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Review

Pollinator Ecology and Management

Pesticide Exposure Assessment Paradigm for Solitary Bees

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Abstract

Current pesticide risk assessment for bees relies on a single (social) species, the western honey bee, *Apis mellifera* L. (Hymenoptera: Apidae). However, most of the >20,000 bee species worldwide are solitary. Differences in life history traits between solitary bees (SB) and honey bees (HB) are likely to determine differences in routes and levels of pesticide exposure. The objectives of this review are to: 1) compare SB and HB life history traits relevant for risk assessment; 2) summarize current knowledge about levels of pesticide exposure for SB and HB; 3) identify knowledge gaps and research needs; 4) evaluate whether current HB risk assessment schemes cover routes and levels of exposure of SB; and 5) identify potential SB model species for risk assessment. Most SB exposure routes seem well covered by current HB risk assessment schemes. Exceptions to this are exposure routes related to nesting substrates and nesting materials used by SB. Exposure via soil is of particular concern because most SB species nest underground. Six SB species (Hymenoptera: Megachilidae - *Osmia bicornis* L., *O. cornifrons* Radoszkowski, *O. cornuta* Latreille, *O. lignaria* Say, *Megachile rotundata* F., and Halictidae - *Nomia melanderi* Cockerell) are commercially available and could be used in risk assessment. Of these, only *N. melanderi* nests underground, and the rest are cavity-nesters. However, the three *Osmia* species collect soil to build their nests. Life history traits of cavity-nesting species make them particularly suitable for semifield and, to a lesser extent, field tests. Future studies should address basic biology, rearing methods and levels of exposure of ground-nesting SB species.

Key words: risk assessment, pollinator, *Osmia*, *Megachile*, *Nomia*, ecotoxicology

Bees (Hymenoptera: Apoidea, Anthophila) are an extraordinarily speciose group, with more than 20,000 species worldwide (Michener 2007, Ascher and Pickering 2017) and comprising a wide range of biological traits and life histories. Although social species (such as honey bees, bumblebees, and stingless bees) are most known and recognized by the general public, most bees (*ca.* 70% in temperate ecosystems) are solitary. Solitary life implies that each female builds and provisions her nest and raises her offspring alone, with no cooperation from other individuals. Another substantial portion of bee species (*ca.* 20% in temperate ecosystems) are cleptoparasitic. These species lay their eggs in the nests of other (mostly solitary) bee species and feed on their hosts' provisions. The remaining bee species are social, i.e., they live in colonies with one reproductive female and a number of nonreproductive workers (from tens to tens of thousands, depending on the species).

Bees provide pollination services to 87% of wild flowering plants (Ollerton *et al.* 2011) and 75% of cultivated crops (Klein *et al.* 2007). Although most agricultural pollination traditionally has been attributed to the western honey bee, *Apis mellifera* L. (Hymenoptera: Apidae) (Carreck and Williams 1998), other bee species also contribute decisively to crop pollination. This contribution comes not only from wild bee populations (Garibaldi *et al.* 2013), but also from a handful of managed species used as commercial pollinators (Johansen *et al.* 1978, van Heemert *et al.* 1990, Bosch and Kemp 2002, Pitts-Singer and Cane 2011, Peterson and Artz 2014, Isaacs *et al.* 2017).

In recent decades, declines in bee diversity have been documented in various parts of the world (Biesmeijer *et al.* 2006, Potts *et al.* 2010, Cameron *et al.* 2011, Bartomeus *et al.* 2013, Burkle *et al.* 2013). The drivers of these declines are at least partially known and include habitat destruction and fragmentation, insufficient floral resources, and pesticide use (Kluser and Peduzzi 2007, NRC 2007, Vanbergen *et al.* 2013, Potts *et al.* 2016). For this reason, bee conservation has become a priority in many countries, and several initiatives have been undertaken at global and regional scales to reverse bee declines and secure pollination services (Dias *et al.* 1999, Byrne and Fitzpatrick 2009, Potts *et al.* 2016). One of these initiatives involves the review of environmental risk assessment schemes required for the registration and re-evaluation of plant protection products. Regulatory agencies in the European Union and the United States have already started this process with the publication of scientific opinion and guidance documents (EFSA 2012, EFSA 2013, USEPA et al. 2014). Until now, pesticide risk assessment for bees has relied on a single species, the western honey bee, *Apis mellifera* L. (EPPO/OEPP 2010). This approach assumes that the worst-case scenarios used in honey bee risk assessment schemes are sufficiently conservative to protect other bee species, or that predictions for other bee species can be extrapolated from honey bee results. However, details of the interspecific differences in exposure and potential impacts of pesticides are lacking. In fact, an increasing body of knowledge shows that the impact of pesticides on bees strongly depends on specific life history traits, that ultimately determine routes and levels of exposure, as well as on differences in sensitivity among different taxa (Brittain and Potts 2011, Arena and Sgolastra 2014, Thompson 2016, Stoner 2016, Kopit and Pitts-Singer 2018). Consequently, the aforementioned EFSA and USEPA documents on bees and pesticides highlight knowledge gaps that may impede efforts to develop risk assessment schemes that are more inclusive of the variation in life histories found among such a diverse group of organisms. The EFSA document (EFSA 2013), in particular, considers separate risk assessment schemes for honey bees, bumblebees, and solitary bees.

This paper focuses on solitary bees and is one in a series of documents generated at the Workshop on 'Pesticide Exposure Assessment Paradigm for non-*Apis* bees' held in 10–12 January 2017, at the United States Environmental Protection Agency (USEPA) in Arlington, Virginia (USA). The aim of the workshop was to focus on routes of pesticide exposure and to understand whether the western honey bee sufficiently serves as a surrogate for pesticide risk assessment for all bee species. This paper summarizes the results of the workshop and reviews relevant facts and data with the following objectives: 1) to provide a comparison of solitary bee and honey bee life history traits relevant for risk assessment; 2) to summarize current knowledge about comparative levels of pesticide exposure for solitary bees and honey bees; 3) to identify gaps in our knowledge of exposure and research needs; 4) to ask if the current honey bee risk assessment paradigm provides coverage of all the routes and levels of exposure of solitary bees; and 5) to identify potential solitary bee model species for pesticide risk assessment.

Life History Differences Between Honey Bees and Solitary Bees and Implications for Pesticide Risk Assessment

As mentioned, the vast majority of bees in temperate ecosystems are either solitary or cleptoparasites of solitary species. Like social bees (Human *et al.* 2007), adult solitary bees feed mostly on nectar, but they also ingest small amounts of pollen (especially females that require protein to mature their eggs) (Cane 2016). Female solitary bees build nests composed of multiple cells. In each cell, the nesting female forms a pollen-nectar provision upon which an egg is laid. The provision mass serves as food for the developing larva. Solitary bees, therefore, are mass-provisioners, in contrast to social bees whose workers typically feed larvae progressively.

Most solitary bees (*ca.* 65%) excavate their nests underground. Underground nesting is typical of species in the families Andrenidae, Halictidae, Melittidae, Stenotritidae, and some Apidae and Colletidae. Most ground-nesting solitary bees line their nest cells with glandular secretions. The rest of the species (most Megachilidae, some Colletidae and some Apidae) nest above-ground. Most above-ground nesters use existing cavities, such as hollow stems and abandoned beetle burrows in dead wood, but some excavate their nests in dead wood or in soft-pith stems. Many of these species collect one or more natural materials to build their nest cells (soil, leaves, resin, plant pubescence, floral oils, etc.), and some line their cells with glandular secretions. In contrast to social species, most solitary bees are short-lived. Individual females live about 20–30 d, and the flight season of a population at a given site may span 2–3 mo. In contrast to the reproductive members of social bee colonies, fecundity is low in solitary bees (10–40 eggs per female). In temperate climates, most solitary bee species are univoltine (have a single generation per year), but some may complete two or more generations per year (multivoltinism) under conducive environmental conditions.

