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**REVIEW ARTICLE**

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**Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees****J. Bosch<sup>1\*</sup> and W.P. Kemp<sup>2</sup>**

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**Abstract**

The development of a bee species as a new crop pollinator starts with the identification of a pollination-limited crop production deficit and the selection of one or more candidate pollinator species. The process continues with a series of studies on the developmental biology, pollinating efficacy, nesting behaviour, preference for different nesting substrates, and population dynamics of the candidate pollinator. Parallel studies investigate the biology of parasites, predators and pathogens. The information gained in these studies is combined with information on the reproductive biology of the crop to design a management system. Complete management systems should provide guidelines on rearing and releasing methods, bee densities required for adequate pollination, nesting materials, and control against parasites, predators and pathogens. Management systems should also provide methods to ensure a reliable pollinator supply. Pilot tests on a commercial scale are then conducted to test and eventually refine the management system. The process culminates with the delivery of a viable system to manage and sustain the new pollinator on a commercial scale. The process is illustrated by the development of three mason bees, *Osmia cornifrons* (Radoszkowski), *O. lignaria* Say and *O. cornuta* (Latreille) as orchard pollinators in Japan, the USA and Europe, respectively.

**Introduction**

Of the more than 16,000 bee species (Hymenoptera: Apoidea) described worldwide (Michener, 2000), only a handful are managed commercially as crop pollinators. These include both social and solitary species, mostly nesting in pre-established cavities (Bohart, 1972; Parker *et al.*, 1987; Torchio, 1987, 1991a; Cane, 1997). Among social species, the honey bee, *Apis mellifera* Linnaeus (Hymenoptera: Apidae), is used throughout the world on a vast array of cultivated

plants (McGregor, 1976; Free, 1993), and several bumblebee species, *Bombus* spp. (Hymenoptera: Apidae), are extensively managed for pollination of tomato and other greenhouse crops (van Heemert *et al.*, 1990; van den Eijnde *et al.*, 1991). Cavity-nesting solitary species developed as crop pollinators include the alfalfa leafcutting bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Megachilidae), mostly managed for alfalfa pollination (Bohart, 1962; Stephen, 1962; Hobbs, 1967; Richards, 1984) and several species of mason bees, *Osmia* spp. (Hymenoptera: Megachilidae), mostly managed for fruit tree pollination (Yamada *et al.*, 1971; Maeta & Kitamura, 1974; Maeta, 1978; Torchio, 1981, 1985; Bosch, 1994a; Bosch & Kemp, 2001). Two ground-nesting solitary

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bees, the alkali bee, *Nomia melanderi* Cockerell, and the grey-haired alfalfa bee, *Rhophitoides canus* (Eversmann) (both Hymenoptera: Halictidae), are used as alfalfa pollinators in western USA and eastern Europe, respectively (Bohart, 1958; Stephen, 1959; Torchio, 1966; Johansen *et al.*, 1982; Ptacek, 1989; Dobrynin, 1998).

This small group of pollinators, manageable at the commercial crop production scale, represents a diverse collection of natural histories. Besides differences in nesting substrates and sociality mentioned above, these species differ widely in their seasonality (from short-lived spring species to species remaining active for most of the year), life cycle (from strictly univoltine solitary species to social species forming perennial colonies), and pollen preferences (from oligolectic to widely polylectic). Equally diverse are the agricultural systems within which these pollinators are being used, ranging from rich nectar- and pollen-producing, self-incompatible fruit trees in orchards, to nectarless, self-compatible tomatoes in glasshouses. Despite this diversity, the establishment of these managed pollinators in different parts of the world has followed similar sequential patterns (Torchio, 1990), with the exception of *A. mellifera*, which was first managed for honey and wax production and later for pollination.

The aim of this review is to illustrate the process leading to the development of a wild bee species as a manageable crop pollinator, using the example of three *Osmia* species, *O. cornifrons* (Radoszkowski), *O. lignaria* Say, and *O. cornuta* (Latreille) (Hymenoptera: Megachilidae) developed as fruit tree pollinators in Japan, the USA and Europe, respectively. This review does not attempt to provide a comprehensive coverage of the information available on *Osmia* biology and management, as these subjects are already treated in other publications (Yamada *et al.*, 1971; Maeta & Kitamura, 1974; Maeta, 1978; Torchio, 1985, 1989a; Bosch, 1994b; Bosch & Kemp, 1999, 2001), but rather to outline a series of steps that the authors believe should be followed in a logical sequence to establish new agricultural pollinators. As other species are investigated as potential crop pollinators (Parker *et al.*, 1987; Torchio, 1987, 1991a; Crane, 1991; Cane, 1997; Heard, 1999), the steps outlined herein will hopefully assist researchers and practitioners in identifying areas in need of further study for each particular pollinator–crop system under consideration. Following Torchio (1987, 1991a), the word ‘development’ is used throughout this review to describe the process of developing the necessary techniques to manage an initially unmanaged bee species, and the word ‘establishment’ to describe the process that leads to the commercial use of a manageable species. Although the focus of this review is on *Osmia* spp. and orchard pollination, other pollinators and crops are occasionally referenced to illustrate particular aspects of the process.

### Recognition of a pollination problem

The development of a new crop pollinator is summarized in fig. 1. The process starts with the recognition of a pollination problem in agriculture. Although obvious, this step deserves attention because poor orchard yields may have many causes aside from insufficient pollinator populations. Most almond, plum, sweet cherry, pear and apple cultivars are self-incompatible, and must be planted with particular pollinizer cultivars (Free, 1993). Poor yields in self-incompatible cultivars following frequent pollinator visitation can result from insufficient pollinizer tree distributions, from

pollinizer and main cultivars not being inter-compatible, or flowering during periods that do not overlap sufficiently (Westwood, 1993; Nyéki, 1996; Soltész, 1996).

Weather has a direct effect on pollinator activity, but can also influence fruit or seed production in other ways. Cold temperatures during early spring can result in low pollen production and reduced pollen viability (Faust, 1989), as well as ovule sterility (Williams, 1969). On the other hand, some apple cultivars develop sterile pollen if spring temperatures reach 20°C (Faust, 1989). Poor fruit tree yields can also result from low temperatures hindering pollen germination, pollen tube growth, or fertilization (Bubán, 1996). Inhibited pollen tube growth, as well as decreased ovule longevity, can also result from application of certain chemicals (Bubán, 1996). Post-flowering weather conditions also have an important effect on fruit set. Insufficient sunlight hours in the 10-day-period immediately after flowering significantly reduces fruit set, even after an optimal pollination period (Williams, 1991).

