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Review article

Cavity-nest boxes for solitary bees: a century of design and research

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Abstract – A variety of solitary bee species that naturally nest in wood and plant stems aboveground also readily accept nest boxes, which are human-made devices that aggregate these nesting conditions. Nest boxes are sheltered bundles of hollow plant stems, bamboo or reeds, and holes drilled into wood or cavities made of other materials such as glass or polystyrene. In this paper, I examine the best practises in nest box material selection and construction, and the use of nest boxes to address four basic objectives related to our understanding of bee biology and enhancement of pollination services. A variety of materials and cavity dimensions are included in nest boxes that are used to monitor local bee diversity or to address fundamental questions in community ecology and environmental change. Others examine bee biology, physiology and behaviour that use nest boxes to obtain bees for further experimentation. The majority of studies use nest boxes in agricultural landscapes and in alternative pollinator management; these studies improve nest box design for target bee species to augment their numbers. Continued design and data sharing, as well as the refinement of nest box construction and deployment for specific objectives, will ensure they remain useful tools for bee science, conservation and alternative pollinator management.

cavity-nesting bees / alternative pollinator management / wild bees / biodiversity / agroecosystems / trap nest / bee hotel / pollinator garden

1. INTRODUCTION

Different survey methods and sampling tools are available to study wild bees in their natural habitats. Some of these techniques sample broadly, such as pan traps (Kearns and Inouye 1993; Gezon et al. 2015), window traps (Rubene et al. 2015), Malaise traps (Malaise 1937; Darling and Packer 1988), sweep netting (Richards et al. 2011) and observations of visitors to flowers (Deguines et al. 2016). Other survey methods target certain taxa by creating analogues of their nesting habitat. A few examples include Fussell and Corbet (1992) making wood and clay-brick nest sites for bumble bees (1.5 % colonized of N = 654 nests set out over 3 years), Sheffield et al. (2014) setting out overturned flower pot saucers ('nesting saucers') for *Osmia inermis* (Zetterstedt) which nest at the surface of the ground under stones (10 % colonized of N = 60), and Silva et al. (2014) using plastic bottles treated with propolis and wax to attract nesting colonies of stingless bees (five species, 3.5 % colonized of N = 720 over 2 years).

Another method having far greater success in attracting a target community of bees are nest boxes (also 'trap nests', 'bee condos', 'bee hotels', 'bee boxes') (Maeta and Kitamura 1964; Krombein 1967; Bosch and Kemp 2002; Tylianakis et al. 2005; Westphal et al. 2008; Holzschuh et al. 2009; Barthélémy 2012; MacIvor et al. 2014). These bee species are solitary and in each nesting cavity, a reproductive female will construct brood cells in a linear series

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from the back of the tunnel to the front. Depending on the species, she will partition each brood cell using materials that are taxon-specific and can include cut pieces of leaves, tree resins, mud or pebbles (Krombein 1967; Cane et al. 2007). As a group, these bees are referred to as cavity nesters and naturally nest in hollow plant stems, cavities in wood or other structures above ground, including those in human-made infrastructure such as nail holes (Raw 1972) and cracks in mortar between bricks (Blochtein and Wittmann 1988). As central place foragers, once a suitable nesting site is found, bees will forage within a range around this site, provisioning the nest with the various resources they seek (Gathmann et al. 1994; Peterson and Roitberg 2006). As a result, identifying the nesting location of a bee provides information on its resource use and the environment in which it is living, not just where it is passing through (Grixti and Packer 2006).

Nest boxes have been used to observe and study cavity-nesting bees for more than a century and initially were largely inspired by observations of bees constructing nests in naturally occurring materials. In 1918, the naturalist and writer Jean-Henri Fabre described the nest building activities and homing abilities of mason bees nesting in the straw thatching that formed his roof (Fabre 1918). Balfour-Browne's (1925) 'bee wall' used bricks to hold elderberry stems and glass tubes in place to survey local cavity-nesting bees in his residential garden. Over time, different materials were tested for field durability, ease of maintenance and use by different species, including glass tubes (Hartman et al. 1944), plant stems (Rau 1937; Hicks 1937; Frost 1943) and holes drilled in wooden blocks (Peck and Bolton 1946; Bohart 1955). These early investigations and field observations led to the use of nest boxes in agriculture as a means of augmenting solitary bee pollinators of flowering crops (Bohart 1955; Medler 1958; Fye 1965a; Raw 1972; Maeta and Kitamura 1974; Torchio 1976).

