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Notes and Discussion

Generalist Bees Pollinate Red-flowered Penstemon eatonii: Duality in the Hummingbird Pollination Syndrome

Abstract.—The red tubular flowers of *Penstemon eatonii* (Plantaginaceae) typify the classic pollination syndrome for hummingbirds. Bees are thought to diminish its seed siring potential, but we found that foraging female generalist bees (*Apis, Anthophora*) deposited substantial amounts of conspecific pollen on *P. eatonii* stigmas. In the absence of hummingbirds, bee pollination of cultivated *P. eatonii* annually generated massive seed yields from a 1.5 ha field. Most penstemons with red tubular flowers like *P. eatonii* present a symmetrically flared floral opening that facilitates landing by foraging bees. Derived floral traits that attract and position nectar-foraging hummingbirds for efficient pollen export (red deeply tubular flowers secreting abundant dilute nectar) need not compromise pollination and seed production that result from visitation by generalist bees seeking pollen and/or nectar.

Introduction

To varying degrees, all pollinators use just a subset of the floral diversity presented by plant communities. Pollination syndromes have been used to conveniently classify associations between kinds of pollinator and correlated suites of floral traits (Faegri and van der Pijl, 1979; Wilson *et al.*, 2004). The hummingbird floral syndrome is especially striking. In western North America, species representing at least 15 eudicot families have evolutionarily converged on a narrowly defined suite of floral traits adapted for hummingbird attraction, foraging and pollination (Grant and Grant, 1968), including 10 or more lineages within *Penstemon* (Wilson *et al.*, 2007). The implicated traits include: a red, deep, narrowly tubular corolla; a lack of evident scent; absence of any conspicuous ''landing platform''; and, anthers/stigmas exserted just enough to daub and pick up pollen on the hovering hummingbird's facial feathers as it imbibes nectar (Grant and Grant, 1968; Wilson *et al.*, 2004). This suite of floral traits has been shown to favor hummingbird foraging and their efficient acquisition, export and later deposition of pollen (Castellanos *et al.*, 2003, 2004). By that measure of male fitness, limited experiments indicated that nectaring bumblebees were inferior to hummingbirds in pollinating one species, *P. barbatus* (Castellanos *et al.*, 2003). However, can bees contribute substantially to maternal fitness (*e.g.,* seed production) by any of these archetypal hummingbird flowers?

We report here that scarlet tubular-flowered *Penstemon eatonii* Gray (Plantaginaceae), when farmed for seed in the western U.S., generated massive seed yields for multiple years in the absence of hummingbirds. The flowers in this population were solely visited and effectively pollinated by foraging generalist bees.

Methods

The native seed farm is near Worland, Wyoming (44°57′N, 117°58′W) in an agricultural strip along the Bighorn River. The surrounding sagebrush-steppe habitat supports Broad-tailed, Calliope, and Rufous hummingbirds (USGS Bird Checklists of the United States). Since 2000, the short-lived native perennial *P. eatonii* has been continuously grown in monoculture on a 1.3 ha field (Fig. 1). The original seed came from the wild near American Fork, Utah. Neighboring fields (each 0.2–5 ha) included coflowering *P. angustifolia, Prunus besseyii* (Rosaceae), and *Hedysarum boreale* (Fabaceae), all wildflowers visited abundantly by honeybees and native bees. Any hummingbirds were noted since 2003.

Bees were surveyed at blooming *P. eatonii* during warm calm sunny weather on 9 Jun. 2008. Bees at flowers were identified and counted during a walking scan census along three 30 m lengths of row. After 5–6 h of bee activity, 14 fresh *P. eatonii* flowers were randomly taken along three 10 m lengths of row, one per plant. Flowers were carefully emasculated and refrigerated. The next day, their stigmatic pollen loads were counted while viewing intact stigmas microscopically. Seed of *P. eatonii* was mechanically harvested, cleaned, and weighed late each summer (2002–2008).

FIG. 1.—Seed production field of *P. eatonii* in Worland, Wyoming. *Inset* Honey bee probing flower of *P. eatonii* for nectar. Photo by JHC

More insights came from *P. eatonii* grown in a suburban garden in Logan, Utah where plants could be daily observed and manipulated. Nectar that had accumulated in eight virgin flowers was withdrawn at 1100 h using a 5 µl microcapillary pipette. Volume was calculated from the pipette's measured height of nectar. Sugar concentrations were measured using a hand-held refractometer (Bellingham and Stanley Ltd., Tunbridge Wells, U.K.). Ovules were counted for one of the pair of locules of 10 dissected fresh flowers. Potentially UV-reflective floral surfaces were microscopically examined while using a portable 365 nm LED UV lamp (Nichia Corp., Tokushima, Japan). Anther morphology was viewed microscopically using herbarium material cleared in ethanol. Lastly, during 5 y at the Logan garden, the foraging rounds of the *Penstemon* specialists (=oligoleges), *Osmia brevis* (Megachilidae), and *Pseudomasaris vespoides* (Masaridae) were observed at a mix of penstemons that included *P. eatonii*. Quantitative data are summarized in the results as the mean +/−1 SD.

