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A scientific note on pollinators' ability to overcome exploitation barriers: deep hummingbird-evolved corollas and small-sized bees

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Mexican *Salvia* / *Lasioglossum* / lever mechanism / behavioural flexibility / nectar robbing

For most people, it is common to associate flowers and bees. Ideally, they will combine by gathering reciprocal benefits: the bee will find resources, pollen and nectar, to sustain itself and its progeny; the flower will get the service of cross-pollination to give rise to the next plant generation. This view is sustained by natural-history observations that helped to draw hypotheses on how co-evolution shaped the interactions between bees and flowers. However, it is a complex matter and the interactions may take different paths, where the players are actually competing to be the best performers (Danforth et al. 2019).

Studies on flower morphologies and/or bees have highlighted the variability of traits involved in the exchange: i.e., shape, colour, scents, floral display in flowers; mouthparts, memory, foraging strategies in bees. Many of these traits were/are employed to predict the selective pressures that shape the observed interactions, as

described in the seminal work of Faegri and Van der Pijl (1979) on pollination syndromes. Pollination syndromes should indicate the route from the flower morphological traits to its pollinator guild. Although pollination syndromes and flower traits are still a vibrant field of research, there are potential caveats on how literature addresses concepts and data (Dellinger 2020). Pollination syndromes proved to be weak at a large scale: increasing the number of species and scale affects the predictive power of floral syndromes (Lanuza et al. 2023; Ollerton et al. 2009). The flower-centric approach, carried out by focusing on floral traits, may pose limits in understanding other forces which do not fit with “flower” predictions. For example, anemophilous flowers evolved traits facilitating pollen dispersal by wind: therefore, apparently there is no call for the involvement of bees. However, when the plants are flowering, abundant pollen is available: an appetizing yield for bees that actively visit many anemophilous species (Giovanetti and Aronne 2011; Saunders 2018). Similarly, in the classical view, red flowers are predicted to attract mostly birds: the plant

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genus *Penstemon* Schmidel has been an excellent case-study to separate bird- or bee-pollinated species, depending on floral traits (Castellanos et al. 2004). However, Mediterranean red flowers have also been investigated to understand how they attract other pollinators when no bird pollinators are available in temperate areas. These flowers may match red with other colour signals (UV-red flower type spectra and/or patterned flowers) so as to attract bees (León-Osper and Narbona 2022).

Another way to tackle the interaction between flowers and bees is by addressing animal foraging patterns: therefore, by taking a bee perspective. Optimal foraging should, for example, drive selection towards abundant resources (Fowler et al. 2016): we should record more bee species interested in these resources, and more visits paid to resource-abundant flowers. At the community level, large quantities of floral resources attract more pollinators, but up to a certain threshold and depending on the resource, i.e., nectar (Fantinato et al. 2021). Number of flowers might not be the trait highlighting patterns in the pollination network of a given environment. However, nectar abundance may not be the ultimate driver: for example, foragers of *Apis mellifera* do not select to visit the nectar-richest of *Robinia pseudoacacia* L. flowers, since plenty of nectar also reflects previously unmanipulated flowers, difficult to handle (Giovanetti 2019).

Animals can count on behaviour and learning ability. Flexibility in foraging choices may be a powerful tool, matching the resource options with evolutionary traits and constraints, and may unveil interactions otherwise neglected. A good example of flexibility is bee visits to alien unfamiliar plants, such as the exotic ornamentals: plants introduced into the environment, not co-evolved with native bees, but which can be added to the list of their botanical sources of food. Among ornamentals, especially renowned are those belonging to the very large genus *Salvia* L. (Lamiaceae), distributed worldwide in Asia, America, and Europe, and largely employed in medicine, food, and cosmetics. *Salvia* spp. are similar to *Penstemon* spp. in that they can be matched to their preferred pollinator based on