The life history traits of solitary bees and honey bees that are relevant to pesticide exposure are outlined in Table 1. Differences between these two groups of bees in body size, foraging range, level of pollen and nectar consumption, and exposure to various environmental materials (soil, leaves, plant pubescence, etc.) may result in different routes and levels of exposure. Social versus solitary life history traits may also entail different ecological consequences. For example, in solitary bees, the death of a nesting female results in a complete cessation of its reproductive output, whereas in social bees, the deaths of nonreproductive individuals can be buffered by the survival of other colony members and the production of new members (i.e., superorganism resilience) (Straub *et al.* 2015).

Potential Surrogate Species to Estimate Exposure for Solitary Bees

It is obviously not feasible to examine every bee species. The use of surrogates is a common procedure in risk assessment, and a good surrogate species should: 1) be commercially reared so that sufficiently large managed populations are available; 2) be easily handled in laboratory, semifield and field conditions; and 3) show behavioral and life history traits representative of other species of the same taxonomic or ecological group. In addition, surrogate species would ideally be natively distributed over a large geographic area.

In spite of their diversity and importance as crop pollinators, only a few solitary bee species are commercially reared or propagated (Johansen *et al.* 1978, Richards 1984, Bosch and Kemp 2001, 2002, Pitts-Singer and Cane 2011, Peterson and Artz 2014). These include: *Osmia cornifrons* Radoszkowski (the hornfaced bee) in eastern Asia, *Osmia cornuta* Latreille (the horned mason bee) and *Osmia bicornis* (= *rufa*) L. (the red mason bee) in Europe, *Osmia lignaria* Say (the blue orchard bee), *Megachile rotundata* F. (the alfalfa leafcutting bee), and *Nomia melanderi* Cockerell) (the alkali bee) in North America (Fig. 1).

N. melanderi (Hymenoptera: Halictidae) is the only ground-nesting species propagated for large-scale pollination (of alfalfa) (Pitts-Singer 2008). Although it is representative of the nesting behavior found most commonly in solitary bees, nesting aggregations only occur in very restricted regions of the western United States. Due to its ground-nesting behavior, *N. melanderi* is difficult to rear and manipulate in laboratory or semifield conditions, and limited attempts to

Table 1. Life history traits of honey bees compared with solitary bees and implications for risk assessment

Traits	Honey bees	Solitary bees	Implications for risk assessment
Level of sociality	Eusocial	Solitary	Due to colony resilience in social bees, extrapolation of fitness effects from the individual to the population level is easier in solitary bees. Nesting activity and reproductive output of individual females can be measured in solitary bees, thus facilitating the detection of certain sublethal effects. Reproductive output of a honey bee colony is much more difficult to measure.
Fecundity	Circa 1,500 eggs per day	Usually no more than 2 eggs per day (10–40 eggs over entire life span)	Supply of bees for toxicological assays is much higher for honey bees.
Trophallaxis	Present	Absent	In solitary bees, only individual feeding is feasible in laboratory tests. Individual feeding is more labor intense, but the amount of solution ingested by each individual can be accurately controlled.
Nesting substrate	Large cavities; hives	Most species nest underground. Others nest in small cavities above ground.	Pesticide exposure via excavation and dwelling in soil is an important route of exposure in ground nesting solitary species. Natural cavities used by honey bees and above-ground solitary bees are unlikely exposure routes.
Nesting material	Wax and propolis	Mud, soil, leaves, resin, floral oil, etc.	Several environmental matrices may be highly relevant to solitary bees but less so to honey bees.
Foraging range	Mean: 1.5 km Maximum: 16 km	Mean: 100 m; Maximum: 2 km[a]	The typical size of test fields (1 ha) is much more representative of the foraging area of solitary bees than honey bees. For full field testing in honey bees, distance between test hives needs to be very large to avoid overlap of control and treatment colony foraging areas (exposure uncertainty).
Amenability to nest in confined conditions	Low	High	The behavior of solitary bees is much less affected by confinement (greenhouses, screened cages). Due to their reduced foraging range and short life span, the entire nesting period of single nesting females can be monitored in semi-field conditions.
Nesting period	All or most of the year	Usually 2–3 mo in spring or summer	Adult solitary bees are only available for some months (3–4 with appropriate temperature management) in spring or summer.
Pollen transport	On hind legs (in corbiculae); pollen wetted with nectar and glandular secretions	Most species carry dry pollen on hind legs or ventral abdomen (in scopae). Some species carry pollen mixed with nectar inside crop.	Risk of exposure via pollen is probably greatest in bees that carry pollen inside their crop.
Body size	~100 mg (workers)	2–400 mg[b]	Because exposure level and sensitivity are body-size dependent, a possible extrapolation factor from honey bees to solitary bees should consider the large body size variability. Solitary bees also show greater intraspecific variability.
Adult food	Nectar + small amounts of pollen	Nectar + small amounts of pollen	The amounts and identity of nectar and pollen consumed may vary widely depending on body size, natural history and physiological traits (known for very few species). Honey bees prefer to visit flowers with high sugar concentration. Pollen ingestion in foraging honey bees is not relevant. Nurse honey bees ingest pollen in the form of beebread (stored pollen mixed with nectar/honey). Solitary bee females ingest freshly-collected pollen, not mixed with nectar.
Flower preferences	Broad generalists. Colonies typically collect pollen and nectar from many sources.	Most are generalists, but many show a marked preference for certain plants. Some are oligolectic (collect pollen from only one plant family)	In open field tests, honey bees are expected to collect pollen from the field test and from other sources within their foraging range. In semi-field test, solitary species will forage and develop normally on non-preferred host plants. However, in field tests they may ignore the test field if other preferred pollen sources are available within their foraging range.
Larval food	Royal jelly, bee bread, and honey	All use pollen mixed with nectar; some species also consume floral oil.	In honey bees, larval exposure is 'filtered' by nurse bees (raw food is processed and larvae are fed glandular secretions by workers). Solitary bee larvae consume unprocessed food.

Table 1. Continued

Traits	Honey bees	Solitary bees	Implications for risk assessment
Larval food provisioning	Progressive feeding	Mass-provisioning	In honey bees, the food consumed by an individual larva may have been collected over a long period of time, and the time between provisioning and feeding may be long. In solitary bees, the larval food is collected over a short period of time (1–2 d), and the larva starts feeding within a few days (e.g., 7 in *Osmia*, 3 in *Megachile*) after egg is laid.
Larval feeding period	5 d	Highly variable: from a few days to 1 mo, depending on the species	Solitary bee larvae may feed for considerably longer periods than honey bees.

[a]Data from agricultural fields.
[b]Data for European species.

