

Pollen specialization by solitary bees in an urban landscape

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Abstract Many polylectic bee species are known to specialize locally on one or a few pollen types to increase foraging efficiency. What is relatively unknown is how different landscapes influence foraging decisions, and whether habitat alteration, such as that resulting from urbanization, influences broad-scale foraging activities of bees. This study evaluates the type and diversity of pollen collected by two solitary bees that are common in Toronto, Ontario, Canada, the native *Osmia pumila* and the exotic *O. caerulescens*, sampled in trap nests set up in urban parks and gardens. We found that the dominant pollen in every successful brood cell was either of one widespread, cosmopolitan lawn-invasive plant species (*Trifolium repens*) or one of two wind-pollinated tree genera (*Quercus* spp. and *Betula* spp.). In combination, these three represented more than 90 % of all pollen collected by each bee species. Despite considerable overlap in the dominant pollen types collected by each bee species, the exotic *O. caerulescens* was significantly more specialized than the native *O. pumila*. Brood cells with *Betula* as the dominant pollen type were more pollen species-rich than those cells having *Trifolium* or *Quercus* as dominant, perhaps a result of the comparatively low protein content in *Betula* pollen.

Keywords *Osmia* · Exotic species · Trap nests · Pollen nutritional content · Wind pollination

Introduction

Many species of bee possess traits that permit their survival in urban landscapes. Elucidating these traits is an important field of study for predicting how fragmentation and other anthropogenic disturbances alter species assembly (Niemela et al. 2000) and pollination services (Williams et al. 2010). Cities are model landscapes for investigating the effects of fragmentation and anthropogenic disturbance, both of which vary in intensity and frequency, usually increasing towards the urban core (McDonnell et al. 1997). In urban areas, the majority of bee species recorded are polylectic, collecting pollen and nectar from a variety of

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native and exotic, ornamental, and invasive flowering plants, shrubs, and trees (Matteson et al. 2008). Despite many studies evaluating the diversity of wild bees in urban and suburban landscapes (Tommasi et al. 2004; Smith et al. 2006; Fetridge et al. 2008; reviewed in Hernandez et al. 2009; Banaszak-Cibicka and Zmihorski 2011), none has assessed pollen use by urban bees. Analyzing and identifying pollen grains from nests provides a more useful record of the floral host use over an extended period of time than does floral observations in the field (Cane and Sipes 2006), and acknowledging these relationships can have implications in sustaining native pollinators and pollination services (Kearns and Inouye 1997; Jones and Jones 2001; Fontaine et al. 2006; Müller et al. 2006; Bosch et al. 2009; Ollerton et al. 2011).

In cities, knowledge of pollen, nectar, and nesting requirements of bees is important for advancing the integration of ecology into landscape design in support of plant-pollinator assemblages (Cane 2005). This is important because urbanization and the associated loss of vegetation have been shown to generally have a negative effect on bee populations (Zanette et al. 2005; Winfree et al. 2009). At the same time, citizens are becoming increasingly engaged in socio-economic activities requiring pollination, such as wildlife gardening and urban agriculture (Smit and Nasr 1992; Drescher 2004). This could include selecting combinations of plant species that provide floral resources all season, which is particularly important for social bees active all season (Pleasants 1980), while also fulfilling other important city planning criteria such as canopy cover and shading using flowering trees (Dwyer et al. 1992). Indeed, many large-scale urban re-forestation and vegetation initiatives are underway. In New York, an initiative of PlaNYC is to re-vegetate the boroughs with one million planted trees by 2017 (Rosenthal and Brechwald 2013). Another initiative in the city of Toronto aims to double the tree canopy cover from 17 % to 34 % by 2050 (City of Toronto 2007). In these reforestation plans, canopy-providing tree selection has the potential to modify, either positively or negatively, the activity of non-target, pollen-dependent insects (Dreistadt et al. 1990).

