

The oligolectic bee *Osmia brevis* sonicates *Penstemon* flowers for pollen: a newly documented behavior for the Megachilidae

James H. CANE

USDA-ARS Pollinating Insect Research Unit, Utah State University, Logan, UT 84322-5310, USA

Received 7 December 2013 – Revised 21 February 2014 – Accepted 2 April 2014

Abstract – Flowers with poricidally dehiscent anthers are typically nectarless but are avidly visited and often solely pollinated by bees that sonicate the flowers to harvest pollen. Sonication results from shivering the thoracic flight muscles. Honey bees (*Apis*) and the 4,000+ species of Megachilidae are enigmatic in their seeming inability to sonicate flowers. The oligolectic megachilid bee *Osmia brevis* was found audibly sonicating two of its beardtongue pollen hosts, *Penstemon radicosus* and *P. cyananthus*. The bees' high-pitched sonication sequences are readily distinguishable from flight sounds in audiospectrograms, as well as sounds that result from anther rasping. Instead, floral sonication by *O. brevis* resembles the familiar sounds of bumblebees buzzing, in this case while visiting *P. strictus* flowers.

Apiformes / Megachilidae / buzz pollination / *Penstemon* / floral sonication / pollen foraging / porose anthers

1. INTRODUCTION

The anthers of many species of flowering plants do not freely shed their pollen, but rather dehisce pollen through terminal pores, slits, or valves that serve to limit the pollen accessible to individual foraging pollinators. Dispensing pollen to sequential visitors can enhance pollen dispersal and thus male fitness (Harder and Thomson 1989). The widespread trait is reported from 72 plant families representing about 7 % of flowering plants (Buchmann 1983; De Luca and Vallejo-Marin 2013). A similarly diverse group of bees, most notably the bum-

blebees, are known to sonicate these poricidal anthers, as well as cones of introrse anthers, to enhance their acquisition of pollen (Buchmann 1985; Buchmann 1983; De Luca and Vallejo-Marin 2013).

Such sonication or “buzz pollination” is achieved by rapid contractions of a bee's thoracic flight muscles (King et al. 1996). The sound produced during floral sonication is higher pitched and audibly distinct from that of flight. For bumblebees (*Bombus*) and large carpenter bees (*Xylocopa*), most of the sound energy of sonication is in the second harmonic frequency above that of flight sounds (King and Buchmann 2003). The temporal patterning of sonication is also distinctive from that of flight, often consisting of stereotypical pulses or prolonged bouts of buzzing (e.g., Cane and Buchmann 1989).

Multiple representatives of all bee families but the Megachilidae have well-documented abilities to sonicate flowers (Buchmann 1983).

Electronic supplementary material The online version of this article (doi:10.1007/s13592-014-0286-1) contains supplementary material, which is available to authorized users.

Corresponding author: J. Cane,
Jim.Cane@ars.usda.gov
Manuscript editor Peter Rosenkranz

Only two instances of floral sonication have been reported from the Megachilidae, a large bee family comprising one-fifth of all bee species (4,125 described species) (Gonzalez et al. 2012). Neff and Simpson (1988) reported hearing several females of the leaf-cutting bee *Megachile mendica* Cresson faintly buzzing the porose anthers of *Chamaecrista fasciculata* Michx. (Fabaceae). This legume is a classic nectarless buzz-pollinated flower that is sonicated loudly by other visiting bees (Thorp and Estes 1975). Dukas and Dafni (1990) mentioned hearing an unidentified *Hoplitis* species buzzing flowers of *Trichodesma* in Israel. No other literature reports have been found.

