

Diversity of cavity-nesting bees (Hymenoptera: Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada

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Abstract—Solitary cavity-nesting bees, especially trap-nesting Megachilidae, have great potential as commercial pollinators. A few species have been developed for crop pollination, but the diversity, abundance, and potential pollination contributions of native cavity-nesting bees within agricultural systems have seldom been assessed. Our objectives were to compare the diversity and fecundity of cavity-nesting bees in Nova Scotia in natural ecosystems with those in apple orchards under three levels of management, using trap nests, and to determine whether any native bees show promise for development as pollinators. Our results show that species richness and numbers of bees reared from trap nests in commercially managed orchards, abandoned orchards, and natural habitats were similar, and species' compositional patterns were not unique to specific habitats. Trap nests can be used to increase and maintain cavity-nesting bee populations within Nova Scotia apple orchards. *Osmia tersula* Cockerell (Megachilidae), which accounted for almost 45% of all bees captured and was the most abundant species nesting in all habitats evaluated, should be assessed for potential as a commercial pollinator of spring-flowering crops. The influence of natural cavities on bee species richness in trap-nesting surveys is also discussed.

Résumé—Les abeilles solitaires qui nichent dans les cavités, particulièrement les Megachilidae qui logent dans les nids-pièges, représentent un important potentiel de pollinisateurs commerciaux. Quelques espèces ont été utilisées pour la pollinisation des cultures, mais on a rarement évalué la diversité, l'abondance et la contribution potentielle à la pollinisation des abeilles qui nichent dans les cavités dans les systèmes agricoles. Notre objectif est de comparer à l'aide de nids-pièges la diversité et la fécondité des abeilles qui nichent dans les cavités dans les écosystèmes naturels et dans des pommeraies gérées sous trois régimes différents en Nouvelle-Écosse, ainsi que de déterminer s'il y a des abeilles indigènes qui offrent un potentiel pour servir à la pollinisation. Nos résultats montrent que la richesse spécifique et le nombre d'abeilles obtenues dans les nids-pièges sont semblables dans les pommeraies sous gestion commerciale, dans les pommeraies abandonnées et les habitats naturels; de plus, les patrons de composition spécifique ne sont pas propres aux différents habitats. Dans les pommeraies de Nouvelle-Écosse, les nids-pièges peuvent servir à augmenter et à maintenir les populations d'abeilles qui nichent dans les cavités. *Osmia tersula* Cockerell (Megachilidae), qui représente presque 45 % de toutes les abeilles capturées et qui est l'espèce la plus abondante à nicher dans tous les habitats étudiés, devrait être évalué en vue d'une utilisation éventuelle comme pollinisateur des cultures qui fleurissent au printemps. Nous discutons aussi de l'influence des cavités naturelles sur la richesse spécifique des abeilles dans les inventaires faits à l'aide de nids-pièges.

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Introduction

Bees (Hymenoptera: Apoidea) are the most important pollinators (Kevan and Baker 1983; Free 1993), and releasing them into agricultural landscapes is the fastest and most effective way to provide sufficient numbers to meet the pollination requirements of many crops. This is achieved most often with the use of honey bee, *Apis mellifera* L. (Apidae: Apini), colonies (Free 1993), and more recently with managed colonies of bumble bees (Apidae: Bombini), which are commercially available year-round and have proved invaluable in greenhouse settings (Kevan *et al.* 1991; Thorp 2003, and references therein). In tropical areas, stingless bee (Apidae: Meliponini) colonies have also shown potential for management as crop pollinators (Heard 1999).

For solitary bees, nesting biology often dictates the ease with which they can be developed and managed for pollination; although many ground-nesting species are important crop pollinators (Free 1993), only the alkali bee, *Nomia melanderi* Cockerell (Halictidae: Nomiinae), has been extensively studied and successfully developed for commercial pollination of any crop (Free 1993; Stephen 2003, and references therein). Cavity-nesting bees, especially those of the family Megachilidae, have shown the greatest potential for development as manageable pollinators, as many species readily accept artificial nesting materials, including trap nests (Krombein 1967; Stubbs and Drummond 2001; Cane *et al.* 2007). Trap nests have been used to study nesting biology (*e.g.*, Krombein 1967), develop and evaluate potential crop pollinators (*e.g.*, Torchio 2003), conduct studies of species diversity (*e.g.*, Steffan-Dewenter 2002, 2003), and provide additional nesting sites for increasing and conserving bee populations (*e.g.*, Stubbs and Drummond 2001).

Several megachilid bee species show floral preferences and can be exploited for pollination of specific crops. Examples include *Megachile rotundata* (Fabr.) for alfalfa pollination (Stephen 2003) and *Osmia* Panzer species for tree fruits (Bosch and Kemp 2001; Torchio 2003). However, the commercial status of *Osmia* spp. in general is not known (Stephen 2003), although they have certainly shown great potential in previous studies of pollination of tree fruit crops, including apple (Bosch and Kemp 2001; Torchio 2003).

Many megachilid bees can be trap-nested in a multitude of habitats and subsequently released

back into agricultural systems (Torchio 2003). Unfortunately, agricultural practices often make these systems unfavourable for many beneficial organisms through pesticide use (Kevan 2001) as well as causing loss of natural habitat and plant diversity through fragmentation (Banaszak 2000; Steffan-Dewenter 2002; Steffan-Dewenter and Leschke 2003), altering natural margins (Corbet 1995; Marshall and Moonen 2002), and reducing nesting-site availability (Westrich 1996). Furthermore, the impact of agricultural practices on overall species richness and subsequent utilization of cavity-nesting bees for pollination within these systems has seldom been assessed.