Members of the solitary bee genus *Osmia* (Hymenoptera: Megachilidae) are often common in urban landscapes (Tommasi et al. 2004; Everaars et al. 2011). Many *Osmia* are polylectic, with each female constructing its own nest after mating in spring and early summer (Cripps and Rust 1989). The success of *Osmia* may be mediated in part by flexibility in nest selection, and the availability of accidental human-made nesting sites. Many *Osmia* will build their nests in woody or non-woody plant stems, branches, or logs, but also holes drilled into building material such as wooden boards, brick, or mortar, and even intentionally bundled nests of cardboard paper tubes or reeds (Krombein 1967; Free and Williams 1970; Sheffield et al. 2008; Mader et al. 2010). An *Osmia* nest consists of a gallery of brood cells, each cell provisioned with pollen and nectar produced, in sequence, from the back of the nest to the front. Each cell is lined with masticated leaves and/or mud and the same material is usually used to plug the entrance to the gallery when complete (Cane et al. 2007).

The developmental success of *Osmia* larva is unaffected by the richness of pollen provisioned, with brood able to develop successfully on even a single pollen type (Williams and Tepedino 2003). Such specialization presumably minimizes time spent foraging (Raw 1974; Strickler 1979; Chittka et al. 1999; Müller et al. 2006) while simultaneously reducing rates of parasitism through decreasing the duration of absences from the nest (Goodell 2003). Specialization in this case would particularly increase the efficiency of brood provisioning in the springtime, when there are fewer foraging alternatives and weather conditions are less stable (Radmacher and Strohm 2010). Like adaptive specialization of foraging behaviour in suboptimal weather, bees that can specialize on pollen in less predictable or fragmented environments might have greater population persistence in city landscapes.

In this study we investigate the pollen diversity and preference of one native, *O. pumila*, and one exotic, *O. caerulea*, bee species to determine whether pollen use by *Osmia* in a

city landscape is consistent with observations of pollen specialization by *Osmia* in naturalized (Raw 1974; Cripps and Rust 1989; Rust 1990; Kraemer and Favi 2005) and orchard agricultural landscapes (Torchio 1976; Vicens and Bosch 2000). Further, since pollen collection by exotic solitary bees is poorly known (Goulson 2000), the study will examine differences between the co-occurring native and exotic species.

Methods

Sampling

From May to October 2011, 190 trap nests were set up in the city of Toronto in private gardens, community gardens, green roofs, and parks. Each trap nest was constructed from a 30 cm piece of recyclable PVC piping of 10 cm diameter with one end fitted with a pipe cap, the other with a faceplate bearing 30 cardboard tubes (Custom Paper Tubes, Cleveland, OH), 10 of each of three different widths (3.4 mm, 5.5 mm and 7.6 mm) that were plugged at the capped end of the pipe. Once recovered, all cardboard tubes were opened and the contents analyzed. Average trap nest colonization was 33.6 % with *O. pumila* and *O. caerulescens* representing 16.7 % and 10.3 % of the total sample, respectively.

Pollen analysis

Osmia pumila and *O. caerulescens* were identified and 20 galleries containing *O. pumila* and 11 containing *O. caerulescens* were selected so to best reflect the entire sampling area (Fig. 1). This resulted in 160 successful *O. pumila* brood cells from 10 nesting locations and 58 successful *O. caerulescens* brood cells from 7 locations (see Fig. 1). Pollen was collected from each of these brood cells from the frass that is excreted just prior to pupation (Raw 1974; Davidson and Evans 2010). Each frass-pollen sample was transferred to a slide with two drops of water and pulverized with the blunt end of a spatula, followed by a thorough mixing and re-distribution on the slide with an insect mounting pin (Teper 2007). The spatula was cleaned between each slide preparation and a fresh mixing pin was used each time to avoid contamination among samples. Pollen was then air-dried for 60 min, and a drop of glycerin and a drop each of fuchsin and methyl green in 70 % ethyl alcohol were added to each sample to make the pollen microstructure more visible for identification (Raw 1974; Kearns and Inouye 1997). All pollen grain samples are preserved and placed in storage at the Packer Collection at York University, Toronto, Canada.

Pollen grains from each of the prepared samples were examined using a Canon E05 40D camera with a K2 lens and a 10× lens attachment and photographed using a Microoptics ML 1,000 fiberoptics illuminating system at the highest flash setting and highest magnification. Photographs of several fields of view (moving 2× above and 2× below the original magnification) were taken. The images were uploaded to Adobe Photoshop Lightroom 3 and exported to Helicon Focus 5.2×64, which compiles multiple fields of view of a single location to provide a composite image with a greater depth of field. Data were obtained from each of a minimum of three locations on the slide in an attempt to ensure that at least 600 pollen grains (maximum 200 per slide location) could be identified in each sample.

