., Eckel, K., Everaars, J., Dormann, C.F. (2011) On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie* **42**(5), 564–576
- Haider, M., Dorn, S., Müller, A. (2012) Intra- and interpopulational variation in the ability of a solitary bee species to develop on non-host pollen: implications for host range expansion. *Funct. Ecol.* **27**(1), 255–263
- Haider, M., Dorn, S., Sedivy, S., Müller, A. (2013) Phylogeny and floral hosts of a predominantly pollen generalist group of mason bees (Megachilidae, Osmiini). *Biol. J. Linn. Soc.* (in press)
- Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J.F., Aupinel, P., Aptel, J., Tchamitchian, S., Decourtye, A. (2012) A common pesticide decreases foraging success and survival in honey bees. *Science* **336**(6079), 348–350
- Hermann, M. (2008) Ertragsförderung & Qualitätssicherung durch optimale Bestäubung—Ansiedlung von einheimischen Mauerbienen. *Öko-Obstbau* **19**(4), 17–19 (in German)
- Hermann, M. (2010) Einsatzmöglichkeiten und Haltung von Mauerbienen (*Osmia* sp.) in intensiven Obstkulturen. *Obstbau* **2**, 66–69 (in German)
- Holm, S.N. (1973) *Osmia rufa* (Hymenoptera: Megachilidae) as a pollinator of plants in greenhouses. *Entomol. Scand.* **4**(3), 217–224
- Holzschuh, A., Dudenhoffer, J.H., Tschamtkke, T. (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* **153**, 101–107
- Kemp, W.P., Bosch, J., Dennis, B. (2004) Oxygen consumption during the life cycles of the prepupa-wintering bee *Megachile rotundata* and the adult-wintering bee *Osmia lignaria* (Hymenoptera: Megachilidae). *Ann. Entomol. Soc. Am.* **97**(1), 161–170
- Kitamura, T. (1969) Studies on the pollination of apple by *Osmia* (III) preliminary report on the homing ability of *Osmia cornifrons* (Radoszkowski) and *O. pedicornis* Cockerell. *Kontyu* **37**(1), 83–90
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtkke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B-Biol. Sci.* **274**(1608), 303–313
- Kornmilch, J.C. (2010) Einsatz von Mauerbienen zur Bestäubung von Obstkulturen; Handbuch zur Nutzung der Roten Mauerbiene in Obstplantagen und Kleingärten. Bienenhotel, Rostock (in German)
- Kronic, M., Stanisavljevic, L. (2006) Augmentation of managed populations of *Osmia cornuta* and *O. rufa* (Hymenoptera: Megachilidae) in Southeastern Europe. *Eur J Entomol* **103**(3), 695–697
- Kronic, M., Stanisavljevic, L., Brajkovic, M., Tomanovic, Z., Radovic, I. (2001) Ecological studies of *Osmia cornuta* (Latr.) (Hymenoptera, Megachilidae) populations in Yugoslavia with special attention to their

- diapause, in: Benedek, P., Richards, K.W. (Eds.), Acta Hort. (ISHS) **561**, 297–301
- Kronic, M., Stanisavljevic, L., Pinzauti, M., Felicioli, A. (2005) The accompanying fauna of *Osmia cornuta* and *Osmia rufa* and effective measures of protection. Bull. Insectology **58**(2), 141–152
- Kuhn, E.D., Ambrose, J.T. (1984) Pollination of delicious apple by megachilid bees of the genus *Osmia* (Hymenoptera, Megachilidae). J. Kansas Entomol. Soc. **57**(2), 169–180
- Ladurner, E., Recla, L., Wolf, M., Zelger, R., Burgio, G. (2004) *Osmia cornuta* (Hymenoptera Megachilidae) densities required for apple pollination: a cage study. J. Apic. Res. **43**(3), 118–122
- Maccagnani, B., Ladurner, E., Santi, F., Burgio, G. (2003) *Osmia cornuta* (Hymenoptera, Megachilidae) as a pollinator of pear (*Pyrus communis*): fruit- and seed-set. Apidologie **34**(3), 207–216
- Maccagnani, B., Betti, F., Fontan, P. (2004) The role of ecological infrastructures in pollinators management: *Osmia cornuta* (Hymenoptera Megachilidae) in pear orchards. Redia **87**, 191–194
- Maccagnani, B., Burgio, G., Stanisavljevic, L.Z., Main, S. (2007) *Osmia cornuta* management in pear orchards. Bull. Insectology **60**(1), 77–82