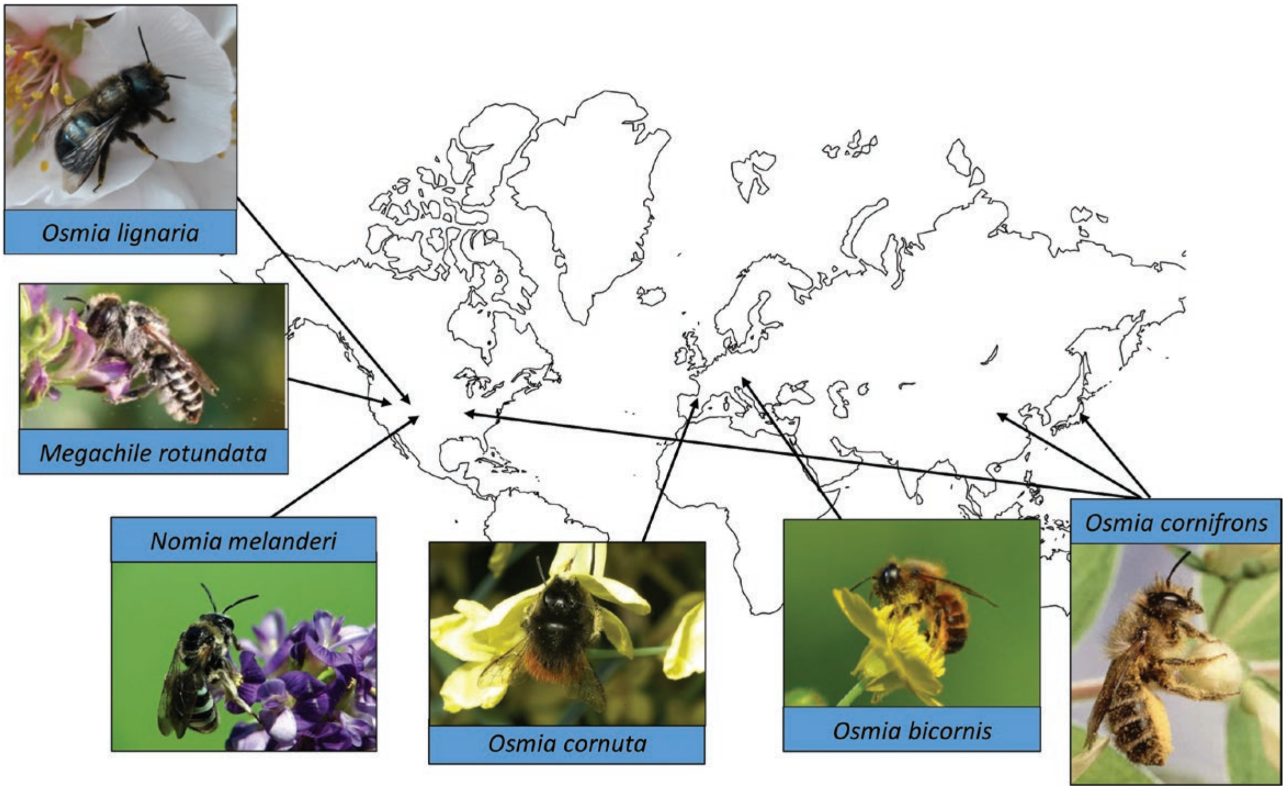

Fig. 1. Solitary bee species commercially available in different parts of the world. Photo credits: *Osmia lignaria* (Derek Artz), *Megachile rotundata* (Theresa Pitts-Singer), *Nomia melanderi* (James Cane), *Osmia cornuta* (Fabrizio Santi), *Osmia bicornis* (Laura Bortolotti), *Osmia cornifrons* (Suzanne Batra).

create artificial rearing protocols have failed. Consequently, information on its biology is scarce.

Commercially available *M. rotundata*, *O. lignaria*, *O. cornifrons*, *O. cornuta*, and *O. bicornis* are cavity-nesting species in the family Megachilidae. Unlike ground-nesting species, they do not excavate their nests, and readily accept a variety of artificial nesting sites. They are fairly easy to rear and manipulate. Large *M. rotundata* and *O. cornifrons* populations are commercially available in North America and eastern Asia (Japan, China, South Korea), respectively. Supplies of *O. lignaria* are becoming more widely available in the western United States, and *O. cornifrons*, which was introduced to the United States from Japan in the 1980s (Batra 1998), can be purchased from a few vendors in the Eastern United States where those bees have become established and wild populations occur. *Osmia cornuta* and *O. bicornis* are increasingly becoming available for commercial use in various countries in Europe. The biology of both *Megachile* and *Osmia* is well known.

Studies on the effects of pesticides on *N. melanderi* are sparse (Torchio 1973, Johansen *et al.* 1984). Better studied is the ecotoxicology of *M. rotundata* (Torchio 1973 1983; Johansen *et al.* 1984; Abbott et al. 2008; Huntzinger et al. 2008a,b; Scott-Dupree *et al.* 2009; Hodgson *et al.* 2011; Artz and Pitts-Singer 2015) and especially *Osmia* spp. (Ladurner *et al.* 2003, Tesoriero *et al.* 2003, Ladurner *et al.* 2005, Abott et al. 2008, Ladurner *et al.* 2008, Scott-Dupree *et al.* 2009, Biddinger *et al.* 2013, Hinarejos et al. 2015, Sandrock *et al.* 2014, Artz and Pitts-Singer 2015, Jin *et al.* 2015, Roessink *et al.* 2015, Ründlof et al. 2015, Sgolastra *et al.* 2015, Heard et al. 2017, Peters *et al.* 2016, Spurgeon at al., 2016, Uhl *et al.* 2016, Sgolastra *et al.* 2017). *O. cornuta* and *O. bicornis* are the two risk assessment model species proposed by EFSA (European Food Safety Authority) in Europe (EFSA 2013). Standard protocols for laboratory and semifield tests are currently being ring-tested in Europe by the non-*Apis* working group of the International Commission for Plant-Pollinator Relationships (ICPPR) (Roessink *et al.* 2015).

Life History of *N. melanderi*

N. melanderi is native to the Western United States (Fig. 1). It is a gregarious species that excavates nests in alkaline soils. Each cell is provisioned with nectar and pollen and sealed with a polished soil cap. This bee is active from late June to late August. The larval period lasts *ca.* 15 d, and the fifth instar overwinters as a prepupa. Development is completed in the summer, and the pupal period lasts 10–15 d. Most populations are univoltine, but in southern California they may produce a second generation (or more) whose adults nest in the same summer as their mother and, thus, have an extended flight period (Fig. 2). *N. melanderi* are propagated for alfalfa pollination in certain locations of Washington State and Oregon where natural bee beds are protected and artificial beds are created for new establishments near alfalfa fields. Aggregations are occasionally found in other states (e.g., California, Utah, Wyoming, and Colorado) where they were once more abundant than now.

Life History of *Osmia* Species

The four aforementioned *Osmia* species (*O. lignaria* in North America, *O. cornifrons* in Asia and North America, *O. cornuta* and *O. bicornis* in Europe) (Fig. 1), often referred to as mason bees, belong to the same subgenus *Osmia (Osmia)* and have very similar natural histories. As mentioned, *O. cornifrons* was introduced into the United States in the 1980s and has become feral in some states, especially in the higher latitudes of the eastern part of the country. These *Osmia* spp. overwinter as cocooned adults, emerge in early spring, and produce only one generation per year (i.e., are univoltine). Adult females are active for *ca.* 2 mo between February and May, depending on the species and the geographic area. They use mud to build cell partitions and to seal the nest entrance. The larval feeding period lasts *ca.* 1 mo. The prepupal period lasts 1–2 mo, and the pupal period *ca.* 1 mo. Adults eclose in late summer, but do not emerge from cocoons until the following spring (Fig. 3). All four species have been developed as orchard pollinators in different parts of the world.

Life History of *M. rotundata*

M. rotundata is native to Europe and southwestern Asia. The species was unintentionally introduced into North America around the early 1940s and currently occurs across most of the United States and southern Canada (Pitts-Singer and Cane 2011). Adults are active for *ca.* 3 mo starting in June-July depending on the latitude. They usually produce a partial second generation (and sometimes a third and fourth generation), especially in southern latitudes. Adult females use cut-leaf pieces to line each brood cell and to cap the nest entrance. The larval period last *ca.* 20 d, and the pupal period 15 d. They overwinter as prepupae (Fig. 4). *M. rotundata* is the most important alfalfa pollinator for seed production in central Canada and the western United States. Management protocols for *M. rotundata* are well developed.