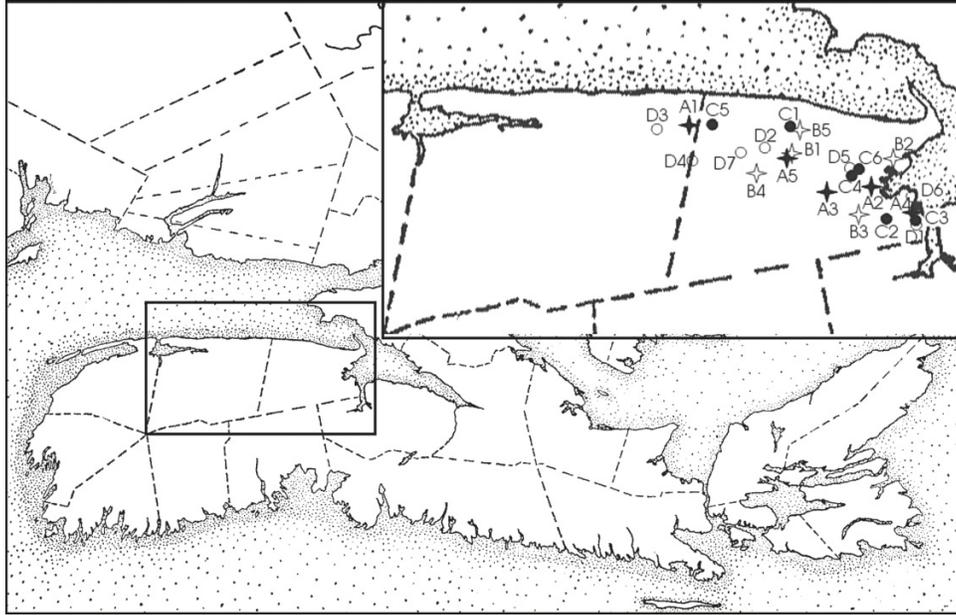
The main objective of our study was to compare the diversity and relative fecundity of cavity-nesting bees within apple orchards in Nova Scotia under three levels of management with those of bees in natural ecosystems. Our expectations were that richness and abundance of cavity-nesting bees would be lowest in sites within habitats with the most intense levels of agricultural management, and would increase with decreasing habitat management; high similarity among sites within each habitat type and low similarity among habitats were expected. A second objective was to determine if any indigenous bee species show promise for development as managed pollinators. To address these objectives we used trap nests to conduct a 3-year survey of cavity-nesting bees within four habitat types: three were apple-orchard systems and one comprised non-agricultural habitats.

Materials and methods

Study sites

In total, 23 sites within Nova Scotia's main agricultural and horticultural region, the Annapolis Valley (Fig. 1), were used during the 3 years of this study. For various reasons not all sites could be used each year; 20 were used in 2000 and 19 in 2001 and 2002 (for details see Appendix A). The sites represented four habitat types: (1) COMM-A: sites A1–A5, which were commercially managed apple orchards within agricultural landscapes surrounded by adjacent orchard blocks or other agricultural crops, *etc.*, routinely mowed and (or) treated with herbicides, and subject to pesticide use; (2) COMM-B: sites B1–B5, which were commercially managed orchard blocks isolated from other agricultural areas and (or) usually surrounded by adjacent woodland or non-agricultural land, also routinely mowed and

Fig. 1. Map of Nova Scotia, Canada. The insert (44.93339–45.31580°N, 64.19303–65.90454°W) shows study sites in four different habitat types in the Annapolis Valley (◆, sites in COMM-A habitat; ◇, sites in COMM-B habitat; ●, sites in ABAND habitat; ○, sites in WILD habitat). For details of sites see Appendix A.



(or) treated with herbicides, and subject to pesticide use; (3) ABAND: sites C1–C6, which were abandoned and (or) unmanaged orchard sites that had not been mowed or sprayed with pesticides for at least 10 years; and (4) WILD: D1–D7, which were mixed natural meadow/woodland habitats at least 5 km from any other sites. Sites within each habitat were at least 5 ha, and were selected to represent varying levels of management and floral-resource availability, COMM-A sites representing one extreme (assumed low floral-resource availability, based on management practices and inspection) and WILD habitats the other (a variety of native floral resources available throughout the season). Site selection was facilitated by data collected for “*Tree Fruit Census of the Annapolis Valley*” (Craig 1998), particularly the “*Orchard Mapping Project*” conducted by the Nova Scotia Department of Agriculture and Marketing in 1995, and through personal scouting and communication with apple growers, integrated pest management consultants, researchers, and (or) extension staff.

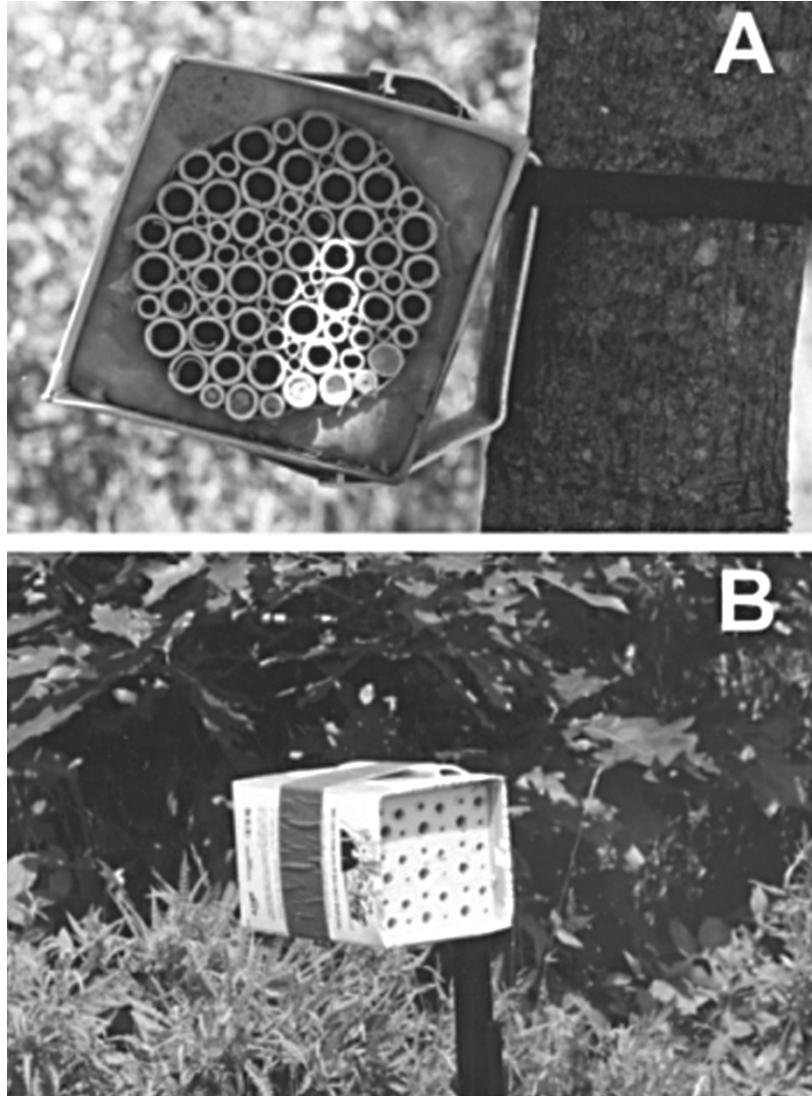
Methods of surveying cavity-nesting bees

