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V. J. Tepedino
*USDA–ARS Bee Biology and Systematics Lab, Utah State University, Logan, UT*, vince.tepedino@usu.edu

T. L. Griswold
*USDA–ARS Bee Biology and Systematics Lab, Utah State University, Logan, UT*, terry.griswold@ars.usda.gov

J. E. Freilich
*The Nature Conservancy, Wyoming Field Office, Lander, WY*, stonefly@olypen.com

P. Shephard
*The Nature Conservancy, Wyoming Field Office, Lander, WY*, pshephard@greatlandtrust.org

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# SPECIALIST AND GENERALIST BEE VISITORS OF AN ENDEMIC BEARDTONGUE (*PENSTEMON CARYI:* PLANTAGINACEAE) OF THE BIG HORN MOUNTAINS, WYOMING

V.J. Tepedino[1,5], T.L. Griswold[1], J.E. Freilich[2,3], and P. Shephard[2,4]

ABSTRACT.—Insect exclusion from the flowers of *Penstemon caryi* showed that fruits are not produced unless pollen is moved between flowers by pollinators. We recorded over 30 species of bees visiting the flowers, and about a third of the bee species were common. Flower visitors were primarily pollen-collecting female bees, most of which also carried pollen on areas of the head that strongly implicated them as pollinators. While larger bees were generally more common on the flowers than smaller bees, there appeared to be no difference between size groups in (1) the percent of females collecting *Penstemon* pollen, (2) the percent of collected pollen that was *Penstemon* pollen, or (3) the percent of individuals that carried pollen in areas likely to effect pollination. Two long-tongued species, *Anthophora ursina* (Apidae) and *Osmia brevis* (Megachilidae), dominated the collections. These 2 species have very different host associations with *Penstemon* flowers: the specialist *O. brevis* collects pollen only from species of beardtongues in the western United States, while the generalist *A. ursina* uses a wide spectrum of plant species for pollen and seems to express fidelity to *Penstemon* flowers only when those flowers are abundant. There was no evidence that specialists are superior to generalists as pollinators of *P. caryi.*

RESUMEN.—La exclusión de insectos de las flores de *Penstemon caryi* mostró que no hay producción de frutos a menos que el polen se mueva entre las flores mediante un polinizador. Registramos a más de 30 especies de abejas que visitaron las flores, de las cuales alrededor de un tercio eran especies comunes. Principalmente fueron abejas hembras recolectoras de polen quienes visitaron las flores; la mayoría de estas abejas también llevaba polen en ciertas partes de sus cabezas, lo que implicó fuertemente que eran polinizadoras. A pesar de que fue más común encontrar abejas de mayor tamaño en las flores, en comparación con abejas más pequeñas, al parecer no hubo ninguna diferencia entre los grupos de diferentes tamaños en materia de (1) el porcentaje de hembras que recolectaron polen de *Penstemon;* (2) el porcentaje de polen recolectado que fue de *Penstemon;* o (3) el porcentaje de individuos que llevaban polen en las áreas que más comúnmente afectan la polinización. Hubo dos especies de lenguas largas que dominaron la colecta de polen: *Anthophora ursina* (Apidae) y *Osmia brevis* (Megachilidae). Estas 2 especies tienen una asociación ecológica muy diferente con las flores *Penstemon.* La especialista *O. brevis* solo recolecta polen de especies de *Penstemon* al occidente de los Estados Unidos; por su parte, la generalista *A. ursine* utiliza una amplia gama de especies de plantas para obtener polen y al parecer muestra lealtad a las flores *Penstemon* solamente cuando tales flores abundan. No se encontró evidencia de que las especialistas son superiores a las generalistas en cuanto a su desempeño como polinizadoras de *P. caryi.*