Megachilids do harvest pollen from some flowers with porose anthers. In particular, the nectar-bearing species of *Vaccinium* (Ericaceae) are worked for pollen by some species of *Megachile* (Cane et al. 1996) and especially *Osmia* (Torchio 1990; Rust and Osgood 1993; Cane et al. 1985; Maeta et al. 1990b; Sampson et al. 2004; Stubbs et al. 1997). These megachilids use their legs to stroke or drum the staminal column to release blueberry or cranberry pollen, a foraging behavior likewise employed by the honeybee, *Apis mellifera* L. (Cane et al. 1993). Several of these *Osmia* species are even *Vaccinium* oligoleges (taxonomic pollen specialists) (Cane et al. 1985; Rust and Osgood 1993; Stubbs et al. 1997) despite their apparent inability to sonicate anthers.

Here, I report that a common *Penstemon* oligolege, *Osmia brevis* Cresson, regularly sonicates the anthers of at least two of its natural hosts, *P. radicosus* Nelson and *P. cyananthus* Hooker. The first acoustical recordings and audiospectrographs of floral sonication for any megachilid are shown to be similar to sonication of *P. strictus* Benthams by the much larger bumblebee, *B. nevadensis* Cresson.

2. MATERIALS AND METHODS

2.1. Natural history and foraging observations

Female *O. brevis* were observed collecting pollen from flowers at two patches of *P. radicosus* growing

at the margins of two past wildfire near Tuscarora, Elko County, Nevada USA on June 5–6, 2013. Later, in July, female *O. brevis* also were observed sonicating and their pollen foraging sounds recorded as they visited flowers of *P. strictus* in mountain meadows east of Logan, Utah USA. For comparison, I recorded sounds of the bumblebee *B. nevadensis* sonicating flowers of *P. strictus* in a diverse xeriscape garden in Logan. Plant vouchers were deposited with the Intermountain Herbarium and voucher bees were placed in the collections of the USDA-ARS Pollinating Insect Research Unit, both at Utah State University in Logan.

2.2. Sound analysis

Foraging sounds of *Osmia* and *Bombus* at *Penstemon* were recorded outdoors using a handheld digital audio recorder (Model H2, Zoom Corp, Tokyo, Japan). Sounds were amplified on the recorder and exported to a computer as digital files. Sound clips were edited and the displays optimized, then analyzed from oscillograms, audiospectrograms, and Discrete Fourier Transformation (DFT) using RavenPro1.4 software (Bioacoustics Research Program, The Cornell Lab of Ornithology, Ithaca, NY).

3. RESULTS

3.1. Pollen foraging behaviors at *Penstemon* flowers

On a calm, quiet morning, ten female *O. brevis* were each followed for ten *P. radicosus* flower visits. They audibly sonicated every one of the 100 visited flowers that were observed; most of the females also carried visible abdominal scopal loads of pale *Penstemon*—colored pollen as well. In mountain meadows east of Logan, *O. brevis* audibly sonicated every visited flower of *P. strictus* (no formal sample counts kept) (Online Resource 1). At both species, the sonicating females stood upright on the floor of the floral throat, such that the dorsal surfaces of the bee's thorax were opposite and close to the anther sutures of these nototribic flowers.

3.2. Sounds of sonication

Floral sonication by *O. brevis* consisted of 1–3 trains of brief pulsed buzzes while the bee stands upright in a given *Penstemon* flower. The acoustic frequencies of their buzzing sounded much higher pitched than their flight sounds (Online Resource 1). The audiospectrograms show distinct differences between flight sound and the intermittent sound pulses produced during floral sonication at *Penstemon*. Sonication sounds have many more overlying harmonics running into the higher frequencies (Figure 1). From the DFT trace, which plots sound power (dB) against frequency, the dominant sound frequency of *O. brevis* flight was 440 Hz, with slightly smaller peaks at 230, 680, and 913 Hz. The bees' sounds of floral sonication were at higher pitches, the largest peaks being at 1,360 and 1,800 Hz, with the three next largest peaks at 918, 2,300, and 2,700 Hz. A similar dichotomy, but at lower pitches, was evident in acoustical recordings of the much larger *B. nevadensis* as it sonicated flowers of *P. strictus* (Figure 1).