The causes of low fruit yields can also be intrinsic to particular cultivars, and pollen viability is of special concern. For example, several triploid apple cultivars are known to produce abundant, but mostly non-viable pollen (Soltész, 1996). In some cherry and apricot cultivars, ovule longevity is very short, and ovule degeneration of 50% and higher have been observed as early as anthesis (Faust, 1989). Apparent poor yields may simply be due to the low bearing capacity of some species or cultivars. For example, in some avocado cultivars the percentage of flowers that set is less than 1%, even when hand-pollinated with abundant viable pollen (Davenport, 1982). Biennial bearing patterns, resulting in poor flower production following years of heavy fruit sets, are common in most fruit trees (Westwood, 1993).

Methods to determine whether the production of a particular crop would benefit from increased pollination are provided in several reviews and manuals (Corbet *et al.*, 1991; Free, 1993; Kearns & Inouye, 1993; Nyéki, 1996). Essentially, these methods are based on the comparison of yields in open-pollinated flowers versus flowers pollinated with abundant pollen (which can be accomplished either through hand-pollination or through insect pollination in pollinator-saturated cages). Because fruit- and seed-set are often limited by plant physiology and resources other than pollen (Stephenson, 1981), large numbers of flowers per individual plant should be hand-pollinated, and yields in experimental (hand-pollinated) flowers should be compared to yields in control (unpollinated) flowers from both experimental and control individual plants (Zimmerman & Pyke, 1988). Lower yields in trees located far from pollinator nesting sites or from pollinizer rows may also be an indication of insufficient pollen transfer (Free, 1962).

### Survey of floral visitors

Once the need for increased insect visitation has been established, one or more candidate pollinator species must be selected among the flower visitors of the target crop (fig. 1). Field and literature surveys are complementary ways to select candidate species. Because of pesticide use, and lack of nesting substrates and alternative floral resources in intensively cultivated areas, field surveys may yield higher numbers of pollinator species in small or abandoned orchards near wild lands compared with intensively managed orchards. Field surveys provide not only useful

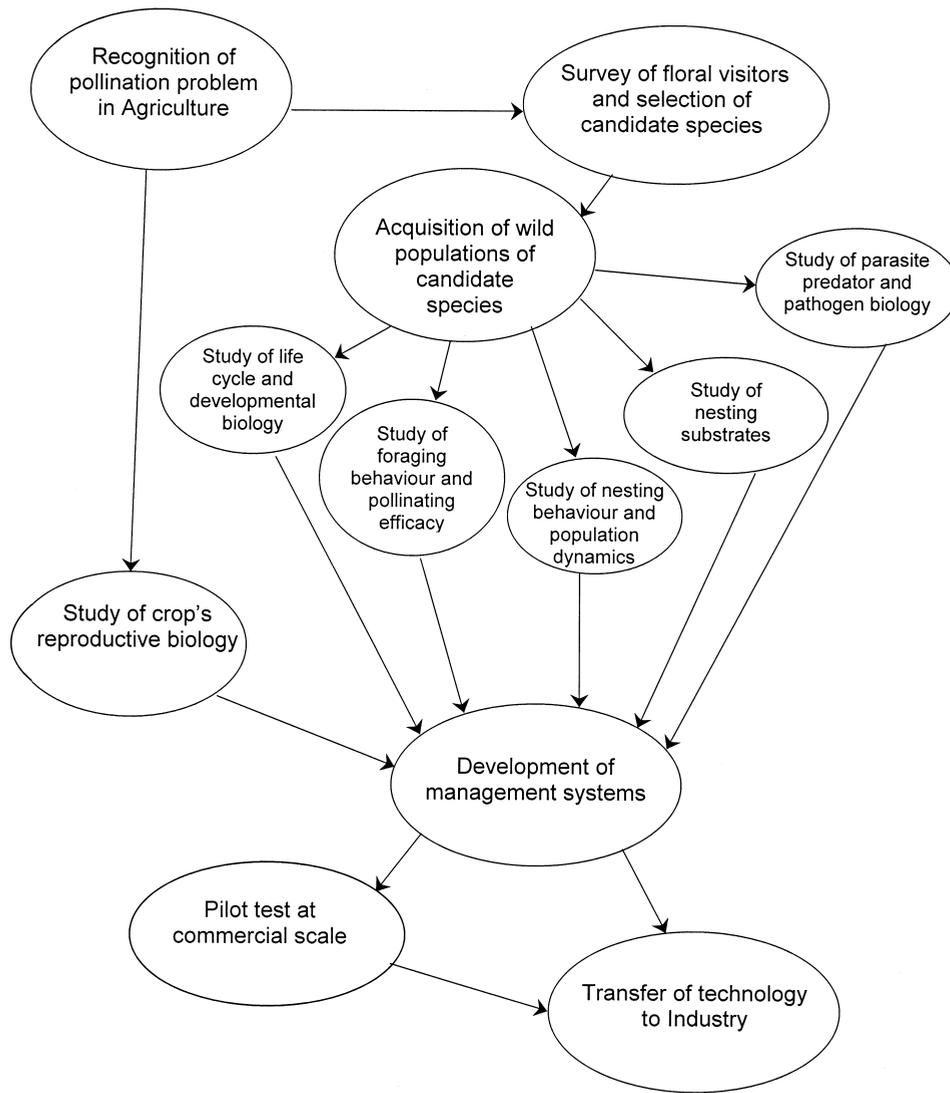


Fig. 1. Diagram of steps involved in the development of a wild bee species into a commercially managed crop pollinator (After Torchio, 1990; Bosch, 1992a).

information on the identity of local flower visitors, but also preliminary observations on their foraging behaviour, rates of stigma contact, daily and seasonal activity patterns, and pollen/nectar source preferences (Løken, 1958; Chansigaud, 1972; Kendall, 1973; Boyle-Makowski & Philogéne, 1985; Scott-Dupree & Winston, 1987; Jacob-Remacle, 1989). Once flower visitors have been identified, museum collection records and available literature provide critical supporting information on their phenology, pollen records, and geographical distribution. As in the case of *O. cornifrons*, observant growers are often the first to call attention to a particular bee species with potential as a crop pollinator (Maeta, 1990; Batra, 1998).

