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Bees assess pollen returns while sonicating *Solanum* flowers

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Summary. Can bees accurately gauge accumulating bodily pollen as they harvest pollen from flowers? Several recent reports conclude that bees fail to assess pollen harvest rates when foraging for nectar and pollen. A native nightshade (*Solanum elaeagnifolium* Cavanilles) that is visited exclusively for pollen by both solitary and social bees (eg. *Ptiloglossa* and *Bombus*) was studied in SE Arizona and SW New Mexico. The flowers have no nectaries. Two experiments were deployed that eliminated "pollen feedback" to the bees by experimentally manipulating flowers prior to bee visits. The two methods were 1) plugging poricidal anthers with glue and 2) emptying anthers of pollen by vibration prior to bee visitation. Both experiments demonstrated that bees directly assess pollen harvest on a flower-by-flower basis, and significantly tailor their handling times, number of vibratile buzzes per flower and grooming bouts according to the ongoing harvest on a given flower. In comparison to experimental flowers, floral handling times were extended for both *Bombus* and *Ptiloglossa* on virgin flowers. Greater numbers of intrafloral buzzes and numbers of times bees groomed pollen and packed it into their scopae while still on the flower were also more frequent at virgin versus experimental flowers. Flowers with glued androecia received uniformly brief visits from *Bombus* and *Ptiloglossa* with fewer sonications and virtually no bouts of grooming. Curtailed handling with few buzzes and grooms also characterized visits to our manually harvested flowers wherein pollen was artificially depleted. Sonicating bees respond positively to pollen-feedback while harvesting from individual flowers, and therefore we expect them to adjust their harvesting tempo according to the currency of available pollen (standing crop) within *Solanum* floral patches.

Key words: Buzz pollination – Vibratile – *Bombus* – *Ptiloglossa* – Nightshade

A cosmopolitan genus of more than 2000 species, *Solanum* (Solanaceae) is the second largest genus of flowering plants. The genus offers floral biologists unique opportunities to monitor pollen production, floral cues for pollen advertisement, and depletion dynamics resulting from pollen-foraging activities of specialist and generalist bees. Nightshade (*Solanum*) species often have large showy flowers. The white or blue perianth strongly contrasts with the brilliant yellow androecium, which consists of five greatly enlarged stamens. Although these flowers are showy and sometimes fragrant, they offer no nectar, although "pseudonectaries" (greenish shiny areas at the perianth base) may be present.

Pollen is the sole reward for bees visiting *Solanum*. It may be present in large amounts (2–6 mg per flower and 100000–200000 pollen grains per flower). Pollen from several *Solanum* species have been studied nutritionally. Their pollen is extremely rich in nitrogen (about 6.1–8.8% of dry wt.), and protein (40–56%) relative to pollen from other bee-pollinated species in the Solanaceae (see Buchmann (1986) for additional data on *Solanum* pollen chemistry). *Solanum* pollen also is energy rich, containing 5400–5800 joules per gram (Buchmann, unpublished work).

Nightshades typify several androecial adaptations to conserve pollen. Their sizeable anthers do not shed pollen by complete stomial rupture, as in most angiosperms, but rather through minute apical pores. Poricidal dehiscence of pollen is found among 27 orders, 72 families, 544 genera and an estimated 15000–20000 species of plants, constituting about 8% of the world's angiosperm species (Harris 1905; Buchmann 1983). Many of these species visually advertise apparent pollen abundance. Their androecia remain turgid and bright yellow even after their anthers have been emptied of pollen by bee visitation. Such flowers "sham pollen copiousness" with their pronounced male function advertisements (Vogel 1978). Although *Solanum* pollen is abundant and nutritious, it is hidden from the usual direct visual and contact chemosensory inspection employed by scrabbling pollen harvesting methods common among bees and other pollen-collecting insects.