Nest boxes today are made from a wide range of materials with no two designs the same. Many are small and sold in stores to gardeners, ready-made or as DIY projects. Those used in agriculture are usually much larger than those in home gardens or public spaces (Wilson et al. 1999). In all cases, basic features of a nest box include a sheltered set of a few to several hundred nesting cavities made of porous materials such as wood, cardboard or polystyrene, opened at one end only, and (optimally) about 15–20 cm in length and an internal diameter of <1 cm.

Studies that use nest boxes can be grouped in two ways: (1) those intending to study bees in a natural setting and (2) those augmenting numbers to obtain bees for pollination services or for experimental research. In the first example, using nest boxes to study bees has led to a significant understanding of key aspects of their ecology, diversity, nesting, and foraging biology, as well as how environmental factors impact their populations. Using nest boxes to study how bees respond to landscape changes, such as those resulting from urbanization (MacIvor and Packer 2015; Fortel et al. 2016) or climate change (Forrest and Thomson 2011) could be extrapolated to impacts experienced by all bees (Westphal et al. 2008). In these studies, nest boxes are a key component of the experimental design; for example, researchers consider its design, how many and where they are placed to best answer a set of questions. In the second example, nest boxes are simply tools used to increase the number of bees for pollination services or for further experimentation ancillary to the nest box used to obtain the bee specimens. In each example, nest boxes play an important role but require different designs, materials and implementation.

In this paper, I identify best practises for material selection and construction of nest boxes for cavity-nesting bees and recommend design criteria to address four primary objectives. Two of these objectives require nest boxes to monitor bees in their environment and two utilize nest boxes to enhance numbers of bees for management or further experimentation. A secondary goal in surveying the literature on this topic is to highlight to readers the broad applications of nest boxes as tools in the study of bees and in bee education, to enhance target species for pollination and engage local communities with wild (e.g. non-honey bee) pollinators.

2. DESIGN CONSIDERATIONS

A variety of materials are used to construct nest boxes to house cavity-nesting bees (see https://resonatingbodies.wordpress.com). Many factors impact the effectiveness of nest boxes including the material and dimensions (length, width) of the nesting cavities, as well as pattern and colour of the nest box, and its positioning, orientation and the timing of placement in the habitat studied (Krombein 1967; Bohart 1972; Budrienė et al. 2004; Gaston et al. 2005; Everaars et al. 2011). As a result, there is no general consensus on the 'best' nest box and researchers tend to use their own designs based on regionally available materials (Dicks et al. 2010). In general, the materials used to make nest box cavities can be delineated into four main types: (1) holes drilled in wood; (2) bamboo, reeds and hollow plant stems; (3) cylindrically rolled paper or cardboard tubes and (4) artificial materials such as glass, polystyrene or other plastic (Table I).

2.1. Nesting materials

Wooden nest boxes, especially those set out over multiple seasons (Fairey and Lieverse 1986), are generally more attractive to bees than any other materials (Figure 1), including vermiculite boards (Martins et al. 2012) and polystyrene (Torchio 1984), but rarely are the type or species of wood used identified in studies. Pine (*Pinus*: Pinaceae) is most commonly identified and other wood types used include fir (*Abies*: Pinaceae) (Coville and Griswold 1984), aspen (*Populus*: Salicaceae) (Peck and Bolton 1946), cedar (*Thuja*: Pinaceae) (Jennings and Parker 1987), oak (*Quercus lobata* Née: Fagaceae) (Barthell et al. 1998), and redwood (e.g. Torchio 1981).