their flower traits: colour, corolla length, and nectar abundance are expected to indicate either hummingbird- or bee-pollination. Moreover, a peculiar lever mechanism poses a limit to flower visitors: the lever needs to be released to access the nectar by exerting a given pressure at the entrance of the corolla tube (Claßen-Bockhoff et al. 2003), thus also selecting the pollinator based on individual strength. During a research project on plant-pollinator interactions in a botanical garden, we had the chance to record bee visits to two exotic species: *Salvia blepharophylla* Brandegees ex Epling and *Salvia greggii* A. Gray, both native to Mexico. As with other hummingbird-pollinated species, their corollas are especially deep and red, with abundant nectar. We were not expecting many visits to these sage flowers since there are no hummingbirds in temperate areas, but we hypothesized that some large bees might be successful in pressing the lever and reaching the nectar at the base of the corollas. We did actually record a large bee, as predicted: *Xylocopa violacea* (Linnaeus) was visiting *S. greggii* looking solely for nectar (Malabusini et al. 2019; Giuliani et al. 2020). However, this bee was paying illegitimate visits, placing its tongue between calyx and corolla to get the nectar. It is not forced to do so by physical constraints: *X. violacea* frequently applies this strategy, even when visiting native food sources (Vicidomini 2006). Therefore, this is a matter of a species-intrinsic behavioural trait, rather than of plasticity applied to a peculiar food source. Surprisingly, we also recorded very small bees belonging to the genus *Lasioglossum* Curtis, on both sage species. *Lasioglossum* bees did contact the reproductive parts while collecting pollen. Females landed on the lower petal or on top of the upper petal and then reached the anthers by walking: they collected pollen while hanging and grasping the petals. Due to the anthers' position, enclosed within the upper petal, and bee size (4–9 mm), the bees invested some time to reach the anthers and take a suitable position to collect the resource. They grasped a single anther entirely, moving their legs to release and collect the pollen. Pollen grains could later be easily detected on different bee body parts (antennae,

head, thorax, abdomen, legs). Finally, the exotic-tropical plant, which possibly evolved as hummingbird-flowers, got a pollination service from very small native-temperate bees.

More intriguing were a few observations of *Lasioglossum* bees visiting the flowers to collect nectar. What are the pros and cons of visiting such flowers for nectar? Certainly, on the one hand, nectar abundance, and even a possible nectar replenishment during the day as found in another sage, *Salvia przewalskii* Maximovich (Ye et al. 2017): nectar may be a very powerful encouragement for bee foragers. However, on the other hand, the lever mechanism is a strong barrier: Wester et al. (2020) found that mechanical bee exclusion is very efficient in hummingbird-pollinated sage species. During our field observations, *Lasioglossum* bees did in fact employ some time in forcing the lever mechanism, finally entering into the corolla tube with their entire body. After the bee enters, the lever mechanism goes back into position and, hence, a possible drama occurs (entire sequence in Figure 1): from inside, it was not possible to move the lever so to achieve the way out and the bee found itself trapped inside. Not able to exit in the same way they entered, bees employed their mandibles to cut the corolla. From the outside, the two mandibles emerged after having punctured the flower tissue. This cut allowed the enlarging of a small hole from which the bee makes an effort to push first the head and continues by slowly emerging with the other body parts (see the thorax in the picture). The bee can finally press the entire body through the hole until getting free. As it is clearly illustrated by the sequence of the photographic record, when the bee is finally able to fly away, the corolla is left with noticeable damage. This damaged area can be further employed by other bees, therefore avoiding the sequence just described. Were we witnessing a new foraging strategy? We checked for evidence of the presence and frequency of damage to the perianths of individual flowers: all *S. greggii* flowers showed some holes in the corolla tube, up to 8 on the same flower. Presence of damage on *S. blepharophylla* was much rarer, the difference

between the two species being statistically significant (z test statistic = 7.2243, $p = < 0.00001$). We measured nectar volume (in the field, with 10 μ l microtubes) and sugar concentration (by a hand-held refractometer) in a random sample of flowers ($n = 80$) at different times of the day. Results showed *S. greggii* as lower in quantity ($1.37 \pm 1.88 \mu$ l, $n = 45$) but higher in sugar concentration ($34.2 \pm 3.74 = ^\circ$ Bx RDS, $n = 28$) than *S. blepharophylla* ($1.99 \pm 1.51 \mu$ l, $n = 35$ and $28.11 \pm 3.09 = ^\circ$ Bx RDS, $n = 27$, respectively). It is generally expected that lower nectar volumes with higher sugar concentrations are preferred by bees, while higher nectar volumes with more dilute sugar solutions are more attractive to birds, bats and lepidopterans (Baker and Baker 1983). This difference may explain the higher number of damaged flowers we recorded on *S. greggii*.

