

# Pollen preferences of two species of *Andrena* in British Columbia's oak-savannah ecosystem

JULIE C. WRAY<sup>1</sup> and ELIZABETH ELLE<sup>1</sup>

## ABSTRACT

Although understanding the requirements of species is an essential component of their conservation, the extent of dietary specialisation is unknown for most pollinators in Canada. In this paper, we investigate pollen preference of two bees, *Andrena angustitarsata* Vierick and *A. auricoma* Smith [Hymenoptera: Andrenidae]. Both species range widely throughout Western North America and associated floral records are diverse. However, these species were primarily associated with spring-blooming Apiaceae in the oak-savannah ecosystem of Vancouver Island, BC, specifically *Lomatium utriculatum* [Nutt. ex Torr. & A. Gray] J.M. Coult. & Rose, *L. nudicaule* [Pursh] J.M. Coult. & Rose, and *Sanicula crassicaulis* Poepp ex. DC. Floral visit records and scopal pollen composition for these species from two regions on Vancouver Island indicate dietary specialisation in oak-savannah habitats where Apiaceae are present. Both species were also caught in low abundances in residential gardens where Apiaceae were scarce, sometimes on unrelated plants with inflorescence morphology similar (to our eyes) to Apiaceae. Further study of these species is needed to understand whether preferences observed locally in BC exist elsewhere in their range. Our findings contribute to understanding pollen preference in natural and urban areas, and highlight an important factor to consider for species-specific conservation action in a highly sensitive fragmented ecosystem.

**Key Words:** Andrenidae, Apoidea, oligolecty, pollen preference

## INTRODUCTION

Relationships between flowering plants and bees (Hymenoptera: Apoidea, Apiformes) range from extreme pollen specialisation, or oligolecty, to extreme generalisation, or polylecty. Perhaps as many as half of all non-parasitic bee species exhibit dietary specialisation at some level, but for most bees the extent of specialisation is unknown (Cane and Sipes 2006; Michener 2007). Bee species are considered to exhibit narrow oligolecty if females consistently provision offspring with pollen from a small related clade of plants (typically genus level; Linsley and MacSwain 1958; Müller 1996; Cane and Sipes 2006). Broad oligolecty could potentially comprise a larger number of related plant species or genera, but differs from polylecty in that many to most of the available pollen sources are not utilized (Cane and Sipes 2006). Facultative oligolecty occurs in some bee species, which normally specialize on a host plant, but may use non-host pollen when the usual host is unavailable (e.g., Williams 2003; Sipes and Tepedino 2005). Use of non-host pollen by oligolectic species can sometimes have substantial fitness consequences (Praz et al. 2008a), which may have conservation implications and explain why specialists tend to be more sensitive to disturbance (Elle et al. 2012).

Evaluating specialisation can be challenging. The identity of plant species from which bees are collected has frequently been used to describe foraging preferences, but we have known since the landmark work of Charles Robertson that bees visit a broader array of flowers for nectar than for pollen (Robertson 1925). Similarly, foraging preferences of male bees, which do not provision nests with pollen (they forage only for

---

<sup>1</sup> Evolutionary and Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, Canada, V5A 1S6; (778) 782-4592, eelle@sfu.ca

nectar), should not be considered when evaluating dietary specialisation. Floral records that do not include information on gender and behaviour simply have limited utility (Cane and Sipes 2006). Instead, it is important to consider not only constancy of floral visits by female non-parasitic bees, but also the composition of pollen they collect for offspring provisioning.