4. DISCUSSION

Several species of *Osmia*, including *O. brevis*, are oligolectic for *Penstemon*. Tepedino et al. (2011) reviewed the floral associations of *O. brevis* using published reports and museum collections. They concluded that this specialist visits at least 42 species of *Penstemon*. No prior report mentions sonication of any *Penstemon* species (or any other flowering plant) by any *Osmia* species, however, including *O. brevis*. Sonication of *Penstemon* by *O. brevis* is not a novel trait of one population. The behavior was observed for most or all floral visits to two different species of *Penstemon* that were 400 km apart. Floral sonication of at least some *Penstemon* hosts by *O. brevis* appears to be a species-specific trait.

The sound produced during floral sonication by bees is noticeably higher pitched than their flight sounds. For *Bombus* and *Xylocopa*, most of the sound energy is reportedly in the second harmonic frequency above that of flight (King

and Buchmann 2003); the multiple harmonics above this frequency have less sound energy (De Luca and Vallejo-Marin 2013). Sonication by *O. brevis* was consistent with this pitch difference, its dominant harmonics during floral sonication being threefold higher than those of flight, as revealed by the discrete Fourier transforms. These frequency differences, as well as the temporal patterning of the buzzes (Figure 1), make sonication sounds of *O. brevis* audibly distinct from those of flight. By comparison with audio recordings of *Bombus* sonicating *Penstemon* flowers (Figure 1), it seems evident that buzzing sounds produced by *O. brevis* while harvesting pollen from flowers of some species of *Penstemon* are comparable and so generated by flight muscle contractions as well.

Both *O. brevis* and the pollen wasp *Pseudomasaris vespoides* remove pollen from anthers of some *Penstemon* species by a second mechanism, anther rasping. The wasp or bee stands beneath the anthers and rapidly rocks to and fro, its punctate thoracic scutum rasping across the teeth of the anther sutures. The sound resembles faint scratching of loosely held paper. Though pulsed, it is audibly different from buzzing and coincides with the visible rocking behavior. Pollen rains out of the vibrated anthers onto the insect's dorsum. For *P. vespoides* visiting flowers of *P. cyananthus*, Torchio (1974) described the behavior as manifesting from the wasp repeatedly head-butting the vertical bend of the staminode (sterile stamen) as it probes past the staminode to reach the nectaries. Torchio (1974) described specialized hair arrays on the thoracic scutum to receive the pollen. Comparable behavior by *O. brevis* was readily seen and heard, but it is rarely mentioned and not yet described in the literature, despite reports that the thoracic scutum of *O. brevis* carries more *Penstemon* pollen than any other body part (Tepedino et al. 1999). Inasmuch as the much smaller bee visibly worked first one and then the other pair of anthers (Tepedino et al. 1999), anther rasping by *O. brevis* may involve more than a struggle to reach the nectaries.

