The Canadian Field-Naturalist

Parasitism and brood mortality in Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius)), nesting in vacated comb cells of European Paper Wasp (*Polistes dominula* (Christ))

J. Scott MacIvor

Department of Biological Sciences, University of Toronto Scarborough, 1265 Military Trail, Toronto, Ontario M1C 1A4 Canada; email: scott.macivor@utoronto.ca

MacIvor, J.S. 2021. Parasitism and brood mortality in Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius)), nesting in vacated comb cells of European Paper Wasp (*Polistes dominula* (Christ)). Canadian Field-Naturalist 135(4): 377–382. https://doi.org/10.22621/cfn.v135i4.2649

Abstract
Social paper wasps (Hymenoptera: Vespidae) construct comb nests of tens to hundreds of brood cells that are abandoned each year before winter. The nests are positioned where they are protected from inclement weather and may remain intact for several years. Here, I detail observations of nests provisioned by the non-native, solitary Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius, 1787); Hymenoptera: Megachilidae) in individual brood cells in vacated combs of the invasive, social European Paper Wasp (*Polistes dominula* (Christ, 1791)) on a green roof in Toronto, Ontario. A total of 12 paper wasp combs were dissected and 280 *M. rotundata* nests (one per wasp comb cell) were recovered; 22 nests were provisioned in 2013 consisting of 32 individual *M. rotundata* brood cells. Parasitism by *Melittobia* and *Monodontomerus* wasps accounted for 46.9% of *M. rotundata* mortality in the cells in 2013; mortality from all causes, including parasitism, was 78.1%. In contrast, total mortality of *M. rotundata* in brood cells provisioned in a human-made bee nest box on the same roof in 2013 was 4.2% and there was no parasitism. Mortality by parasitism and total brood mortality in 391 brood cells provisioned in 41 nests in the bee nest box in 2011–2013 were 2.0% and 21.2%, respectively. Therefore, the use of vacated paper wasp comb cells resulted in an overall >20-fold increase in parasitism and >3-fold increase in brood mortality over that observed in the bee nest box when all years are combined.

Key words: Megachilidae; Vespidae; non-native; invasive; parasitoids; urban ecology; bee nest box

Introduction
Alfalfa Leafcutting Bee (*Megachile rotundata* (Fabricius, 1787); Hymenoptera: Megachilidae) is one of the most widely distributed and economically important solitary bees in the world (Pitts-Singer and Cane 2011). Introduced into North America and subsequently established in the late 1930s (Stephen 1961; Mitchell 1962), its utility as a managed commercial pollinator has blossomed since the 1960s (Stephen and Torchio 1961). It now exists as feral populations throughout the continent and its ubiquity is most pronounced in urban and agricultural areas where it visits a variety of flowering species.

Megachile rotundata has immense flexibility in its use of nesting materials and cuts leaves from a wide range of plants (MacIvor 2016), sometimes flower petals (Klostermeyer and Gerber 1969), and even plastic shopping bags (MacIvor and Moore 2013) to enfold and partition brood cells. Each brood cell in a nest contains an individual egg on top of a ball of pollen and nectar provided by the female. The bee is also flexible in where the nest is constructed. As an aboveground "renter", *M. rotundata* is a cavity-nester with females searching for holes excavated by beetles in wood or hollow plant stems (Pitts-Singer and Cane 2011). It will also nest in a variety of human-made materials, such as plastic straws (Stephen and Every 1970), polystyrene boards (Richards 1978), or rolled paper tubes (Sheffield *et al.* 2008) and has even been found in the radiator of an antique tractor (Sheffield 2017).

Interest in the management of *M. rotundata* populations for pollination services, or simply as a hobby, has increased dramatically with the development and retailing of human-made bee nest boxes (MacIvor 2017). The boxes are made of pre-formed horizontal cavities of a variety of materials (e.g., holes drilled into wood, bundled hollow plant stems, or rolled paper and cardboard tubes) that provide nesting cavities for *M. rotundata* and other solitary bee and wasp species to lay and provision their eggs (Krombein 1967; Tscharntke *et al.* 1998; Sheffield *et al.* 2008;

Staab *et al.* 2017). *Megachile rotundata* will readily nest in aggregated conditions; thus, tens to thousands of cavities may be grouped together. Further, females are attracted to previously used nests, so large populations are possible (Pitts-Singer 2007).