The criteria used to select candidate pollinator species undoubtedly vary from crop to crop, but some general rules apply. In principle, promising pollinator species should show a preference for foraging on flowers of the target crop (Torchio, 1976; Maeta, 1978; Márquez *et al.*, 1994). Candidate pollinator species should also be effective pollinators. High

rates of stigma contact are strongly related to the pollinator's behaviour on the flower, including the way the flower is handled and the resources collected (nectar and/or pollen). It is well known that *A. mellifera* nectar collectors often side-work fruit tree flowers, a behaviour that results in low rates of stigma contact, whereas pollen collectors are much more efficient pollinators of these crops (Roberts, 1945; Free, 1960; Robinson, 1979; Bosch & Blas, 1994a; Monzón, 1998; Vicens & Bosch, 2000a). Rates of stigma contact are sometimes also related to the body size of the pollinator relative to the size of the crop flower. In general, small bee species are not the best pollinators of large-flowered plants (Inouye, 1980).

A good match between the activity period of the bee species and the flowering period of the crop is very important, although, as discussed below, both phenological processes can often be modified through informed management. For fruit trees, with short, seasonal flowering periods, univoltine pollinators with relatively short nesting periods are desirable, as they eliminate the need to provide

alternative floral resources once the crop has been pollinated (Parker *et al.*, 1987). Considerable effort has been devoted to understanding and reducing partial bivoltinism in *M. rotundata* populations managed for alfalfa pollination (Parker & Tepedino, 1982; Tepedino & Parker, 1986; Rank & Rank, 1989; Kemp & Bosch, 2001). The feasibility of congregating large numbers of bees in a small area should be also considered an important selection criterion (Maeta, 1990).

### Acquisition of wild populations of candidate species

Once a species has been selected as a potential pollinator, it is necessary to obtain populations in order to begin studying its biology and potential for management (fig. 1). As mentioned, literature, museum collections and flower records provide valuable information on where and when to locate wild populations. For cavity-nesting species such as *O. cornifrons*, *O. lignaria* and *O. cornuta*, trap-nesting (placement of artificial nesting materials in areas where wild populations of the candidate species occur) is a very effective way to obtain initial populations. Trap-nesting is also a useful way to expand the information on the phenology, distribution, and natural history of the candidate species. Specimens of the candidate pollinator species can be captured and transported in cold-temperature and high-humidity containers (Parker & Potter, 1974), and released in a confined environment, such as a cage or greenhouse. When released at open sites, most females disperse, but some can be induced to resume nesting activities, especially if released after dark (Parker & Potter, 1974).

### Life cycle and developmental biology

Basic knowledge of the life cycle and developmental biology of the candidate pollinator is essential to develop adequate rearing and management systems (fig. 1). The life cycle of the three *Osmia* species considered herein can be divided into seven partially overlapping periods: nesting, development, pre-wintering, wintering, incubation, mating and pre-nesting. Nesting typically takes place in spring, and development from egg to adult, including a dormant prepupal phase, proceeds from spring until late summer or early autumn. For a brief period, newly formed adults are exposed to temperatures above developmental threshold (pre-wintering period), until the onset of cool (wintering) temperatures. Adults remain inside their cocoons in a dormant stage throughout the wintering period. The incubation period starts in late winter or early spring, when wintered adults are exposed to generally increasing temperatures, which trigger their emergence. Most females mate shortly after emergence and then experience a short pre-nesting period, presumably to allow for ovary maturation, before starting nesting activities.

The effect of temperature regimes on the life cycle of the three *Osmia* species considered herein has been investigated in several studies (Maeta & Kitamura, 1974; Maeta, 1978; Torchio, 1982a; Torchio *et al.*, 1987; Bosch & Blas, 1994b; Monzón, 1998; Bosch & Kemp, 2000a,b). Some of the aspects addressed in these studies are: temperature thresholds for development, comparisons between constant and fluctuating temperatures, respiration rates, diapausing or non-diapausing nature of dormant periods, and timing, duration and temperature of pre-wintering, wintering and post-wintering treatments. Temperature regimes have a

direct effect not only on survival, but also on the timing of emergence. For instance, *Osmia* pre-wintered for excessively long periods consume their fat body reserves and have high winter mortality, and, because they are exposed to a shortened wintering period, exhibit protracted pre-emergence and emergence periods when incubated in the spring (Bosch & Kemp, 2000b; Bosch *et al.*, 2000). Protracted pre-emergence and emergence periods are undesirable when pollinating short-blooming crops such as fruit trees.

Within a species, the nesting and developmental phenology can vary considerably among populations from different geographical areas. For example, in *O. cornuta* and *O. lignaria*, early-flying populations from warmer areas have extended prepupal dormancy periods in comparison to later-flying populations from generally cooler areas, so their developmental period from egg to adult lasts longer (Bosch *et al.*, 2000; Bosch & Kemp, 2000b, 2001). Populations from warmer areas also require higher temperatures for prepupal summer dormancy completion (Monzón, 1998; Bosch & Kemp, 2000b, 2001). On the other hand, bees from warmer areas require shorter wintering periods (Bosch & Blas, 1994b; Bosch & Kemp, 2001). Management systems need to be tailored according to these phenological differences among populations. For example, late-flying (April–May) *O. lignaria* from northern Utah can be reared at constant 22°C, whereas a high proportion of early-flying (February–March) *O. lignaria* from southern Texas fail to complete prepupal dormancy at this temperature (Bosch & Kemp, 2001).

### Foraging behaviour and pollinating efficacy

Studies on the foraging behaviour and pollinating efficacy of the candidate pollinator are typically conducted at the early stages of the process of developing a new crop pollinator (fig. 1). This information is necessary to eventually establish adequate population densities for optimal pollination. Some of the variables commonly measured in studies of *Osmia* species as potential fruit tree pollinators are visit legitimacy (stigma contact), visitation rates (number of flowers visited per minute), number of flowers visited per tree and frequency of flights between rows or cultivars (Yamada *et al.*, 1971; Maeta, 1978; Torchio, 1979; Torchio & Asensio, 1985; Kuhn & Ambrose, 1984; Bosch & Blas, 1994a; Monzón, 1998; Vicens & Bosch, 2000a). Visit legitimacy approaches 100% in all three *Osmia* species on all fruit trees studied. However, stigma contact does not necessarily guarantee pollen deposition. Even when pollen deposition does occur, and under favourable ambient conditions, fertilization may be precluded due to incompatibility or non-viability phenomena. For the same reason, counting pollen grains on the pollinator's body does not provide a good indication of its pollinating ability.