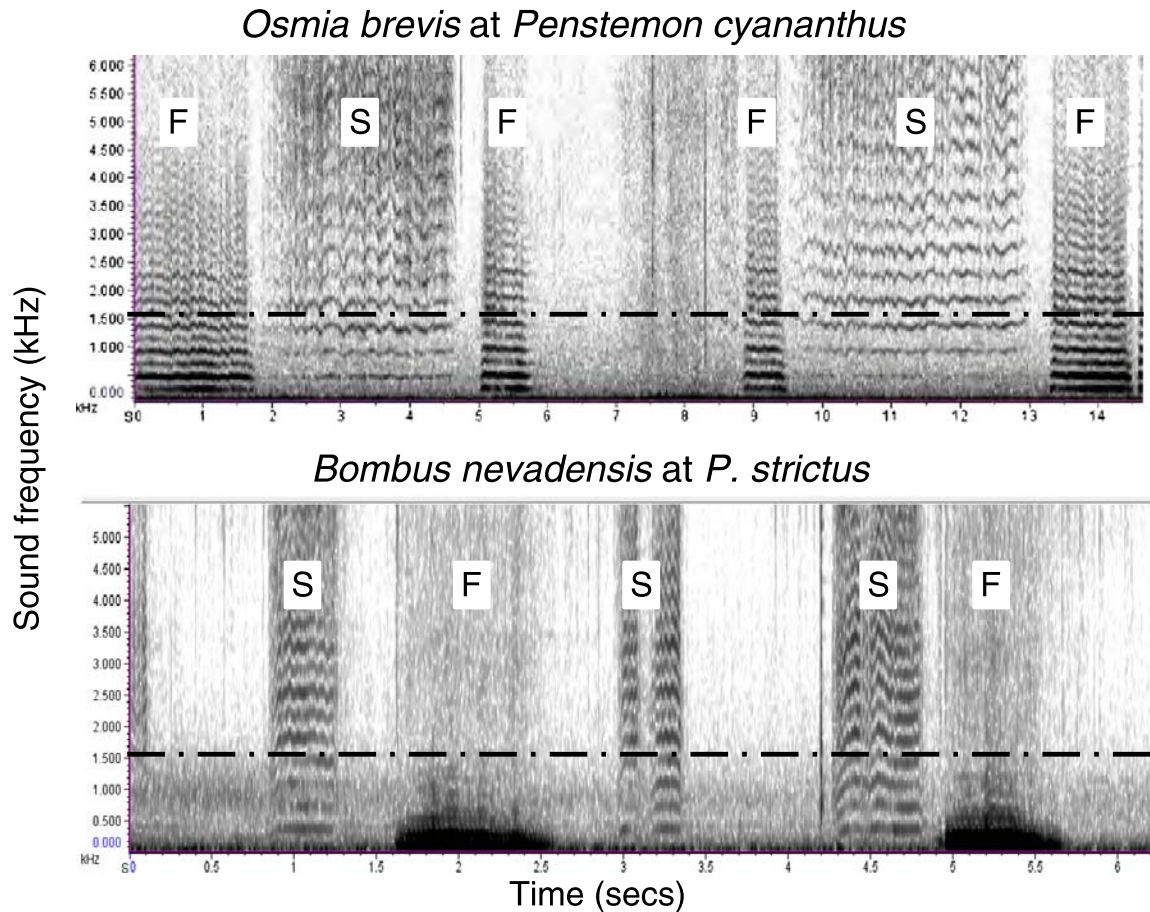


Figure 1. Audiospectrograms from sound recordings of *Osmia brevis* sonicating flowers of *P. cyananthus* (upper trace) and *Bombus* sonicating flowers of *Penstemon strictus* (lower trace). The labels refer to flight (F) and sonication (S) sounds. A dashed reference line is provided at 1,500 Hz.

It seems likely that *O. brevis* will be found sonicating additional *Penstemon* species. Both of the sonicated hosts reported here present mid-sized blue flowers, common traits for *Penstemon* species (Nold 1999). Taxonomically, *P. radicosus* belongs to section *Penstemon*, *P. cyananthus* to section *Glabri*. Anther morphologies differ between these two sections; those of *P. radicosus* dehisce along their full length but do not open widely, whereas those of *P. cyananthus* dehisce only from their distal ends (Nold 1999). In the PIRU collections, host labels for *O. brevis* include 16 other *Penstemon* species in these two sections alone. Close observation of pollen foraging *O. brevis* at additional *Penstemon* species is needed, distinguishing between floral sonication, anther rasping, or clear absence of these audible

foraging behaviors. Less common *Penstemon* specialists (e.g. *O. penstemonis*) should be included, as should several other *Osmia* sometimes common in *Penstemon* guilds (e.g. *O. ednae*) (Tepedino et al. 1999).