While inspecting a bee nest box on a green roof at York University campus in Toronto, Ontario, I discovered ~20 vacated comb nests constructed by the invasive, social European Paper Wasp (*Polistes dominula* (Christ 1791); Hymenoptera: Vespidae) on the underside of awnings of vaulted windows along the inner perimeter of the roof. The paper wasp nests consisted of exposed combs of unenveloped, vertically oriented cells and were located in places protected from inclement weather (Downing and Jeanne 1986). *Polistes dominula* has spread throughout North America, displacing native wasps, and the species is common in cities (Cervo *et al.* 2000), where food resources are abundant and buildings provide shelter (Höcherl and Tautz 2015). The paper comb nests are vacated by the wasps after one year but, if protected, the structure may remain for several more. On close inspection, I noticed that many of the paper wasp comb cells were being used as nesting cavities by leafcutting bees (Figure 1a–c). Hundreds of comb cells contained individual nests made by *M. rotundata*, which have a distinct small size and brood cell construction pattern compared with other leafcutting bees in the region.

Here, I describe the results from dissecting these paper wasp combs and compare the survival, parasitism, and brood mortality of the *M. rotundata* nests found in the paper wasp comb cells with those from a nearby bee nest box on the same building.

Methods

In July 2013, 12 individual vacated paper wasp combs that contained *M. rotundata* nests were dissected. The combs were located on the fourth-storey roof of York University's Computer Science Building (43°46′26.24″N, 79°30′18.73″W), which is northwest of downtown Toronto, Ontario. The unirrigated green roof was originally seeded in 2001 (for details, see Toronto and Region Conservation Authority 2006) and is a mix of extensive (<15 cm substrate depth) and intensive (>15 cm) growing media substrates. Flowering plants included in the original seed mix, such as Lance-leaved Tickseed (*Coreopsis lanceolata* L., Asteraceae), False Sunflower (*Heliopsis helianthoides* (L.) Sweet, Asteraceae), Foxglove Beardtongue (*Penstemon digitalis* Nuttall ex Sims, Plantaginaceae), and Black-eyed Susan (*Rudbeckia hirta* L., Asteraceae), persist on the roof. Many other flowering plants have arrived spontaneously, including Common Milkweed (*Asclepias syriaca* L., Apocynaceae), Annual Fleabane (*Erigeron annuus* (L.) Persoon, Asteraceae), White Sweet-clover (*Melilotus albus* Medikus, Fabaceae), Tall Goldenrod (*Solidago altissima* L., Asteraceae), White Clover (*Trifolium repens* L., Fabaceae), and Common Dandelion (*Taraxacum officinale* F.H. Wigg., Asteraceae).

All *M. rotundata* nests (one nest per paper wasp comb cell) in the 12 combs were dissected and determined to be either provisioned pre-2013 or in 2013.