- Maddocks, R., Paulus, H.F. (1987) Quantitative aspects of the breeding biology of *Osmia rufa* L. and *Osmia cornuta* Latr. (Hymenoptera: Megachilidae) a comparative study of competition-reducing mechanisms in 2 closely related bee species. Zool. Jahrb. Abt. Syst. Oekol. Geog. Tiere **114**(1), 15–44
- Maeta, Y. (1978) Comparative studies on the biology of the bees of the genus *Osmia* in Japan, with special reference to their management for pollination of crops (Hymenoptera, Megachilidae). Bull. Tohoku Nat. Agric. Exp. Stat **57**, 1–221 (in Japanese)
- Maeta, Y. (1990) Utilization of wild bees. Farming Japan **24**(6), 13–22
- Maeta, Y., Kitamura, T. (1974) How to manage the Mame-ko bee (*Osmia cornifrons* Radoszkowski) for pollination of fruit crops. Ask. Co. Ltd, Naganoshi (in Japanese)
- Marquez, 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**(4), 353–359
- Michener, C.D. (2007) The bees of the world, 2nd edn. The Johns Hopkins University Press, Baltimore
- Mitchell, T.B. (1962) Bees of the Eastern United States. Technical bulletin. The North Carolina Agricultural Experiment Station, Raleigh
- Monzon, V.H., Bosch, J., Retana, J. (2004) Foraging behavior and pollinating effectiveness of *Osmia cornuta* (Hymenoptera: Megachilidae) and *Apis mellifera* (Hymenoptera: Apidae) on “Comice” pear. Apidologie **35**(6), 575–585
- Müller, A. (2013). Palaeartic osmiine bees. <http://blogs.ethz.ch/osmiini> (accessed on 12 Jun 2013)
- Naug, D. (2009) Nutritional stress due to habitat loss may explain recent honeybee colony collapses. Biol. Conserv. **142**(10), 2369–2372
- Park, Y.L., Kondo, V., White, J., West, T., McConnell, B., McCutcheon, T. (2009) Nest-to-nest dispersal of *Chaetodactylus krombeini* (Acari, Chaetodactylidae) associated with *Osmia cornifrons* (Hym., Megachilidae). J. Appl. Entomol. **133**(3), 174–180
- Pitts-Singer, T.L. (2007) Olfactory response of megachilid bees, *Osmia lignaria*, *Megachile rotundata* and *M. pugnata*, to individual cues from old nest cavities. Environ. Entomol. **36**(2), 402–408
- Pitts-Singer, T.L., Bosch, J., Kemp, W.P., Trostle, G.E. (2008) Field use of an incubation box for improved emergence timing of *Osmia lignaria* populations used for orchard pollination. Apidologie **39**(2), 235–246
- Radmacher, S., Strohm, E. (2010) Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). Apidologie **41**(2), 169–177
- Radmacher, S., Strohm, E. (2011) Effects of constant and fluctuating temperatures on the development of the solitary bee *Osmia bicornis* (Hymenoptera: Megachilidae). Apidologie **42**(6), 711–720
- Rust, R.W. (1974) The systematics and biology of the genus *Osmia*, subgenera *Osmia*, *Chalcosmia* and *Cephalosmia* (Hymenoptera: Megachilidae). Wasmann J. Biol. **32**(1), 1–94
- Rust, R.W., Torchio, P.F. (1991) Induction of *Ascospaera* (Ascomycetes, Ascospaerales) infections in field populations of *Osmia lignaria propinqua* Cresson (Hymenoptera, Megachilidae). Pan-Pac. Entomol. **67**(4), 251–257
- Rust, R.W., Torchio, P.F. (1992) Effects of temperature and host developmental stage on *Ascospaera torchioi* Youssef and McManus prevalence in *Osmia lignaria propinqua* Cresson (Hymenoptera, Megachilidae). Apidologie **23**(1), 1–9
- Sampson, B.J., Cane, J.H. (2000) Pollination efficiencies of three bee (Hymenoptera: Apoidea) species visiting rabbiteye blueberry. J. Econ. Entomol. **93**(6), 1726–1731
- Sampson, B.J., Stringer, S.J., Cane, J.H., Spiers, J.M. (2004) Greenhouse evaluations of a mason bee *Osmia ribifloris* (Hymenoptera: Megachilidae) as a pollinator for blueberries in the southeastern United States. Small Fruits R. **3**(3–4), 381–392
- Sampson, B.J., Cane, J.H., Kirker, G.T., Stringer, S.J., Spiers, J.M. (2009) Biology and management potential for three orchard bee species (Hymenoptera: Megachilidae): *Osmia ribifloris* Cockerell, *O. lignaria* (Say) and *O. chalybea* Smith with emphasis on the former. In: Hummer, K.E. (Ed.), Acta Hort. (ISHS) **810**, 549–555.