Routes of Pesticide Exposure

The relative importance of different exposure routes to adult and larval honey bees and solitary bees of the three potential surrogate taxa is summarized in Table 2. Exposure via air particles (dust and spray) and nectar consumption are important routes of exposure in both honey bee and solitary bee adults (EFSA 2013, USEPA et al. 2014) (Table 2). Adult honey bee workers consume bee bread (aged

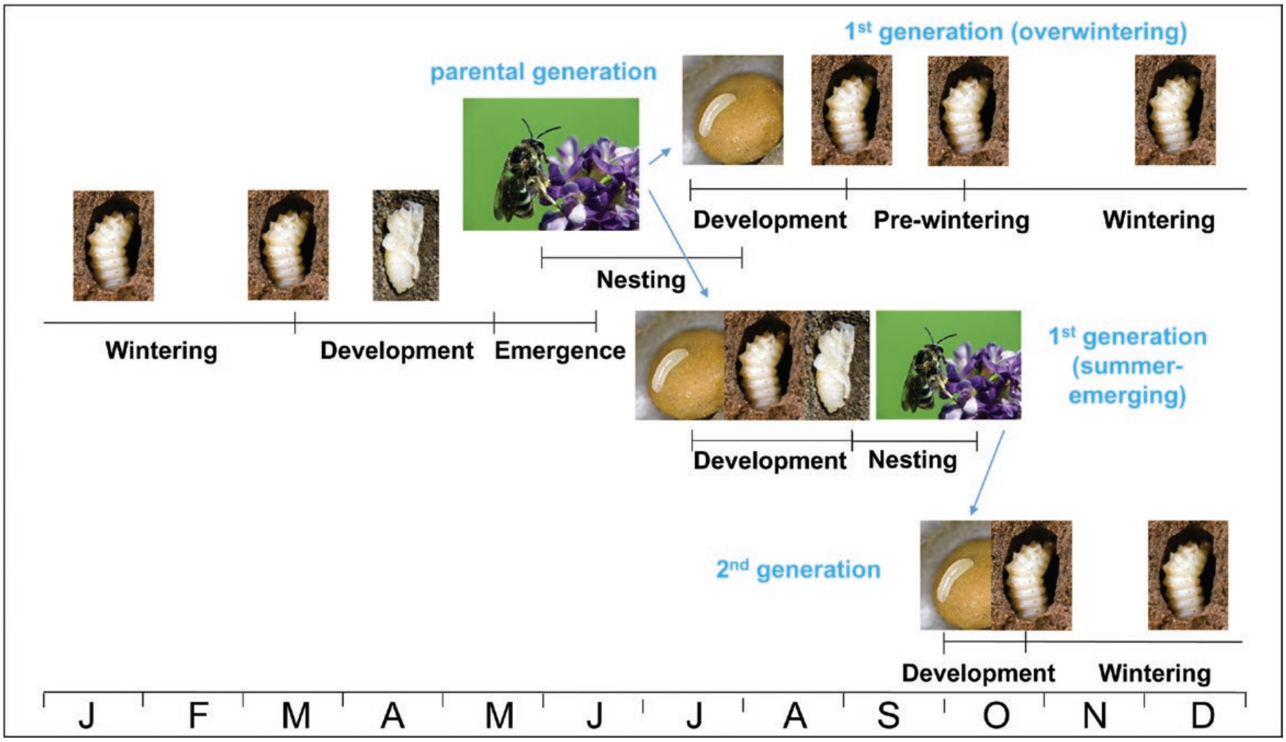

Fig. 2. Life cycle of *Nomia melanderi.* Photo credits: egg (James Cane), prepupa (James Cane), pupa (Bill Nye), adult (James Cane).

pollen mixed with nectar) during the first 2 wk of their life while they are nurse bees. In contrast, female solitary bees consume fresh pollen throughout their entire life span (Cane 2016). In contrast to honey bees, there are no reports that solitary bees consume honeydew or guttation water in natural conditions (Table 2).

Soil is not likely to be an important route of exposure for honey bees, but it is very relevant for species like *N. melanderi* that nest underground (Table 2). *Osmia* females collect soil to build nest cell partitions, and, therefore, are also directly exposed to residues in this material. *M. rotundata* females cut pieces of leaves to line and cap their nests, and, therefore, are likely to be exposed to residues in plant tissues and on their surfaces.

In larvae, exposure via nectar and pollen is highly relevant in all bee species (Table 2). However, honey bee larvae consume food that may have been collected from various sources over a longer expanse of time and stored for an extended period in the form of bee bread (pollen with some nectar) and honey (nectar). Bee bread and honey are ingested and processed by nurse bees before being regurgitated into larval cells. Thus, the pollen and nectar eaten by larvae have undergone complex aging and enzymatic transformation. In contrast, solitary bees consume recently-collected provisions of unprocessed (often single-sourced) pollen mixed with nectar. On the other hand, solitary bee larvae may take much longer than honey bee larvae to consume the entire food provision. These differences

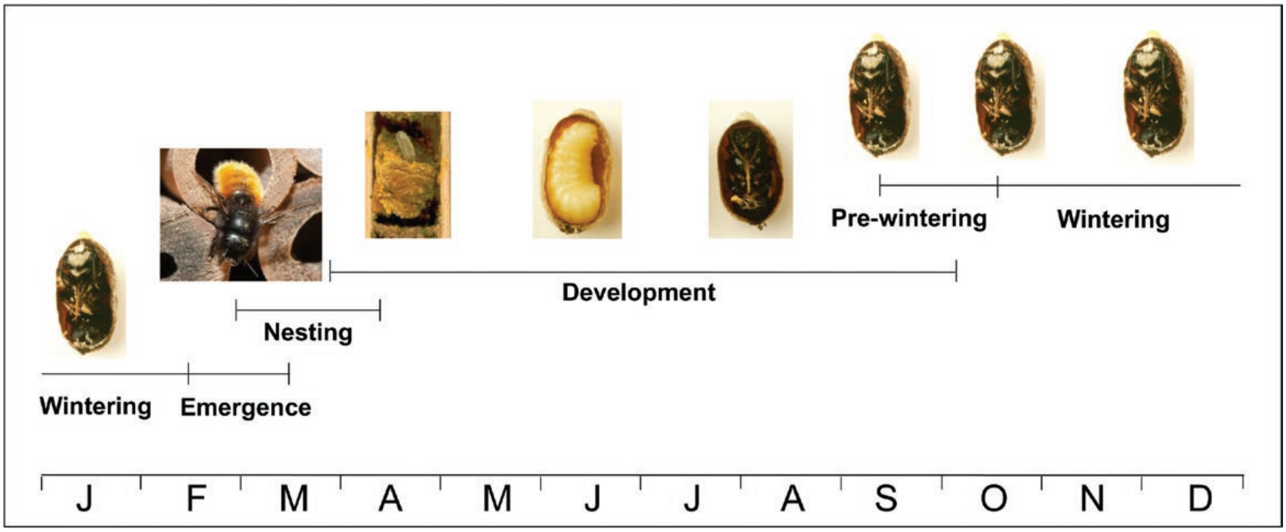

Fig. 3. Life cycle of *Osmia* spp. Photo credits: egg (USDA), prepupa (USDA), pupa (USDA), cocooned adult (USDA), emerged adult (Serena Magagnoli).