Pollination biologists predict the kinds of visitors to flowers using characteristics such as flower color, size, morphology, and resource delivery (e.g., Waser et al. 1996, Fenster et al. 2004). One taxon whose flower attributes and pollinators have attracted much recent attention is the beardtongues, genus *Penstemon* (Plantaginaceae). Thomson, Wilson, and colleagues (Thomson et al. 2000, Castellanos et al. 2003, 2006, Wilson et al. 2004, 2006, 2007) have cast most beardtongues into 2 readily recognizable pollination syndromes: hummingbird- and bee-adapted species. They describe 2 suites of associated flower characteristics. In general, hummingbird flowers are pink to bright red, with relatively narrow and long corollas and exserted anthers. These flowers produce dilute nectar and dispense pollen liberally with each effective visit. In contrast, bee flowers are blue to violet, with relatively short and wide corollas and anthers of various degrees of in- and exsertion. These flowers produce sugar-rich nectar and dispense their pollen gradually in small portions. It is more difficult to predict the types of bees associated with bee-syndrome beardtongue species; the clearest connection appears to be between size of flower and visitor (Wilson et al. 2004).

Here we describe the pollinators associated with the rare *Penstemon caryi* Pennell (section

[1]USDA ARS Bee Biology and Systematics Lab, Department of Biology, Utah State University, Logan UT 84322-5305.
[2]The Nature Conservancy, Wyoming Field Office, 258 Main Street, Suite 200, Lander WY 82520.
[3]Present address: U.S. National Park Service, Olympic National Park, 600 East Park Ave., Port Angeles, WA 98362.
[4]Present address: Executive Director, Great Land Trust, 619 E Ship Creek Ave., Anchorage AK 99501.
[5]E-mail: andrena@biology.usu.edu

*Habroanthus;* Wolfe et al. 2006), an endemic of the Big Horn Mountains of north central Wyoming and south central Montana. Cary's penstemon is a former candidate for listing under the U.S. Endangered Species Act, a current USDA Forest Service sensitive species, and a species of concern in Wyoming and Montana (Heidel and Handley 2004). Pollination is an important process for rare plants (Kearns et al. 1998) and a concern for those who manage their populations, as most rare plants are unable to reproduce sexually unless pollen is transferred between the flowers (e.g., Tepedino 2000).

Our first objective was to determine if sexual reproduction by *P. caryi* flowers was enabled by pollinators. Our second objective was to determine if color and size of *P. caryi* flowers accurately predicted the kinds of insects that visited and were likely pollinators. The flowers of *P. caryi* are blue to purple, with violet nectar guides. The flowers are also large (20–28 mm in length) and strongly bilabiate, with an abruptly inflated throat and a slightly exserted staminode (C.C. Freeman, "*Penstemon*" in *Plantaginaceae, Flora of North America*, Vol. 17, submitted); they augur large bees. Our third objective was to classify bee species visiting penstemon flowers as specialists or generalists based on our pollen-collection records and information in the literature. Our last objective was to determine if pollen specialists (oligoleges) were more efficient foragers or more important pollinators than were generalists (polyleges).

## METHODS

We studied *P. caryi* at The Nature Conservancy's Ten Sleep Preserve in Washakie County, Wyoming, on the west slope of the Big Horn Mountains. The site covers about 40 acres and supports over 3000 *P. caryi* ramets. More detailed site descriptions and locations can be found in Fertig (2002) and Heidel and Handley (2004), which also list associated species.

To determine if *P. caryi* flowers set fruit without pollinator visitation (autogamy), we used 1-mm$^2$ white tulle bags to cover one inflorescence, with a variable number of flowers, on each of 20 randomly selected plants before any flower buds had opened. At the same time, a similarly sized, but unbagged, inflorescence on a nearby plant was marked as an open-pollinated comparison. Inflorescences from these 2 treatments were subsequently collected, and the number of fruits (but not seeds) per flower were recorded and compared.

Visitors to *P. caryi* flowers were collected at 2 sites with abundant blooming plants on the Ten Sleep Preserve on 3 days (28–29 May 1998, 17 June 1999). Both sites were surrounded by juniper/sagebrush grasslands (Heidel and Handley 2004). Collections were made from midmorning to late afternoon as 2 collectors walked among the plants for several hour-long periods. Bees were captured with a butterfly net and transferred immediately to cyanide vials. Bees were subsequently pinned, labeled, and taken to the laboratory for identification, measurement, and examination of pollen (taxonomy follows that of Michener 2000; specimens are in the collection of the USDA ARS Bee Biology and Systematics Lab, Utah State University, Logan, UT).