Another common method for constructing nest boxes is to bundle together hollow stems, or stems having soft pith which is excavated by certain bee species (Figure 1). These stems range considerably in internal diameter (2 to 20 mm as in Gathmann et al. 1994; Tscharntke et al. 1998; Matsumoto and Makino 2011). 'Bamboo' is used generically to describe nesting cavities in numerous papers without a clear indication of which species was used (Figure 1a). 'Reed' is also used often to describe the source of nesting cavities, and the dominant reed identified to species is *Phragmites australis* (Cav.) Trin. ex Steud. (Family: Poaceae), with one other reed species used *Saccharum spontaneum* L. (Poaceae) (Kessler et al. 2009). Three globally invasive plant species, *Phyllostachys aurea* C.R. Riviere (Poacaeae) (Musicante and Salvo 2010), *Arundo donax* L. (Poaceae) and *Fallopia japonica* (Houtt.) Ronse Decr. (Polygonaceae) are also used and collecting them for nest boxes could contribute to management and outreach (Table II). Among hollow and pithy stems and branches, the most commonly used are elderberry (*Sambucus*: Adoxaceae) (Hicks 1937; Cane et al. 2007), raspberry and blackberry (*Rubus*: Rosaceae) (e.g. Hicks 1937; Danks 1971) (Table II).

Extruded polystyrene nesting boards can support large populations of solitary bees and have been developed for managing them for pollination services in agricultural systems (Rothschild 1979; Kemp and Bosch 2001; Radmacher and Strohm 2010, 2011) (Figure 1). Richards (1978) found polystyrene supported higher numbers of viable offspring than other nest box materials including paper and cardboard tubes. Brood cells in boards can be mechanical harvested and easily cleaned and this innovation has made the production of *Megachile rotundata* (Fabricius) a profitable industry and a model system for other cavity-nesting bee species managed as alternative pollinators.

2.2. Nesting cavity dimension

Nesting cavity length and diameter vary widely between studies, and choosing the correct dimensions can improve colonization by the species of interest (Fye 1965a; Krombein 1967). Among studies that report nesting cavity diameters, these range from as low as 2–3 mm to as high as 25 mm (e.g. Kessler et al. 2009). Bees select cavities that match their own body width to ensure the brood cells fit tightly and reduce pathways for parasites to access brood deeper in the nest. For example, studies interested in small cellophane bees (*Hylaeus* spp.) should use diameters between 1 and 4 mm, whereas diameters between 5 and 8 mm should be used for medium-sized bees

Table I. Most common materials used to create nest boxes for cavity-nesting bees

Cavity material	Description	Opportunities	Limitations
Wood	Cavities drilled into a solid block of wood or a series of identically sized wood planks of no more than a few centimetres in width all with drill holes along one exposed side and planks bound together	Highly attractive to bees. Cavities in planks bundled together are easily opened, cleaned and reused (Cane et al. 2011). Clear acetate sheets in between planks used so brood can be inspected midseason without disruption (Hallett 2001). Paper rolled into cavities is used so that nests can be removed with minimal cleaning required for reuse, but colonization is less	Cavities drilled directly into solid pieces of wood cannot be opened or easily cleaned, as a result are less useful year-over-year. Paper rolled into cavities reduce colonization because the inner walls are not stabilized inside the cavity
Bamboo, reeds, hollow and pith-bearing stems	Cut, dried, bundled and protected with a nest box enclosure. Stems are closed at one end with an internal diameter of 20 mm or less. Pithy stems are used less often but can attract specific bee taxa	Used often because they are widely available and free to collect. Some well documented stem options, such as *Phragmites australis* and *Phyllostachys aurea* are globally invasive and nest boxes can be built to contribute to controlling spread	Some stems can be difficult to split because of non-linearity and irregularity in the stems selected. Cracks in stems permit parasites and bees will avoid these stems
Cardboard paper tubes	Corrugated cardboard strips or rolled tubes can be custom made for consistency in tube length, wall thickness and internal cavity diameter (O'Neill and O'Neill 2010)	Thicker cavity walls reduce ability of parasites to bore through (Stubbs et al. 1994). Rolled tubes can be opened by unravelling them from one end for easy removal of brood cells for further study (Figure 1)	Extra work needed to open, replace and maintain individual cavities. Can decompose or easily destroyed by wildlife if unprotected. Bundled in milk cartons (Sheffield et al. 2008a), PVC pipe (MacIvor et al. 2014), wooden boxes (Everaars et al. 2011)
Glass	Glass tubes are blown with thin internal diameters and plugged at one end with a stopper. Clear glass tubes are kept in enclosures to minimize light penetration	Glass tubes were used early in the development of nest boxes because manipulation of other materials had not been invented and they permitted viewing of nest building behaviour (Balfour-Browne 1925; Hartman et al. 1944; Frohlich and Parker 1983)	Expensive and much less available versus drilled wood and plant stems. Easily broken, not permeable and moisture promotes mould that increases mortality (Medler and Fye 1956)
Plastic	Any form of plastic-based product manipulated into cavities of the dimensions used by nesting bees (Levin 1957). Extruded polystyrene boards are used often in management of *M. rotundata*	Uncommon; include drinking straws (Stephen 1961; Sekita and Yamada 1993), 'plastic tubes' (Gerber and Klostermeyer 1970), rubber tubing (Medler 1965), corrugated plastic sheets (Stephen and Every 1970) and polystyrene boards (Rothschild 1979)	Not permeable so mortality is high (Fye 1965a). Plastic straws showed up to 90% mortality in *M. rotundata* due to mould (Stephen and Every 1970)