Pollinating efficacy of *Osmia* species on fruit trees, often in comparison to *A. mellifera*, has been evaluated through single-visit experiments, in which virgin bagged flowers are allowed to be visited once by a pollinator (Maeta & Kitamura, 1981; Bosch & Blas, 1994a; Monzón, 1998; Vicens & Bosch, 2000a). Although this technique only provides an approximation to pollinating efficacy in non-manipulated flowers, it is a practical, widely-accepted approach in pollination biology studies (Corbet *et al.*, 1991). Accumulation of nectar in virgin bagged flowers may result in long visitation times and increased pollen deposition (Thomson & Plowright, 1980), and non-manipulated flowers

exposed to open pollination may be visited more than once, and by different pollinators. In fact, the relative pollinating efficacy of a single pollinator is not independent of pollen and nectar removal by other flower visitors (Thomson & Thomson, 1992). Ideally, deposition of viable, compatible pollen grains should be used as a measure of pollinating efficacy, but many fruit tree species are self-incompatible and pollen grains from different cultivars within a species cannot be identified through light microscopy. However, pollen from some apple and almond cultivars can be identified through scanning electron microscopy (Thorp, 1979; DeGrandi-Hoffman *et al.*, 1992). Because incompatibility in fruit trees is gametophytic (Bubán, 1996), fluorescence microscopy procedures to count pollen tubes growing down the style (Kearns & Inouye, 1993; Nyéki, 1996) do not provide an adequate estimate of compatible pollen grain deposition. For these reasons, fruit-set, and seed-set in multi-seeded fruit tree species, have been used as an indirect measure of pollinating efficacy (Maeta & Kitamura, 1981; Bosch & Blas, 1994a; Monzón, 1998; Vicens & Bosch, 2000a). Other studies have measured pollinating efficacy on trees in cages in which low numbers of *Osmia* were released (Torchio, 1979), or on limbs near *Osmia* nesting sites (Kuhn & Ambrose, 1984).

Two other factors contributing to the pollinating capacity of a pollinator species are flower fidelity and foraging activity thresholds. A pollinator species may readily visit the target crop when given no other choice, as in cage or greenhouse trials, but be attracted to other plants in open field situations. Although *O. cornifrons*, *O. lignaria* and *O. cornuta* are polylectic species, they have a strong preference to forage on fruit trees. Pollen analysis of provision or faecal samples from populations released in orchards yield high percentages (85–100%) of fruit tree pollen (Torchio, 1976, 1981, 1982a; Maeta, 1978; Márquez *et al.*, 1994; Monzón, 1998; Vicens & Bosch, 2000a). Information on temperature, wind, humidity and solar radiation thresholds for foraging is important to evaluate the potential performance of a pollinator on different crops and in different climatic areas (Vicens & Bosch, 2000b). For spring-flowering crops, pollinator species capable of flying under relatively unfavourable conditions are particularly desirable (Torchio, 1984a; Torchio & Asensio, 1985; Bosch, 1994b; Vicens & Bosch, 2000b). Commercial yields in *Osmia*-pollinated orchards are achieved even in years with poor weather during bloom (Bosch & Kemp, 1999, 2001).

### Nesting behaviour and population dynamics

Basic knowledge on the nesting behaviour of the candidate species is important at an early stage of the pollinator development process, to provide adequate nesting resources and quantify populations (fig. 1). At later stages, the population dynamics of the species need to be well known, to determine which factors limit population growth and to establish whether the pollinator is sustainable in agricultural environments. Several variables related to nesting behaviour and population dynamics, such as the number of foraging trips necessary to provision a cell, and the duration of foraging trips, coupled with flower visiting rates, are useful for estimating the pollinating capacity of an individual female, and eventually for establishing bee densities that achieve adequate pollination.

The nesting behaviours of *O. cornifrons*, *O. lignaria* and

*O. cornuta* are very similar (Maeta, 1978; Torchio, 1989a; Bosch, 1994b). All three species nest in pre-established cavities, where they build linear series of cells, and use mud to construct cell partitions and nest plugs. In all three species, females (resulting from fertilized eggs) are, on average, larger than males because they receive larger pollen-nectar resources than males (resulting from unfertilized eggs). Typical population sex ratios are 1.7 males per female. Female progeny are usually produced in the innermost cells within a nest, and early in the season, when nesting females are young and capable of provisioning cells at a faster rate (Tepedino & Torchio, 1982a; Sugiura & Maeta, 1989; Vicens, 1997).

Because female progeny in the three *Osmia* species considered are more 'costly' to produce than male progeny, populations nesting under stressed situations (poor weather, insufficient pollen-nectar resources, inadequate nesting substrates, etc.) tend to produce an excessively male-biased progeny. For this reason, fecundity counts should consider both sexes separately. Because males do not participate in nest construction and visit many fewer flowers than females, the over-production of males does not result in increased fecundity or pollination. With unlimited resources and under ideal nesting conditions (e.g. in greenhouses) an *Osmia* spp. female may lay as many as 30 eggs over the course of her life, and more than a third of these may be fertilized (Maeta, 1978; Torchio *et al.*, 1987; Torchio, 1989a). In orchard environments, however, *O. cornifrons*, *O. lignaria* and *O. cornuta* female cell production typically ranges from 2.5 to 6 per nesting female, depending on weather and availability of floral resources (Maeta, 1978; Bosch, 1994a, 1994c; Monzón, 1998; Bosch *et al.*, 2000; Vicens & Bosch, 2000a).

Progeny mortality can be divided into developmental mortality, wintering mortality, and 'parasitism' (mortality caused by parasitoids, predators and pathogens). Because of its particular nature, the latter is discussed below in a separate section. Developmental and wintering mortality are very much dependent on the rearing and management methods used. Mortality levels typically decrease as knowledge on the developmental biology of the pollinator increases, and rearing methods are improved. For instance, *O. cornuta* populations from north east Spain expressed 18% winter mortality when wintered for 75 days compared to 4% mortality when wintered for 105 days (Bosch, 1994a). In the same species, failure to terminate prepupal summer dormancy declined from 22% to 4% when rearing temperatures were raised from 20–25°C to 22–30°C (Bosch, 1994a).