Each specimen was examined under a binocular microscope for the presence of pollen in the scopa (the hairy pollen-collecting apparatus of bees, either on the hind legs or, for megachilids, on the ventral abdomen) and on areas that would contact the anthers and stigma of *P. caryi* flowers (i.e., the frons, clypeus, and the supraclypeal parts of the head). Pollen of pollen-collecting bees was sampled from the scopa with a clean forceps, transferred to a slide, stained with Calberla's solution (Kearns and Inouye 1993), and identified at 400X as either *Penstemon* or non-*Penstemon* pollen using a pollen reference collection. Although we were unable to distinguish pollen among different species of contemporaneously blooming Plantaginaceae, other *Penstemon* species were over 500 m away and other members of the family were few in number. Thus, we are confident that most pollen was from *P. caryi.*

## RESULTS

The results of our experimental pollination comparisons were unequivocal: no flower from any bagged inflorescence ($n$ = 20) produced fruit, while 89.1% (SD = 12.5) of open-pollinated flowers on marked inflorescences produced seeded fruits ($n$ = 17; 3 inflorescences were lost). Thus, pollinators were required for sexual reproduction to occur in *P. caryi*.

We collected over 30 species of bees on the flowers of *P. caryi*, the overwhelming majority of which were solitary (only members of the genus *Bombus* were eusocial); other potential

TABLE 1. Family and species of bees captured on *Penstemon caryi* on 3 days at Ten Sleep Preserve, Wyoming. N = total females captured (males noted ♂); L = mean length of females (mm); PER = percent of females collecting *Penstemon* pollen; PPP = percent of collected pollen that was *Penstemon* pollen; PH = percent of individuals carrying *Penstemon* pollen on the head.

| | N | L | PER | PPP | PH |
|---|---|---|---|---|---|
| Andrenidae | | | | | |
| *Andrena sola* | 4 | 11.0 | 0 | — | 0 |
| Apidae | | | | | |
| *Anthophora pacifica* | 6 | 17.1 | 33.3 | 82.6 | 100.0 |
| *Anthophora ursina* | 52 | 15.7 | 75.0 | 96.6 | 73.1 |
| *Bombus* spp.[a] | 13 | >15.0 | — | — | — |
| *Eucera frater* | 4 (2♂) | 13.9 | 50.0 | 100.0 | 75.0 |
| Halictidae | | | | | |
| *Lasioglossum sisymbrii* | 13 | 8.7 | 92.3 | 76.1 | 38.5 |
| Megachilidae | | | | | |
| *Osmia albolateralis* | 11 | 11.0 | 81.8 | 85.3 | 63.6 |
| *Osmia brevis* | 46 | 10.5 | 56.5 | 100.0 | 82.6 |
| *Osmia bruneri* | 9 | 9.0 | 33.3 | 98.6 | 100.0 |
| *Osmia densa* | 7 | 12.5 | 57.1 | 73.9 | 100.0 |
| *Osmia ednae* | 2 | 8.5 | 100.0 | 100.0 | 100.0 |
| *Osmia gaudiosa* | 5 | 6.5 | 40.0 | 81.5 | 100.0 |
| *Osmia sanrafaelae* | 2 | 9.0 | 100.0 | 100.0 | 100.0 |
| *Osmia trevoris* | 3 | 10.0 | 33.3 | 89.2 | 100.0 |
| *Osmia tristella* | 2 | 8.5 | 100.0 | 96.5 | 100.0 |

[a]Specimens misplaced and unavailable for examination; length conservatively estimated based on size of queens of most abundant species in northern Wyoming.

pollinating insects, such as wasps or flies, were uncommon or absent. Bee species represented by more than one individual are shown in Table 1 (a list of uncommon species is available from Tepedino). Species richness of *Penstemon* flower-visitors was dominated by members of the bee genus *Osmia* (9 common and several uncommon species). Two species of long-tongued bees in 2 families numerically dominated the collection: *Anthophora ursina* (Apidae) and *Osmia brevis* (Megachilidae). Conspicuous because of their low numbers or total absence were the usually common, small sweat bees of the subgenus *Lasioglossum* (*Dialictus*) (all <7 mm in length) and pollen wasps (*Pseudomasaris* spp.).