Figure 1. Different nest boxes and materials used to construct them. **a** , **b** Bamboo reeds (**a** photo credit: Stephen Humphreys). **c** , **d** Drilled holes in wood blocks. **e** , **f** Wood cartridges. **g** Cardboard paper tubes. **h** Extruded plastic tubes.

(e.g. *Megachile* or *Osmia* spp.). Nesting cavity diameter can influence bee sex ratios, such that less-desirable nest sizes result in a reduction in female offspring (Stephen and Osgood 1965). Studies investigating the consequences of an altered sex ratio on population dynamics and resulting pollination levels use nest cavities of varying diameters so that these comparisons can be made (Krombein 1967; Rothschild 1979; Longair 1981).

In general, nesting cavity lengths should be approximately 150 mm, but some range up to 200–300 mm, and others much shorter. For example, 50 mm in Paini (2004), 58–85 mm in Gazola and Garófalo (2003), 70 mm in Zillikens and Steiner (2004), 75 mm in Wilson and Holway (2010), 100 mm in Kuhn and Ambrose (1984) and 115 mm in Vinson et al. (2010). Lengths shorter than 150 mm have been linked to increases in male production (Gerber and Klostermeyer 1970; Gruber et al. 2011), but others have found no effect (Jay and Mohr 1987). Seidelmann (2006) attributes the bias to females provisioning less costly offspring (e.g. males) nearer the nest entrance where the risk of parasitism or nest predation is highest.

2.3. Patterning and colour

Patterning and colouration of the area around the nest box entrance can improve nest recognition when multiple suitable cavities are available (Krombein 1967; Fauria and Campan 1998; Fauria et al. 2004; Guédot et al. 2006; Lee-Mäder et al. 2010). The colour of the nest box entrance can improve bee productivity: Artz et al. (2014) found that *Osmia lignaria* provisioned 1.4 and 2.6 times more females in nest boxes that were light blue compared to orange- and yellow-coloured nest boxes. Excess patterning can confuse bees at the nest entrance too; for example, Guédot et al. (2007) found increasing disorientation at nests with high levels of contrasting colours and patterns. Disorientation can extend the duration of return foraging bouts, reducing the time dedicated to provisioning offspring and nest building, and so it is recommended that some patterning and colour be used on the exteriors of the nest box (Figure 1).

Table II. List of plant species whose stems are collected to construct nest boxes to study cavity-nesting bees (and wasps)