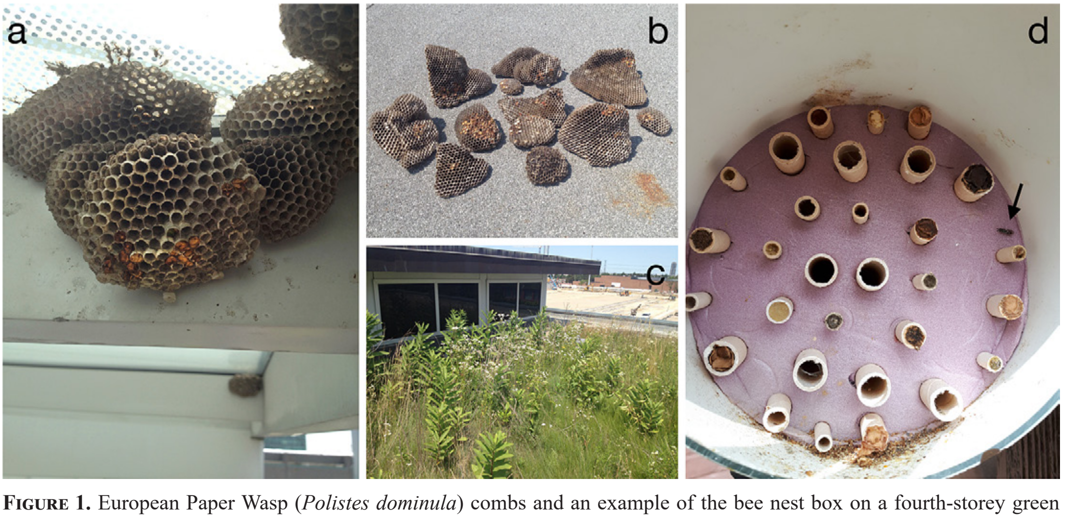

FIGURE 1. European Paper Wasp (*Polistes dominula*) combs and an example of the bee nest box on a fourth-storey green roof in Toronto, Ontario, Canada. a. Vacated unenveloped paper wasp comb cells where provisioned Alfalfa Leafcutting Bee (*Megachile rotundata*) nests were observed. b. A collection of paper wasp nest combs with *M. rotundata* nests visible. c. The green roof where the observations were made. d. Example of the bee nest box from which *M. rotundata* were obtained for comparison, with parasitoid *Monodontomerus* present (arrow). Photos: a–c. J.S. MacIvor. Photo: d. Kathy Bosci.

Those presumed to be provisioned before 2013 were mouldy and decomposed and sometimes contained the remnants of a dead larva or an emergence hole indicating that a bee or parasitoid(s) had matured and left the nest; these were not included in further analyses. Nests provisioned in 2013 with one or more brood cells containing uneaten fresh pollen or a living bee larva or parasitoid(s) were included in my analysis. Uneaten pollen can include a shrivelled early instar larva indicated that the nest cell had failed (e.g., Danks 1971).

Living larvae suspected to be *M. rotundata* were individually stored in 24-well assay trays at room temperature, moved to a 4°C refrigerator to simulate late-fall and winter (October–April), and then to 26°C and 60–65% humidity in spring until emergence. Adult female and male bees were identified using Sheffield *et al.* (2011).

Parasitized nest cells were also collected, and the parasitoids allowed to pupate. Adults were identified to either genus *Melittobia* Westwood, 1848 (Hymenoptera: Eulophidae) or *Monodontomerus* Westwood 1833 (Hymenoptera: Torymidae) using the dichotomous key in Peck (1969). No vouchers were collected so identification to species is not possible. Both parasitoid wasp taxa are gregarious and multivoltine. Mated females use olfactory cues to locate a prepupal bee in its brood cell, sting it, then lay eggs externally on the host surface (Eves 1970; Matthews *et al.* 2009). *Melittobia* are small (1.0–1.5 mm in length) and must gain entry inside the brood cell to access the host, whereas *Monodontomerus* (2.0–4.0 mm) may insert their ovipositor through the brood cell (Eves 1970). Larvae hatch from eggs quickly and begin to feed on the immature bee, emerge as adults, then chew through the brood cell ready to attack other immature bees in a nest or aggregation (Farkas *et al.* 1985; Matthews *et al.* 2009).

A bee nest box (Figure 1d) on the same green roof was part of a larger study detailed in MacIvor and Packer (2015). From it, 30 horizontally oriented cardboard nesting tubes of three widths (3.4 mm, 5.5 mm, and 7.6 mm), all 15 cm long, were useable by *M. rotundata* (although the 5.5 mm tubes were used primarily). All specimens from nesting tubes were reared to adults (as above), identified to species, and the number of failed (e.g., mouldy, shrivelled) and parasitized brood cells counted. Representative vouchers of *M. rotundata* from the bee nest box for all three years are curated in the Biodiversity of Urban Green Spaces (BUGS) lab at the University of Toronto Scarborough (2011-163A6, 2012-303B1, and 2013-307C2).

Brood mortality was defined as the sum of the number of brood cells that failed because they were parasitized or from other causes.