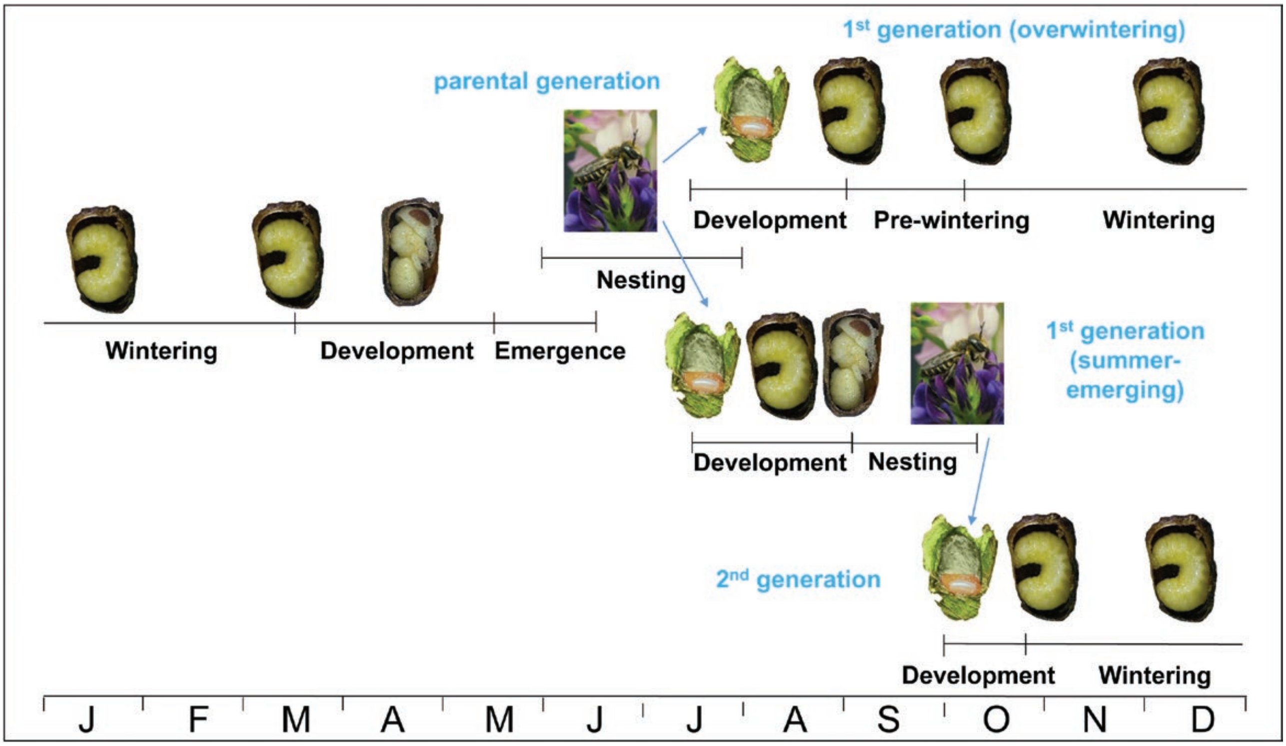

Fig. 4. Life cycle of *Megachile rotundata*. Photo credits: egg (Bill Nye), prepupa (Alan Anderson), pupa (Alan Anderson), adult (Theresa Pitts-Singer).

Table 2. Relative importance (based on expert knowledge) of pesticide exposure routes to honey bees, *Osmia* spp., *Megachile rotundata* and *Nomia melanderi*

Exposure route	Life stage	*A. mellifera*	*Osmia* spp.	*M. rotundata*	*N. melanderi*
Air Particles (Contact)	Adults	4/0/1	4	4	4
	Larvae	0	0	0	0
Nectar (Oral)	Adults	4/3/2	4	4	4
	Larvae[a]	4	4	4	4
Pollen (Oral)	Adults	1/3/1	4	4	4
	Larvae[b]	4	4	4	4
Mud/Soil (Contact)	Adults[c]	0/0/0	2	0	4
	Larvae	0	1	0	4
Wax (Contact)	Adults	1/3/3	0	0	0
	Larvae	4	0	0	0
Water (Oral)	Adults	4/1/1	1	1	1
	Larvae	1	0	0	2
Plant Surfaces (Contact)	Adults	3/0/0	3	4[d]	3
	Larvae	0	0	4	0
Propolis/Resin (Contact)	Adults	3/1/1	0	0	0
	Larvae	0	0	0	0
Honeydew (Oral)	Adults	4/2/0	0	0	0
		-	-	-	-
Gutattion Water (Oral)	Adults	1/1/1	0	0	0
		-	-	-	-

Values are intended for comparisons across taxa (rows), not for within-taxon comparisons (columns).

Designated values rank from 0 (marginal or no likelihood of exposure) to 4 (high likelihood of exposure), for both adults and larval bees. Under each exposure route identified, the primary category of exposure (contact or oral) is specified. For honey bees, relative values are provided for foragers, in-hive bees and overwintering bees, respectively.

[a] All larvae are also subject to contact exposure through nectar.

[b] All larvae are also subject to contact exposure through pollen.

[c] Adult *Osmia* spp. and *N. melanderi* are also subject to oral exposure through mud/soil.

[d] Adult *M. rotundata* are also subject to oral exposure via plant surfaces.

in feeding strategies between honey bees and solitary bees may have consequences on the degradation and dilution of chemical residues found in pollen and nectar that are eventually consumed by the larvae (Table 1).

N. melanderi and *Osmia* larvae may be orally and topically exposed to residues from soil, whereas, *Megachile* larvae, as well as larvae of other solitary bees using plant materials in their nests, may be exposed to residues from leaf surfaces that wick into the provision (Table 2). Larvae of ground-nesting bees such as *N. melanderi* may additionally be exposed to residues in water that are incorporated into the cell through the soil matrix.

To further understand how differences in the natural history of honey bees and solitary bees may have consequences for pesticide exposure, we scored the relative importance of different pesticide exposure routes within each bee group (Table 3). For adults, exposure via air particles (by contact) and via pollen and nectar (oral) are the most important exposure routes (score = 4) in both honey bees and solitary bees. However, other routes of exposure are more important for certain solitary bees than for honey bees. Evaluation of exposure routes indicate that the worst-case exposure scenario for honey bee adults used in current risk assessment schemes may be sufficient to evaluate the potential effects on other bees, except in three cases: 1) the likelihood of exposure via contact with pollen is substantially greater for solitary bees because they collect large amounts of pollen throughout their activity period; honey bees collect pollen only for a limited period of time, and they mix it with nectar and glandular secretions for transportation to the nest; 2) pesticide exposure via soil is more biologically relevant in ground-nesting species such as *N. melanderi* and in species that collect mud such as *Osmia* spp.; and 3) all bee species are susceptible to exposure to pesticides through contact with plant surfaces, but *M. rotundata* adults are also orally exposed because they may ingest small amounts of plant material while cutting leaf pieces.

As for larvae, the exposure routes that are insufficiently covered by the current honey bee risk assessment are: 1) exposure via soil, which is highly relevant in *N. melanderi* and *Osmia* spp., but not in honey bee larvae, which are never exposed to soil; 2) oral and contact exposure via water, which is relevant in *N. melanderi*, because both larvae and their pollen/nectar provision are in direct contact with the cell soil and, therefore, may absorb contaminated water; and 3) exposure via plant surfaces in *M. rotundata* larvae, because their cells are lined with leaf cuttings.