Pollen grains were identified to genus because of the difficulties associated with a finer taxonomic assessment; this level has been shown to be sufficient for examining pollen specialization (Eltz et al. 2001; Radmacher and Strohm 2010). Pollen identities were determined using keys in McAndrews et al. (1973) and Crompton and Wojtas (1993).

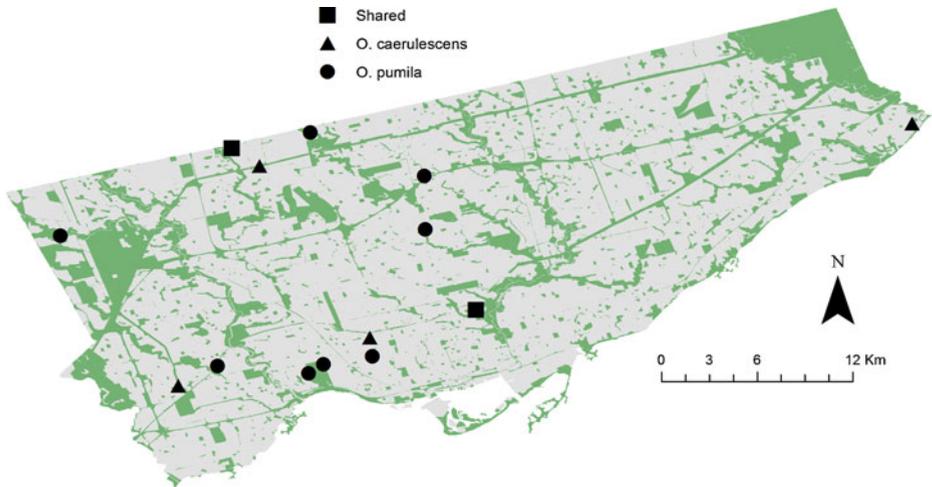


Fig. 1 Map of study site localities in and around Toronto, Ontario, Canada, created using ArcGIS 10 software (ESRI, Toronto, Canada). Open areas and City parks and recreation land are highlighted in green. One sampling site located north of the city boundary is omitted from the map

Pollen grains that made up less than 1 % of the total count were considered contaminants (Eltz et al. 2001), or as having been haphazardly collected while bees were foraging for nectar (Radmacher and Strohm 2010) and omitted from analysis.

Statistical analysis

Average pollen richness was calculated as the average number of pollen grain types both within a brood cell and within a nesting gallery for each *Osmia* species. Pollen grain specialization was calculated per brood cell, gallery, and trap nest location using Levins' standardized measure of niche breadth (B_n) (Feinsinger et al. 1981). A B_n value nearing 1 reflects higher specialization on a single pollen type and values approaching 0 represent increasing breadth of pollen species collection. A Welch's two-sample t-test ($\alpha=0.05$) (assuming unequal variance) was used to compare the number of brood cells per gallery constructed, pollen richness per gallery, and pollen specialization between the two species. A linear regression analysis tested whether specialization within a gallery of each species were associated with an increase in the number of brood cells constructed by an individual, since specialization has been shown to increase productivity in oligolectic bees (Strickler 1979). Finally, an analysis of variance with a Tukey HSD post-hoc analysis was used to detect significant differences in the dominance of pollen grain types in the brood cells between the two species. All statistics were completed using R version 2.15.2 (R Foundation for Statistical Computing 2012).

Results

The native *O. pumila* collected significantly more pollen types ($n=8$) than the non-native *O. caerulescens* ($n=6$) ($t_{29}=-2.59, p=0.015$) and was significantly less specialized on the dominant pollen it collected compared to the non-native *O. caerulescens* ($t_{15}=2.42, p=0.029$) (Table

1). That said, high specialization was noted in both species, with instances in which 100 % of the pollen mass was of a single pollen type (3 % of all brood cells). Moreover, 79 % of *O. caeruleascens* cells were provisioned with >95 % (by proportion) of a single host species compared to only 37 % of *O. pumila* cells. Despite the difference in pollen specialization, the number of brood cells per gallery was not significantly different between species ($t_{22}=-0.466$, $p=0.646$), nor was there any effect of specialization on the number of brood cells produced within *O. pumila* ($p=0.862$) or *O. caeruleascens* ($p=0.389$).