RESULTS

Only bees visited flowers of *P. eatonii* on the Wyoming farm since 2002. On 9 Jun. 2008, only honey bees were seen at *P. eatonii* flowers (28–29 bees per 30 m of row), which was generally true during bloom that year. From 2002–2008, no hummingbirds were seen or heard during daily casual observation of farmed *P. eatonii*, although they are in nearby Worland. In 2008, honey bees came from 40 hives placed 950 m distant from the *P. eatonii* field. In the six preceding years, honey bee hives were absent. In 2004, numerous females of the solitary bee *Anthophora ursina* foraged for pollen but not nectar at *P. eatonii*. This bee was seen at *P. eatonii* flowers in the Logan garden but not at concurrently blooming blue-flowered *P. cyananthus, P. speciosus,* or *P. strictus*. These latter species were daily visited by *Penstemon* specialists (*O. brevis* and *P. vespoides*) seeking pollen and nectar. Neither specialist visited adjacent *P. eatonii*.

All honey bees landed upright and faced into the corollar opening of a *P. eatonii* flower (Fig. 1). They may have been attracted at close range by the bright UV-reflectance of the dentate rims of the anther sutures, which are visible from the corollar opening. Most foragers inserted their heads fully into the corolla, proboscis extended, to drink from the basal nectary. By midday, new virgin flowers had 4.4 +/− 1.6 µl of dilute nectar (20–28% w/w concentration). No robbery holes were seen. At flowers of *P. eatonii*, 11 of 20 surveyed honey bee foragers carried corbicular pellets of pale pollen resembling that of *P. eatonii*. Honey bees periodically groomed and packed loose pale pollen while foraging at *P. eatonii*. Extrapolating these bee surveys to the 1.3 ha field on 9 Jun., 10,500 honey bees foraged at *P. eatonii* in the 11,200 m of farmed rows.

Stigmas from freely visited new flowers of *P. eatonii* bore only tiny pale tricolpate grains typical of *Penstemon*. After 5–6 h, visiting honey bees had cumulatively deposited 52 +/− 30 pollen grains on each of 14 stigmas (range 10–104 grains). Ten locules had 46 +/− 3 ovules, or 92 ovules per flower.

The field of *P. eatonii* yielded 123–312 kg/ha/yr of clean seed each year (differences mostly due to weather). The larger value approaches the maximum predicted seed yield for cultivated *P. eatonii* (Stevens *et al.*, 1996). Harvested seed yield in 2008 was 2 g/plant, or about 1400 seeds, given that there are 690,000 seeds/kg (Stevens *et al.*, 1996), or 15 floral-equivalents if all ovules are fertilized. Pollination solely by bees thus yielded up to 1/4 billion seeds of *P. eatonii* annually from the Worland seed field.

DISCUSSION

The more obvious floral traits of *P. eatonii* clearly fit the hummingbird syndrome, but *P. eatonii* had massive seed yields at the Worland farm though pollinated solely by generalist bees. Multivariate analyses of floral traits by Wilson *et al.* (2004) grouped *P. eatonii* with other red tubular-flowered penstemons visited by hummingbirds. The generous volumes of dilute nectar that we measured match other red-flowered penstemons (Wilson *et al.*, 2007). Nonetheless, polylectic (generalist) bees were key pollinators of *P. eatonii* in our study, as shown both by stigmatic pollen loads and the yield of several billion seeds produced over 6 y. Apparently, *P. eatonii* has traits favoring pollination by hummingbirds without hindering pollination by mid-sized polylectic bees, at least in terms of maternal fitness. Manipulative floral experiments with *Dudlyea greenei* likewise showed that floral specialization for hummingbirds accommodated generalist bees as pollinators (Aigner, 2004). An evolutionary order of derivation–bee, then hummingbird–is supported by a *Penstemon* phylogeny (Wilson *et al.*, 2007; Wolfe *et al.*, 2006). If that evolutionary transition is gradual, then intermediate stages should engage both bees and hummingbirds, as is the case for *P. eatonii*.