Levels of Pesticide Exposure

Even when different species share similar exposure routes, the levels of exposure may be highly species-dependent. Table 4 provides estimates of nectar and pollen intake for adult honey bees, *Osmia* spp., *M. rotundata* and *N. melanderi*, as well as estimates of the amounts of water, soil and leaves collected by these bees. Of all the nectar collected by adult bees (both honey bees and solitary species), some is regurgitated into the nest, and some is consumed by the foraging bee. For this reason, direct measures of the level of exposure via nectar in adult bees are difficult to obtain. Current approaches rely on estimates of flight duration, energy requirements for sustained flight, amounts of nectar collected, and nectar sugar concentration. Using this approach, EFSA (2012) estimated nectar consumption per foraging trip and day for honey bees (Table 4). These estimates are based on the following information: sugar consumption per unit time during flight (8–12 mg/h) (Balderrama *et al.* 1992), foraging trip duration (30–80 min in nectar foragers, 10 min in pollen foragers) (Winston 1987), proportion of this time

Table 3. Relative importance (based on expert knowledge) of pesticide exposure routes to honey bees, *Osmia* spp., *Megachile rotundata* and *Nomia melanderi*

	Exposure route	Air particles		Nectar		Pollen		Mud/Soil		Wax		Water		Plant Surfaces		Propolis/Resin		Honeydew		Guttation Water	
Bee group	Life stage	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral	Contact	Oral
Apis mellifera	Larvae	0	0	4	4	4	4	0	0	3	0	0	1	0	0	0	0	0	1	0	1
	Adults	4	0	1	4	1	4	0	0	2	0	0	2	3	0	1	1	0	1	0	1
Osmia spp.	Larvae	0	0	4	4	4	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	Adults	4	0	0	4	2	4	2	1	0	0	0	0	3	0	0	0	0	0	0	0
M. rotundata	Larvae	0	0	4	4	4	4	0	0	0	0	0	0	2	0	0	0	0	0	0	0
	Adults	4	0	0	4	2	4	0	0	0	0	0	0	3	2	0	0	0	0	0	0
N. melanderi	Larvae	0	0	4	4	4	4	4	0	0	0	2	2	0	0	0	0	0	0	0	0
	Adults	4	0	0	4	0	4	4	1	0	0	0	0	3	0	0	0	0	0	0	0

Values are intended for comparison across exposure routes within each taxon (rows), not for comparisons across taxa (columns).

Designated values rank from 0 (marginal or no likelihood of exposure) to 4 (high likelihood of exposure), for both adults and larval bees. Under each exposure route identified, separate rankings are provided for contact or oral exposure.

spent flying (80%) (Rortais *et al.* 2005), and 10 foraging trips per day (Winston 1987). In these estimates, sugar content in nectar was assumed to be 15% (w:w). The sugar concentration of nectar loads brought into a honey bee hive ranges from 15 to 65% (Seeley 1985). Therefore, 15% can be considered a realistic worst-case scenario (at higher sugar concentrations bees would require less nectar and consequently would be exposed to lower pesticide levels). There are two problems with these kinds of estimates of nectar consumption per bee. First, each of the five parameters involved in the calculations (i.e., quantity of sugar required for flight, number of foraging trips per day, duration of a foraging trip, fraction of the foraging trip spent flying, and nectar sugar concentration) is highly variable. For example, metabolic rates of honey bees in flight are highly dependent on a number of factors such as ambient temperature, flight speed, load carriage, and bee ontogeny and genetic makeup (Harrison and Fewell 2002). Yet, available measures are usually limited to a small number of individuals and environmental conditions (often from a single study). Second, information on the distribution of values across the observed ranges is often missing. To avoid over-estimates that would result from using the upper ranges of the various parameters, results in Table 4 (nectar foragers: 213 mg/day; pollen foragers: 70 mg/day) are based on the lower estimates of each parameter, and, therefore, should be considered a conservative estimate.

Independent estimates of nectar consumption were calculated by USEPA et al. (2012). USEPA assigned a distribution (either lognormal or uniform) to each of the five parameters involved and then used Monte Carlo simulations to randomly select values from each distribution. The USEPA et al. (2012) analysis also accounted for the energy requirements of bees while at rest and assumed mean sugar content in the nectar to be 30% based on measurements on various plants. Using this approach, median nectar ingestion by nectar foragers was estimated at 292 mg/day (95th percentile: 499 mg/day) (Table 4). For in-hive honey bees (brood-attending nurse bees), nectar consumption was estimated to be at least 113 mg/day (USEPA et al. 2012). This result is based on Rortais *et al.* (2005) and assumes a nectar sugar concentration of 30%. In another study (Decourtye *et al.* 2005), consumption values for newly emerged bees were 22–45 mg/day with a nectar sugar concentration of 500 g/liter. The lower values in the Decourtye *et al.* (2005) study are probably a consequence of holding bees in laboratory cages at 33°C and without brood. Under these (resting) conditions bees are expected to show lower metabolic consumption rates than bees inside a hive. Estimates of sugar (nectar) and protein (pollen) ingestion rates for solitary bees are currently not available. Information on the number of foraging trips per day and number of flowers visited per trip is available for *Osmia* (Bosch 1994, Bosch and Kemp 2001), but information on energy budgets during flight that might be used to calculate sugar consumption are lacking. However, consumption of sugar solution (330 g/liter) in newly emerged *O. bicornis* females maintained under laboratory conditions averaged 59.8 (range: 31.7–104.2) µl/day (Sgolastra et al., unpublished data).

The quantity of pollen consumed per day by honey bees has been estimated at 6.5–12 mg for in-hive worker bees and 0.04 mg for foraging worker bees (Table 4). Solitary bees (especially females) are known to ingest pollen throughout their adult life, but consumption estimates are lacking (Cane 2016; Cane *et al.* 2017). For example, a *N. melanderi* female refills its crop with pollen two to three times per day, and each pollen refill contains *ca.* 34,000 alfalfa pollen grains (Cane *et al.* 2017). Thus, the amount of pollen consumed by *N. melanderi* could be estimated by obtaining weight measurements of fresh alfalfa pollen. A pollen load and a nest provision are *ca.* 200,000 and *ca.* 4.25 million alfalfa grains, respectively (Cane *et al.* 2017).

Daily rates of water collection were estimated by EFSA (2012) for honey bees by assuming that individuals conduct an average of 46 water trips per day with a crop capacity of 30–58 µl. Comparable data are not currently available for solitary bees, but water ingestion has rarely been observed in this group of bees. There is a critical need for research to understand if water is directly taken in by solitary bees (adults and larvae), and if this activity is ubiquitous among all solitary bees or restricted to certain life histories or environmental conditions.

Body surface area of a bee is a useful measure for estimating topical exposure. Using X-ray computed tomography, and the residues found on the body surface after a spray application with a Potter tower, Poquet *et al.* (2014) estimated the body surface area of honey bee workers (Table 4). To our knowledge, this kind of information represents another knowledge gap for solitary bees.

Amounts of mud collected throughout the nesting period in *O. cornuta* are 2.2–4.4 g (dry weight), corresponding to 1.1 g per nest (Bosch and Vicens 2005). In *M. rotundata*, a female can collect up to 4.9 g of leaves throughout her nesting period (Klostermeyer *et al.* 1973). A possible calculation for chronic pesticide exposure (µg of active ingredient/day) via plant surface for the adults of *M. rotundata* is estimated with the formula:

$$Exposure = AR * F * TC * ET$$

Where:

AR = pesticide application rate (µg a.i./cm^2);

F = % fraction of application rate available for transfer to bees (USEPA 1996);

TC = transfer coefficient (cm^2/unit time);

ET = exposure time to foliage (unit time/day).