Trap nests were used to survey the diversity and abundance (*i.e.*, overall fecundity) of cavity-nesting bees in all the study sites. In 2000 each trap nest consisted of a tight bundle of paper

nesting tubes (20 tubes each of 3, 5, 7, and 9 mm internal diameter; all were 15 cm in length; Jonesville Papertube Corporation, Jonesville, Michigan) placed within a modified 2 L milk carton. The bundle was supported in the milk carton with foam insulation sprayed into the cavity surrounding the tube bundle and allowed to dry (Fig. 2A). For 2001 and 2002 a new design was developed because of problems with the previous design: the absence of spacing between individual nesting tubes (Fig. 2A) was believed to be a deterrent to nesting activity for some bee species (Bosch and Kemp 2001), and moisture getting into the surrounding cavity caused mould problems. For the new design, a front piece of 4 cm thick blue high-density polystyrene foam was placed in the milk carton and nine tubes of each diameter were arranged in a grid pattern within each trap nest (Fig. 2B).

In all years, six trap nests were placed in each site 1–1.5 m above ground level, with southern exposure. Trap nests were fastened to trees or fence posts, or were attached to 1 m high plastic fencing stakes (Fig. 2B) along the periphery of the orchard sites. A strip of Tanglefoot® was placed on the supporting structure of each trap nest approximately 30 cm above the ground to prevent raiding by ants and

Fig. 2. (A) Trap nest design used in 2000 but not in 2001–2002 because the absence of spacing between tubes was believed to discourage nesting. (B) Trap nest design used in 2001–2002; this particular trap is mounted on a fencing stake.



earwigs. In addition, all vegetation blocking nest entrances was removed throughout the season. Trap nests were put out in April (prior to bee flight) and removed in late September each year.

At the end of the bee flight season, trap nests were collected from all sites, labelled, and stored in a screened building until late October. Nesting tubes were then removed from trap nests, sorted according to tube size and type of nesting material collected by the occupants, and then placed in cold storage at 4 °C (60%–70% RH). In late winter (February–March), nesting tubes were placed

in small transparent containers in an incubator at 30 °C. The containers were checked daily for emergence. Emerged insects were collected and later prepared for identification. Total emergence time (in days) was recorded for each trap-nested bee. Specimens collected in this study are currently held in the Packer Bee Collection, York University, Toronto, Ontario. Synoptic collections of voucher species will be retained in the Packer Bee Collection and also placed in the Department of Environmental Biology, University of Guelph, Guelph, Ontario and the Canadian National Collection, Ottawa, Ontario.

Data analyses

Trap nests as a sampling unit consist of nesting tubes containing related individuals (*i.e.*, eggs laid by one nesting female); the “capture” data for individuals are therefore not independent. Therefore, taxon sampling curves and methods of comparison based on random and independent resampling of data (*i.e.*, rarefaction) were deemed inappropriate. To summarize the relationship between the species collected and the number of individuals reared for each habitat type, rank-abundance plots were prepared using data pooled for all 3 years. Species richness and the number of bees reared for each habitat and year were compared using two-factor analysis of variance (ANOVA) (Minitab Inc. 2000); Tukey’s test ($P = 0.05$) was used to examine possible pairwise differences. The Berger–Parker dominance index (Magurran 2004) was determined for each site, and habitat/years were compared by two-factor ANOVA as above. This index was chosen because it provides a comparable measure of dominance for the most abundant species within a site (Magurran 2004). Similarly, species dominance (SD) (*i.e.*, total proportional abundance of each species) was determined using the following formula:

$$SD = (S_i/S_{tot}) \times 100$$

where S_i represents the number of individuals of species i and S_{tot} represents all bees collected during the 3-year study. In addition, frequency of occurrence (FO) was calculated for the 3 years using the following formula (after Buschini 2006):

$$FO = (SM_i/SM_{tot}) \times 100$$

where SM_i represents samples containing species i and SM_{tot} represents the total number of samples. For each species, FO was calculated at two levels for each habitat for all 3 years: (1) trap nests and (2) sites within each habitat.

Chi-square analysis (Zar 1999) was employed to determine within-habitat variability in productivity (*i.e.*, total number of bees reared from each site within a habitat) for each year. Fecundity (*i.e.*, number of bees per nesting tube) for each habitat was also compared using χ^2 analysis (Zar 1999); expected values for each habitat were calculated using the following formula:

$$\hat{E} = T_{hab} \times (N/T_{tot})$$

where T_{hab} is the number of nesting tubes recovered in each habitat, N is the total number of

bees recovered, and T_{tot} is the total number of nesting tubes recovered; data for all years were pooled.

To determine which habitats showed the highest levels of internal similarity (*i.e.*, among sites within each habitat), values of Jaccard’s incidence-based similarity index (S_j) (Magurran 2004) for all site-pair comparisons within each habitat for 2000–2002 were pooled and compared using ANOVA with Tukey’s tests ($P = 0.05$) to examine the possible pairwise differences. Species composition was also compared among the sites using Jaccard’s incidence-based dissimilarity index ($1 - S_j$) for 2001–2002, calculated using Community Analysis Package 3.2 (Seaby *et al.* 2004). The resulting matrix was analyzed by means of cluster analysis using average linkage, and a dendrogram was produced. Cluster analysis was chosen over ordination techniques because there were *a priori* reasons for suspecting that the data would fall into four discrete groups based on the chosen habitat types (Seaby *et al.* 2004).

The nest tube diameter preference of each bee species was summarized using Levins’ (1968) normalized niche breadth measure (B). B values ranged from 0.25 (the females of that species chose only nesting tubes of one diameter to provision) to 1.0 (nesting tubes chosen by a species were equally distributed across diameters).