Another important factor affecting the growth of managed *Osmia* populations is the dispersal of pre-nesting females. Some fraction of any female population released in an orchard disperses and nests somewhere else. Dispersal of pre-nesting females increases when populations are released as loose cocoons instead of natal (whole) nests (Maeta, 1978; Torchio, 1984a, 1985; Bosch, 1994c). Pre-nesting dispersal also increases when populations are released in environments with insufficient floral resources (Maeta & Kitamura, 1974; Maeta, 1978; Bosch, 1995). Poorly managed populations, for example bees exposed to stressful temperature regimes during development or wintering, have low levels of establishment (J. Bosch, unpublished), although it is difficult to discern whether this is due to dispersal, to post-emergence mortality, or both. Pre-nesting dispersal needs to be considered when determining

adequate population densities for crop pollination. *Osmia cornifrons* populations in Japan are managed assuming 50% female establishment (Maeta & Kitamura, 1974; Maeta, 1990), but percentages near 75% can be achieved when bees are released from natal nests or from cocoons inserted in nesting cavities (Bosch, 1994a,c; Bosch & Kemp, 2001).

A better understanding of the factors influencing nest site fidelity in solitary bees would likely prove useful to increase female establishment in *Osmia* spp. populations managed for pollination. Females of the alfalfa leafcutting bee, *M. rotundata* show a clear preference for nesting in previously used, rather than new, nesting cavities, and several volatile compounds have been extracted from *M. rotundata* cells (Buttery *et al.*, 1981). However, when the effect of these compounds was tested in the field, extract-treated nesting materials failed to attract a higher proportion of females than untreated nesting materials (Parker *et al.*, 1983). In various solitary bees, secretions from the mandibular glands are known to attract conspecifics of both sexes, and are believed to serve as aggregation pheromones at nest sites (Batra 1978; Hefetz *et al.*, 1979). Several *Osmia* species, including *O. cornuta*, use individual scents to mark their nest entrances (Steinmann, 1976; Raw, 1992; Rosner, 1994). It is very likely that future studies analysing the potential role of individual nest-marking as aggregation pheromones will yield exciting results.

### Nesting substrates

Studies on nesting requirements need to be intensified (fig. 1), in order to eventually obtain one or more nesting substrates that allow for large-scale management. Cavity-nesting Megachilidae normally accept a variety of artificial or semi-artificial nesting materials, including holes drilled in wood or styrene, wood or styrene grooved boards, paper or cardboard tubes, and reed sections (Yamada *et al.*, 1971; Maeta, 1978; Torchio, 1982b, 1984a; Bosch, 1995). Adequate nesting materials need to be not only attractive to female bees, but also affordable and manageable. Nesting materials should also offer protection from light, excessive heat and humidity, parasites and predators. Progeny from less-preferred nesting materials tend to be excessively male-biased and/or express high developmental mortality (Torchio, 1982b, 1984b; Bosch, 1995).

In cavity-nesting Megachilidae, preferred nest hole diameters are correlated with female body size, but smaller species are more plastic, accepting a wider range of cavity dimensions than larger species (Krombein, 1967; Vicens *et al.*, 1993). Cavity dimensions affect not only female establishment and nesting success, but also sex ratio and body size of progeny, as well as overall progeny survival. Nesting cavities of narrow diameter and/or short length produce increasingly male-biased progenies (Yamada *et al.*, 1971; Maeta, 1978; Torchio, 1989a; Tepedino & Torchio, 1989; Bosch, 1994a,c). Progeny of both sexes produced in narrow-diameter cavities tend to be smaller than progeny produced in larger-diameter holes. Small *O. lignaria* and *O. cornuta* progeny express higher development and wintering mortality (Tepedino & Torchio, 1982a; Vicens, 1997). Nesting success, number of cells per nest, and sex ratio of progeny vary substantially among sites and years, mostly due to variations in weather conducive to foraging activity, and availability of floral resources (Tepedino & Torchio, 1982b). Thus, different nesting materials and cavity dimensions

should be compared under standard or controlled conditions.

### Parasitoids, predators and pathogens

Initially, resident populations of parasitoids, predators and pathogens (henceforth parasites) are typically low in agricultural environments, so parasitism in 'clean' experimental populations is typically lower than in wild populations (Maeta, 1978; Bosch, 1992b; Bosch *et al.*, 2000). However, some management practices create favourable conditions for the proliferation of certain parasites, that may otherwise be scarce in wild populations. In these cases, parasitism may rapidly increase, and studies on the biology of the parasites of concern (fig. 1) need to be directed toward the development of control methods that can be incorporated into the management system of the pollinator. Because population dynamics of parasites and predators are so dependent on specific management practices, control methods are typically designed and applied at the later stages of the establishment of the new pollinator.

For example, chalkbrood, a disease caused by pathogenic fungi, *Ascosphaera* spp. (Ascomycota: Ascospaeraceae), is rarely encountered in wild *M. rotundata* populations, but is responsible for mortality levels reaching up to 50% in populations managed for alfalfa pollination in the USA (Peterson *et al.*, 1992). High bee densities and re-use of old, poorly sanitized nesting materials typically result in enhanced chalkbrood incidence. In cavity-nesting species, removal of nests from nesting materials facilitates host location by parasitoids and increases cell exposure (Eves *et al.*, 1980; Bosch, 1992b). High temperatures used to incubate bee populations during development can increase the number of generations in certain parasitoids (Eves *et al.*, 1980).

Several studies on *Osmia* examine mortality levels caused by parasites and describe their biology and behaviour (Yamada *et al.*, 1971; Maeta & Yamane, 1974; Maeta, 1978; Youssef *et al.*, 1985; Torchio, 1989b, 1992; Bosch, 1992b; Torchio & Bosch, 1992; Bosch & Kemp, 2001). As described in the section on management systems, some of this information has been applied to establish prophylactic and control measures against specific enemies. Several genera of parasitoids, cleptoparasites and nest scavengers, e.g. *Leucospis* (Hymenoptera: Leucospidae), *Melittobia* (Hymenoptera: Eulophidae), *Monodontomerus* (Hymenoptera: Torymidae), *Trichodes* (Coleoptera: Cleridae), *Ptinus* (Coleoptera: Pfinidae), *Chaetodactylus* (Acari: Chaetodactylidae), are commonly associated with all three *Osmia* species discussed in this article. Other parasitic genera, e.g. *Chrysuria* (Hymenoptera: Chrysididae), *Sapyga* (Hymenoptera: Sapygidae), *Stelis* (Hymenoptera: Megachilidae), *Cacoxenus* (Diptera: Drosophilidae), *Argyramoeba* (Diptera: Bombyliidae), *Ascosphaera*, have only been found as common associates in one or two of the species. Within a given *Osmia* species, the main enemies vary in frequency from area to area and year to year, partly because of the relative timing of parasite activity and *Osmia* nesting periods (Bosch, 1992b; Torchio & Bosch, 1992).