The near absence of floral sonication among species of *Osmia* is not for the lack of evolutionary opportunities. Admittedly, many of the plant species with porose anthers are tropical (Buchmann 1983), whereas the genus *Osmia* is Holarctic, largely exclusive of the warm deserts (Michener 2007). Nonetheless, the Ericaceae is rich in species with porose anthers, especially the genus *Vaccinium* (blueberries, huckleberries, cranberries, etc.). Many of these occur in north temperate regions, where their flowers are sonicated by diverse bee species, especially bumblebees. Species of *Osmia* are

often present but rarely common at *Vaccinium* flowers (reviewed in MacKenzie and Eickwort 1997), foraging for both nectar and pollen (Maeta et al. 1990a; Cane et al. 1985). A few *Osmia* are even *Vaccinium* oligoleges (Rust and Osgood 1993; Stubbs and Drummond 1997) and effective blueberry pollinators (Stubbs and Drummond 1997). These *Osmia* have never been reported to audibly sonicate ericaceous flowers for pollen. Rather, species of *Osmia* (and *Megachile* and *Apis*) dislodge pollen by using their legs to stroke or drum the column of *Vaccinium* anthers (Torchio 1990; Cane et al. 1985; Cane et al. 1996; Cane et al. 1993), a behavior that precludes a stance for effective sonication.

Some other Holarctic plant genera of other families commonly sonicated by bees include *Borago*, *Dodecatheon*, *Pedicularis*, *Polygonatum*, *Pyrola*, *Symphytum*, and *Trichodesma*, as well as northern representatives of some mostly tropical buzz-pollinated floral genera (e.g. *Chamaecrista* and *Rhexia*). Bumblebees regularly visit and buzz flowers of most of these taxa, often acquiring the pollen ventrally (Corbet et al. 1988; Larson and Barrett 1999; Knudsen and Olesen 1993). Often, they are joined by other bee taxa, but never by co-occurring *Osmia* (Macior 1964; Macior 1973; Macior 1993; Larson and Barrett 1999; Knudsen and Olesen 1993; Dukas and Dafni 1990). The one exception is *Pedicularis semibarbata*. Its flowers are not rostrate and therefore do not need to be vibrated to release pollen. It is visited solely by *Osmia tristella*, which does not buzz its flowers (Macior 1977), consistent with the generalization that *Osmia* species do not visit classic buzz-pollinated flowers.

The regular sonication of flowers of several species of *Penstemon* at distant locations by *O. brevis* suggests that this is a species-wide behavioral trait. Was the behavior lost in an ancestral *Osmia*, only to be derived anew in a single species oligolectic for a plant genus with flowers atypical among buzz-pollinated flowers? Perhaps it is a novel trait of *O. brevis* that has facilitated its radiation onto a number of beardtongue hosts. It nonetheless seems enigmatic that species of

Osmia either eschew visiting flowers with porose anthers altogether (those with anther cones) or harvest their pollen through seemingly inefficient anther stroking using their legs (e.g., Ericaceae). Despite the many studies of *Penstemon* pollination and the prevalence of *Osmia* in many of its floral guilds [half the bees collected at Rocky Mountain beardtongues (Clements and Long 1923)], floral sonication by *O. brevis* had not been reported before. It seems reasonable that vibratile pollination by some other species of *Osmia* also has been somehow overlooked and therefore awaits documentation.

ACKNOWLEDGMENTS

Research was funded by the Great Basin Native Plant Selection and Increase Project funded through the USDI-BLM Great Basin Restoration Initiative and the USDA-FS Rocky Mountain Research Station. Dr. Noel Holmgren kindly identified the penstemons. Vincent Tepedino and Michael Mesler provided helpful reviews. I dedicate this study to the memory of Philip Torchio, an astute observer of solitary bees.