Estimates of nectar and pollen intake for the larvae of honey bees and non-*Apis* bees are summarized in Table 5. Total nectar consumption by a honey bee worker larva has been estimated by USEPA et al. (2012) based on total food consumed (120 mg) during days 4 and 5 (only royal jelly is consumed in the first 3 d), minus the amount of pollen (5.4 mg), and corrected by the percentage of sugar in honey (45%) and nectar (30%). Daily nectar consumption has been estimated based on rates of food consumption and exponential growth during the last 2 d of larval development (USEPA et al. 2012). Overall pollen consumption of honey bee larvae has been estimated

Table 4. Available estimates of food (nectar and pollen) and water intake and other parameters relevant to pesticide exposure levels in honey bees, *Osmia* spp., *Megachile rotundata* and *Nomia melanderi* adults

Exposure route	*Apis mellifera* (by task)		*Osmia* spp.	*Megachile rotundata*	*Nomia melanderi*
Nectar consumption/foraging trip	Nectar forager[a]:	≥21.3 mg;	?	?	?
	Pollen forager[a]:	≥7 mg			
Nectar consumption/day	Nectar forager[a,b]:	≥213 mg; 292 mg	?	?	?
	Pollen forager[a]:	≥70 mg			
	In-hive bee[b,i]:	≥113 mg; 140 mg			
Pollen consumption/day	Nectar forager[c]:	0.041 mg;	?	?	?
	Pollen forager[c]:	0.041 mg*			
	In-hive bee[d]:	6.5–12 mg			
Body surface area	Worker[e]:	1.05 cm^2	?	?	?
Amount of soil/leaves collected during life span	NR		2.2–4.4 g[g]	≥ 4.9 g[h]	?
Water collected/day	Water forager[f]:	1.4–2.7 ml	NR	NR	NR

Values presented herein are supported by the following references: [a]EFSA (2012); [b]USEPA (2012); [c]Crailsheim et al. (1992, 1993); [d]Rortais *et al.* (2005); [e]Poquet *et al.* (2014); [f]EFSA (2012); [g]Bosch and Vicens (2005); [h]Klostermeyer *et al.* (1973); [i]USEPA (2014).

*Forager pollen exposure is predominantly through contact.

NR: Not relevant.?: Unknown.

Table 5. Available estimates of food intake and other parameters relevant to pesticide exposure levels in honey bee, *Osmia* spp., *Megachile rotundata* and *Nomia melanderi* larvae

Route of exposure	*Apis mellifera*	*Osmia* spp.	*Megachile rotundata*	*Nomia melanderi*
Life span nectar consumption	172 mg[a]; 59.4 mg (sugar)[b]	87 mg[d]	31 mg[e]	?
Daily nectar consumption	Day 4: 56 mg[c]-60 mg[f] Day 5: 117[c]-120 mg[f]	2.9 mg[d]	3.1 mg	?
Life span pollen consumption	1.5–5.4 mg[b]	455 mg[d]	62 mg[e]	?
Daily pollen consumption	2.7 mg[c] Day 4: 1.8 mg[f] Day 5: 3.6 mg[f]	15.2 mg[d]	6.2 mg	?
Wax contact	?	NR	NR	?
Soil contact	NR	?	NR	?
Leaf contact	NR	NR	?	NR

Values presented herein are supported by the following references: [a]USEPA (2012); [b]EFSA (2013); [c]Rortais *et al.* (2005); [d]Independent EFSA (2013) estimates of sugar and pollen consumption in *Osmia* larvae are 54 and 387 mg, respectively; [e]EFSA (2012); [f]USEPA (2014).

NR: Not relevant.?: Unknown.

from 1.5 (maize pollen) to 5.4 (red clover pollen) mg, (Rortais *et al.* 2005), which corresponds to 0.75–2.7 mg of pollen per day.

The ratio of nectar to pollen in the provision of solitary bees varies widely across species. For example, provisions have a higher nectar content in *M. rotundata* (nectar/pollen weight ratio: 2:1 (Cane *et al.* 2011) than in *O. cornuta* (nectar/pollen weight ratio: 1:3, Ladurner *et al.* 1999). Even after accounting for this degree of variability, pollen consumption appears to be higher in solitary bees than in honey bees. In *O. cornuta*, nectar and pollen consumption was estimated by EFSA (2013) based on mean female provision weight (542 mg) (Bosch and Vicens 2002) and the nectar/pollen weight ratio (Ladurner *et al.* 1999). Daily rates of food consumption were calculated assuming a feeding period of 30 d under field conditions (Bosch *et al.* 2008). Nectar and pollen consumption of *M. rotundata* was estimated by EFSA (2012) based on provision weight (90–94 mg), percentage of pollen and nectar weight in the provision (33–36 and 64–67, respectively) (Cane *et al.* 2011), and larval feeding period (10 d) (Kemp and Bosch 2000). Comparable information is not available for *N. melanderi*.

Information needed to estimate the levels of exposure via wax in honey bees, and via soil in *Osmia* spp. and *N. melanderi* is insufficient. However, combined contact and oral exposure via leaves in *M. rotundata* can be possibly estimated again with the formula:

$$Exposure = AR * F * TC * ET$$

Which can be simplified to

$$\text{Exposure} = AR^{*} F^{*} SAi$$

Where:

SAi = internal surface area of nest cell (cm^2)

assuming a worst-case scenario under which pesticide residues of the leaf surface in contact with the pollen-nectar provision are completely transferred (TC = 1) and incorporated by the bee throughout its larval life span.

Discussion

The aim of this paper is to examine differences between life history traits between honey bees and solitary bees that reveal to what extent the current honey bee risk assessment is sufficient for evaluating pesticide exposure in solitary bee species.

Exposure routes adequately addressed by current honey bee-based risk assessment schemes include routes that are more relevant for honey bees than for solitary bees (e.g., honeydew, wax, guttation fluid and water in adults), as well as those that are shared by both bee groups (air particles, nectar in adults). Other routes of exposure show important differences between honey bees and solitary bees, but might be well covered by current honey bee risk assessment schemes, which rely on conservative worst-case scenario assumptions (e.g., that the entire food provision consumed by a larva is contaminated, and that no pesticide degradation occurs over time). However, larval exposure to pollen and nectar is very different between honey bees and solitary bees. First, overall pollen consumption per larva is much greater in solitary bees. Second, in honey bees, pollen and nectar larval exposure is 'filtered' by nurse bees, whereas larvae of solitary bees consume unprocessed food and are, therefore, more directly exposed. Third, honey bee larvae consume food that may have been collected and stored over a longer period of time and, thus, may have been exposed to a long aging period, potentially allowing for greater degradation and dilution of chemicals. Lastly, some solitary bees have longer feeding periods than honey bees. The expected effects of a pesticide (and its degradation products) will vary due to the aforementioned differences in food provisioning and feeding behavior, as well as the chemical properties of the compound.

Some exposure routes relevant for solitary bees are not relevant for honey bees, or represent higher levels of exposure for solitary bees than honey bees, and therefore are not sufficiently addressed by the current honey bee risk assessment paradigm. One particularly important route for solitary bees is exposure via soil, including contact with the soil itself, as well as contact and ingestion of water from the soil. This route of exposure is obviously very important for both adults and larvae of species nesting underground. *N. melanderi* would be a good surrogate solitary bee to study this exposure route, but this species is only available in limited numbers in small areas of the Western United States. The three *Osmia* species considered in this review use mud to build their nest cells and, therefore, are also exposed to soil contaminants, although to a lesser extent than ground nesting species. These *Osmia* species could be used as surrogates for ground-nesting bees until a better alternative becomes available. Plant surfaces are an exposure route relevant to both leaf-cutting bees and other solitary species that use plant material to build their nests (e.g., masticated leaf pulp in many *Osmia* species; plant pubescence in *Anthidium* species (Hymenoptera: Megachilidae)). As such, *M. rotundata* would be a good species for studies that quantify this route of exposure. Importantly, soil and mud are only two of the various natural products used by solitary bees to construct and line their nests. Some species use resin (e.g., *Heriades*, some *Megachile* and some Anthidiini; Hymenoptera: Megachilidae), and some use floral oils (e.g., some *Centris*; Hymenoptera: Apidae). To our knowledge, potential levels of contamination in these matrices have not been investigated.