Results

Abundance and richness patterns

Throughout the 3-year study period, 4102 individual bees representing two families and 18 species were reared from approximately 400 provisioned trap nest tubes from the sites surveyed, 5 of which were cleptoparasites from the megachilid genera *Coelioxys* Latreille and *Stelis* Panzer (Table 1). *Hylaeus verticalis* (Cresson) (Apoidea: Colletidae) and two megachilid species, *Heriades carinata* Cresson and its cleptoparasite *Stelis coarctatus* Crawford, are new records for Nova Scotia (see Sheffield *et al.* 2003). A fourth species, *Megachile pugnata* Say, though not reported by Sheffield *et al.* (2003), was previously reported from Nova Scotia from two specimens by Ivanochko (1979). In 2001, 17 of the 18 species were collected; 9 species were collected in 2000 and 14 in 2002 (Table 1). The total number of bees reared from individual sites showed great variability within habitats (Table 2), but significant differences were not observed across habitat

Table 1. Bee species trap-nested in the Annapolis Valley of Nova Scotia throughout 2000–2002, showing the years of collection, Levins' (1968) normalized niche breadth measure (*B*), species dominance (SD), and frequency of occurrence (FO) for all nests and across sites within four habitat types.

Species*	Habitat														
	COMM-A				COMM-B				ABAND				WILD		
	2000	2001	2002	<i>B</i>	SD	FO _{nests}	FO _{site}								
<i>Hylaeus annulatus</i> (L.)	Yes	Yes	Yes	0.38	2.8	2.2	13.3	4.4	20	5.1	30.8	8.9	40	—	—
<i>H. verticalis</i> (Cresson)	No	No	Yes	0.25	0.2	—	—	1.1	6.7	—	—	1.1	6.7	—	—
<i>Megachile centuncularis</i> (L.) ^A	No	Yes	Yes	0.57	3.6	11.1	40	—	—	—	—	—	—	—	—
<i>M. inermis</i> Provancher ^B	Yes	Yes	Yes	0.32	13.8	13.3	46.7	14.4	46.7	20.5	69.2	20	46.7	—	—
<i>M. pugnata</i> Say	No	Yes	Yes	0.56	6.0	13.3	33.3	2.2	13.3	2.6	15.4	6.7	26.7	—	—
<i>M. relativa</i> Cresson ^{A,B,C}	Yes	Yes	Yes	0.52	21.4	22.2	66.7	7.8	40	23.1	61.5	27.8	73.3	—	—
<i>M. rotundata</i> (Fabr.)	No	Yes	Yes	0.25	0.9	4.4	13.3	—	—	1.3	7.7	—	—	—	—
<i>Hoplitis spoliata</i> (Provancher) ^D	No	Yes	Yes	0.45	1.4	3.3	20	—	—	11.5	15.4	—	—	—	—
<i>Osmia atriventris</i> Cresson	Yes	Yes	No	0.67	0.5	—	—	2.2	13.3	1.3	7.7	—	—	—	—
<i>O. bucephala</i> Cresson	Yes	Yes	No	0.25	0.5	—	—	1.1	6.7	1.3	7.7	—	—	—	—
<i>O. coerulea</i> (L.)	Yes	Yes	Yes	0.56	1.8	3.3	13.3	—	—	7.7	23.1	—	—	—	—
<i>O. tersula</i> Cockerell	Yes	Yes	Yes	0.45	43.4	28.9	60	27.8	86.7	42.3	69.2	42.2	86.7	—	—
<i>Heriades carinata</i> Cresson ^E	No	Yes	Yes	0.25	0.9	—	—	1.1	6.7	1.3	7.7	1.1	6.7	—	—

<i>Coelioxys funeraria</i> Smith ^B	Yes	Yes	Yes	0.47	1.1	5.6	26.7	6.7	26.7	6.4	15.4	13.3	40	—	—
<i>C. moesta</i> Cresson ^A	No	Yes	Yes	0.60	1.0	5.6	20	—	—	3.8	23.1	2.2	13.3	—	—
<i>C. porterae</i> Cockerell ^C	Yes	Yes	No	0.50	0.05	—	—	1.1	6.7	—	—	—	—	—	—
<i>Stelis submarginata</i> (Cresson) ^D	No	Yes	Yes	0.37	0.2	—	—	1.1	6.7	5.1	15.4	—	—	—	—
<i>S. coarctatus</i> Crawford ^E	No	Yes	No	0.25	0.05	—	—	—	—	1.3	7.7	1.1	6.7	—	—

Note: For a description of the four habitat types see the text. Underlined FO values are the highest in that column.

*Species followed by the same letter are matched non-cleptoparasitic hosts (above the broken line) or cleptoparasites (below the broken line).

Table 2. Chi-square values for total bee numbers compared among sites within the four habitat types in the 3 years of the study.

	2000	2001	2002
COMM-A	19.7	119.9	800.8
COMM-B	48.4	66.6	136.2
ABAND	38.4	59.2*	224.0*
WILD	98.5	47.5	823.9

Note: For a description of the four habitat types see the text. Critical values are as follows: $\chi^2_{0.05,4} = 9.488$ and $\chi^2_{0.05,3} = 7.815$ (for values with an asterisk) (Zar 1999).

categories ($F_{3,42} = 1.13$, $P = 0.347$) (Table 3). Three sites yielded more than 300 bees in 2002: sites A3 and A4 in the COMM-A habitat and D1 in the WILD habitat. The total number of bees reared from trap nests increased by a factor of 1.8 between 2000 (485 individuals) and 2001 (855 individuals) and by 3.1 between 2001 and 2002 (2762 individuals). Significantly more bees were collected per habitat in 2002 than in 2000 and 2001, but numbers did not differ between the latter 2 years ($F_{2,42} = 11.39$, $P > 0.001$; Tukey's test, $P = 0.05$) (Table 3). The WILD and COMM-A habitats yielded the greatest abundance of bees overall, although the ABAND habitat was also productive in 2002 (Table 3). No significant interactions between site and year were observed ($F_{6,42} = 0.85$, $P = 0.542$).