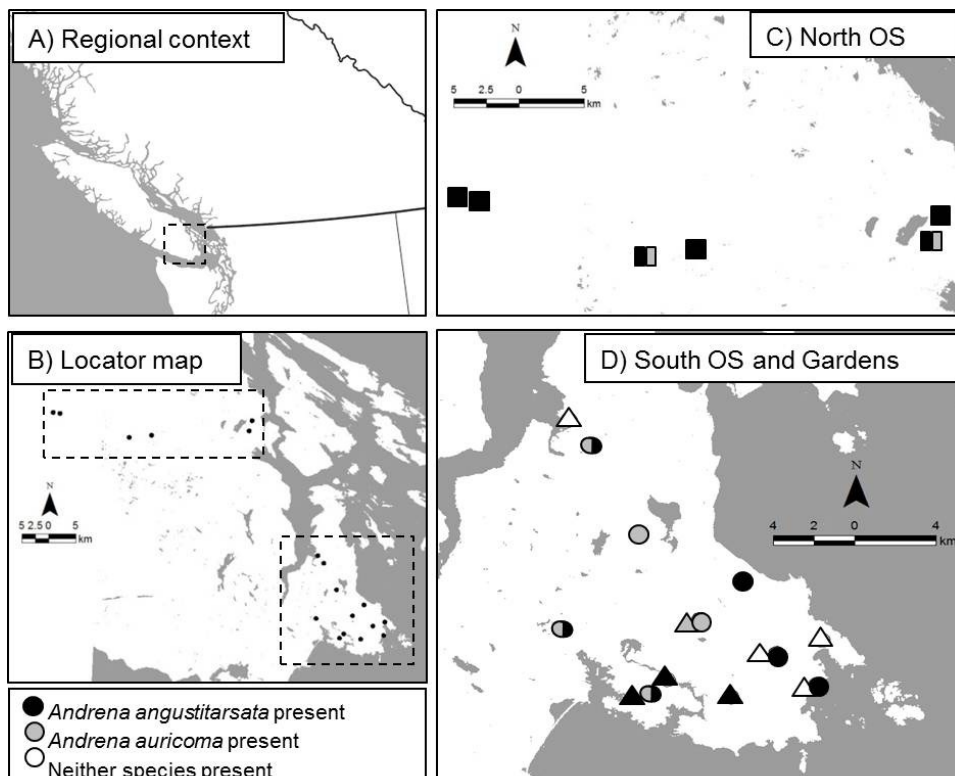
Habitat loss and fragmentation is predicted to have negative effects on biodiversity unless organisms can use the surrounding landscape (or “matrix”) for food or nesting resources (Dunning *et al.* 1992; Fahrig 2001; Wray and Elle 2015). Dietary specialists are expected to be negatively impacted by habitat conversion because the plant species upon which they rely are generally not available in the non-habitat matrix. In studies examining the effects of habitat loss on pollinating insects, specialists consistently decline with reduction in natural habitat (Steffan-Dewenter and Tschamtko 2000; Burkle *et al.* 2013). Britain and the Netherlands experienced parallel declines in bee-dependent plants and specialist bees (Biesmeijer *et al.* 2006), in some cases, because the plant species required by the bees have been locally extirpated. Documenting dietary specialisation, therefore, is important for recognition of threats to bees of particular conservation concern, the plants upon which they rely for offspring provisioning, and potentially how reproductive output of those plants would be impacted by pollinator loss. Such research can be especially interesting in human-dominated landscapes where host plants may vary in availability (MacIvor *et al.* 2014).

We investigated potential pollen specialisation of two mining bees, *Andrena angustitarsata* Vierick and *A. auricoma* Smith (Hymenoptera: Andrenidae) in a highly fragmented oak-savannah ecosystem. Less than 5% of this habitat remains due to residential expansion, agricultural development, and the introduction of invasive species (Fuchs 2001). We noticed that collections of these bees at our study sites were primarily from two species of *Lomatium* (Apiaceae), spring gold (*L. utriculatum* [Nutt. ex Torr. & A. Gray] J.M. Coult. & Rose) and Indian consumption plant (*L. nudicaule* [Pursh] J.M. Coult. & Rose), suggesting the bees may be oligolectic. However, the range of both bees comprises the majority of Western North America, and the floral records included in species descriptions are quite diverse (LaBerge and Ribble 1975; LaBerge 1989). We have also more recently been working in urban and suburban neighborhoods near oak-savannah fragments, where the host plants are not available (Wray and Elle 2015). We were therefore interested in documenting the proportion of visits by *A. angustitarsata* and *A. auricoma* females to Apiaceae (at our field sites, the two *Lomatium* species and *Sanicula crassicaulis* Poepp ex. DC) vs. other plant species, and the composition of pollen collected by females for nest provisioning, to better understand whether these *Andrena* spp. are facultative oligolectes in our region.

## METHODS

As part of two larger research projects, bees were collected directly from flowers in oak-savannah fragments of the Cowichan Valley (“North OS”, 2008–2010), and oak-savannah fragments and urban residential gardens on the Saanich Peninsula (“South OS”, “South Gardens”, 2012) of Vancouver Island, British Columbia (Fig. 1, Gielens 2012; Wray and Elle 2015). Bees collected from flowers of a single plant species (or genus in gardens, where botanical cultivars were common) were euthanized in the same cyanide tube during the duration of a sample period. For North OS sites, two 15-minute plant-species-specific samples were collected on each day sampling occurred (Gielens 2012). In South OS sites and gardens, two 30-minute samples were taken on each day of sampling, with collections made from any plant species in flower, although collected insects were still kept separate by plant species (Wray and Elle 2015). For both studies, collection dates comprised the majority of the flowering season of our sites, from April to July. Bees of the species of interest were collected from 11 April to 27 June, depending on year and site, with the majority collected in May. Because of the variability in

numbers of bees collected at different sites, we calculated the proportion of *A. angustitarsata* and *A. auricoma* collected on different plant species within a geographic region (i.e., North OS, South OS, South Gardens), rather than by sites within a region.