Species	Family	Common name	Example reference	Example taxa
'Bamboo'	–	'Bamboo'	Rubene et al. (2015)	Multi
'Reed'	–	'Reed'	Krewenka et al. (2011)	Multi
Phragmites australis (Cav.) Trin. ex Steud.	Poaceae	Common Reed	Tscharntke et al. (1998)	Multi
Saccharum spontaneum L.	Poaceae	Kans grass	Kessler et al. (2009)	Multi
Phyllostachys aurea Riviere & C.Riviere	Poaceae	Golden Bamboo	Musicante and Salvo (2010)	*Trypoxylon* *
Arundo donax L.	Poaceae	Giant Cane	Tylianakis et al. (2006)	Multi
Fallopia japonica (Houtt.) Ronse Decr.	Polygonaceae	Japanese knotweed	Klein et al. (2004)	Multi
Ricinis communis	Euphorbiaceae	Castor	Abrol et al. (2015)	Megachilidae
Xanthorrhoea minor R.Br.	Xanthorrhoeaceae	Grasstree	Bull and Schwarz (1996)	*Exoneura bicolor*
Sambucus sp.	Adoxaceae	Elderberry	Frohlich and Parker (1983)	*Megachile pugnata*
Rubus fruticosus L. sens.str.	Rosaceae	Blackberry	Danks (1971)	Multi
Rubus strigosus Michx.	Rosaceae	Raspberry	Vickruck and Richards (2012)	*Ceratina*
Erythrina poeppigiana (Walp.) O.F. Cook	Fabaceae	Dadap	Eickwort (1967)	*Chilicola ashmeadi*
Dipteryx alata Vogel	Fabaceae	Baru Tree	Loyola and Martins (2008)	Multi
Melia azedarach L.	Meliaceae	Chinaberry	Fye (1965a)	Multi
Conium maculatum L.	Apiaceae	Poison Hemlock	Rust et al. (1974)	*Osmia nigrifrons*
Ailanthus altissima (Mill.) Swingle	Simaroubaceae	Tree of Heaven	Tormos et al. (2005)	Crabronidae*
Rhus typhina L.	Anacardiaceae	Sumac	Koerber and Medler (1958)	Multi

*Refers to studies that examine cavity-nesting wasps

However, more work is needed that examines the mechanisms behind nest recognition and associated improvements in productivity.

2.4. Placement

Local environmental factors impact the type and number of colonizers in nest boxes and so, placement requires careful attention to the surroundings (Gaston et al. 2005). Securing the nest box so that it does not move or fall over (e.g. a fence, pole, shed wall) is critical. Nest boxes not visited often also benefit from protective screens over the entrance to guard against attacks by birds or other wildlife (Krunic et al. 2005). In an urban environment, Everaars et al. (2011) found more colonization of the target species *Osmia bicornis* (Linnaeus) in nest boxes attached to balconies and carport walls versus those attached to trees and shrubs. Another study found colonization of nest boxes on green roofs declined with increasing building height suggesting there are vertical limitations to where a nest box can be set up and colonization expected (MacIvor 2015). Nest boxes are also colonized less if facing prevailing winds (Martins et al. 2012). In general, placement is best facing south east and above the flower line so that the entrance is not blocked by vegetation.

3. MOTIVATIONS

3.1. Objective 1: to assess bee diversity and populations in natural settings

Nest boxes can be constructed in a standardized way, and set up *en masse* to monitor regional diversity, mortality and natural history in both space and time (Tscharntke et al. 1998; Loyola and Martins 2006; Sheffield et al. 2008a; Gazola and Garófalo 2009; Forrest and Thomson 2011; Fabian et al. 2014). Nest boxes used to sample diversity of bees should include cavities with different internal diameters to accommodate species of different body sizes (O'Neill and O'Neill 2013). Sampling diversity within an environment or along a gradient should use many nest boxes to cover as wide a sampling area as possible, rather than single large nest boxes that are cumbersome. Access to larva may be required and so, designs that can easily be opened (wood panels) or are inexpensive so that they can be destroyed (cardboard/paper) are best.

Nest boxes allow researchers to assess numerous aspects of bee biology to interpret environment conditions; this includes pollen (Abel and Wilson 1998; MacIvor et al. 2014; Eckhardt et al. 2014) and nectar preferences (Burkle and Irwin 2009; Cane et al. 2011), as well as the spread of parasites (Paern et al. 2015), introduced species (e.g. *Osmia tanneri* Sandhouse: Torchio 1984) and invasive ones (e.g. *Megachile sculpturalis* Smith: Mangum and Sumner 2003). Saturating habitats with nest boxes can help monitor community change, range expansions or track target species. Colonized nest boxes can be moved between sites, altered in orientation or positioning, or bee cocoons 'seeded' in or removed (Fründ et al. 2013). The degree of manipulation and flexibility in studies using nest boxes allows for simple, low-cost and data-rich sampling to address questions in community ecology (Steffan-Dewenter 2002; Sheffield et al. 2008a; Westphal et al. 2008; Schüepp et al. 2011; Steckel et al. 2014). Most studies are carried out over 1 or 2 years but there are several that sample over 3+ years. For example, a 17-year study of change in nest box colonizers with the introduction of the Africanized honey bee in Mexico (Roubik and Villanueva-Gutierrez 2009), and another that monitored *Osmia rufa* off-and-on over 27 years in Ukraine (Ivanov 2006). Nest boxes can provide insight into multitrophic interactions to address bee conservation of species and the complexity of their needs (Tylianakis et al. 2006; Veddeler et al. 2010; Ebeling et al. 2012; MacIvor 2016).