In the WILD habitat, 10 species were collected in trap nests during the 3-year period, fewer than in all other habitat types (Fig. 3). The ABAND habitat supported the highest species richness (15 species), followed by COMM-B (13 species) and COMM-A (12 species) (Fig. 3). However, no significant differences in the number of species per habitat were found ($F_{3,42} = 1.44$, $P = 0.244$), although differences were observed among years ($F_{2,42} = 9.91$, $P > 0.001$), with significantly more species per habitat in 2002 than were observed in 2000, and numbers in 2001 not differing significantly from those in either of those years (Tukey's test, $P = 0.05$). No significant interactions between site and year were observed ($F_{6,42} = 1.71$, $P = 0.143$). The maximum number of species collected at any site within the 3 years was 9 (COMM-A, site A3, in 2002). Two other COMM-A sites (A2 and A4) had moderate (≥ 7 species) species diversity in 2002, as did one COMM-B site (B1), two ABAND sites (C3 in 2001, C6 in 2002), and one WILD site (D4).

Overall fecundity varied significantly among habitats ($\chi^2_{0.05,3} = 76.75$), being much higher than expected in the WILD habitat and lower than expected in the ABAND habitat, while the COMM-A and COMM-B habitats yielded close to the expected number of bees (Fig. 4). No significant variation in the Berger–Parker dominance index was observed across habitats ($F_{3,42} = 0.86$, $P = 0.470$), but variation was observed across years ($F_{2,42} = 5.13$, $P = 0.01$), values being lower in 2000 than in 2002 (Tukey's test, $P = 0.05$). No significant interactions between site and year were observed ($F_{6,42} = 1.58$, $P = 0.176$). The most abundant species was *Osmia tersula* Cockerell, which accounted for 43.4% of the total bees reared from all sites in the 3 years (see SD values in Table 1) and was the most common species encountered in all habitats (Fig. 3). *Osmia tersula* was the most frequently collected species, using 27%–29% of the trap nests within the commercial orchards (COMM-A and COMM-B) and just over 42% in the ABAND and WILD habitats (see FO_{nest} values in Table 1). It was found in more sites per year ($FO_{\text{site}} = 60\text{--}86.7$) than any other species, although *Megachile relativa* Cresson was slightly more widespread in the COMM-A habitat (Table 1). *Megachile relativa* was the second most abundant species (SD = 21.4%), and with *M. inermis* Provancher (SD = 13.8%) and *M. pugnata* (SD = 6.0%) made up the majority of the remaining bees collected (Table 1). *Stelis coarctatus* was only observed in 2001 (Table 1).

S_j values among sites within each habitat were low (< 0.45 in all cases; data pooled across years), although the WILD habitat showed significantly higher compositional similarity than COMM-A and ABAND; no differences were observed among the other sites ($F_{3,92} = 4.67$, $P = 0.004$; Tukey's test, $P = 0.05$) (Fig. 5). Sites showed no predictable patterns of clustering based on species presence/absence, and sites classified within each of the four habitat categories showed high levels of dissimilarity, each site often appearing in separate groups containing sites from different habitat categories (Fig. 6).

Nesting preferences

Most bee species trap-nested showed a preference for nesting tubes with one or two diameters, as summarized by B values, which were averaged for each species across the 3 years (Table 1). However, 8 of the 18 species provisioned/parasitized fewer than five nesting tubes within the 3-year period. The B value for

Table 3. Summary statistics for trap nest captures, showing numbers of bees reared, numbers of species (mean \pm standard deviation (SD)), and minimum and maximum values observed within each habitat category for 2000–2002 and pooled for all years.

Year	Habitat*	<i>n</i>	Number of individuals		Number of species	
			Mean \pm SD	Range	Mean \pm SD	Range
2000	COMM-A	5	9.4 \pm 6.8	0–19	1.6 \pm 1.1	0–3
2000	COMM-B	5	27.8 \pm 18.3	15–59	2.8 \pm 0.8	2–4
2000	ABAND	5	21.4 \pm 14.3	5–41	2.0 \pm 1.0	1–3
2000	WILD	5	38.4 \pm 30.7	0–86	2.4 \pm 1.5	0–4
2001	COMM-A	5	64.0 \pm 59.8	27–169	4.0 \pm 1.6	2–6
2001	COMM-B	5	21.6 \pm 18.8	0–41	2.2 \pm 1.6	0–4
2001	ABAND	4	68.0 \pm 36.6	30–118	5.0 \pm 1.6	3–7
2001	WILD	5	42.6 \pm 22.5	14–64	3.4 \pm 0.9	3–5
2002	COMM-A	5	168.4 \pm 183.6	0–400	5.0 \pm 4.2	0–9
2002	COMM-B	5	71.4 \pm 49.3	27–131	3.4 \pm 1.9	2–6
2002	ABAND	4	141.8 \pm 102.9	72–291	5.0 \pm 2.2	2–7
2002	WILD	5	204.8 \pm 195.5	13–513	5.2 \pm 1.3	3–6
Pooled	COMM-A	15	80.6 \pm 123.8	0–400	3.5 \pm 2.9	0–9
Pooled	COMM-B	15	40.3 \pm 37.6	0–131	2.8 \pm 1.5	0–6
Pooled	ABAND	13	72.8 \pm 75.8	5–291	3.8 \pm 2.1	1–7
Pooled	WILD	15	95.3 \pm 133.3	0–513	3.7 \pm 1.7	0–6

*For a description of the four habitat types see the text.

Fig. 3. Rank-abundance plots of numbers of trap-nested bees from the four habitat types for 2000–2002. Species are coded as follows: 1, *Hylaeus annulatus*; 2, *H. verticalis*; 3, *Megachile centuncularis*; 4, *M. inermis*; 5, *M. pugnata*; 6, *M. relativa*; 7, *M. rotundata*; 8, *Hoplitis spoliata*; 9, *Osmia atriventris*; 10, *O. bucephala*; 11, *O. coerulea*; 12, *O. tersula*; 13, *Heriades carinata*; 14, *Coelioxys funeraria*; 15, *C. moesta*; 16, *C. porterae*; 17, *Stelis submarginata*; 18, *S. coarctatus*.