**Figure 1.** Maps illustrating locations of study sites and which focal species were collected at each. Land is white and ocean is grey. Dashed boxes indicate the area magnified in subsequent panels. A) Vancouver Island in the broader regional context of British Columbia (from iMapBC, <http://maps.gov.bc.ca/ess/sv/imapbc/>). B) Locator map of southern Vancouver Island, with two regions of study outlined. C) North Oak-Savannah (OS) sites (squares). D) South OS (circles) and South Gardens (triangles). Symbol colour indicates species collected (black: *Andrena angustitarsata*; grey: *A. auricoma*; split symbols: both species; white: neither).

Female bees were visually examined for the presence of scopal pollen, and a random sample of those individuals was included in the analysis. Only pollen from the tibial scopa and propodeal corbicula (i.e., pollen-carrying regions of *Andrena*) was analysed because our intention was to investigate the pollen collected for offspring provisioning. Using pollen from these areas also reduced the likelihood of any contamination by non-scopal pollen from our cyanide tubes. The pollen load from the scopa of one leg was scraped into a 1-mL centrifuge tube with a sterilized needle. In addition, the leg and propodeum were washed with 1mL of 70% alcohol. The pollen/alcohol mixture was centrifuged at 3500 rpm for 5 min, discarding the supernatant after centrifuging. Pollen pellets were left in centrifuge tubes to dry for 30 min. We added 10uL Caberla solution (6mL glycerin, 12mL 95% ethyl alcohol, 18mL distilled water, 50mg basic fuchsin stain [pararosaniline]), and 10uL glycerin to the pollen pellet, and tubes were agitated to suspend pollen in solution. We transferred the entire 20-uL sample to a glass slide, covered the pollen solution with a cover slip, and used clear nail polish to seal the edges.

We identified pollen under a light microscope at 400X magnification with the assistance of reference pollen slides made from flowers collected from our sites and from the SFU Palynology Lab. Pollen grains were identified to “type” at the lowest possible taxonomic level—species, genus, or family (Table 1). Pollen morphology is often conserved within a genus or family and so identification to species is frequently not possible. When pollen was identified to genus or family, but could not be unambiguously assigned to species using our reference collection, we inferred likely species based on vegetation-sampling data from our sites (Gielens 2012; Wray and Elle 2015) and include a note in the table. Pollen grains were counted in four random “transects” of the cover slip (as in Müller 1996). Samples with insufficient pollen (<50 grains) were not included in results. Any pollen types that contributed less than five percent to the total pollen count on a slide were deleted to account for the possibility of trace contamination (Cane and Sipes 2006). However when averaged across all samples within a geographic region (North OS, South OS, South Gardens), some pollen types still contributed less than five percent to the total pollen count across all slides from that region. In addition to presenting the average proportion of pollen types for different regions, we include information on the incidence of “pure” loads (100% host pollen once trace contaminants comprising <5% removed, as in Cane and Sipes 2006)

**Table 1**

Description of pollen types, including the family, genera, and species combined into the different types. When pollen could not be attributed to a particular plant species using our reference collection, likely species identities listed in the table are based on our vegetation surveys, as indicated.