Nest boxes that contain many cavities provide opportunities to increase the numbers of observations and replication in studies that examine bee behaviour (Trostle and Torchio 1994). Traditionally, studies that monitor activity at natural nesting cavities of bees are dependent on the search effort required of researchers to locate sufficient numbers of nests (e.g. Scott 1993). For example, Dobson and Peng (1997) collected nests of *Chelostoma florisomne* (Linnaeus) from dried stems of *Phragmites* comprising a thatched roof on an old farm in rural Sweden. Others document the nests of bees in the stems of different plants, such as *Ceratina mikmaqi* Rehan & Sheffield and *Ceratina calcarata* Robertson in *Dipsacus fullonum* L., *Rubus strigosus* Michx. and *Rhus typhina* L. (Vickruck and Richards 2012) or *Augochlora esox* (Vachal) in the bromeliad, *Aechmea lindenii* (E. Morren) Baker (Zillikens et al. 2001). Natural history observations and reporting on the natural nesting materials used by bee species is critical to inform best practises for nest box design and implementation.

Nest boxes can also be used as the (nesting) point of reference to quantify the time spent foraging (Klostermeyer and Gerber 1969) or the minimum and maximum foraging distances travelled to a resource from the nest (Gathmann and Tscharntke 2002). Zurbuchen et al. (2010a) studied maximum flight distances using nest boxes and found they are considerably shorter and within dozens of meters of the nest for small bodied species. Manipulating the location or distance of nest boxes from marked resources can determine maximum foraging distances and help interpret landscape factors that support wild bee foraging requirements (Williams and Tepedino 2003). Marking and recapturing bees from nest boxes can be used as a method to examine floral availability or preference of different taxa

(Steffan-Dewenter and Schiele 2004; Zurbuchen et al. 2010b; Yamamoto et al. 2014).

3.2. Objective 2: to examine environmental factors that impact their populations

In studies that use nest boxes to explore how environmental factors impact wild bees, it is recommended that standardized nest boxes that are easily replicated and durable for deployment over large geographic areas are used. Nest boxes should contain cavities with differently sized widths and that can be replaced so that sufficient and diverse nesting options are not limited to cavity-nesting bees throughout the entire sampling period. Durability in nesting material and the nest box exterior is key to withstand different and extreme environmental conditions.

Studying cavity-nesting bees with nest boxes has led to findings on how different environmental factors impact pollinators (Schüepp et al. 2011) and species diversity (Tscharntke et al. 1998; Tylianakis et al. 2007; Dorado et al. 2011; Fabian et al. 2013). Colonization and diversity in nest boxes along environmental gradients can be studied to understand the impacts of landscape change on bee communities (e.g. wetlands: Moroń et al. 2008; forest canopy cover: Sobek et al. 2009; heavy metal contamination: Moroń et al. 2012; mass-flowering agricultural crop: Diekötter et al. 2014; urban land use: Fortel et al. 2016) as well as the effects of fragmentation (Klein et al. 2006; Krewenka et al. 2011; Coudrain et al. 2014). Landscape changes have been linked to foraging and diet inefficiency in cavity-nesting bees (Levin and Haydak 1957; Raw 1974; Williams 2003) and increasing interactions with parasites (Münster-Swendsen and Calabuig 2000; Kruess and Tscharntke 2002). For example, Peterson and Roitberg (2006) found a decline in resources allocated to offspring in *M. rotundata* in nest boxes at further distances from a large floral patches.