Our own sensory biases might downplay the possibility of a mixed pollination syndrome for some red-flowered penstemons. Several defining hummingbird syndrome traits are large and visually striking. Conversely, floral traits that attract or favor bees can be less apparent to us. We found, for instance, that the anther rims of *P. eatonii* brightly reflect ultraviolet light. Experiments by Lunau *et al.* (2011) showed that foraging orchid bees were attracted more to artificial red flowers that reflected UV wavelengths too; hummingbird visits continued apace. Thus, UV-reflective red flowers can attract visits from both bees and hummingbirds without compromise.

Bees at *P. eatonii* were all floral generalists (polylectic), both in this study and for earlier collections. The two western oligolectic bees of *Penstemon, O. brevis* and *O. penstemonis,* were rare among bees taken at *P. eatonii* (4 of 259 specimens in the USDA-ARS Pollinating Insect Research Unit (PIRU), Utah State University, Logan, UT, collection). Instead, these two oligoleges frequent a host subgroup with blue or purple flowers (1/3 of the 272 *Penstemon* species). Their anthers commonly dispense pollen through narrow slits rimmed with pointed teeth (Lodewick and Lodewick, 1999). Torchio (1974) described how females of a pollen-wasp butt the staminode to reach the nectaries, thereby rasping their punctate thoracic dorsa against the dentate anthers. In response, pollen rains down from the anther slits. This action was seen and heard daily by females of this pollen-wasp and the two specialist *Osmia* bees foraging at blue-flowered penstemons in the Logan garden. These oligoleges were never seen at coflowering, adjacent *P. eatonii*.

Curiously, *P. eatonii* anther sacs are dentate too, but they open more widely, enabling generalist bees to forage by standing outside of the corolla tube, scrabbling with their legs to dislodge pollen. In so doing, they effected pollination. A narrowed corolla, like that of *P. eatonii*, positions a nectar-foraging

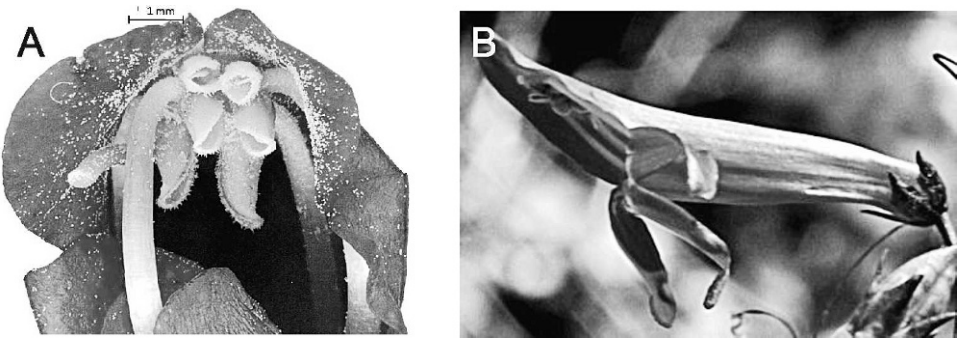

FIG. 2.—A. Mouth of a *P. eatonii* flower, showing the radially symmetrical flared stubby petal lobes and open, forward-facing anther sutures. Photo by JHC. B. Deeply reflexed lower petal lobes of the *P. barbatus* flower. Photograph courtesy of the Dale A. Zimmerman Herbarium, Western New Mexico University

hummingbird to more consistently pick up and later transfer pollen (Castellanos *et al.*, 2004). The forward-facing, openly dehiscent anthers of *P. eatonii* (Fig. 2) are suited for this purpose but likely preclude the peculiar, but effective, anther rasping used by *Penstemon* oligoleges while they stand beneath the overarching stamens. For the combination of hummingbird and oligolectic bee, fitness trade-offs seem inevitable. As a corollary to Aigner's (2004) insights, then, we predict that no *Penstemon* of the hummingbird syndrome will be frequented by *Penstemon* specialists. Observations by Wilson *et al.* (2004) are supportive; they found no specialist *Pseudomasaris* wasps at flowers of any red-flowered *Penstemon*.

Narrowly tubular red corollas were posited to restrict attraction and access to just hummingbirds while deterring bees that take pollen and nectar to feed their brood, thereby depleting the plant's rewards and pollination potential (Castellanos *et al.*, 2004). Hummingbirds do visit wild *P. eatonii* (Wilson *et al.*, 2004); bees do also (Bateman, 1980). Tiny bees readily ''steal'' nectar and pollen from *P. eatonii* without stigma contact. They comprise 83% of the 259 individuals (36 of 56 species) taken at *P. eatonii* flowers and housed in the PIRU collections; only 2% were bumblebees. Multiple regressions of floral visitor classes on floral traits of *Penstemon* (Wilson *et al.*, 2004) likewise found that small generalist bees (*e.g., Lasioglossum*) were strongly associated with red tubular hummingbird flowers rather than the typical bee-pollinated species. Floral traits of *P. eatonii* may attract, reward, and position hummingbirds for pollen transfer, but they fail to exclude the very nectar or pollen thieves that were posited to be the targets of ''anti-bee'' adaptations. Conversely, it would be maladaptive for *P. eatonii* to deter visits by larger generalist bees because of their pollination value.