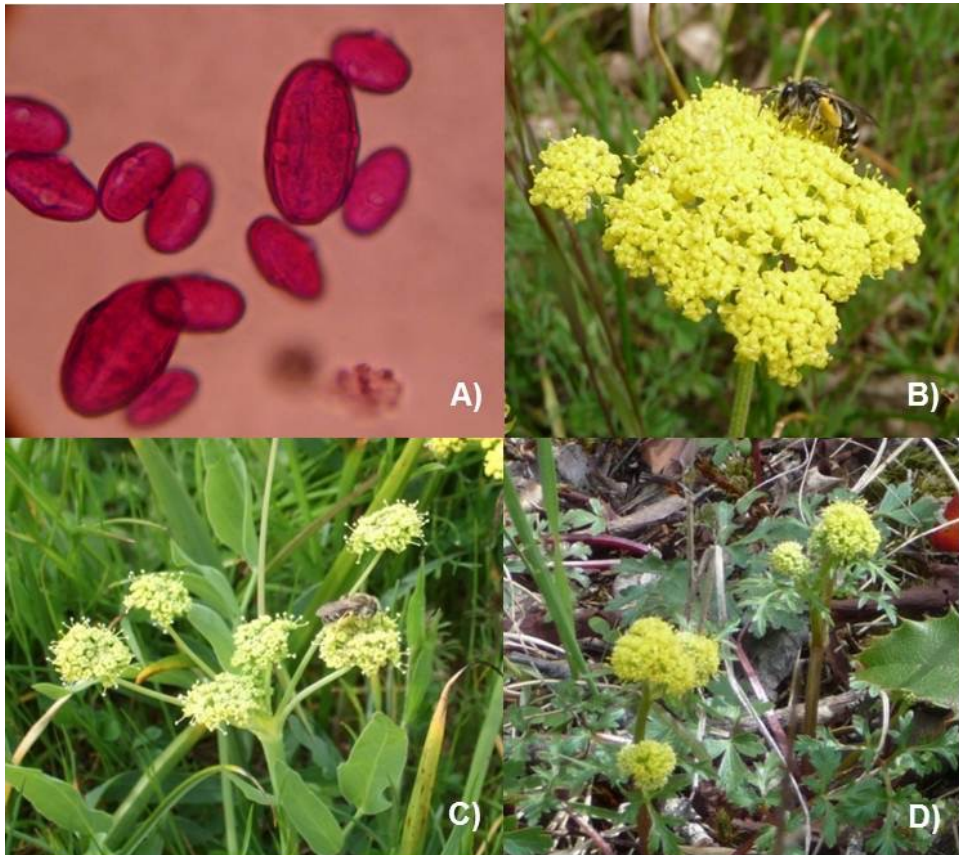
Pollen type	Family/genera/species included
Apiaceae-1	<i>Lomatium utriculatum</i> , <i>L. nudicaule</i>
Apiaceae-2	<i>Sanicula crassicaulis</i>
Asteraceae	Many species possible. Based on our vegetation surveys, this pollen type could include <i>Achillea millefolium</i> , <i>Balsamorhiza deltoidea</i> , <i>Bellis perennis</i> , <i>Eriophyllum lanatum</i> , <i>Hypochaeris radicata</i> , and/or <i>Taraxacum officinale</i>
Brassicaceae	Likely <i>Brassica</i> spp., based on our vegetation survey
Rhamnaceae	<i>Ceanothus</i> spp. (probably <i>C. thrysiflorus</i> cv. “Victoria” as this was commonly planted in gardens)
Rosaceae-1	<i>Sorbus</i> spp. (usually <i>S. aucuparia</i> , according to our vegetation survey)
Rosaceae-2	<i>Rosa nutkana</i>
<i>Trifolium pratense</i>	<i>Trifolium pratense</i>
<i>Trifolium repens</i>	<i>Trifolium repens</i>
Other	Caryophyllaceae, Ranunculaceae, Unknown-1

## RESULTS

Two pollen types that could be assigned via morphology to Apiaceae were detected in our samples. Based on our reference collection, Apiaceae-1 is consistent with *Lomatium* spp., and so could be either *L. utriculatum* or *L. nudicale*. The larger grains of Apiaceae-2

are consistent with *Sanicula crassicaulis* (Fig. 2). Inflorescence morphology for these three species is also shown in Figure 2, and all are comprised of dense heads of small flowers.

***Andrena angustitarsata*.** We collected a total of 141 females of this species from oak-savannah fragments in the Cowichan Valley (“North OS”) and on the Saanich peninsula (“South OS”), and from residential gardens on the Saanich Peninsula (“South Gardens”; Table 2). Most were collected from flowers of Apiaceae; 89% in North OS sites, and 98% in the South OS sites (Table 2). In South Gardens, only 11 *A. angustitarsata* were collected, none from flowers of Apiaceae. No plants from this family were blooming in residential gardens during the spring flight period of this bee, although some Apiaceae genera bloom in gardens in July and August (*Astrantia*, *Eryngium*, *Foeniculum*, *Pastinaca*). In gardens, bees were collected from a number of plant species with diverse floral morphologies, including small flowers densely arranged in compact heads or umbels (e.g., *Ceanothus* Linnaeus [Rhamnaceae], *Sorbus* Linnaeus [Rosaceae], *Spiraea* Linnaeus [Rosaceae]) and simple flowers with easily accessible pollen and nectar rewards (*Brassica* spp. Linnaeus [Brassicaceae]).