Results

The 12 dissected paper wasp combs yielded 280 *M. rotundata* nests constructed in downward facing (i.e., vertically oriented) cells (Figure 1a). From this total, 258 nests were determined to be provisioned pre-2013 and each contained an unknown number of brood cells per nest. Only 22 *M. rotundata* nests consisting of 32 brood cells (average 1.5 brood cells/nest cell, reflecting the depth of each comb cell ~3 cm) could be confirmed as having been provisioned in 2013 (Table 1) and were retrieved from five separate paper wasp combs. Seven larvae in these 32 brood cells survived to adulthood (two female, five male), 15 were parasitized by *Monodontomerus*, and 10 perished because of mould or other unknown causes (e.g., disease/virus; Table 1). The average (± SE) number of parasitoids per parasitized brood cell was 4.4 ± 1.7. No *Melittobia* were found in the paper wasp combs. Dermestid (*Trogoderma*) beetles (Coleoptera: Dermestidae) were also recovered from three paper wasp combs and near (or in) former *M. rotundata* nests, indicating that they may have scavenged on the remains of pollen provisions and immature bees (Bohart 1972).

From the bee nest box, 41 *M. rotundata* nests (one nest per nesting tube) consisting of 391 brood cells

Table 1. Number of nests and brood cells provisioned, as well as survival, parasitism, and failure of Alfalfa Leafcutting Bee (*Megachile rotundata*) in European Paper Wasp (*Polistes dominula*) comb cells and in a bee nest box on a fourth-storey green roof in Toronto, Canada.

Nest type	Year	No. nests	No. brood cells	Average no. brood cells/ nest	Brood outcome, no. (%)		
					Survival to adult	Parasitized	Mould/failed
Paper wasp comb	2013	22	32	1.5	7 (21.9)	15 (46.9)	10 (31.2)
Nest box	2011	13	186	14.3	121 (65.1)	0 (0.0)	65 (34.9)
	2012	20	181	9.1	166 (91.7)	8 (4.4)	7 (2.2)
	2013	8	24	3.0	21 (87.5)	0 (0.0)	3 (4.2)
	All years combined	41	391	9.5	308 (78.8)	8 (2.0)	75 (19.2)

were recorded in 2011–2013, with an average of 9.5 brood cells/nest (Table 1). In 2013, none of the 24 brood cells in eight nests was parasitized, but three failed as a result of unknown causes. In 2011, 13 nests contained 186 brood cells, of which 121 survived, 65 failed, and none was parasitized. In 2012, I recorded 20 nests containing 181 brood cells: 166 survived to adulthood, seven failed, and eight were parasitized by either *Melittobia* (n = 5) or *Monodontomerus* (n = 3).

The number of *M. rotundata* in the bee nest box fluctuated among years presumably because of competition for nesting opportunities with other species. For example, the number of *M. rotundata* nests was lower in 2011 and 2013 than in 2012 because the spring-active and non-native Blue Mason Bee (*Osmia caerulescens* (L., 1758); Hymenoptera: Megachilidae) filled nesting tubes that would otherwise be available for summer-active species such as *M. rotundata*. There was no evidence of *O. caerulescens* nesting in paper wasp combs.

Altogether, parasitism and brood mortality occurred >20 and >3 times more often, respectively, in *M. rotundata* brood cells provisioned in the paper wasp combs compared with the bee nest box.

Discussion

The observations reported here confirm the nesting flexibility that others have shown for *M. rotundata* (e.g., Stephen and Every 1970; Richards 1978; Sheffield *et al.* 2017) and demonstrates that the species can also opportunistically use vacated *P. dominula* paper wasp comb cells as nesting cavities. However, the rates of parasitism and brood mortality were higher in the paper wasp combs than in a nearby bee nest box, at least during one year on one green roof in Toronto.