For *Solanum*, and similar flowers with staminal-pores, pollen can only be efficiently harvested by bees which sonicate the anthers. Using rapid contractions of their pterothoracic flight muscles, they transmit strong substrate vibrations to the flower androecium. Such vibrations rapidly propel the small light pollen out the small pores in distinct streams or clouds of grains which strike the venter of the sonicating bees (Buchmann et al. 1977; Buchmann 1978; Buchmann 1983, 1985, 1986; Buchmann and Hurley 1978). Such floral sonications usually last one to several seconds per flower and enable such buzzing bees to handle flowers from poricidal flowers much more rapidly than if they "milked" the anthers with their legs and mouthparts (Cane and Buchmann 1989). Many bees, including solitary and social species, and both generalists and specialists, routinely use floral sonication to harvest pollen (including bees in at least seven families and over 50 genera). Bee families

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with few species which use sonication include the Megachilidae and the Andrenidae (with the exception of *Protandrena* and a few specialist *Andrena*). Three tribes of the Apidae (eg. Bombini, Euglossini, some Meliponini) routinely buzz flowers, although two genera (*Apis* and *Trigona*) have never been observed to sonicate poricidal flowers.

The morphological features of *Solanum* flowers, especially their small numbers of enlarged durable pored anthers, makes them uniquely predisposed to measurements of pollen production and release. Simple experimental manipulations can interrupt, change or otherwise block bees from accessing to the visually concealed pollen rewards without overtly altering morphological or olfactory cues of pollen advertisement. Since *Solanum* species produce no floral nectar, pollen presentation is "decoupled" from nectar rewards, the bee flight fuel.

We took advantage of these features of *Solanum* flowers to experimentally determine whether specialist (native solitary oligoleges) and generalist (native social polyleges) bees could discern quantitative returns in pollen harvested. We compared harvest at control flowers with flowers manipulated to block or remove pollen available to sonicating bees. We present data suggesting that bees can and do quantitatively assess pollen rewards as it is being harvested, on a per flower or plant basis, and tailor their foraging behaviors to the pollen rewards available in a given nightshade flower.

Methods and materials

Data were collected between August 14 and August 20, 1987, in Chihuahuan desertscrub 2 km north of Portal, Cochise County, Arizona (109°10′W × 31°56′N at 4700′ elevation) along the Foothills Hwy. The *Solanum* patch grew at a cattle stocktank on the property of the Crown Dancer Ranch. Fifteen species of bees have been observed to collect pollen from *S. elaeagnifolium* during our five years of observation at this site (Cane and Buchmann, unpublished work) which closely parallels the taxonomic constitution of this bee guild of *S. elaeagnifolium* as reported previously by Linsley and Cazier (1963) working in neighboring localities. The honey bee (*Apis mellifera* L.) is a rare visitor which uses scrabbling or proboscis insertion, both inefficient methods of gleaning to collect pollen "dregs" which legitimate floral sonicators leave behind.

During the present study, however, we focused on only two species, one a polylectic generalist and the other a narrow pollen oligolege, which harvested the majority of *Solanum* pollen from plants in our study population. The specialist buzzing bee during this time was *Ptiloglossa arizonensis* Timberlake, a large diphaglossine colletid (Colletidae). The generalist was the common low elevation Sonoran Desert bumble bee, *Bombus sonorus* Say (Apidae). Foraging females of the two species are of similar size and foraged concurrently in the patch at dawn. Bees visiting *Solanum* within the patch were pollen foragers only, since no nectar rewards are offered by this plant. All floral visits were accompanied by one or more sonications of the anthers.

The floral biology of this *Solanum* is similar to that for other nightshades (Buchmann et al. 1977; Bowers 1975).