Both bee species shared a surprisingly similar diet breadth, concentrating primarily on White Clover, *Trifolium repens* (Fabaceae), and two wind-pollinated tree genera: Oak (likely *Quercus rubra* and/or *Quercus alba*), and Birch (likely *Betula papyrifera* and/or *Betula alleghaniensis*) (Fig. 2). Clover pollen was the dominant grain type in 75 % of *O. pumila* and 54 % of *O. caeruleascens* galleries, followed by Oak dominant in 15 % for *O. pumila*, 27 % for *O. caeruleascens*, and Birch (10 % for *O. pumila*, 9 % for *O. caeruleascens*). Interestingly, when Birch was dominant in a brood cell of *O. caeruleascens*, the proportion of other co-occurring pollen types was proportionally significantly greater than when either Clover or Oak was dominant ($F=5.75$, $p=0.025$) (Fig. 3). Pollen was also collected in small amounts (<5 % each) from Willow (likely *Salix discolor*, *Salix nigra*, and/or *Salix alba*), Maple (likely *Acer saccharum*, *Acer saccharinum*, and/or *Acer platanoides*), Cherry (*Prunus* spp.), Vetch (likely *Vicia sativa*), and Dandelion (*Taraxacum officinale*).

Discussion

In this study, we find that two solitary bees abundant in an urban landscape exhibit high pollen specialization on wind-pollinated trees (*Quercus* spp., *Betula* spp.) and on a nitrogen-fixing legume common in pastures and now an abundant lawn-invading cosmopolitan weed (*Trifolium repens*). *Trifolium repens* has a near worldwide distribution and is common in urban areas (Turkington and Burdon 1983). Having a moderately high protein content (35.4 %) (Roulston et al. 2000), it is visited by many bee species including both *O. pumila* (Goodell 2003) and *O. caeruleascens* (Hennig and Ghazoul 2011). The other two primary pollen types collected by both bee species were from predominantly wind-pollinated trees:

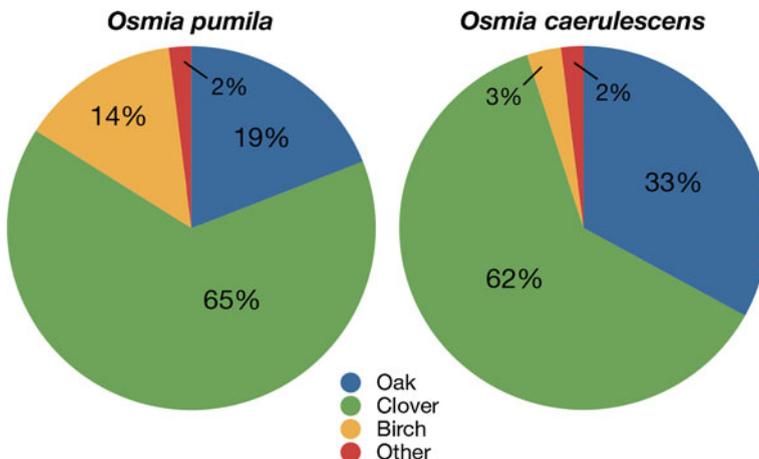


Fig. 2 Total proportion of each of the specialized pollen types collected by *O. pumila* and *O. caeruleascens*

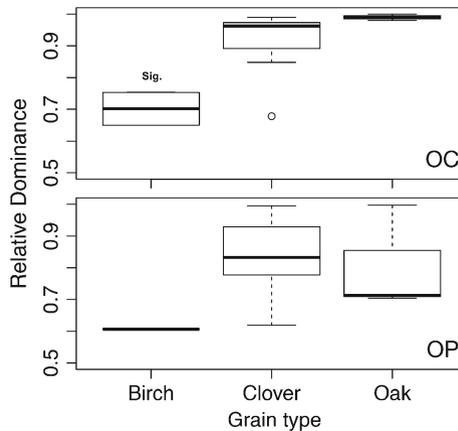


Fig. 3 A boxplot for each commonly collected pollen genera, demonstrating the difference between their relative dominance when they are the dominant grain in the brood cells of either *O. caerulescens* (OC) and *O. pumila* (OP). A post-hoc Tukey HSD analysis revealed that Oak (p -adjusted = 0.02) and Clover (p -adjusted = 0.05) were significantly more dominant than Birch in brood cells of *O. caerulescens* (Birch denoted with a “Sig.” to mark significance), but no difference was evident for *O. pumila*