About foraging strategies, “cutting” itself is a practice that other bees adopt: for example, in Australia the bee species *Hylaeus* (*Hylaeteron*) *douglasi* Michener, 1965 was recorded extracting pollen from pre-anthesis flowers of *Grevillea excelsior* Diels by cutting a hole in the perianth limb (Jacobi and Newman 2012). *Lasioglossum zephyrum* (Smith) was recorded manipulating a flower to open it before natural anthesis and getting first access to the pollen by cutting and removing a sheath covering the flower (Wall et al. 2002). Notwithstanding some similarities, our observations indicate a certain degree of risk that the “cutting” strategy does not imply. It would be interesting to better understand what forces are involved in this interaction. The single report we could find resembling our observations is that of Li et al. (2008). They described *Lasioglossum* spp. visiting an orchid species, also risking getting trapped inside the flower, possibly to the point of death (one actual record), while escapees renounced paying any more visits to the same type of flowers in the future.

For bees, it is expected that a trade-off will occur, balancing the caloric value of nectar rewards with the cost of nectar collection (Heinrich 2004), which explains the behavioural efforts to visit flowers that impose some extra foraging effort. However, energy saving does not

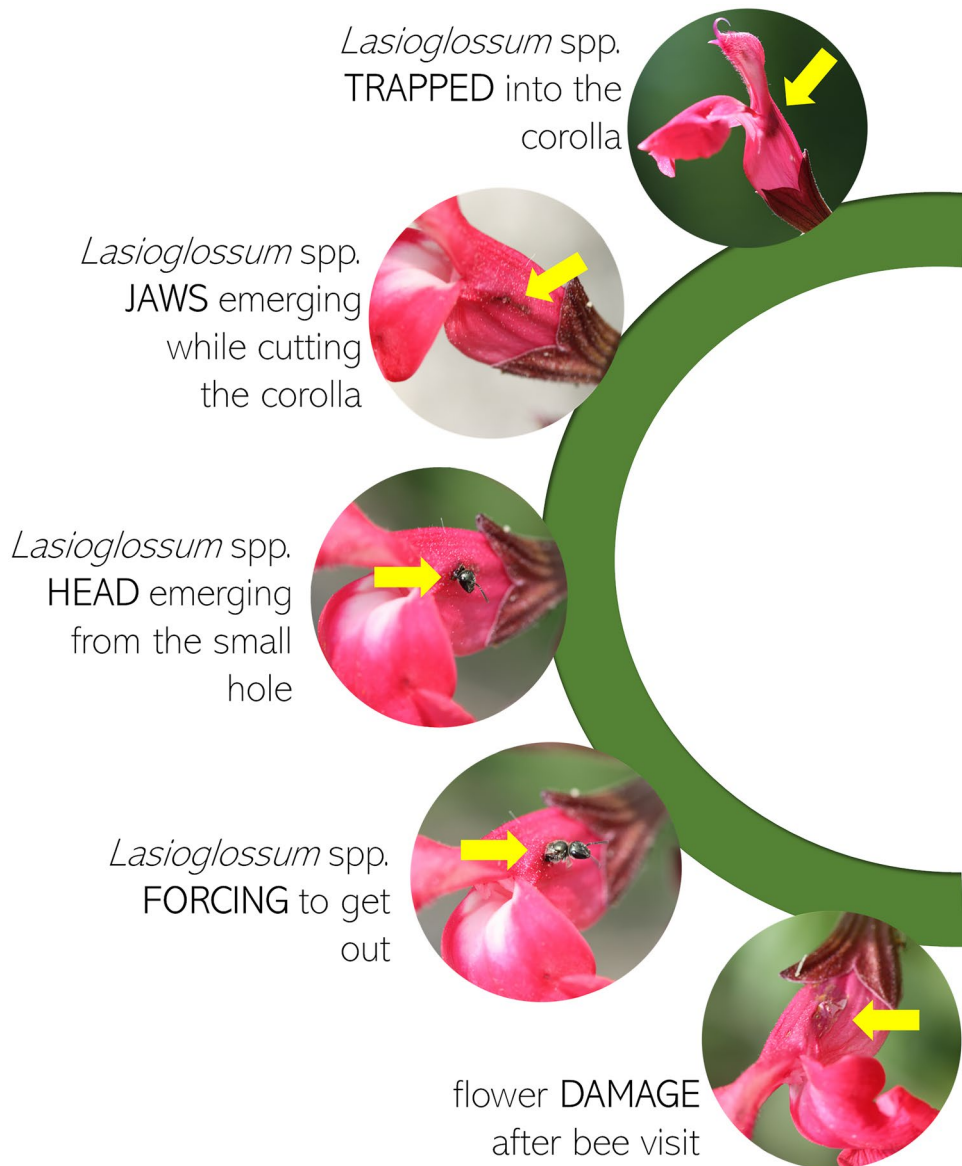


Figure 1. Photographic sequence of trapped *Lasioglossum* sp. individual inside the corolla tube of a *Salvia greggii* flower, until the point of escape after having cut the corolla tissue.

seem the more fitting explanation for our observations. A compulsory cue may be the reason: the concealed nectar released by *S. greggii* possibly deposited in the belly-shaped corolla may facilitate a mechanical or olfactory detection and finally boost bee visits even at the risk of getting trapped inside. A reinforced or overwrite signal

could induce this visit, by ranking top in a “perceptual hierarchy” (Ruedenauer et al. 2023) of getting an abundant/special resource, moreover considering that a solution to overcome the trap exists: to cut the flower tissue.

On the plant side, there is a cost still not evaluated. In Brazil, *Trigona fulviventris*