For the two experiments detailed below, two plots of 1–2 m^2 were chosen daily which were separated by 3 m. In each plot, one observer watched his own experimental and control flowers. The day prior to the experimental day, 15–20 pollination bags (15 × 20 cm grey, "no-see-um" netting bags with drawstrings) were placed over large purple buds that would open the following morning. Each flower was further given an identifying number and color-coded plastic tag 2–4 cm down the stem. Each morning (at or slightly before 0500 h MST) we unbagged flowers to use in two treatments. The first group (controls) were left unmodified except that each anther was given a small droplet of Elmer's Glue-all at the middle extrorse region. Thus, these controls were "sham-glued" virgin flowers offering a full complement of pollen, but serving as an odor control for the presence of the glue. A second group of treated flowers had their androecia emptied of pollen by touching them 5–10 times with a vibrating 512 Hz tuning fork. Experimental flowers each received small droplets of the same glue (about 0.05 µl per flower) to completely cover and seal the apical pores on all five anthers. Glue, applied with a toothpick, dried in 3–5 min. Subsequent dissection of visited flowers showed that these glued pores remained effective barriers to pollen collection after repeated bee sonications. We were similarly unable to discharge pollen from glued anthers by vibration with a 512 Hz tuning fork.

We allowed bees access to virgin control flowers for only one visit after which a new flower was unbagged and sham-glued to take its place. Experimental flowers, with anther pores glued shut, were visited repeatedly over the course of a morning (from 0500–1000 MST). Observers watched about 120 individual bees visit our experimental patches. We have no evidence that bees in this system scent-mark and subsequently avoid already visited flowers. Indeed, watching cohorts of unbagged flowers on other mornings indicated that, on average, flowers received a total of 5–17 visits by bees of various species during a morning at two neighboring m^2 census plots (871 total visits to 51 flowers). These "glued-flower" experiments were conducted on the mornings of August 15, 16 and 17, 1987.

Data on three related variables (handling times, buzzes/flower, and grooms/flower) were recorded for each bee visitation to either a control or experimental flower. A stopwatch was started and handling time (to 0.1 s) recorded from the time a bee first touched a flower until its departure. The sum of discrete bouts of floral sonication a bee applied to a given flower was easily determined by listening, as audible buzzes are always concomitant with the biophysical act of pollen harvesting at *Solanum* flowers. Similarly, we noted the number of times a bee groomed, combing pollen with its legs from all over its body and finally packing it into their scopae for transport. Bees groomed while on the flowers or neighboring leaves, stroking their bodies vigorously, followed by a brief quiescent period, often hanging from one tarsus at the flower just buzzed. Thus, the logical indication of "pollen feedback" to the bee, number of grooms, could be accurately determined.

We analyzed our data statistically using SAS and PC SAS (SAS Institute 1985). We compared the number of buzzes delivered by bees (*Bombus* and *Ptiloglossa*) to control flowers with the glued and the emptied flowers using a Kruskal-Wallis test following our unsuccessful attempts to transform the data to a normal distribution. We then compared these 2 species for their relative numbers of buzzes at control, emptied and glued flowers. For this repeated univariate test, we set $P \leq 0.01$. We also compared these 2 species for the number of buzzes per flower they delivered to flowers elsewhere in the patch, using slow-play-

Table 1. Intrafloral bee pollen-harvesting behavior for *S. elaeagnifolium* at Crown Dancer popl. from August 15–17, 1987. Means are followed by 1 SE while ranges given in parentheses. Sample sizes are below ranges

	Virgin flowers (controls)[a]			Glued-pore flowers (experimentals)[b]		
	Handling time (s)	Buzzes/flwr	Groomings/flwr	Handling time (s)	Buzzes/flwr	Groomings/flwr
Ptiloglossa arizonensis	12.51 ± 2.06 (4.5–35.2) 18	6.17 ± 0.85 (2–14) 18	4.44 ± 0.93 (0–13) 18	1.98 ± 0.15 (0.4–6.1) 64	1.91 ± 0.11 (1–4) 64	0.03 ± 0.02 (0–1) 64
Bombus sonorus	17.44 ± 2.20 (5.5–42.0) 20	9.55 ± 0.96 (3–20) 20	2.75 ± 0.49 (0–7) 20	6.08 ± 0.91 (0.7–24.3) 34	3.94 ± 0.47 (1–12) 34	0.03 ± 0.03 (0–1) 34
All bees	15.11 ± 1.54 (4.5–42.0) 38	7.95 ± 0.70 (2–20) 38	3.55 ± 0.52 (0–13) 38	3.40 ± 0.38 (0.4–24.3) 98	2.61 ± 0.20 (1–12) 98	0.03 ± 0.02 (0–1) 98