Oak (*Quercus*) and Birch (*Betula*). Wind-pollinated trees are not reliant on insect pollination but provide an abundant source of pollen for bees (Molina et al. 1996). The pollen of Oak, like White Clover, contains a relatively high proportion of protein (38.8 %), but Birch contains much less, approximately 28 % (Roulston et al. 2000). Although there is no evidence that bees assess the nutritional content of pollen while foraging (Roulston and Cane 2000), low protein content may have resulted in both Birch being only the third most commonly collected pollen and, when used, to be associated with a greater species richness of pollen sources than the other two main pollen sources. Similarly, in related bee genera, Praz et al (2008) found that species specializing on pollen having low protein content were more flexible in their use of pollen from different plant families.

The City of Toronto’s Urban Forestry department commonly specifies both Oak and Birch for landscaping and reforestation projects (City of Toronto 2012). These trees, along with Willow and Maple, which were found in some *Osmia* cells in this study, bear easily accessible pollen concentrated on catkins having many small open flowers with little or no corolla (Giovanetti and Aronne 2011). With large trees permeating the urban landscape, each having potentially many thousands of flowers in a single season, these species might prove locally significant resources for pollen collecting insects within the urban matrix, potentially increasing connectivity in fragmented habitat (Ricketts 2001).

Our results reflect those of other studies examining pollen loads of *Osmia* in less urban environments. In particular, in rural England, Raw (1974) found 83 % of the pollen provisioned in opened brood cells of *O. caerulescens*, *O. rufa*, and *O. leaiana* came from the combination of a wind-pollinated tree (*Quercus* spp.) and a lawn weed (*Ranunculus* spp.). Another study on a suburban university campus in Germany found 38.8 % of all brood cells of *O. bicornis* contained >95 % of a single pollen type, most often the wind-pollinated *Quercus* or the partially wind-pollinated *Acer* (Maple) (Radmacher and Strohm 2010). In our study, both *O. pumila* and *O. caerulescens* specialized on one of each of the three dominant pollen types (*Trifolium*, *Quercus*, and *Betula*) all of which are widespread in the city. It is evident that inherent local pollen specialization by polylectic bees on one or a few grain types might reflect a trait

suites for persistence in urban landscapes. In this case, specialization on whichever dominant grain is found in the neighbourhood would ensure foraging success in these increasingly novel environments.

Different from other investigations of pollen collection by *Osmia* that examined native species only (e.g. Raw 1974; Cripps and Rust 1989; Radmacher and Strohm 2010) we report that pollen collection by the exotic bee species *O. caerulea*, was significantly more specialized than the co-occurring native, *O. pumila*. Although little is known about host plant restrictions of solitary bees in non-native habitats, Goulson (2000) notes that two introduced bees, *Apis mellifera* and *Bombus terrestris*, visit a greater diversity of floral hosts when outside their native range. The significantly greater specialization on a single pollen type by *O. caerulea* could reflect differences in dietary requirements or preference between species, or that *O. caerulea* is more restricted in its pollen collection in a non-native habitat. Despite the difference in degree of specialization, there was no apparent effect of specialization on the number of brood cells provisioned by the two species. Specialization by oligolectic bees has been suggested to increase foraging efficiency and the number of brood cells that can be constructed within a given season (Strickler 1979; Chittka et al. 1999). Although not examined in this study, it is possible that for some bee species, visiting more different types of flowers may not equate to a significant increase in foraging efficiency and brood provisioned because of diverse pollen resources in managed parks and in home and community gardens.

Conclusion

From analyzing pollen extracted from the frass of brood provisioned in trap nests set up throughout the city of Toronto, the native *O. pumila* and exotic *O. caerulea* were found to specialize on the pollen collected to provision their brood. Further, the exotic species was significantly more specialized in foraging than the co-occurring native. The dominant pollen grains for both species were from that of a grass-invading cosmopolitan weed, *T. repens*, and two wind-pollinated tree genera, *Quercus* and *Betula*. No specialization by either *Osmia* species was found to occur on entomophilous native plants, or crops significant for urban agriculture; furthermore it remains unknown whether specialization on abundant cosmopolitan weeds and wind-pollinated trees limits pollination of remnant native plants and crops in urban landscapes.

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