Most bee visitors to the flowers of *P. caryi* were females and pollen-collectors (64.0% overall; Table 1), and most of the pollen collected (total of 105 females) was *Penstemon* pollen (averages between 73.9% and 100%). Pollen loads carried by females of the 2 dominant species, the generalist *A. ursina* and the specialist *O. brevis*, averaged 96.6% and 100% *Penstemon* pollen, respectively. Thus, most female bee visitors were either specialized on, or displaying temporary localized constancy to, *Penstemon* flowers.

In flowers of all but one species of *Penstemon*, both pairs of fertile anthers are located dorsally while the sterile staminode is positioned ventrally; after the anthers have dehisced, the dorsally positioned style develops a hook at the distal end, bringing the receptive stigma into more direct contact with foraging bees. With the exception of the short-tongued species *Andrena sola* and *Lasioglossum sisymbrii*, most female bees carried *Penstemon* pollen on those areas of the head (supraclypeal area, frons, and vertex) likely to contact both anthers and stigma and, therefore, to effect pollination (Table 1). On average, 73.1% (*A. ursina*) and 82.6% (*O. brevis*) of females of the dominant species carried *Penstemon* pollen on one or more areas of the head.

It was difficult to test the expectation that common bee visitors to *P. caryi* flowers exhibit large body sizes, because we have no estimate of the size distribution of all bees active in the community against which to compare them. Our best possible effort was to note that 4 of the 5 most abundant bee taxa collected on *P. caryi* flowers were equal to or greater than the median species body length and that, conversely, 5 of the 7 least common of these species were below the median body size of the collection (Table 1). Thus, it would appear that larger bees are more common on the large flowers of Cary's penstemon, though there are several exceptions.

While larger bees were more common, they were no more likely to collect *Penstemon* pollen (range 56.5%–92.3%) than were small bees (range 33.3%–100.0%). Nor was there a difference in the percent of collected pollen that was *Penstemon* pollen (range: large 76.1%–100.0%, small 81.5%–100.0%) or in the percent of individuals with *Penstemon* pollen on their heads (large 38.5%–82.6%; small 0%–100.0%).

## DISCUSSION

*Penstemon caryi* shares certain reproductive attributes with other beardtongues in section *Habroanthus* (*Penstemon debilis*—McMullen 1998; *Penstemon penlandii*—Tepedino et al. 1999; *Penstemon scariosus* var. *albifluvis*—Lewinsohn and Tepedino 2007) and, indeed, with *Penstemon* species generally: fruit was produced only when pollen was transferred between flowers, and unvisited flowers were barren. Until the necessary experiments are performed, it is unclear if cross-pollination is necessary to achieve maximum fruit and seed set or if *P. caryi* plants are at least partially self-compatible, as is the case in most other *Penstemon* species (Lewinsohn and Tepedino 2007).

In asking whether larger bees were more common on *P. caryi* flowers, as anticipated, it is well to keep in mind that our collections were limited in time and space and that spatiotemporal variability is common in bee communities (Tepedino and Stanton 1981, Herrera 1988). Thus, it is unclear how representative this pollinator collection is. Of the 30+ bee species found on *P. caryi* flowers, a few were very abundant, while only about half were represented by >1 individual (Table 1). While it is likely that the dominant pollinators *O. brevis* and *A. ursina* would be abundant visitors of geographically limited *P. caryi* under most circumstances (both were also very abundant during a brief visit in June 2010), it is also likely that some of the uncommon species, especially those that are reputed to be *Penstemon* oligoleges (e.g., *O. pentstemonis;* Crosswhite and Crosswhite 1966), would have been more abundant had we collected over a greater part of the *P. caryi* flowering season. Thus, the outcome of our size comparisons should be regarded as tentative.