Correlating local and landscape environmental conditions with nest box colonization and diversity can improve our understanding of how land use and planning decisions impact bees and pollination services (Steffan-Dewenter and Schiele 2008; Pereira-Peixoto et al. 2014). This might include proximity to and size of hedgerows, buffer strips, forest patches and other nearby habitat (Steffan-Dewenter 2002; Krewenka et al. 2011) that have landscape management implications and can be encouraged through policy, programs and incentives (Byrne and Fitzpatrick 2009).

3.3. Objective 3: to augment bee abundance for pollination services

A goal of many studies is to enhance the number of bees for pollination services of agricultural crops (Bohart 1972; Bosch and Kemp 2002; Jauker et al. 2012; Sedivy and Dorn 2014). Once a target bee species has been identified, its nesting preferences must be carefully researched to make nest boxes attractive habitat and enhance brood production (Parker and Frohlich 1983; Torchio et al. 1987; Wei et al. 2002; Wilkaniec et al. 2004; West and McCutcheon 2009). When populations have been established, nests can be moved around to target crops or regions of interest (Bosch and Kemp 2002). 'Seeding' bees into nest boxes can fast track the uptake by target species in order to build up large numbers (e.g. Williams and Kremen 2007). Several wild bees are successfully managed for agricultural applications using nest boxes including, for example, *Osmia cornifrons* (Radoszkowski) (Maeta and Kitamura 1974), *O. bicornis* (Gruber et al. 2011), *O. lignaria* (Bohart 1972; Philips and Klostermeyer 1978), *O. cornuta* (Bosch and Kemp 2002), and *M. rotundata* (Bohart 1972; Fairey et al. 1989; Pitts-Singer and Cane 2011).

Nest boxes are used to manage bees and augment their numbers for pollination of a multitude of crops including alfalfa (Wightman and Rogers 1978; Bosch and Kemp 2005), carrot (Tepedino and Frohlich 1984), onion (Giejdasz et al. 2005), rapeseed (Teper and Bilinski 2009), coffee (Laliberté and Tylianakis 2010), almond (Torchio 1981; Bosch 1994), blueberry (Stubbs et al. 1997; Sampson et al. 2004), cherry (Bosch et al. 2006), prune (Torchio 1976), acerola (Pina and Aguiar 2011; Magalhaes and Freitas 2013), apple (Wei et al. 2002; Sheffield et al. 2008b; Gruber et al. 2011) and passion fruit (Junquiera et al. 2012; Yamamoto et al. 2014). Fields containing other economically important plants have been surveyed too; for example, O'Neill et al. (2010) studied feral populations of *M. rotundata* at a wildflower seed farm. Multi-crop systems have been shown to harbour a greater diversity of cavity-nesting bees in nest boxes compared to monocrop systems (Banos-Picon et al. 2013).

There are many facets of nest box design to consider when the aim is to increase the abundance of target bee species (Kim 1992; Bosch and Kemp 2002). Nest boxes should be large and to improve offspring production should not be limited in the number of nesting cavities available (Levin 1957; Stephen 1961; Artz et al. 2014). Some bees are gregarious like *O. bicornis* (Seidelmann 2006) or *M. rotundata* (Pitts-Singer and Cane 2011) and abundantly colonize nest boxes where nesting holes are plentiful. However, aggregating large numbers of specific solitary bee species could facilitate the accumulation of natural enemies (Wcislo 1996; MacIvor and Packer 2015). Managing cavity-nesting bees for pollination management therefore requires large nest boxes that can be easily cleaned to reduce parasites (Cusumano et al. 2012) and pathogens (Goettel et al. 1997), as their accumulation can critically impact bee populations (Hobbs 1968; James 2005).

3.4. Objective 4: to obtain bees for experimental study

Nest boxes can be used as tools for obtaining bees for research that would be otherwise difficult to collect in the field. 'Farming' bees in nest boxes can lead to excess numbers that can be packaged and sold to others needing bees for experimental purposes. Nest boxes used for this objective should be designed to include numerous cavities all of a similar length and internal diameter to match the precise conditions preferred by the bee species of interest. Also, materials that can be easily opened, such as cardboard or paper tubes, so brood cells can be counted and species identified. This permits the control of bee emergence-to-adulthood, parasite levels and sex ratios which can be important criteria to identify prior to further research. Bees collected from nest boxes can be used for study in enclosures in laboratory settings, in flight cages, in green houses, or in the field (Frohlich 1983; Abel and Wilson 1998; Suguira and Maeta 1989; Goodell 2003). For example, by manipulating the diversity of bees seeded into nest boxes in flight cages, Fründ et al. (2013) showed additive impacts of bee diversity on pollination efficacy.