Many leafcutting bees nest in pre-existing cavities in wood or hollow dried plant stems; thus, parasitoids are often restricted to penetrating the nest only through the front entrance. The high rates of parasitism in *M. rotundata* I found in the paper wasp combs may be a result of *Monodontomerus* being able to access bee larvae directly through the thin paper cell walls. Krombein (1967) found that the frequency of ovipositor insertion by parasitoid wasps from outside the cavity into a solitary bee brood cell declined when cavity walls were >2 mm thick. As well, paper wasp comb cell walls may be further weakened and accessible to parasitoids because in sheltered locations (e.g., under a roof awning), *P. dominula* will allocate less protein to paper construction (for waterproofing and strengthening) and more to developing larvae, compared with less-sheltered sites (Curtis *et al.* 2005). Nesting in paper wasp comb cells may represent a habitat sink (Delibes *et al.* 2001) where environmental cues used by *M. rotundata* to differentiate good versus bad nest sites fail and some suffer reduced reproductive fitness as a result. Nest site fidelity, gregarious nesting behaviour, and the "scent" of used nests might attract subsequent *M. rotundata* (Parker *et al.* 1983), enhancing the consequences for these bees.

Although several *M. rotundata* adults emerged successfully from the paper wasp comb cells, brood mortality (parasitized plus failure from all other causes) was higher than in the bee nest box (Table 1). Because nesting tubes in the box are arranged horizontally, eggs are laid on pollen masses on a lateral surface. In the paper wasp combs, cells are vertical or almost so; thus, the provisioned bee eggs could have been laid on the downward facing side of a pollen provision possibly leading to increased mortality if bee larvae fall off the provision. It is typically recommended that bee nest boxes not be moved during a season, as handling may cause mortality (Minckley and Danforth 2019). There may be other examples of natural nest cavities oriented at different angles, but it is unknown whether this increases mortality. Bee nest boxes may enhance reproductive fitness of bee species that accept them, allowing local populations to grow (Steffan-Dewenter and Schiele 2008). Whether bee nest boxes serve as a conservation tool for native bees in urban areas requires more scrutiny given the large number of non-native bees (*M. rotundata* and *O. caerulescens*) produced from this one nest box on a building rooftop.

Vacant paper combs of *P. dominula* are common in urban areas and represent a unique and understudied microhabitat for arthropod communities. Native solitary cavity-nesting wasps, including *Euodynerus foraminatus* (de Saussure) (Hymenoptera: Vespidae), *Parancistrocerus fulvipes* (de Saussure) (Hymenoptera: Vespidae), *Trypoxylon clavatum* Say (Hymenoptera: Crabronidae), and *Auplopus mellipes* (Hymenoptera: Pompilidae; Rau 1944 [first two species], 1928 and Evans 1953, respectively), as well as native solitary cavity-nesting bees such as Blue Orchard Bee (*Osmia lignaria* Say; Hymenoptera: Megachilidae) and *Osmia cordata* Robertson (Hymenoptera: Megachilidae; Rau 1937 and 1928, respectively), have been reported nesting in the vacated comb cells of native paper wasps in non-urban areas. One study in the United States compiled a list of 42 species in 28 invertebrate families that are parasites or symbionts of native *Polistes* and use vacated paper wasp combs as habitat (Nelson 1968), yet no description of *M. rotundata* or other *Megachile* nesting in paper wasp comb cells are present in the literature. However, online images exist (e.g., Prouty 2010) and suggest that the observations documented here may not be an isolated occurrence.

The unusual nesting behaviour I document emphasizes how little we know about the generality and specificity of nesting in solitary wild bees. Others have characterized nesting conditions for various bee species to better understand habitat preferences (e.g., Cane 1991; Sardiñas and Kremen 2014; Antoine and Forrest 2020; Harmon-Threatt 2020), but continued documentation and observation are needed, even for widespread species such as *M. rotundata* that have immense flexibility in nesting requirements. This is critical for implementing design (e.g., bee nest boxes) and management (e.g., removal of invasive paper wasp combs) in urban areas that support the nesting requirements of native bees and do not inadvertently enhance introduced species (Russo *et al.* 2021).

Acknowledgements

I thank Bahar Salehi for assistance in the field and dissection of the paper wasp combs, Dr. Laurence Packer for supervision and lab space, and Tim Haagsma from York University Facilities Management for access to the green roof. I also thank Dr. Alessandro Filazzola, two anonymous reviewers, and the handling editors for their comments on the draft. At the time of this discovery, funding was provided by a Natural Sciences and Engineering Research Council (CGS D 408565) grant.

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Received 23 September 2020
Accepted 30 July 2021
Associate Editor: J.H. Skevington