[a] Controls were previously bagged, virgin (unvisited) flowers with intact pollen standing crops. Their only treatment was a small glue droplet on each anther side ("sham-gluing") as a control for glue odor

[b] Experimentals were previously bagged virgin flowers with full complement of pollen within anthers, now unavailable to bees since all 10 anther pores/flower were closed by gluing

Table 2. Intrafloral bee behavior for *S. elaeagnifolium* flowers at Crown Dancer popl. on August 19, 1987. Means are followed by 1 SE while ranges given in parentheses. Sample sizes are below ranges. Second experiment tuning fork-emptied rather than glued-pore anthers

	Virgin flowers (controls)[a]			Tuning fork-emptied flowers (experimentals)[b]		
	Handling time (s)	Buzzes/flwr	Groomings/flwr	Handling time (s)	Buzzes/flwr	Groomings/flwr
Ptiloglossa arizonensis	11.75 ± 2.26 (2.1–41.9) 17	6.06 ± 0.97 2–17) 17	4.06 ± 0.89 (0–15) 17	1.49 ± 0.31 (0.3–5.5) 22	1.14 ± 0.07 (1–2) 22	0.09 ± 0.06 (0–1) 22
Bombus sonorus	15.8 – 1	9 – 1	4 – 1	2.57 ± 0.42 (0.9–7.0) 13	1.62 ± 0.24 (1–4) 13	0 ± 0 (0–0) 13
All bees	11.97 ± 2.15 (2.1–41.9) 18	6.22 ± 0.93 (2–17) 18	4.06 ± 0.84 (0–15) 18	1.89 ± 0.26 (0.3–7.0) 35	1.31 ± 0.26 (1–4) 35	0.06 ± 0.04 (0–1) 35

[a] Control flowers were previously bagged, contain anthers full of pollen

[b] Experimental flowers were also selected from previously bagged virgin flowers. Prior to bee visitation and data collection, they were vigorously sonicated (at least 10–15 times) with a 512 Hz tuning fork while the androecium was rotated. This treatment produces a flower otherwise identical to controls except that they lacked pollen rewards for visitors

back transcriptions of their taped handling sounds (Cane and Payne 1988).

Floral handling durations were log-transformed to make the variances independent of their means (Sokal and Rohlf 1981), and compared by the general linear models procedure of SAS for a 2-way ANOVA (species by treatment).

Grooming bouts were not discernable on our audio recordings of free-foraging bees. For our glued-anther experiments, however, we performed two statistical analyses. First, we performed a 2-way categorical analysis (CATMOD) of the number of visits that were accompanied by at least one groom, comparing both treatment effects and species differences. Then, since only virgin flowers typically elicited multiple grooming bouts, we compared the two bee species for number of grooms per floral visit, using a 2×6 Chi Square contingency table for 0, 1–2, 3–4, 5–6, 7–8, and more than 8 grooms/floral visit.

Results and discussion

Handling duration per flower

This species, like many other *Solanum* spp., reproduces sexually by outcrossing and also vegetatively by underground rhizomes to produce ramet individuals. Thus, it is difficult to estimate the number of genetic individuals in a population. Our population varied in stem density from 6–15/m^2. Random quadrat sampling (flowers/m^2) during their peak bloom revealed floral densities ranging from 0 to 49 flowers/m^2 ($N = 18$ samples), for a mean of 13 plants/m^2. Each of these flowers produces about 4.0 mg of pollen on a fresh weight basis, therefore our population (1000 m^2 in total area) offered an initial pollen standing crop of 52 g harvestable pollen among the 13000+ flowers each morning during this time period.