**Figure 2.** Pollen grains and inflorescence architecture of focal plant species: A) Smaller pollen grains are Apiaceae-1 (includes both *Lomatium utriculatum* and *L. nudicaule*), and larger grains are Apiaceae-2 (*Sanicula crassicaulis*); B) *L. utriculatum*; C) *L. nudicaule*; D) *S. crassicaulis*.

We investigated composition of actively collected pollen (from scopae and corbiculae) for 73 bees (Table 2). Pollen grains counted per slide ranged from 117 to 11,225 grains, with an average of 2,334 grains per slide. Across all North OS sites, *A. angustitarsata* pollen loads were comprised primarily of Apiaceae-1 (83%, *Lomatium* spp.), followed by Rosaceae-1 (13%, *Sorbus* spp.). Brassicaceae and Rosaceae-2 each contributed less than 2% to the total pollen sample, while unknown pollen types combined into the “Other” category were less than 1% (Fig. 3A). Of the 34 North OS bees included in the pollen analysis, 16 (47%) had “pure” pollen loads of Apiaceae-1.

In South OS sites, pollen was almost exclusively Apiaceae-1 (98%). Brassicaceae, Rosaceae-1 and Other each contributed less than 1% to the total pollen composition (Fig. 3C). Of the 31 South OS bees included in the pollen analysis, 28 (90%) had “pure” pollen loads.

In South Garden sites, there was no Apiaceae pollen in samples that could not be attributed to contamination (e.g., 1-2 grains out of several hundred counted per sample). Instead, samples were comprised largely of Rosaceae-1 (42%), Brassicaceae (21%), Rhamnaceae (17%), and *Trifolium repens* (13%, Fig. 3E). *Trifolium pratense* contributed less than four percent to the total, and Other types less than one percent.

***Andrena auricoma*.** There were a total of 49 female *A. auricoma* collected from oak-savannah fragments (19 North OS sites, 30 South OS sites). Only two females were collected from South Garden sites. Females were predominantly collected from flowers of Apiaceae (95% in North OS, 83% in South OS), the majority from plants in the genus *Lomatium* (Table 2).

Pollen composition was investigated for a total of 32 female bees. We counted between 58 and 4,984 grains per slide, with an average of 1,465 grains. The two females collected from South Garden sites were not included in pollen analysis, due to low numbers of pollen grains (<50 grains counted). In both OS regions (North and South), Apiaceae-1 was the dominant pollen type (North: 61%, South: 75%) followed by Apiaceae-2 (North: 37%, South: 19%; Fig. 3B, D). In North OS sites, Rosaceae-1 and *Trifolium repens* each contributed less than 2% (Fig. 3B). In South OS sites, Rosaceae-1 contributed 5% to total pollen counts, and Asteraceae less than 1% (Fig. 3D).

Of the 11 female bees included from North OS, 9 of 11 (82%) had “pure” pollen loads (combined Apiaceae 1 and 2). Of the 19 females included from South OS sites, 17 (89%) had “pure” loads.

## DISCUSSION

We found evidence of preference for Apiaceae pollen for two bee species in oak-savannah habitats on Vancouver Island. Female *Andrena angustitarsata* and *A. auricoma* predominantly visit *Lomatium* spp. and *Sanicula crassicaulis* in this region, and pollen collected to provision nests is largely from the Apiaceae. Dietary specialization is normally considered a characteristic of species, rather than something that varies across a species’ range. The published floral host records for these species are diverse (LaBerge and Ribble 1975; LaBerge 1989), suggesting polylecty. Further evaluation of pollen collection behaviour throughout the ranges of these species would be useful, as it would allow visits for nectar or by male bees to be distinguished from visits by females actively provisioning nests with pollen. Confirmation of observed preferences, an evaluation of preferences in other parts of the species’ ranges, and clarification of the ecological conditions that promote these preferences in otherwise polylectic bees is clearly required.

It is unlikely that these species are simply foraging on Apiaceae due to disproportionate availability of Apiaceae flowers. For example, during the spring bloom of *Lomatium* spp. and *Sanicula crassicaulis*, these plants combined contributed less than 5% to the total cover of blooming flowers recorded in surveys of South OS sites (Wray and Elle 2015). In addition, other pollen sources (e.g., common camas, *Camassia quamash* [Pursh] Greene [Asparagaceae]; great camas, *Camassia leichtlinii* [Baker] S.