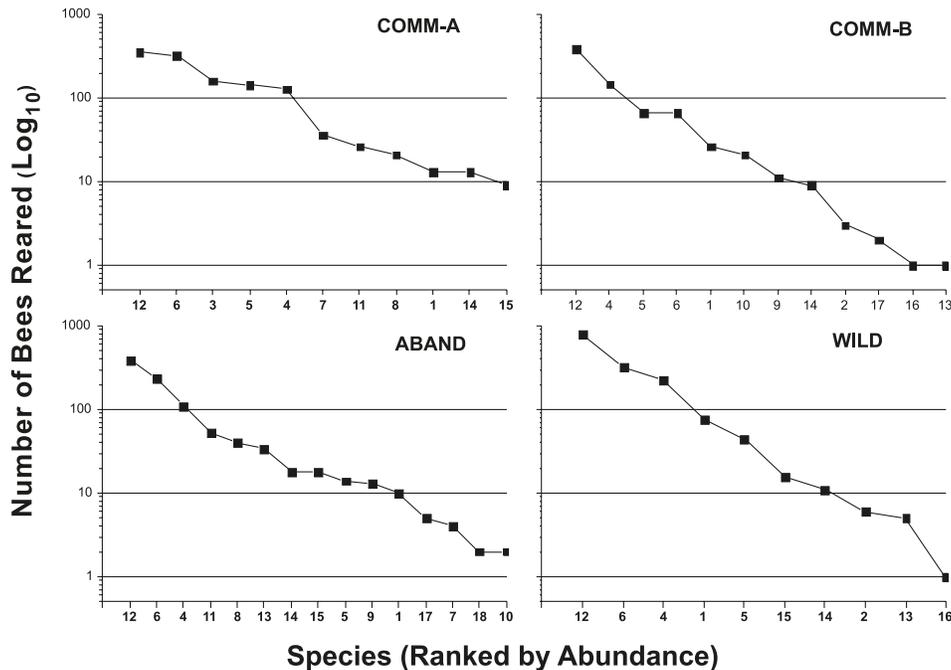


Fig. 4. Observed and expected fecundity (*i.e.*, number of bees produced), based on the number of nesting tubes provisioned in each habitat type; data for 2000–2002 are pooled. The ABAND and WILD habitats accounted for most of the deviation from expected values ($\chi^2_{0.05,3} = 76.75$).

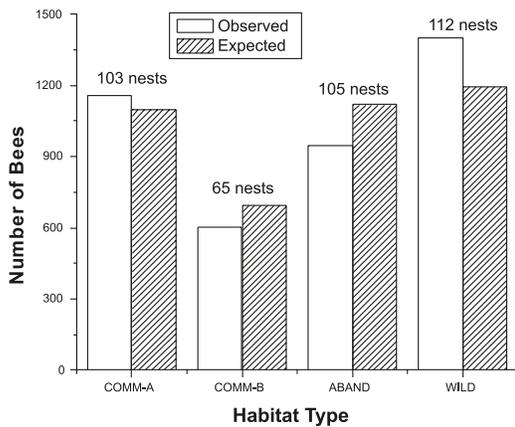


Fig. 5. Mean Jaccard’s incidence-based similarity index values (mean \pm SE) for within-habitat paired-site comparisons; values for 2000–2002 are pooled. Bars with the same letter are not significantly different (Tukey’s test, $P = 0.05$).

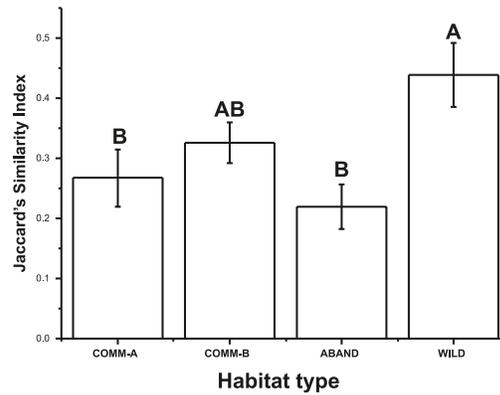
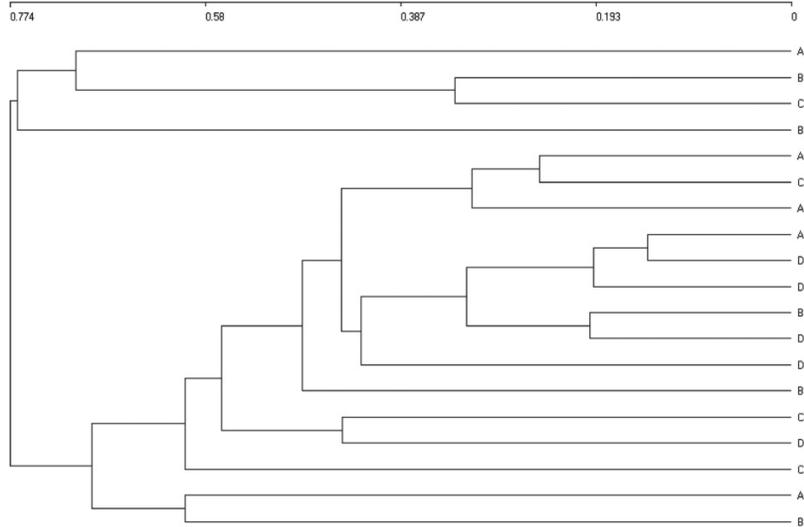


Fig. 6. Dendrogram of Jaccard’s incidence-based dissimilarity ($1 - S_j$) matrix produced by cluster analysis using average linkage methods (Seaby *et al.* 2004); data for 2001–2002 are pooled. Sites are listed at the right-hand side (see Appendix A for an explanation of codes).



O. tersula (0.45) indicated a preference for tubes of two sizes: 5 mm diameter (68%) and, to a lesser extent, 3 mm diameter (29%) tubes were chosen throughout the 3-year study. Although trap-nested less frequently, the other two “small” *Osmia* species (*O. coerulescens* (L.) and *O. atriventris* Cresson) and *H. carinata* also preferred smaller nesting tubes, as did the slightly larger *Hoplitis spoliata* (Provancher) (Table 1). The only non-megachilid bees that

were trap-nested, *Hylaeus annulatus* (L.) and *H. verticalis*, also chose smaller nesting tubes, although a few specimens of *H. annulatus* were reared out of one 9 mm diameter tube in 2002.