Significant differences among groups were detected by 2-way ANOVA for log-transformed handling durations in

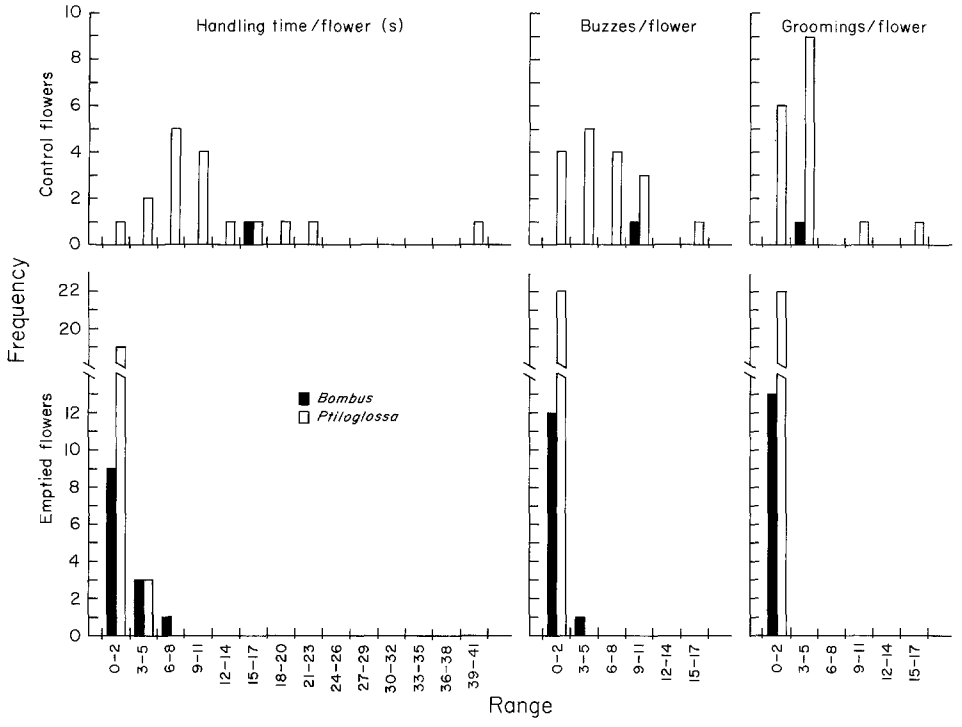

Fig. 1. Frequency histogram summary of pollinator behavior including handling times, number of buzzes delivered to each flower and how often bees groomed and packed pollen into scopae on control flowers (upper three panels) *vs.* glued experimental flowers (lower panels). *Bombus* visits are given in solid black bars while *Ptiloglossa* are shown with open bars

our experiments with glued staminal pores ($F_{3,132}=75.02$, $P<0.0001$). Treatment effects (glued vs. sham-glued pores) and species (*Ptiloglossa* vs. *Bombus*) were both significant sources of variation ($P<0.0001$), as was their interaction ($P<0.025$). Both bee species spent less time working the flowers whose staminal pores were plugged with glue relative to sham-glued flowers (Tables 1, 2). Within a treatment class, *Ptiloglossa* handled flowers faster than *Bombus* (Figs. 1, 2).