Watson [Asparagaceae]) were abundant and available and are consistently used by other solitary mining bees, mason bees, social bumble bees, and honey bees (Gielen 2012; Wray and Elle 2015). Instead, our results indicate a preference for Apiaceae for these two mining bees, particularly plants in the genus *Lomatium*.

**Table 2**

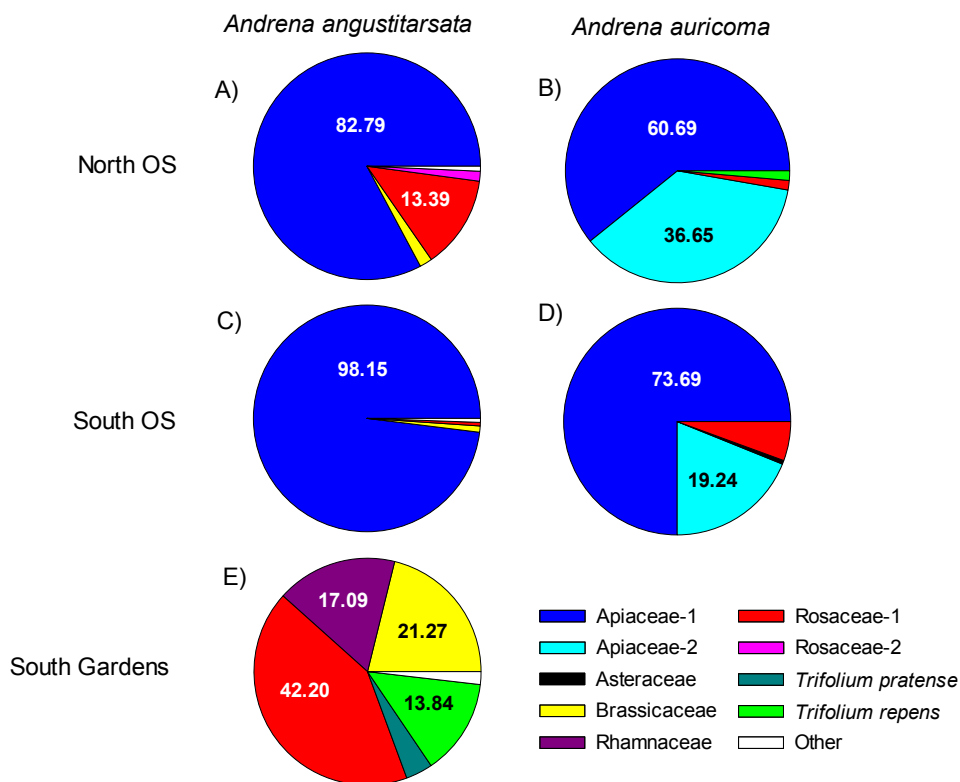
Total numbers of *Andrena angustitarsata* and *Andrena auricoma* collected from different study locations. Of the total collected, we state the number (and percentage, in brackets) of all collected bees that were caught foraging on plants in the Apiaceae, and within Apiaceae, the total that were collected from *Lomatium utriculatum* and *L. nudicaule* combined. The number randomly chosen for pollen analysis is also indicated.

	<i>Andrena angustitarsata</i>			<i>Andrena auricoma</i>	
	North OS	South OS	South Gardens	North OS	South OS
Total number collected	99	42	11	19	30
Collected from Apiaceae	88 (88.9%)	41 (97.6%)	0 (0%)	18 (94.7%)	25 (83.3%)
Collected from <i>Lomatium</i>	85 (85.9%)	40 (95.2%)	0 (0%)	11 (57.9%)	21 (70.0%)
Included in pollen analysis	34	31	8	11	21

Documenting dietary specialisation and/or preference is highly dependent on considering pollinator sex, and evaluating pollen loads used for rearing offspring (Cane and Sipes 2006). *Andrena angustitarsata* is considered a polylectic species, with over 2000 females and 1400 males collected on plants from 61 genera in 24 families in Western North America and included in the revision by LaBerge (1989). These collections include records from multiple species of *Lomatium* and *Sanicula*, as well as *Ceanothus*, *Ranunculus* Linnaeus (Ranunculaceae), *Salix* Linnaeus (Salicaceae), *Brassica*, and *Spiraea*. Similarly, *Andrena auricoma* has been collected from flowers of 44 genera and is also documented to be polylectic (LaBerge and Ribble 1975). The most frequent collections in decreasing order were from *Ranunculus*, *Descurainia* Webb and Berth (Brassicaceae), *Salix*, and *Potentilla* Linnaeus (Rosaceae). However, these collection records do not indicate the sex of the specimen, foraging behaviour (nectar vs. pollen foraging), nor has the pollen collected by female bees been examined. Without this information, one cannot confidently assume these species are polylectic or oligolectic. As such, it is difficult to determine whether Apiaceae preference by *A. angustitarsata* and *A. auricoma* is simply localised to our study region of oak-savannah habitat on Vancouver Island, or if it may be more widespread and present in other habitat types within the broad range of these species. In our region, at least, our data suggest the species should be considered facultative oligolectes, *sensu* Cane and Sipes (2006).