By obtaining bees from nest boxes, researchers can study the mechanisms relating to cavity-nesting bee physiology and development, leading to better management and knowledge relevant for our understanding of all bees. Bees obtained from nest boxes have been used to understand bee incubation and overwintering conditions (e.g. Tepedino and Parker 1986; Kemp and Bosch 2001; Giejdasz and Wilkaniec 2002; Yocum et al. 2005; O'Neill et al. 2011; Fliszkiewicz et al. 2012; Fründ et al. 2013), sex ratio (e.g. Tepedino 1980; Longair 1981; Oku and Nishida 1999; Seidelmann et al. 2010), embryonic change (Torchio 1989), larval instar development (Whitfield et al. 1987), metabolism rates (Wightman and Rogers 1978), changes in egg size (Maeta and Suguira 1990), cocoon size (Tepedino and Parker 1986), larval orientation (Torchio 1980; Martins et al. 2012), diet (Sedivy et al. 2011; Haider et al. 2013), nest site fidelity (Steffan-Dewenter and Schiele 2004), supersedure (Delphia and O'Neill 2012), emergence timing and seasonality (Thiele 2005; Forrest and Thomson 2011), nest material preferences (Horne 1995; MacIvor 2016) and impacts of pesticides and other chemicals on bee health (Waller 1969; Torchio 1983; Alston et al. 2007; Konrad et al. 2008; Sandrock et al. 2014).

4. CONCLUSIONS

Nest boxes are inexpensive, can be set out in a wide variety of habitats and built using porous and preferably natural materials found locally and globally; for example, collected and dried invasive plants like *P. australis* and *P. aurea.* The popularity of nest boxes has greatly diversified the type and number of designs, users, and habitats where nest boxes are deployed. To study bee diversity along environmental gradients or in different habitats it is recommended that nest boxes are set out over as wide an area as possible and contain many cavities of different internal diameters. Nest boxes designed to augment numbers of bees for crop pollination or further experimentation should be made large and of a consistent material and dimension based on the preference of the target bee species.

Although not discussed in this review, numerous species of solitary wasps also use nest boxes (Danks 1971; Taki et al. 2008; Matsumoto and Makino 2011; Ebeling et al. 2012; Diekötter et al. 2014; Staab et al. 2014) and often abundantly (MacIvor and Packer 2015). Many of these cavity-nesting wasps collect aphids, caterpillars and beetles, some of which are garden pests or are hyperabundant (Fye 1965b; Krombein 1967; Fricke 1991; Sears et al. 2001; Krewenka et al. 2011). More work is needed to identify what opportunities there are in using nest boxes to study and enhance cavity-nesting wasps, including the dual functional roles (e.g. pollination, pest-control) that nest boxes might contribute to natural and agricultural systems (Gathmann et al. 1994; Holzschuh et al. 2009; Barthélémy 2012; Fabian et al. 2014).

Nest boxes are increasingly sold at gardening centres and online (MacIvor and Packer 2015). Incorporating nest boxes into gardening practises that support pollinators could increase efforts of citizens to aid in data collection and enhance conditions for wild bees (Everaars et al. 2011). As concern and appreciation for non-honey bee species increases, the use of nest boxes as both a sampling tool and as habitat will increase and expand into new and innovated evidence-based applications.

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Gîtes de nidification artificiels pour abeilles solitaires: un siècle de design et de recherche

Abeilles nichant en cavité / gestion alternative des pollinisateurs / abeilles sauvages / biodiversité / agroécosystème / nid-piège / jardin

Hohlraum-Nistboxen für solitäre Bienen: Ein Jahrhundert über Design und Forschung

Hohlraum-nistende Bienen / Alternatives Bestäubungsmanagment / Wildbienen / Biodiversität / Agrarökosysteme / Nisthilfe / Bienenhotel / Bestäubergarten

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