There is currently insufficient information on adult exposure via pollen in solitary bees compared to honey bees. However, it is known that solitary bee females transport and manipulate large amounts of unprocessed pollen during foraging, flying to the nest, and provisioning throughout their life time. Honey bees, on the other hand, only collect pollen towards the end of their life span, and they mix it with nectar and glandular secretions for transportation. The three solitary bee taxa considered, *Osmia* spp., *M. rotundata* and *N. melanderi*, would be good representatives of most solitary bees to cover this exposure route. In addition to pollen and nectar, an estimated 1.4% of solitary bee species consume floral oils (as adults and/or as larvae) (Buchmann 1987). This route of exposure is not experienced by honey bees or any of the three solitary bee taxa proposed here as surrogate species.

Our review identifies some important gaps in knowledge relating to pesticide exposure levels for solitary bees. Estimates of nectar and pollen consumption in adult *Osmia* spp., *M. rotundata* and *N. melanderi*, in particular, should become a research priority. These estimates could be obtained following the same approach used with honey bees. At least for *Osmia* spp. and *M. rotundata*, most of the parameters needed to calculate pollen and nectar consumption are available, but measures of energetic expenditure during flight are lacking. Importantly, these calculations should account for the high level of variability associated with these measures (Harrison and Fewell 2002). Quantification of the levels of exposure via soil and plant surfaces are also lacking in solitary bees. We provide an approach for the estimation of these levels in *Osmia* spp. and *M. rotundata*, respectively, but further studies are needed to measure some of the parameters involved.

Table 6 shows a comparison of the three solitary bee taxa proposed as model species for risk assessments. *N. melanderi* is the only representative species of the most common nesting behavior found

Table 6. Features of potential solitary bee surrogate taxa for pesticide risk assessment

Management consideration	*Osmia* spp.	*Megachile rotundata*	*Nomia melanderi*
Availability (commercial populations)	+	++	-
Availability (geographical distribution)	North America, Europe, Eastern Asia	North America	Small area in North America
Availability (seasonality)	3–4 mo (spring)	4–5 mo (summer)	4–5 mo (summer)
Rearing and management	+	+	-
Representative of other bees species	-/+ (above-ground-nesting, soil)	- (above-ground-nesting, leaves)	++ (ground-nesting)
General background information	+++	+++	+
Ecotoxicological information	++	+	-

in solitary bees. However, its use as a surrogate species is hindered by its limited availability, its restricted geographical range and the very particular type of soil required for its nesting. For these reasons, we see the study of the basic biology and the establishment of rearing methods for ground-nesting species with more generalist nesting habits as a research priority. The highly speciose and widely distributed genus *Andrena* (Hymenoptera: Andrenidae) could be a good alternative. Although not commercially available, the hoary squash bee (*Peponapis pruinosa* (Say), Hymenoptera: Apidae) is a ground nesting species that is geographically widespread in North America (López-Uribe *et al.* 2016). The ecology and behavior of this specialist pollinator of cucurbit crops (e.g., pumpkin, squash, and watermelon) is comparatively well studied (Hurd *et al.* 1974, Willis and Kevan 1995, Julier and Roulston 2009), with an increasing focus on the potential impacts of pesticide exposure (e.g., Stoner and Eitzner 2012, Health Canada 2014). Recent success establishing populations of nesting females in enclosures (DSW Chan and NE Raine, personal communication) increases the potential of this species for ecotoxicological tests under semifield and field conditions, although utility for laboratory studies remains unknown.

As for cavity-nesters, both *Osmia* spp. and *M. rotundata* are good surrogate species. *M. rotundata* is commercially available in large numbers, but only in North America. *Osmia* spp. are available in smaller numbers, but are more widely spread, and their use as commercial pollinators is increasing. *Osmia* spp. have been suggested as model solitary bees for risk assessment in Europe (EFSA 2013), where test protocols are under development (Roessink *et al.* 2015), and information on their ecotoxicology is accumulating.

Our review of the life history traits of solitary bees reveals that both *Osmia* spp. and *M. rotundata* meet criteria for being practical surrogates for semifield and full-field toxicity tests. Semifield tests are typically conducted with small honey bee colonies in screen cages or plastic tunnels planted with a pollinator-attractive crop such as oilseed rape (*Brassica napus*, Brassicaceae) or lacy phacelia (*Phacelia tanacetifolia*, Boraginaceae). However, even for a small colony, it is challenging to provide sufficient floral resources in an enclosure, and honey bees tend to become stressed in these conditions. By contrast, the behavior of solitary bees is much less affected by confinement. Due to their more localized foraging range, lower food requirements and shorter life span, it is relatively easy to provide sufficient floral resources. Nesting activities of individually-marked females can be monitored, and several variables related to individual reproductive success can be measured (Tepedino and Torchio 1982, Sugiura and Maeta 1989, Peach *et al.* 1995, Ladurner *et al.* 2008, Sandrock *et al.* 2014, Artz and Pitts-Singer 2015, Sgolastra *et al.* 2016). The possibility to monitor individual females throughout their activity period also facilitates the observation of behavioral responses, and, therefore, the detection of sublethal effects. Although both *Osmia* spp. and *M. rotundata* females show preferences for certain pollen types, under confined conditions, they readily collect a variety of pollen/nectar sources (including lacy phacelia and/or oilseed rape in *Osmia* spp.) on which progeny successfully develop. The short foraging ranges and the possibility to measure a number of endpoints related to reproductive success at the individual level (Bosch and Vicens 2006), make these species also appropriate for field tests. However, in this case, the pollen preferences of each species (fruit trees (Rosaceae) for *O. cornuta*, *O. lignaria* and *O. cornifrons*, oak (Fagaceae) for *O. bicornis*, and legumes (Fabaceae) for *M. rotundata*), should be taken into account to ensure that females do most of their foraging in the test field.

In addition to exposure routes and levels of exposure, other factors differ between honey bees and solitary bees in response to pesticides. These factors include the differential sensitivity to pesticide exposure among different bee species (Arena and Sgolastra 2014, Uhl *et al.* 2016, Sgolastra *et al.* 2017). These differences may be due to variability in specific detoxification capacities, and also to differences in body size. Mass-specific metabolic rates increase with decreasing body size. Thus, for a given pesticide concentration in nectar or pollen, smaller bees are expected to ingest larger amounts of pesticides per body mass unit. Similarly, the ratio of body surface area to body volume increases with decreasing body size. Therefore, smaller bees are also likely to be subjected to higher levels of contact exposure per unit of body mass. Future research is needed to address differences in sensitivity to pesticides among bee species, including honey bees, bumblebees, and solitary bees. These studies will be essential not only to detect differences in sensitivity among species but also to establish factors that can be used to extrapolate pesticide toxicity from honey bees to other bee species (Arena and Sgolastra 2014, Thompson 2016). Ultimately, exposure cannot be disassociated from effects (toxicity) in risk assessment, and integration of these two areas of knowledge is imperative to assure bee safety in managed environments.

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