Specialist bees are predicted to be more sensitive to the effects of habitat loss and fragmentation (Davies *et al.* 2000; Henle *et al.* 2004), and our study species were caught in low abundances outside of natural oak-savannah habitat (*A. angustitarsata*: 11 total at three South Garden sites, average 1.4/site out of eight total South Garden sites sampled; *A. auricoma*: 2 total at a single South Garden site, average 0.25/site). The fitness consequences for these bees in gardens are not known, but for other species, the

consequences vary. For example, Praz *et al.* (2008a) found in some oligolectic species, larvae failed to develop on non-host pollen; Haider *et al.* (2013) found within- and among-population variation in offspring development on non-host pollen; and Williams (2003) found no effect on development for specialist larvae reared on non-host pollen. However, successful development on non-host pollen does not necessarily change foraging preference of adults, as Praz *et al.* (2008b) found that larvae successfully reared on non-host pollen preferred their normal host in choice-tests as adults. We do not know if non-Apiaceae pollen would support successful offspring production by these two species in our region, or if such offspring would subsequently maintain oligolecty; this should be studied.



**Figure 3.** Average proportional pollen composition for *Andrena angustitarsata* and *A. auricoma* in North OS (A, B), South OS (C, D), and South Garden sites (E). Numbers in pie sections indicate the percentage a pollen type contributed to the total pollen count.

We found it curious that bees in gardens were collecting pollen from non-host plants that appear (to our eyes) morphologically similar to Apiaceae. *Lomatium utriculatum* has small flowers arranged in flat umbels, and *L. nudicaule* and *S. crassicaulis* have small flowers arranged in spherical clusters (Fig. 2). In gardens, *Sorbus* and *Ceanothus* comprised a large proportion of the diet of the few *A. angustitarsata* collected, and have similar inflorescence architecture to the native host plants. Pollen chemistry has been invoked as an important cue for oligolectic species (e.g., Müller and Kuhlman 2008), but floral morphology may also be important if specialists are limited in their ability to extract resources from flowers with morphology different than that of hosts (Thorp 1979; Müller 1996; Williams 2003). The apparent similarity of visual cues between host and



non-host flowers suggests an investigation of foraging decisions when Apiaceae are unavailable would be worth pursuing in future studies.

Our study provides only a baseline of information on pollen preference in *A. angustitarsata* and *A. auricoma* within BC, and clearly further assessment of pollen provisioning behaviour needs to be done throughout these species' ranges. Our data do suggest that, in the geographically restricted oak-savannah ecosystem on Vancouver Island, *L. utriculatum*, *L. nudicaule*, and *Sanicula crassicaulis* provide vital resources for *A. angustitarsata* and *A. auricoma*. Urban residential gardens in our area support a diversity of bees, including two species in the Megachilidae that are Asteraceae specialists (*Megachile perihirta* Cockerell (Megachilidae) and *Osmia coloradensis* Cresson (Megachilidae); Wray and Elle 2015). Homeowners could consider planting native oak-savannah wildflowers to sustain these, and other specialist bees.

## ACKNOWLEDGEMENTS

Emily Helmer and Rolf Mathewes of the SFU Palynology Lab provided pollen reference slides to complement those made by our research group. Funding was provided by the Natural Sciences and Engineering Council (NSERC) of Canada (Discovery Grant to E. Elle) and by a donation from the SFU "Be Bee Friendly" Campaign (D. McKinley, C. Choi, P. Ficzyz, S. Ghuman, and P. Raimbault). We thank two anonymous reviewers for their comments on the manuscript.