L'abeille oligolectique *Osmia brevis* collecte le pollen des fleurs de *Penstemon* par sonication: un comportement nouvellement mis en évidence pour les Megachilidae

Apiformes / pollinisation vibratile / récolte de pollen / anthères

Die oligolektische Biene *Osmia brevis* beschallt Blüten der Gattung *Penstemon* zum Pollensammeln; ein erstmals dokumentiertes Verhalten für Megachiliden

Apiformes / Megachilidae / Vibrationsbestäubung / florale Beschallung / Pollensammeln / poröse Antheren

REFERENCES

- Buchmann, S.L. (1983) Buzz pollination in angiosperms. In: Jones, C.E., Little, R.J. (eds.) Handbook of Experimental Pollination Biology, pp. 73–113. Van Nostrand Reinhold Co, New York
- Buchmann, S.L. (1985) Bees use vibration to aid pollen collection from non-porocidal flowers. J. Kansas Entomol. Soc. 58, 517–525

- Cane, J.H., Buchmann, S.L. (1989) Novel pollen-harvesting behavior by the bee *Protandrena mexicanorum* (Hymenoptera: Andrenidae). *J. Insect Behav.* **2**, 431–436
- Cane, J.H., Eickwort, G.C., Wesley, F.R., Spielholz, J. (1985) Pollination ecology of *Vaccinium stamineum* (Ericaceae: Vaccinioideae). *Am. J. Bot.* **72**, 135–142
- Cane, J.H., MacKenzie, K., Schiffhauer, D. (1993) Honey bees harvest pollen from the porose anthers of cranberries (*Vaccinium macrocarpon*) (Ericaceae). *Am. Bee J.* **133**, 293–295
- Cane, J.H., Schiffhauer, D., Kervin, L.J. (1996) Pollination, foraging, and nesting ecology of the leaf-cutting bee *Megachile* (*Delomegachile*) *addenda* (Hymenoptera: Megachilidae) on cranberry beds. *Ann. Entomol. Soc. Am.* **89**, 361–367
- Clements, F.C., Long, F.L. (1923) Experimental Pollination: An Outline of the Ecology of Flowers and Insects. Carnegie Inst, Washington
- Corbet, S.A., Chapman, H., Saville, N. (1988) Vibratory pollen collection and flower form: bumble-bees on *Actinidia*, *Symphytum*, *Borago* and *Polygonatum*. *Funct. Ecol.* **2**, 147–155
- De Luca, P.A., Vallejo-Marin, M. (2013) What's the 'buzz' about? The ecology and evolutionary significance of buzz-pollination. *Curr. Opin. Plant Biol.* **16**, 429–435
- Dukas, R., Dafni, A. (1990) Buzz-pollination in three nectariferous Boraginaceae and possible evolution of buzz-pollinated flowers. *Plant Syst. Evol.* **169**, 65–68
- Gonzalez, V.H., Griswold, T., Praz, C.J., Danforth, B.N. (2012) Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. *Syst. Entomol.* **37**, 261–286
- Harder, L.D., Thomson, J.D. (1989) Evolutionary options for maximizing pollen dispersal of animal-pollinated plants. *Am. Nat.* **133**, 323–344
- King, M.J., Buchmann, S.L. (2003) Floral sonication by bees: Mesosomal vibration by *Bombus* and *Xylocopa*, but not *Apis* (Hymenoptera: Apidae), ejects pollen from poricidal anthers. *J. Kansas Entomol. Soc.* **76**, 295–305
- King, M.J., Buchmann, S.L., Spangler, H. (1996) Activity of asynchronous flight muscle from two bee families during sonication (buzzing). *J. Exp. Biol.* **199**, 2317–2321
- Knudsen, J.T., Olesen, J.M. (1993) Buzz-pollination and patterns in sexual traits in North European Pyrolaceae. *Am. J. Bot.* **80**, 900–913
- Larson, B.M.H., Barrett, S.C.H. (1999) The ecology of pollen limitation in buzz-pollinated *Rhexia virginica* (Melastomataceae). *J. Ecol.* **87**, 371–381