damages the flowers of *Eriocnema fulva*, negatively influencing the final fruit set (Rego et al. 2018). Fruit set is also negatively influenced by nectar robbers, usually performed by large bees (Schlindwein et al. 2014). Open questions to be addressed in the future may include: what is the actual damage that flowers sustain, and whether this damage influences flower attractiveness and overall fitness. In the context of the bee-flower interaction that we describe here, nectar collection is not linked to pollen transfer and may not be connected with the plant reproduction. However, it would be interesting to get deeper into the story and find out to what extent this type of nectar visit implies costs to the plant and to the trapped bees. Clearly, much more has to be discovered in relation to the behavioural flexibility of foraging individuals, flower architecture and the ultimate forces driving foragers' selection of food sources. Some authors (van der Kooi et al. 2021) indicate this complexity as the result of a-symmetric relationships between plants and pollinators. We definitely agree with the authors that what can be perceived as a perfect (or not) deal with (possible) reciprocal benefits may finally depend on the perspective taken to interpret the outcome of the relationship. It is of outstanding importance to maintain multidisciplinary in plant-pollinator studies to ascertain the real state of balance for each player. From an evolutionary perspective, the more natural-history observations we acknowledge, the more rethinking is needed on current theories: till the point to finally renounce the concept of the ideal perfect match between flowers and bees for a more outlandish economic perspective of cost–benefit analyses?

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AUTHOR CONTRIBUTION

MG conceived the idea and planned the scientific note; field work was carried out together with DL and CG; MG wrote the manuscript with contributions from DL, CG, GF. All authors have read and agreed to the final version of the manuscript.

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AVAILABILITY OF DATA AND MATERIAL

The authors confirm that the data supporting the findings of this study are available within the article. Rough numbers will be available upon request.

DECLARATIONS

Conflict of interest The authors declare no competing interests.

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