- Schindler, M., Peters, B. (2011) Mason bees *Osmia bicornis* and *Osmia cornuta* as suitable orchard

- pollinators? *Erwerbs-Obstbau* **52**(3–4), 111–116 (in German)
- Sedivy, C., Muller, A., Dorn, S. (2011) Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: evidence for physiological adaptations to digest pollen. *Funct. Ecol.* **25**(3), 718–725
- Seidelmann, K., Ulbrich, K., Mielenz, N. (2010) Conditional sex allocation in the red mason bee, *Osmia rufa*. *Behav. Ecol. Sociobiol.* **64**(3), 337–347
- Sekita, N. (2001) Managing *Osmia cornifrons* to pollinate apples in Aomori Prefecture, Japan, in: Benedek P. Richards K.W. (Eds.), Proceedings of the eight international pollination symposium pollination: integrator of crops and native plant systems. *Acta Hort. (ISHS)* **561**, 303–307.
- Sgolastra, F. (2007) *Ecofisiologia del ciclo biologico di Osmia lignaria* (Hymenoptera: Megachilidae). Università di Bologna, Bologna (in Italian)
- Sgolastra, F., Kemp, W.P., Buckner, J.S., Pitts-Singer, T.L., 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, W.P., 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**(7), 924–933
- Sheffield, C.S., Kevan, P.G., Westby, S.M., Smith, R.F. (2008a) Diversity of cavity-nesting bees (Hymenoptera: Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada. *Can. Entomol.* **140**(2), 235–249
- Sheffield, C.S., Westby, S.M., Smith, R.F., Kevan, P.G. (2008b) Potential of bigleaf lupine for building and sustaining *Osmia lignaria* populations for pollination of apple. *Can. Entomol.* **140**(5), 589–599
- Steffan-Dewenter, I., Schiele, S. (2004) Nest-site fidelity, body weight and population size of the red mason bee, *Osmia rufa* (Hymenoptera: Megachilidae), evaluated by mark-recapture experiments. *Entomol. Gen.* **27**(2), 123–132
- Tepedino, V.J., Torchio, P.F. (1982a) Temporal variability in the sex-ratio of a nonsocial bee, *Osmia lignaria propinqua*—extrinsic determination or the tracking of an optimum. *Oikos* **38**(2), 177–182
- Tepedino, V.J., Torchio, P.F. (1982b) Phenotypic variability in nesting success among *Osmia lignaria propinqua* females in glasshouse environment (Hymenoptera: Megachilidae). *Ecol. Entomol.* **7**(4), 453–462
- Tepedino, V.J., Thompson, R., Torchio, P.F. (1984) Heritability for size in the megachilid bee *Osmia lignaria propinqua* Cresson. *Apidologie* **15**(1), 83–87
- Torchio, P.F. (1976) Use of *Osmia lignaria* (Hymenoptera: Apoidea: Megachilidae) as a pollinator in an apple and prune orchard. *J. Kansas Entomol. Soc.* **49**(4), 475–482
- Torchio, P.F. (1981a) Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards 1. 1975 studies (Hymenoptera, Megachilidae). *J. Kansas Entomol Soc* **54**(4), 815–823
- Torchio, P.F. (1981b) Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards 2. 1976 studies (Hymenoptera, Megachilidae). *J. Kansas Entomol Soc* **54**(4), 824–836
- Torchio, P.F. (1982a) Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards 1. 1975 studies (Hymenoptera, Megachilidae). *J. Kansas Entomol Soc* **55**(1), 136–144
- Torchio, P.F. (1982b) Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards 2. 1976 studies (Hymenoptera, Megachilidae). *J. Kansas Entomol Soc* **55**(4), 759–778
- Torchio, P.F. (1982c) Field experiments with *Osmia lignaria propinqua* Cresson as a pollinator in almond orchards 3. 1977 studies (Hymenoptera - Megachilidae). *J. Kansas Entomol Soc* **55**(1), 101–116
- Torchio, P.F. (1984a) Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson (Hymenoptera, Megachilidae) in apple orchards 3. 1977 studies. *J. Kansas Entomol Soc* **57**(3), 517–521
- Torchio, P.F. (1984b) Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards 4. 1978 studies (Hymenoptera, Megachilidae). *J. Kansas Entomol Soc* **57**(4), 689–694