Nonetheless, we found support for the expectation that bee visitors to the large flowers of *P. caryi* should also be large. Most of the more common species collected were at the large end of the size-frequency distribution of bees captured. It is less clear that these larger species were more effective foragers, or pollinators, than smaller species. There appeared to be no difference between species with large and small females in the percent that collected *Penstemon* pollen or in the percent of *Penstemon* pollen that they collected (Table 1). Thus, apt foraging behavior, learned or instinctive, may compensate for a suboptimal size match between bee and flower. Most importantly, from the plant's perspective, there was no difference between large and small females in the percent that carried *Penstemon* pollen on areas of the head likely to contact a receptive stigma. While our preliminary findings suggest minimal differences in pollination performance between bees in different size categories, only more detailed comparisons of pollination efficiencies and pollen-harvesting efficiencies among bee species can resolve these issues.

A second comparison of interest is between specialist (oligoleges) and generalist (polyleges) pollen collectors: specialists are frequently hypothesized to be superior to generalists in foraging efficiency and pollination on their preferred host plant (Minckley and Roulston 2006). Both types of pollen foragers were present in our collections. Of the 2 dominant species, one, *O. brevis*, is an oligolege, while the other, *A. ursina*, is a polylege. In addition, 9 of the 15 most common bee species were members of the genus *Osmia*, many of whose species have an affinity for visiting and collecting pollen from *Penstemon* flowers (Crosswhite and Crosswhite 1966, Tepedino et al. 1999). Indeed, all of the *Osmia* species collected from *P. caryi* have been recorded visiting other beardtongues, though it is not clear how many are polyleges as opposed to oligoleges. A few of these predictable *Penstemon* visitors in the western United States (e.g., *O. brevis* and *Osmia ednae*) also possess basket-forming proclinate hairs on the supraclypeal and frons areas of the head that seem to be adaptations for collecting pollen from nototribic flowers (Müller 1996), such as penstemons (Tepedino et al. 1999). While this pollen-collecting apparatus is also possessed by some other *Penstemon* specialists (Griswold and Rightmeyer unpublished data), it is unclear that its absence is a disadvantage for other common *Penstemon* foragers (e.g., *Osmia albolateralis*, *Osmia bruneri*, *Osmia gaudiosa*, *Osmia sanrafaelae*, and *A. ursina*; Table 1).

An instructive comparison is between the 2 dominant visitors of *P. caryi* flowers: the specialist *O. brevis*, which possesses proclinate hairs, and the generalist *A. ursina*, which lacks them. These species are quite different in their association with beardtongue flowers. *Osmia brevis* is a *Penstemon* oligolege that, in addition to *P. caryi*, has been recorded collecting pollen from *Penstemon secundiflorus* and *Penstemon spectabilis* (Crosswhite and Crosswhite 1966), *Penstemon debilis* and *Penstemon caespitosus* (McMullen 1998), *Penstemon harringtonii* (Nielson 1998), *Penstemon penlandii* (Tepedino et al. 1999), *Penstemon scariosus* var. *albifluvis* (Lewinsohn and Tepedino 2007), *Penstemon haydenii* (Tepedino et al. 2007), *Penstemon speciosus* and *Penstemon kingii* (J.H. Cane personal communication), and is known to visit at least an additional 31 other *Penstemon* species (Griswold unpublished data). In contrast, *A. ursina*, a polylege, collects pollen from many plant families. For example, the USDA ARS bee collection in Logan, Utah, harbors 112 individuals (*P. caryi* visitors omitted) that have been recorded from 15 plant families of primitive (e.g., Ranunculaceae) to derived (e.g., Asteraceae) status. A brief trip to the Ten Sleep Preserve in June 2010 yielded numerous female *A. ursina* visiting *Penstemon* (2 species), *Astragalus* (several species), *Lupinus*, *Castilleja*, and *Cerastium*.

These differences between the dominant visitors in host-plant associations, and in the presence of the pollen-collecting apparatus on the head, have not resulted in any obvious corresponding difference in pollen-foraging efficiency or in likelihood of pollination. Most females of both species (indeed, of almost all common species) collected a high percent of *Penstemon* pollen on a given foraging trip and carried pollen on the head, irrespective of the presence of a pollen basket (Table 1). Thus, *Penstemon* oligoleges do not appear to be superior to polyleges as pollinators of *Penstemon* flowers. Again, only more detailed observations and comparisons can determine if specialized females with or without proclinate hairs are more efficient *Penstemon* pollen foragers and pollinators than are generalized females without such hairs.

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