At a time of increasing globalization, some pollinator species have been accidentally or purposely introduced in recent decades in areas beyond their historical distribution range (Cane, 2001; Thorp, 2001). Adequate information on parasite incidence and biology is necessary to understand

the risks associated with such introductions. *Varroa* spp. mites (Acari: Varroidae) are unfortunate examples of how parasites can switch between closely-related hosts, causing havoc to species with which they did not co-evolve (Anderson, 2000; Anderson & Trueman, 2000). The genus *Osmia* has approximately 135 species in North America and over 160 in the Palaearctic (Michener, 2000). The accidental introduction of some of the parasites listed above, especially of those genera found in only one geographic area, could have serious consequences for local wild and managed *Osmia* populations.

### Development of management systems

The knowledge obtained through studies described above needs to be combined with information on the reproductive biology of the plant to develop adequate management systems (fig. 1) that result in both appropriate pollination levels and sustainable bee reproduction. The breeding systems of the crop, its blooming phenology, flowering habits (e.g. biennial bearing), pollen and nectar production, receptivity periods, effective pollination periods and bearing capacities, are all factors that need to be considered (McGregor, 1976; Free, 1993; Nyéki & Soltész, 1996). Very importantly, pollinator management systems need to be integrated with pest management systems in the target crop. In the Czech Republic, a pest management programme was designed and implemented in alfalfa fields to protect populations of valuable pollinator *R. canus* (Ptacek & Rotrekl, 1990).

A complete management system for *Osmia* spp. populations used in orchard pollination should address the following issues:

1. Rearing methods. How should populations be managed during development, pre-wintering, wintering, and incubation?
2. Releasing methods. How and when should populations be released?
3. Bee density. What densities (bees per ha) should be used to obtain adequate pollination, yet avoid competition for local pollen and nectar resources?
4. Nesting materials. What nesting materials and in what numbers should be used? How should they be distributed in the orchard?
5. Bee supply. Can bee populations be increased on the target crop? If not, can they be increased in some other environment to maintain a continuous supply?
6. Control methods against enemies. What control methods against parasites, predators, and pathogens should be used?

The following paragraphs describe some illustrative examples of how the above questions have been resolved in particular cases. More detailed accounts of management systems for *Osmia* can be found in Maeta & Kitamura (1974) and Bosch & Kemp (2001).

#### Rearing methods

The simplest way to rear *Osmia* populations is under ambient (or close-to-ambient) conditions. This is the way most managed *O. cornifrons* populations are reared in Japan. Emergence of *O. cornifrons* reared under ambient conditions is well timed with cherry bloom, whereas emergence of populations used for apple pollination is delayed by

wintering the bees at 5°C (Maeta & Kitamura, 1974; Maeta, 1990). As mentioned, rearing methods need to be tailored not only to the flowering phenology of the crop, but also to the origin of the population used. For example, *Osmia* populations from cooler geographical regions reared under ambient temperatures in a warmer area will develop fast enough to become adults by mid-summer, at a time when local ambient temperatures may still be very warm. These bees consume a great proportion of their fat body reserves and suffer increased mortality during the winter, or else emerge very weakened, often unable to fly (Monzón, 1998; Bosch & Kemp, 2000b; Bosch *et al.*, 2000).

An example of how emergence dates can be manipulated to improve synchrony between bee activity and flowering periods is provided by the use of *O. lignaria* on almonds. Emergence of late-flying (April–May) *O. lignaria* populations from Utah must be advanced by at least two months to pollinate February-flowering almonds in California. Incubating such populations in late January results in an excessively shortened wintering period, which yields a slow and staggered emergence (Bosch & Blas, 1994b; Bosch & Kemp, 2000b). To circumvent this problem, Bosch *et al.* (2000) reared late-flying populations at a fluctuating temperature regime (14:27°C on 8:16 h day cycle), which results in a shortened prepupal dormancy and a shortened overall development time from egg to adult (Bosch & Kemp, 2000a). As a consequence, bees could be wintered ahead of time and provided with a sufficiently long wintering period, resulting in prompt emergence in synchrony with early-February almond bloom (Bosch *et al.*, 2000). Similar results were obtained when late-flying bees were reared at a temperature regime that did not result in accelerated development (22°C), but were wintered at a warmer temperature (7°C versus 4°C) (Bosch *et al.*, 2000).

#### Releasing methods

For optimal efficiency (in terms of both potential crop yields and bee returns), *Osmia* nesting should be timed to coincide with the beginning of the flowering period. This means bee populations need to be released a few days ahead of first bloom, to allow for complete male emergence, partial female emergence, mating, ovary maturation, and establishment. Artificial feeders or alternative flower resources blooming ahead of the target crop are highly desirable to sustain early-emerging individuals and minimize pre-nesting dispersal (Maeta & Kitamura, 1974; Bosch & Kemp, 1999). Because *Osmia* spp. are strongly attracted to fruit tree flowers, competition from alternative flowering plants for bee visitation is not a concern.

Optimally, *Osmia* populations should be released in natal nests, as this method ensures a higher female establishment at the nesting sites. An interesting example of the trade-off involved with most management practices comes from the alfalfa pollination industry. Alfalfa leafcutting bee, *M. rotundata*, populations are often released as loose cells (rather than from natal nests) to prevent emerging adults from being dusted during emergence with chalkbrood spores, *Ascospaera* spp., from infested larval cadavers (Bohart, 1972; Richards, 1984). This practice is effective at reducing chalkbrood levels, but increases pre-nesting female dispersal.