- Torchio, P.F. (1985) Field experiments with the pollinator species, *Osmia lignaria propinqua* Cresson, in apple orchards 5. (1979–1980), methods of introducing bees, nesting success, seed counts, fruit yields (Hymenoptera, Megachilidae). *J. Kansas Entomol Soc* **58**(3), 448–464
- Torchio, P.F. (1987) Use of non-honey bee species as pollinators of crops. *Proc. Entomol. Soc. Ont.* **118**, 111–124
- Torchio, P.F. (1989) Biology, immature development, and adaptive behavior of *Stelis montana*, a kleptoparasite of *Osmia* (Hymenoptera, Megachilidae). *Ann. Entomol. Soc. Am.* **82**(5), 616–632
- Torchio, P.F. (1990) *Osmia ribifloris*, a native bee species developed as a commercially managed pollinator of highbush blueberry (Hymenoptera, Megachilidae). *J. Kansas Entomol. Soc.* **63**(3), 427–436
- Torchio, P.F. (1991a) Bees as crop pollinators and the role of solitary species in changing environments. *Acta Hort. (ISHS)* **288**, 49–61
- Torchio, P.F. (1991b) Use of *Osmia lignaria propinqua* (Hymenoptera, Megachilidae) as a mobile pollinator of orchard crops. *Environ. Entomol.* **20**(2), 590–596
- Torchio, P.F. (1992) Effects of spore dosage and temperature on pathogenic expressions of chalkbrood syndrome caused by *Ascospaera torchiori* within larvae of *Osmia lignaria propinqua* (Hymenoptera, Megachilidae). *Environ. Entomol.* **21**(5), 1086–1091
- Torchio, P.F., Asensio, E. (1985) The introduction of the European bee, *Osmia cornuta* Latr into the United States 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
- Torchio, P.F., Tepedino, V.J. (1980) Sex-ratio, body size and seasonality in a solitary bee, *Osmia lignaria propinqua* Cresson (Hymenoptera, Megachilidae). Evolution **34**(5), 993–1003
- Torchio, P.F., Asensio, E., Thorp, R.W. (1987) Introduction of the European bee, *Osmia cornuta*, into California almond orchards (Hymenoptera, Megachilidae). Environ. Entomol. **16**(3), 664–667
- Vicens, N., Bosch, J. (2000a) Nest site orientation and relocation of populations of the orchard pollinator *Osmia cornuta* (Hymenoptera: Megachilidae). Environ. Entomol. **29**(1), 69–75
- Vicens, N., Bosch, J. (2000b) Pollinating efficacy of *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae, Apidae) on ‘red Delicious’ apple. Environ. Entomol. **29**(2), 235–240
- Vicens, N., Bosch, J. (2000c) Weather-dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae). Environ. Entomol. **29**(3), 413–420
- Wei, S.G., Wang, R., Smirle, M.J., Xu, H.L. (2002) Release of *Osmia excavata* and *Osmia jacoti* (Hymenoptera: Megachilidae) for apple pollination. Can. Entomol. **134**(3), 369–380
- Westrich, P. (1989) Die Wildbienen Baden-Württembergs. Ulmer, Stuttgart (in German)
- White, J., Son, Y., Park, Y.L. (2009) Temperature-dependent emergence of *Osmia cornifrons* (Hymenoptera: Megachilidae) adults. J. Econ. Entomol. **102**(6), 2026–2032
- Wilkaniec, Z., Giejdasz, K. (2003) Suitability of nesting substrates for the cavity-nesting bee *Osmia rufa*. J. Apic. Res. **42**(3), 29–31
- Wilkaniec, Z., Radajewska, B. (1997) Solitary bee *Osmia rufa* L (Apoidea, Megachilidae) as pollinator of strawberry cultivated in an unheated plastic tunnel. Acta Hort. (ISHS) **439**, 489–493
- Yamada, M., Oyama, N., Sekita, N., Shirasaki, S., Tsugawa, C. (1971) The ecology of the megachilid bee *Osmia cornifrons* and its utilization for apple pollination. Bull. Aomori Apple Exp. Stat. **15**, 1–80 (in Japanese)
- Youssef, N.N., McManus, W.R., Torchio, P.F. (1985) Cross-infectivity potential of *Ascospaera* spp (Ascomycetes, *Ascospaera*) on the bee, *Osmia lignaria propinqua* Cresson (Megachilidae, *Osmia*). J. Econ. Entomol. **78**(1), 227–231
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., Dorn, S. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biol. Conserv. **143**(3), 669–676