The three commonest *Megachile* species also showed preferences, especially *M. inermis*, which was reared most frequently in 9 mm diameter nesting tubes ($B = 0.32$). *Megachile relativa* and *M. pugnata* ($B = 0.52$ and $B = 0.56$, respectively) showed strongest preference

for 7 mm diameter tubes, but were commonly reared out of 5 and 9 mm diameter tubes. Only one *Megachile* species, *M. centuncularis* (L.), was reared out of a 3 mm diameter nesting tube, although it too preferred larger sizes (Table 1). The smallest megachilid, *M. rotundata*, showed a narrow nesting preference, being reared exclusively from 5 mm diameter nesting tubes ($B = 0.25$).

The nest choices of cleptoparasitic Megachilidae were dictated by their hosts. *Stelis submarginatus* (Cresson) ($B = 0.37$) and *S. coarctatus* ($B = 0.25$) were reared out of small nesting tubes with their respective hosts, *H. spoliata* and *H. carinata*. *Coelioxys* species were reared from tubes of multiple sizes ($B \geq 0.47$ for all three species), reflecting their habit of targeting multiple *Megachile* hosts (Table 1).

Discussion

The presence of nesting bees within a given habitat is ultimately related to its suitability, which is influenced by three main factors (after Westrich 1996): (1) the availability of nesting sites (and see Potts *et al.* 2005), (2) the availability of nest-building materials (especially for leafcutters and masons), and (3) sufficient food plants for nectar and pollen. These three resources not only influence the diversity of pollinators within a given habitat by meeting their specific needs, they also strongly affect the abundance and (or) fecundity of certain species through the quantities in which they occur (Müller *et al.* 2006; Williams and Kremen 2007). In this study, one of these resources, nesting sites, was made available to cavity-nesting bees via trap nests.

Overall, the species collected in this survey (Table 1) were representative of Nova Scotia's cavity-nesting bee fauna (Sheffield *et al.* 2003); Sheffield (2006) and Cane *et al.* (2007) recently reviewed the nesting biology of many of these species. Species richness and abundance (*i.e.*, total numbers reared) were expected to be highest within less managed habitats, high similarity was expected among sites within each habitat type, and differences were expected among habitat types based on the management practices in each. These hypotheses were not supported in our study. In fact, the WILD habitat had the lowest species richness (although not significantly so) of the four habitat types (Fig. 3). However, natural habitats within or adjacent to woodlands probably contain abundant

natural nesting sites (*e.g.*, Steffan-Dewenter and Leschke 2003; Morato and Martins 2006), which may decrease trap nest occupation (see Buschini 2006 and references therein). Buschini (2006) compared trap-nesting bees in natural communities in Brazil and found that species richness was lower in forest habitats than in more open swamps and grasslands, and this was attributed to natural-cavity use. To support this observation, other methods of assessing species richness within the same sites are required. However, a complimentary survey using yellow pan traps conducted simultaneously with this study at the same study sites (Sheffield 2006) suggests that many additional species are present and might be using natural nesting cavities within the WILD habitats (Table 4). Cavity-nesting species not utilizing trap nests were collected in pan traps in the WILD habitats, as were species showing a preference for bored or pithy stems, often at abundances several magnitudes higher than those in other habitats (Table 4). This is especially important when one considers the potential fecundity of each female collected in pan traps and its effects on bee population size in subsequent seasons. In our trap nest study, fecundity, measured as the number of bees produced per nesting tube, was much greater in the WILD habitats than in any other habitat (Fig. 4); the unrealized fecundity in the agricultural (and past agricultural) sites may reflect shortages of food plants in these habitats (Williams and Kremen 2007), as weed management occurred routinely, at least within the commercial orchards. Therefore, it seems likely that trap nest surveys alone (*e.g.*, Klein *et al.* 2002; Steffan-Dewenter 2002; Tylianakis *et al.* 2006) provide only a partial picture of potential species richness and abundance of cavity-nesting bees when the results are compared across diverse landscapes.

Diversity and abundance of food plants are important — larger plant communities support larger bee populations and (or) greater fecundity of resident individuals (Müller *et al.* 2006; Williams and Kremen 2007). Often, competition for these food resources affects bee abundance (Forup and Memmott 2005) and fecundity (Paini and Roberts 2004), especially when the main competitors are effective resource exploiters like honey bees. A habitat rich in floral resources is necessary to support bee population growth (Westrich 1996; Potts *et al.* 2003; Müller *et al.* 2006), but management of orchards, particularly weed-control practices

Table 4. Other bee species belonging to the genus *Hylaeus* (Colletidae) and the Megachilidae collected in yellow pan traps within the same sites in four different habitat types in 2000–2002 (data from Sheffield 2006), with notes on nesting biology.

	Nesting biology	Number of pan-trap captures				Source
		COMM-A	COMM-B	ABAND	WILD	
<i>Hylaeus affinis</i> (Smith)	Bored stems?	0	0	0	1	
<i>H. annulatus</i> (L.)	Trap nests	0	0	1	12	This study
<i>H. basalis</i> (Smith)	Bored stems	0	1	4	8	Fye 1965
<i>H. mesillae</i> (Cockerell)	Bored stems?	0	0	6	14	
<i>H. modestus</i> (Say)	Bored stems?	2	11	16	46	Michener 1947
<i>Hoplitis pilosifrons</i> (Cresson)	Dead pithy stems	0	0	2	11	This study
<i>H. spoliata</i> (Provancher)	Trap nests	0	1	2	50	This study; Cane <i>et al.</i> 2007
<i>Osmia atriventris</i> Cresson	Trap nests	1	4	6	7	This study; Cane <i>et al.</i> 2007
<i>O. bucephala</i> Cresson	Trap nests	0	0	1	16	This study; Cane <i>et al.</i> 2007
<i>O. coerulea</i> (L.)	Trap nests	0	2	3	3	This study
<i>O. proxima</i> Cresson	Trap nests	0	0	3	14	Stubbs and Drummond 2001; Cane <i>et al.</i> 2007
<i>O. similima</i> Smith	Trap nests	0	2	14	3	Stubbs and Drummond 2001; Cane <i>et al.</i> 2007
<i>O. tersula</i> Cockerell	Trap nests	2	2	7	19	This study; Cane <i>et al.</i> 2007
<i>Megachile centuncularis</i> (L.)	Trap nests	0	0	0	1	This study
<i>M. inermis</i> Provancher	Trap nests	0	7	6	17	This study
<i>M. pugnata</i> Say	Trap nests	0	0	0	1	This study
<i>M. relativa</i> Cresson	Trap nests	0	1	7	10	This study
<i>Coelioxys porterae</i> Cockerell	Trap nests	0	0	0	2	This study
<i>Stelis foederalis</i> Smith	Trap nests?	1	2	4	8	This study
Total species		4	10	15	19	
Total bees		6	33	82	243	

Note: For a description of the four habitat types see the text.

within and adjacent to blocks, can have an impact on floral-food richness within these settings (Marshall and Moonen 2002; Williams and Kremen 2007), thereby affecting the levels of pollination provided by native bees (Kremen *et al.* 2002). Herbicides targeting broad-leaved weeds can be particularly damaging to bees, which rely on flowers for pollen and nectar. Mowing of vegetation also can have an effect on food-plant availability, although Steffan-Dewenter and Leschke (2003) suggest that this practice may increase the richness of flowering herbs in orchard meadows above levels observed in abandoned ones.