Nesting materials are usually set up in nesting shelters (any kind of structure that provides protection from direct

sunlight, rain and wind). *Osmia* females prefer to nest in shelters oriented to the East, West or South rather than in those orientated to the North (Torchio, 1981). Shelter distribution within the orchard influences not only female establishment, but also pollination. Shelter distribution should be based on female foraging range, roughly 100 m in *Osmia* spp. (Kitamura & Maeta, 1969; Batra, 1982; Yoshida & Maeta, 1988; Vicens & Bosch, 2000c), but is often decided on human convenience. In general, a larger number of small shelters distributed across the orchard will result in better female establishment (Torchio, 1984a,b; Bosch, 1994a), and more even pollination levels (Yamada *et al.*, 1971), particularly during bloom periods with poor weather and small flight windows for pollinators.

#### Bee density

In *O. cornifrons* and *O. cornuta*, recommended bee densities required to pollinate 1 ha of fruit trees are based on estimates of the average number of flowers visited per nesting female in relation to the average number of flowers produced per tree (Maeta & Kitamura, 1974, 1981; Bosch, 1994b; Vicens & Bosch, 2000a). In *O. lignaria*, estimates are based on yields in orchards or cages supplied with different bee densities (Torchio, 1979, 1985, 1991a). Despite this difference in methodology, the bee densities recommended are very similar for all three species (table 1). Because bee density estimates are calculated based on numbers of nesting females, actual population sizes need to be adjusted according to expected dispersal of pre-nesting females (Bosch & Kemp, 2001). Population sizes also need to be adjusted according to biennial bearing patterns of each fruit tree species or cultivar (Bosch & Kemp, 1999). Higher bee densities than those strictly needed to accomplish adequate pollination could be released in orchards with sufficient bloom as a means to increase bee populations, but supersaturating an orchard with bees increases pollination costs and, at the same time, results in high pre-nesting dispersal and high bee progeny mortality due to insufficient pollen-nectar resources (Torchio, 1985).

#### Nesting materials

First and foremost, nesting materials should be designed to accommodate the nesting behaviour of the pollinator. That is, nesting materials should be attractive and, at the same time, yield adequate progeny sex ratios and low mortality. Second, nesting materials should be manageable at the commercial scale. In this regard, low cost and low weight are desirable attributes. Equally important, nesting materials should allow for easy sampling of nest contents, so that bee populations can be quantified and sexed, and parasitism and developmental mortality levels assessed and

controlled. Some nesting materials are adequate for use in experimental studies, but are too costly or difficult to manage in large-scale commercial operations.

An illustrative example of how bee requirements are sometimes compromised by human convenience comes from the alfalfa leafcutting bee industry. Many of the commercially available nesting boards for this pollinator contain holes that are at the low end of the size range (length and diameter) accepted by *M. rotundata* females. Although females nest in these cavities, they tend to produce small-sized and excessively male-biased progeny (Stephen & Osgood, 1965; Gerber & Klostermeyer, 1972). As a result, many commercial *M. rotundata* populations are managed at ratios of 2 or more males per female, when, based on differences between sexes in body size, sex ratios of *M. rotundata* populations should average 1.2 males per female (Klostermeyer *et al.*, 1973). Floral resources invested in the production of surplus males result in diminished female returns and in reduced pollinating potential, as males rarely trip alfalfa flowers (Free, 1993). As mentioned, production of small-sized progeny results in increased developmental and wintering mortality in *Osmia* spp.

#### Bee supply

A reliable source of 'clean' populations needs to be assured to sustain any new pollinator targeted for commercial-scale pollination. In years with fair weather during bloom and, most importantly, following adequate management procedures (especially adequate rearing temperature regimes, and natal nest-release procedures), population increases in the three *Osmia* species considered herein can be accomplished in orchard environments (Torchio, 1985; Yoshida & Maeta, 1988; Maeta, 1990; Bosch, 1994a, 1994c; Bosch & Kemp, 1999; Bosch *et al.*, 2000). Maeta (1990) provides examples of 2- to 3-fold female population increases in *O. cornifrons* following female establishment percentages as low as 42% in apple orchards. Five-fold *O. lignaria* female population increases have been obtained in both pear-apple and cherry orchards (Torchio, 1985; Bosch & Kemp, 1999), and *O. cornuta* female populations have been doubled on almonds (Bosch, 1994a).

In years with very poor weather during bloom, however, and especially in orchards with short blooming periods, progeny production may be compromised. Application of growth regulators to advance or delay bloom in parts of the orchard is one way to provide an extended blooming period and favour bee population increases (Warner, 1999; Traynor, 2000). Other forage plants blooming immediately before or after the target crop can be planted as an under-crop or in the edges of the orchard to provide supplementary pollen-nectar sources. *Osmia* populations can also be moved to a later-flowering orchard, although some losses due to females failing to re-establish at the new site should be expected (Torchio, 1991b; Vicens & Bosch, 2000c). Alternatively, bee populations can be released in wild or cultivated habitats (nurse crops) for increasing progeny numbers. In Japan, *O. cornifrons* populations are routinely released and multiplied in *Astragalus* (Fabaceae) plots planted as a source of nitrogen in rice fields. Populations obtained in this way are used to compensate for losses, due to insecticide sprays and/or short blooming periods, in populations released in apple orchards (Y. Maeta, personal communication). In the USA, meadowfoam, *Limnanthes alba* (Limnathaceae) shows

Table 1. Number of *Osmia* nesting females recommended to pollinate one hectare of almonds or apples (Maeta & Kitamura, 1974; Torchio, 1985, 1991a; Bosch, 1994b; Vicens & Bosch, 2000a).

	Almond	Apple
<i>O. cornifrons</i>	–	550
<i>O. lignaria</i>	740	625
<i>O. cornuta</i>	750	530

promise as a crop to increase *O. lignaria* populations (J. Bosch & W. Kemp, unpublished).

#### Control against enemies

Because of the low numbers of *Osmia* used per ha, nest inspection and manual removal of parasitized cells is feasible in small-orchard operations. For larger operations, other control methods are necessary. Many control methods against *Osmia* enemies are simply based on reducing exposure to parasites or predators. For instance, predation of nesting females by birds can be easily reduced by covering nesting shelters with a screen (Batra, 1982), and nests in reeds or in thick cardboard tubes are effectively protected from *Monodontomerus* chalcid wasps (Maeta, 1978; Batra, 1982). Releasing populations in excluder boxes to avoid re-nesting in old nesting materials is an effective way to reduce *Chaetodactylus* and *Ascospaera* parasitism (Maeta, 1990; Bosch & Kemp, 2001). Retrieving nesting materials from the orchard before the end of the nesting period is an easy way to avoid parasitism by late-flying enemies (Bosch, 1992b; Bosch & Kemp, 2001).