Similar treatment effects on handling duration were detected in our experiments with emptied anthers, which these bee species handled significantly faster than neighboring flowers whose anthers remained full of pollen (one-way ANOVA, $F_{3,60}=57.60$, $P<0.001$; data for single virgin flower visits by *Bombus* supplemented by those of previous morning). The faster handling rates of *Ptiloglossa* compared to *Bombus* in these experiments were mirrored in our simultaneously taped samples of foraging bouts by these bees elsewhere in the *Solanum* patch. Overall significant differences in log-transformed floral handling rates by these bees foraging freely in undisturbed parts of the patch ($F_{14,222}=10.43$, $P<0.0001$) could be partitioned into significant differences between individual foragers ($P<0.0001$) and significantly faster floral handling by *Ptiloglossa* relative to slower *Bombus* ($P<0.005$, nested design using individuals within species as the error term).

Sonications per flower

In our glued-anther experiments, experimental flowers elicited fewer buzzes per visit for both *Bombus* ($X^2=21.4$, $P<0.0001$) and *Ptiloglossa* ($X^2=36.8$, $P<0.0001$) relative to unmanipulated virgin flowers (Figs. 1, 2) by the Kruskal-Wallis test. By the same test, we compared the two species within the two treatments (emptied *vs.* virgin), and found that *Ptiloglossa* delivered fewer buzzes per flower than *Bom-*

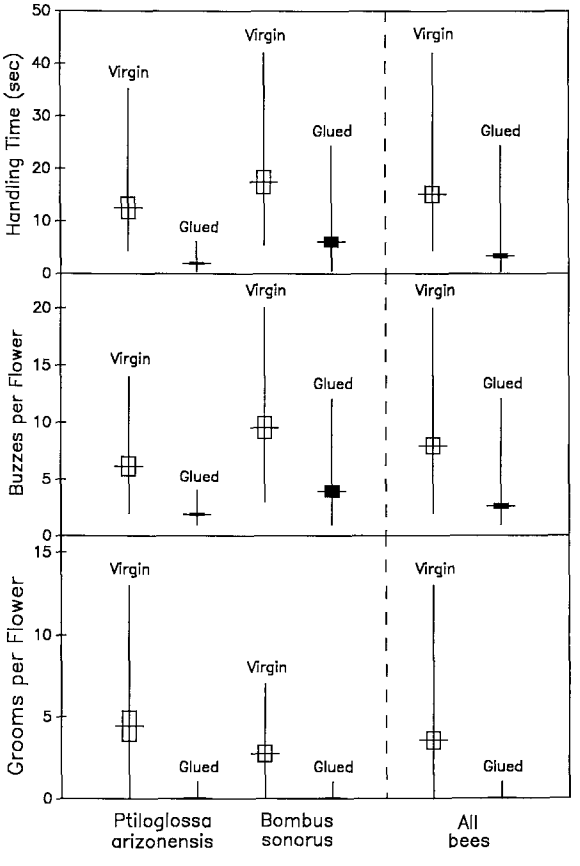

Fig. 2. Dice Gram summary of bee intrafloral behavior including handling time, buzzes per flower and grooming frequency for *Ptiloglossa* and *Bombus* versus values for all bees on virgin (rewarding) flowers compared to flowers with anther pores glued shut (unrewarding). Ranges are given by vertical lines, means as short horizontal bars, and boxes represent one standard deviation

bus for both the experimentally emptied flowers ($X^2=17.3$, $P<0.001$) and the unmanipulated flowers full of pollen ($X^2=6.2$, $P<0.013$) (Figs. 1, 2). Statistical comparison of the numbers of buzzes delivered by *Bombus* vs. *Ptiloglossa* tape recorded outside of our experimental plots during these experiments show that free-ranging undisturbed *Bombus* also deliver more buzzes to a given flower than do *Ptiloglossa* ($X^2=72.2$, $P<0.001$) (Cane and Buchmann, unpublished work).