## REFERENCES

- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., and Kunin, W. E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**: 351–4. doi: 10.1126/science.1127863.
- Burkley, L. A., Marlin, J. C., and Knight, T. M. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence and function. *Science*, **339**: 1611–1615. doi: 10.1126/science.1232728.
- Cane, J. H., and Sipes, S. 2006. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In *Plant-Pollinator Interactions: From Specialization to Generalization*. Edited by N. M. Waser and J. Ollerton. The University of Chicago Press, Chicago, USA. Pp. 99–122.
- Davies, K. F., Margules, C. R., and Lawrence, J. F. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology*, **81**: 1450–1461. doi: 10.1890/0012-9658(2000)081[1450:WTOSPP]2.0.CO;2.
- Dunning, J. B., Danielson, B. J., and Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos*, **65**: 169–175. doi: 10.2307/3544901.
- Elle, E., Elwell, S. L., and Gielens, G. A. 2012. The use of pollination networks in conservation. *Botany*, **534**: 525–534. doi: 10.1139/B11-111.
- Fahrig, L. 2001. How much habitat is enough? *Biol. Conserv.*, **100**: 65–74. doi: 10.1016/S0006-3207(00)00208-1.
- Fuchs, M. A. 2001. Towards a recovery strategy for Garry oak and associated ecosystems in Canada: Ecological assessment and literature review. Technical Report GBEI/EC-00-030.
- Gielens, G. A. 2012. Pollen limitation and network asymmetry in an endangered oak-savannah ecosystem. M. Sc. thesis, Simon Fraser University, Burnaby, Canada.
- Haider, M., Dorn, S., and Müller, A. 2013. Intra- and interpopulational variation in the ability of a solitary bee species to develop on non-host pollen: implications for host range expansion. *Funct. Ecol.*, **27**: 255–263. doi: 10.1111/1365-2435.12021.
- Henle, K., Davies, K. F., Kleyer, M., Margules, C., and Settele, J. 2004. Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.*, **13**: 207–251. doi: 10.1023/B:BIOC.0000004319.91643.9e.
- LaBerge, W. E. 1989. A Revision of the Bees of the Genus *Andrena* of the Western Hemisphere . Part XIII . Subgenera *Simandrena* and *Taeniandrena*. Transactions of the American Entomological Society, **115**: 1–56.

- LaBerge, W. E., and Ribble, D. W. 1975. A Revision of the Bees of the Genus *Andrena* of the Western Hemisphere . Part VII . Subgenus *Euandrena*. Transactions of the American Entomological Society, **101**: 371–446.
- Linsley, E. G., and MacSwain, J. W. 1958. The significance of floral constancy among bees of the genus *Diadasia* (Hymenoptera, Anthophoridae). Evolution, 12: 219–223.
- MacIvor, J. S., Cabral, J. M., and Packer, L. 2014. Pollen specialization by solitary bees in an urban landscape. Urban Ecosyst., **17**: 139–147. doi: 10.1007/s11252-013-0321-4.
- Michener, C. D. 2007. The Bees of the World, Second ed. John Hopkins Press, Baltimore, USA.
- Müller, A. 1996. Host-plant specialization in Western Palearctic anthidine bees (Hymenoptera: Apoidea: Megachilidae). Ecological Monographs, **66**: 235–257. doi: 10.2307/2963476
- Müller, A. and Kuhlmann M. 2008. Pollen hosts of western palaeartic pees of the genus *Colletes* (Hymenoptera, Colletidae): the Asteraceae paradox. Biological Journal of the Linnean Society 95:719–733. doi: 10.1111/j.1095-8312.2008.01113.x
- Praz, C. J., Müller, A., and Dorn, S. 2008a. Specialized bees fail to develop on non-host pollen: Do plants chemically protect their pollen? Ecology 89 (3):795–804. doi 10.1890/07-0751.1
- Praz, C. J., Müller, A., and Dorn, S. 2008b. Host recognition in a pollen-specialist bee: evidence for a genetic basis. Apidologie, **39**: 547–557. doi: 10.1051/apido:2008034.
- Robertson, C. 1925. Heterotropic bees. Ecology 6:412–436.
- Sipes, S. D., and Tepedino, V. J. 2005. Pollen-host specificity and evolutionary patterns of host switching in a clade of specialist bees (Apoidea: *Diadasia*). Biol. J. Linn. Soc., **86**: 487–505. doi: 10.1111/j.1095-8312.2005.00544.x.
- Steffan-Dewenter, I., and Tscharntke, T. 2000. Butterfly community structure in fragmented habitats. Ecol. Lett, **3**: 449–456. doi: 10.1046/j.1461-0248.2000.00175.x.
- Thorp, R. W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. Ann. Missouri Bot. Gard. 66:788–812.
- Williams, N. M. 2003. Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). Oecologia 134: 228–237.
- Wray, J. C., and Elle, E. 2015. Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem. Landscape Ecol., **30**: 261–272. doi: 10.1007/s10980-014-0121-0.