- Macior, L.W. (1964) An experimental study of the floral ecology of *Dodecatheon meadia*. *Am. J. Bot.* **51**, 96–108
- Macior, L.W. (1973) The pollination ecology of *Pedicularis* on Mount Rainier. *Am. J. Bot.* **60**, 863–871
- Macior, L.W. (1977) The pollination ecology of *Pedicularis* in the Sierra Nevada of California. *Bull. Torrey Bot. Club* **104**, 148–154
- Macior, L.W. (1993) Pollination ecology of *Pedicularis palustris* L. (Scrophulariaceae) in North America. *Plant Species Biol* **8**, 35–44
- MacKenzie, K.E., Eickwort, G.C. (1997) Diversity and abundance of bees (Hymenoptera: Apoidea) foraging on highbush blueberry (*Vaccinium corymbosum* L.) in central New York. *J. Kansas Entomol. Soc.* **69**, 185–194
- Maeta, Y., Okamura, S., Ueda, H. (1990a) Blueberry pollinators of south-western Japan, with pollinating behaviors of major species. *Chugoku Kontyu* **4**, 15–24
- Maeta, Y., Okamura, S., Ueda, H. (1990b) Use of the mamekobachi, *Osmia cornifrons* (Radoszkowski) as a pollinator of blueberries (Hymenoptera, Megachilidae). *Unknown* **8**(32), 33–42
- Michener, C.D. (2007) The bees of the world. Johns Hopkins Univ. Press, Baltimore
- Neff, J.L., Simpson, B.B. (1988) Vibratile pollen-harvesting by *Megachile mendica* Cresson (Hymenoptera: Megachilidae). *J. Kansas Entomol. Soc.* **61**, 242–244
- Nold, R. (1999) Penstemons. Timber Press, Portland
- Rust, R.W., Osgood, E.A. (1993) Identification of *Osmia kenoyeri* and *O. virga* (Hymenoptera: Megachilidae), two blueberry pollinators. *Entomol. News* **104**, 113–117
- Sampson, B.J., Stringer, S.J., Cane, J.H., Spiers, J.M. (2004) Screenhouse evaluations of a mason bee *Osmia ribifloris* (Hymenoptera: Megachilidae) as a pollinator of blueberries in the southeastern United States. *Small Fruits Rev.* **3**, 381–392
- Stubbs, C.S., Drummond, F.A. (1997) Blueberry and cranberry (*Vaccinium* spp.) pollination: a comparison of managed and native bee foraging behavior. In: Richards, K.W. (ed.) Pollination: from theory to practice, pp. 341–344. Acta Horticulturae, Leiden
- Stubbs, C.S., Drummond, F.A., Allard, S.L. (1997) Bee conservation and increasing *Osmia* spp. in Maine lowbush blueberry fields. *Northeast. Nat.* **4**, 133–144
- Tepedino, V.J., Sipes, S.D., Griswold, T.L. (1999) The reproductive biology and effective pollinators of the endangered beardtongue *Penstemon penlandii* (Scrophulariaceae). *Plant Syst. Evol.* **219**, 39–54
- Tepedino, V.J., Griswold, T.L., Freilich, J.E., Shephard, P. (2011) Specialist and generalist bee visitors of an endemic beardtongue (*Penstemon caryi*: Plantaginaceae) of the Big Horn Mountains. Wyoming. *Western N. Am. Nat.* **71**, 523–528
- Thorp, R.W., Estes, J.R. (1975) Intrafloral behavior of bees on flowers of *Cassia fasciculata*. *J. Kansas Entomol. Soc.* **48**, 175–184

- Torchio, P.F. (1974) Mechanisms involved in the pollination of *Penstemon* visited by the masarid wasp, *Pseudomasaris vespoides* (Cresson). Pan-Pac. Entomol. **50**, 226–234
- Torchio, P.F. (1990) *Osmia ribifloris*, a native bee species developed as a commercially managed pollinator of highbush blueberry (Hymenoptera: Megachilidae). J. Kansas Entomol. Soc. **63**, 427–436