Bees were essential pollinators of *P. eatonii* at this farm but was that an artifact of cultivation? At another rural seed farm in southwestern Colorado, like-sized fields (0.3 ha) of *P. barbatus* were abundantly visited by broad-tailed hummingbirds (R. Hammon, pers. comm.), a bird also common in the Worland region. Both farms grew *H. boreale* plus two to three other penstemons for seed. The massive display of *P. eatonii* at Worland (Fig. 1) was a ''bonanza resource'' for bees, especially without hummingbirds to deplete nectar. However, for 10,500 honey bees foraging on just 1.3 ha of *P. eatonii*, nectar competition seemed likely. Wild bees might be less inclined to visit blooms at more scattered plants, especially if hummingbirds regularly removed their nectar. However, native bees greatly outnumbered hummingbirds at wild *P. eatonii* growing in central Utah (Bateman, 1980).

Red-flowered penstemons can be sorted by floral morphology into two functional groups relevant to bee access and pollination. The corollar opening of *P. eatonii* is rimmed by stubby petal lobes that are flared like the bell of a trumpet (Fig. 2A) giving pollen-foraging bees a landing platform. In contrast, the lower petal lobes of *P. barbatus* are deeply reflexed (Fig. 2B). The anthers of *P. eatonii* open quite broadly and are at the mouth of the flower (Fig. 2A). A mid-sized bee standing astride the flower's mouth can take pollen using its legs without entry or specialized behavior. From that position, it also

TABLE 1.—List of *Penstemon* species with red tubular corollas, divided into a group lacking landing platforms and those judged to possess a landing platform suitable for foraging bees

Red *Penstemon* lacking platform	Red *Penstemon* with platform
P. barbatus	*P. baccharifolius*
P. cardinalis	*P. centranthifolius*
P. labrosus	*P. fasciculatus*
P. pinifolius	*P. havardii*
P. rostriflorus	*P. isophyllus*
	P. kunthii
	P. lanceolatus
	P. miniatus
	P. murryanus
	P. parryi
	P. subulatus
	P. superbus
	P. utahensis
	P. wrightii

contacts the stigma. Each honey bee seen at *P. eatonii* flowers at Worland sought nectar, thrusting its head into the corolla to reach its tongue to the basal nectary (Fig. 1 inset). In contrast, bumblebees placed on *P. barbatus* flowers (Castellanos *et al.*, 2003) struggled to work the strikingly different corolla opening (Fig. 2B), underscoring how such simple corolla differences matter for foraging bees and pollination.

The floral traits of *P. eatonii* and its mixed pollinator syndrome are shared by *P. centranthifolius* (Mitchell, 1989). Like *P. eatonii*, *P. centranthifolius* has red tubular somewhat drooping flowers with radially flared stubby corolla lobes. It too seems to be effectively pollinated by honey bees and native larger-bodied generalist bees that scrabble at the anthers for pollen, as well as by nectar-foraging hummingbirds (Mitchell, 1989). It evolved independently of *P. eatonii* (Wilson *et al.*, 2007; Wolfe *et al.*, 2006).

What then is the evolutionary trajectory of the mixed pollinator strategy of *P. eatonii* and others like it? They could be transitioning from bee- to hummingbird pollination, a reasonable scenario for this rapidly evolving genus (Wolfe, 2006). Female fitness (seeds) is well-served by mid-sized female bees, but they can take 95–99% of host pollen out of circulation (*e.g.*, Cane *et al.*, 1996; Schlindwein *et al.*, 2005), a potential cost for male fitness (Thomson and Thomson, 1992). Alternatively, these penstemons (Table 1) may embody a mixed but evolutionarily stable pollinator strategy that is overtly adapted for hummingbirds but also served by mid-sized polylectic bees. Pink-flowered *P. pseudospectabilis* maximized seed set when visited by both hummingbirds and bees (Lange and Scott, 1999; Reid *et al.*, 1988); both groups also visit pink-flowered *P. newberryi* (Kimball, 2008). Attracting pollinators with such contrasting life histories as migratory hummingbirds and ground-nesting bees should better stabilize annual visitation intensities; for instance, populations of broad-tailed hummingbirds fluctuated three-fold annually at one montane location (Calder *et al.*, 1983). Manipulative experiments with *P. eatonii* breeding and pollination ecologies could quantify female and male fitness tradeoffs for its contrasting pollinators.

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