In intensely managed systems, wooded or natural corridors and bordering habitats rich in flowering plants are known to promote diversity of beneficial organisms (Marshall and Moonen 2002) including bees (Corbet 1995; Banaszak 2000). Surprisingly, then, the COMM-A habitat yielded many bees, second only to the WILD habitat (Table 3). It is obvious that some of the sites within the COMM-A habitat were much more suitable for bees than were others, as fecundity was not uniform (Table 2; χ^2 values are exceptionally high for 2001 and 2002), indicating that food plants were probably within the flight range of some species (see Gathmann and Tschardt 2002) in a few sites. However, more species were observed in both the COMM-B and ABAND habitats, in both the trap nest (albeit not significant) and the pan trap surveys (Table 4), indicating that natural borders (and lack of chemicals) are indeed important to bee populations. In agro-ecosystems, the history of each site and the existing management practices used within it can ultimately prove to be the factors that influence bee diversity and abundance (Marshall and Moonen 2002). By using practices that are more friendly to beneficial organisms (*i.e.*, appropriate choice of pesticide, time of application, *etc.*), and by promoting diverse plant communities in “no-pesticide zones”, cavity-nesting bees can be encouraged to nest in and adjacent to agricultural landscapes (Kremen *et al.* 2002). Under such conditions, the species richness and fecundity of cavity-nesting bees within a site would be influenced by the presence of nesting sites, both natural and artificial.

Based on our findings, at least 18 indigenous species of cavity-nesting bees can be trap-nested throughout a range of habitats in the Annapolis Valley, possibly more if pithy and (or) hollow stems were to be used in addition to

trap nests with paper nesting tubes (Table 4). Even under conditions of commercial orchard management, a diverse assemblage of bees was trap-nested and exhibited species richness similar to that in unsprayed and (or) wild habitats. In addition, several species (*i.e.*, *O. tersula*, *M. inermis*, *M. centuncularis*, and *M. relativa*) appear to be agrobionts — doing as well or better in agro-ecosystems than in wild sites. Despite the fact that all occupants of trap nests were removed without replacement from the sites each year, the number of bees reared each year continued to increase significantly, especially in 2002.

This study demonstrated the potential of *O. tersula* as a new megachilid bee for commercial pollinator management in orchards. In Nova Scotia, *Osmia* spp. are the only Megachilidae active early in the spring after overwintering as adults, apparently a derived characteristic within the Megachilidae (Bosch *et al.* 2001). The remaining members of the megachilid tribes Osmiini, Anthidiini, and Megachilini in Nova Scotia are strictly summer bees; it would be difficult to synchronize their emergence with the pollination period of spring-flowering crops, including most tree-fruit species. *Osmia tersula* was commonly trap-nested in high numbers in many sites across all habitats (Table 1, Fig. 3). In addition, its early-season emergence and the fact that it visits apple flowers (Sheffield *et al.* 2003) as a pollen source (C.S. Sheffield, unpublished data) suggest its potential as a manageable pollinator of this crop. Knowing that several potentially manageable pollinators are in these systems is encouraging from the standpoint of increasing their numbers. The information gained concerning the nesting biology of these species, including tunnel diameters preferred for maximizing fecundity and promoting a desirable sex ratio, and flower-use patterns, provides the first steps in promoting and developing cavity-nesting species for pollination management.

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Appendix A

Appendix appears on the following page.

Table A1. Coding and locality information for sites in four habitats used in trap nest and pan trap surveys in 2000–2002.

Habitat	Site code	Years used	Location	County	Coordinates
COMM-A	A1	All	Melvorn Square	Annapolis	44.9892°N, 64.9971°W
	A2	All	Pereau	Kings	45.1872°N, 64.4030°W
	A3	All	Upper Canard	Kings	45.1290°N, 64.4617°W
	A4	All	Hortonville	Kings	45.1044°N, 64.2931°W
	A5	All	Grafton	Kings	45.0869°N, 64.6677°W
COMM-B	B1	All	Somerset	Kings	45.0836°N, 64.7322°W
	B2	All	Pereau	Kings	45.1904°N, 64.4153°W
	B3	All	Wolfville	Kings	45.0792°N, 64.3814°W
	B4	All	Morristown	Kings	44.9810°N, 64.7545°W
	B5	All	West Black Rock	Kings	45.1298°N, 64.7383°W
ABAND	C1	All	West Black Rock	Kings	45.1392°N, 64.7302°W
	C2	2000	Gaspereau	Kings	45.0693°N, 64.3266°W
	C3	All	Lockhartville	Kings	45.0850°N, 64.2337°W
	C4	All	Kentville	Kings	45.0628°N, 64.4881°W
	C5	2000	Green Acres	Annapolis	45.0250°N, 64.9299°W
	C6	2001–2002	Upper Canard	Kings	45.1350°N, 64.4890°W
WILD	D1	All	Lockhartville	Kings	45.0727°N, 64.2198°W
	D2	2000	Burlington	Kings	45.0765°N, 64.7940°W
	D3	All	Middleton	Annapolis	44.9650°N, 65.0575°W
	D4	All	East Torbrook	Kings	44.9266°N, 64.9301°W
	D5	2000	Kentville	Kings	45.0793°N, 64.4828°W
	D6	2001–2002	Avonport	Kings	45.1198°N, 64.2730°W
	D7	2001–2002	Aylesford	Kings	44.9783°N, 64.8103°W

Note: For a description of the four habitat types see the text.