Other control methods involve actively killing parasites and predators. Black light traps are used to attract and kill *Monodontomerus* (Eves *et al.*, 1980). Acaricide and thermal shock treatments applied during the most resistant bee stage (dormant prepupa) are used in Japan to reduce numbers of *Chaetodactylus* mites (Yamada, 1990). An illustrative example of how results from basic studies are applied to establish control methods is provided by Torchio's work on the alfalfa leafcutting bee cleptoparasite, *Sapyga pumila* Cresson (Hymenoptera: Sapygidae). Males of this wasp were found to selectively spend the night in cavities measuring 2.5 mm in diameter (Torchio, 1972a). Subsequently, traps with holes of this size were designed to attract and kill *S. pumila* males and effectively reduce parasitism levels (Torchio, 1972b).

#### Pilot tests

Once a prototype management system has been developed, pilot tests must be conducted (fig. 1) to ensure that the results obtained at the commercial scale meet expectations, in terms of both pollination and bee return (Yamada *et al.*, 1971; Torchio, 1985; Maeta, 1990; Bosch & Kemp, 1999). Fruit yields in orchards pollinated with the new pollinator can be compared to yields from years during which other pollinators were used (Bosch & Kemp, 1999), or to yields from hand-pollinated branches, or from trees in pollinator-saturated cages. Decreasing yields at increasing distances from the pollinator nesting site can also be used to measure the pollinating contribution of the new pollinator (Yamada *et al.*, 1971; Maeta, 1990; Monzón, 1998). Results obtained in pilot tests are used to refine management techniques until consistent results are obtained and the new pollinator can be delivered with confidence to the industry. For instance, if pollination levels are adequate but bee returns are not sufficient or consistent, one should consider reducing the bee density or providing an alternative pollen-nectar source to increase bee numbers.

#### Technology transfer

The last step in the process of establishing a new pollinator is the transfer of technology from research to

producers and pollination providers. Awareness of the new pollinator among growers, beekeepers and custom pollination companies is usually accomplished through technical and popular articles. Pilot tests are an effective way to locally demonstrate the potential of the new pollinator. Management systems can be communicated to wider audiences through the publication of manuals (Maeta & Kitamura, 1974; Bosch & Kemp, 2001), as well as through training courses and workshops.

The eventual establishment of any new pollinator depends on its pollinating performance, sustainability, and manageability, as well as on its economic cost. A less efficient pollinator may be preferred because of its low cost. Alternatively, a more costly pollinator may be chosen because it provides a more consistent pollinating service, even in years with poor weather during bloom, or because substantial population increases provide added profitability from the sale of surplus bees (Bosch & Kemp, 1999). New pollinators are typically costly in the first years of their commercial establishment, generally because demand tends to exceed supply. Subsequently, however, prices tend to stabilize as larger populations become available from increasing numbers of suppliers, and production efficiency improves through new discoveries and refined management techniques. The first commercial *Bombus* colonies available in the USA sold for \$700 in the early 1990s, whereas better colonies (with more workers) are now available for \$250. Populations of the alfalfa leafcutting bee, *M. rotundata*, currently available in the USA at roughly \$50 per gallon (approximately 10,000 bees; 2600 bees l<sup>-1</sup>), sold for \$200 per gallon in the early 1980s (Bitner, 2000).

#### Concluding remarks

The three *Osmia* species discussed in this article are very similar in biology and management. *Osmia cornuta* populations are being used in almond orchards in Spain (Calzadilla *et al.*, 1997) and France (J.-P. Torré Grossa, personal communication), and in apple orchards in Yugoslavia (Krunić *et al.*, 1991). With recent reduction in numbers of both feral and managed honey bee colonies in North America (Finley *et al.*, 1996; Traynor, 1998; Campbell, 2000), *O. lignaria* is becoming commercially established in the USA and Canada (Bosch & Kemp, 1999, 2001). Commercial populations are being used, especially in Utah, Washington, and California, on apples, cherries and almonds. The use of *O. cornifrons* in Japan has increased from 10% of the total apple production area in 1981, to 50% in 1990, and over 70% in 1996 (Maeta, 1990; Sekita *et al.*, 1996; Batra, 1998). In the late 1970s and early 1980s, *O. cornifrons* populations from Japan were introduced into eastern USA (Batra, 1979, 1998), where they are now becoming established as commercial orchard pollinators. *Osmia cornifrons* is also becoming established as a commercial pollinator in Korea and China (Xu *et al.*, 1995).

Information on the contribution of wild pollinators to the pollination of flowering crops is mostly lacking. Even for those crops in which pollinator surveys exist, little is known about the pollinating abilities of each species and their potential as manageable pollinators, and management systems have been developed for only a few of those species that have actually been studied as potential crop pollinators. Often, insufficient effort is given to the development of rearing methods and management systems for otherwise

promising, effective pollinators. Notwithstanding the influence of economical and sociological aspects on the establishment of a new pollinator, only those species for which a reliable supply has been resolved are likely to ever become established as viable commercial pollinators.

A word of caution must be added concerning the movement of pollinator species beyond their native geographical distribution ranges. The honey bee and bumblebee industries provide several examples of the threats involved with pollinator introductions. As mentioned, the spread of exotic parasites and diseases constitutes a very serious threat (Kraus & Page, 1995; Goka *et al.*, 2000; Hood, 2000; Stanghellini *et al.*, 2000). Although difficult to measure, a second risk is the potential displacement of native pollinators by introduced bee species (Dafni & Shmida, 1996; Hingston & McQuillan, 1999; Roubik & Wolda, 2001). Introduced bee species could also disrupt pollination relationships between native floras and pollinators (Butz Huryn, 1997; Kearns *et al.*, 1998), or enhance weed spread (Butz Huryn & Moller, 1995; Barthell *et al.*, 1995). In most areas with crop pollination deficits, bee faunas are sufficiently rich to find suitable candidate species, and the development of native species should be attempted before considering exotic introductions. The genus *Osmia* illustrates the availability of suitable orchard pollinators in large areas on three different continents. Hopefully, the knowledge gained from these species can be applied to successfully develop other native species and provide improved stability to those crops that rely on insect pollination.

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