Grooming pollen packing bouts per flower

Visit by either bee species to sham-glued virgin flowers were significantly more likely to be accompanied by an episode of grooming when compared to visits to flowers whose staminal pores had been glued shut ($X^2=44.89$, $P<0.001$) (Fig. 1). Individual *Ptiloglossa* and *Bombus* were equally likely to groom during visits to flowers within either of the two treatments ($X^2=3.58$, $P=0.058$). When visiting the pollen-laden, sham-glued flowers, significant differences did not exist in the number of grooming bouts associated with a given visit ($X^2=8.3$, $P=0.14$, $N=34$), although *Ptiloglossa* gave twice as many visits with 5 or more grooming bouts, while *Bombus* usually groomed less than 4 times per floral visit (Figs. 1, 2; Tables 1, 2).

Few studies have examined pollen foraging by bumble bees (Haynes and Mesler 1985; Zimmermann 1982). A recent study of movement patterns involving bumble bee species (*Bombus*) concluded that as bumble bees species foraged for pollen and nectar, the bees apparently did not assess pollen returns (harvested pollen accumulating on their bodies) on a per plant or per flower basis (Hodges and Miller 1981). These authors studied bumble bees (*Bombus appositus* Cresson, *B. bifarius* Cresson, *B. flavifrons* Cresson, and *B. occidentalis* Greene) foraging for pollen (and nectar?) on flowers of *Aquilegia caerulea* (Ranunculaceae). They concluded that if their bees had monitored pollen harvest per flower in the case of relatively high overall standing crops, then a characteristic pollen collection time (handling time per flower) should have existed, i.e., there should have been a higher probability of departing a flower after some interval of time and a lower probability of departings sooner or later than this characterizable handling time. If, however, the bees were not detecting differences in available pollen of different flowers, then they predicted that there would be a constant probability of leaving a flower after any pollen collection time indicating to them that pressures to avoid revisitations should not have influenced the *Bombus* pollen-collection tactics (Hodges and Miller 1981). These authors also suggested that accurate monitoring of pollen-feedback, once grains were on the bees but prior to pollen-combing and corbicular-packing, may be difficult for bees (*Bombus*) since the pollen is scattered over the body and not ingested. They further suggested that a bee may assess pollen returns only after visiting multiple flowers (and/or plants) and following grooming and redistribution to its corbiculae, and remarked that "even biologists find it difficult to measure a bumble bee's pollen uptake from a single flower!" Obviously, they neglected scaling theory and failed to realize that pollen grains are large recognizable objects to bees.

In a recent study (Pellmyr 1988), discriminatory behavior by bumble bees (*Bombus honshuensis* and *B. diversus*) in favor of young pollen-rich flowers of *Anemonopsis macrophylla* Ranunculaceae was demonstrated. Observations by Pellmyr indicate that these bees use age-related morphological differences (sepal arrangement) to select pollen rewarding flowers before alighting. This is apparently the first case where visual distant (morphological and/or olfactory?) pollen assessment has been documented for bees. After alighting on *Anemonopsis*, these two *Bombus* utilize floral sonication to rapidly harvest pollen.

We used a local native *Solanum* (*Solanum elaeagnifolium* to experimentally test the interfloral or intraplant pollen-feedback assessment hypothesis rejected by Hodges and Miller using two bee species; a social polylege (*Bombus sonorus*) and a solitary sonication oligolege (the colletid bee *Ptiloglossa arizonensis*) as they harvested *Solanum elaeagnifolium* pollen grains in a SE Arizona nightshade population.

Using experimental manipulations that blocked bee access to pollen we demonstrated that both the generalist polylege (*Bombus*) and a specialist oligolege (*Ptiloglossa*) did assess bodily pollen buildup and adjusted their handling times/rates and behaviors according to available pollen in an individual flower. Such direct positive pollen feedback while sonicating the nectarless *Solanum* flowers presumably enables these bees to harvest more protein-rich pollen and convert it into more larval bees (i.e., "bee units" of pollen) per minute of foraging effort by tailoring their foraging efforts to the available pollen rewards. Ours is the first empirical demonstration of direct positive pollen feedback influencing pollen harvesting by bees on a flower-by-flower basis.

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