Accepted refereed manuscript of: Pritchard DJ & Vallejo-Marín M (2020) Buzz pollination. *Current Biology*, 30 (15), pp. R858-R860.
https://doi.org/10.1016/j.cub.2020.05.087

Quick Guide to Buzz Pollination

David J. Pritchard* & Mario Vallejo-Marín

Biological and Environmental Sciences. University of Stirling. FK9 4LA. Stirling, Scotland, United Kingdom.

* Author for correspondence

What is buzz pollination?

Buzz pollination is a pollination syndrome in which bees use vibrations to extract pollen from flowers, incidentally fertilising them (Figure 1). The buzzing behaviour that some bees display on flowers to extract pollen has also been called "floral sonication" due to the distinctive sound the vibrations produce. Buzz pollination is relatively widespread; flowers with buzz-specialised morphology are found across more than 20,000 species of flowering plants, including economically important crop species such as tomatoes, potatoes and kiwis, while flower buzzing has been observed in 74 genera comprising about 58% of bee species.

How do bees produce floral vibrations?

When buzzing a flower, a bee holds onto the anther or other floral structure and produces vibrations using its thoracic muscles, while keeping the wings folded. These vibrations release pollen onto the bee's body which she will later groom into place to carry back to the nest. To produce floral vibrations, bees use their flight muscles: specifically, the dorsal longitudinal and dorso-ventral muscles that fill the inside of the thorax and provide the power for flight. These muscles are *asynchronous,* meaning that the rate of muscle contraction is different to the rate of neural impulses received by the muscles. This disconnect between neuron firing rate and muscle contraction is due to *stretch-activation*. When one of the muscle sets contracts, it stretches the other set, triggering those latter muscles to contract. While insects with stretch-activated muscles can use neural impulses to control the overall power produced, this self-perpetuating cycle of muscle contractions allows the production of vibrations at much higher frequencies than would be possible without stretch activation. Floral vibration frequencies can exceed 300 Hz (cycles a second), with some species approaching 400 Hz. The vibrations produced during floral vibrations are not exactly the same as those produced during flight. During flower-buzzing bees vibrate their thorax at higher frequencies and higher amplitudes than during flight. These higher frequency vibrations appear to be partly due to the wings being folded over the abdomen, reducing the effect of drag and inertia on the vibrations, and partly due to differences in the pattern of neural impulses sent to the muscles. The properties of floral vibrations therefore depend on both the nervous system of the bees and biomechanics of the body.

Can all bees buzz flowers?

No. Only about half of bee species can buzz flowers, including large carpenter bees as well as minute sweat bees. We do not currently know why some species do not buzz flowers. On a mechanistic level, some bees might not be able to generate the forces required to release pollen, and so there is little point in buzzing flowers. Bumblebees and carpenter bees can produce buzzes with accelerations sufficient to release pollen from poricidal anthers, but honeybees (*Apis mellifera)* cannot reach the required acceleration. We still do not know why, on an evolutionary level, bee species differ in the buzzes they can produce.

How does a buzz-pollinated flower look?

Bees vibrate flowers of diverse floral morphologies (Figure 1). However, the vast majority of buzz-pollinated flowers possess anthers that conceal pollen inside anthers that open only though small pores or slits at their tip (poricidal anthers). The anthers of these species are enlarged, brightly coloured, and presented prominently to the approaching visitors. The petals are often reflexed away from the anthers, which in some cases form a cone at the centre of the flower. There are more than 20,000 species of flowering plants with poricidal anthers and these are mainly pollinated by bees that use floral vibrations to remove pollen. Classic examples of buzz-pollinated flowers with poricidal anthers include the 1,300 or so species of *Solanum* (including tomatoes, potatoes and aubergines) as well as most species in the tropical family Melastomataceae. Other plant species have evolved different floral morphologies that conceal pollen and which require bee vibrations to remove it efficiently. For example, some *Pedicularis spp.* (Orobanchaceae) keep their anthers inside a tubular structure made of modified petals that release pollen only through a small terminal pore-like opening, while an unusual species of *Dalechampia* (Euphorbiaceae) in Madagascar has modified entire male flowers that take the functional role of a poricidal anther. Curiously, flowers of some species of Fabaceae combine poricidal anthers with highly modified, curved (*Senna spp.*) or even tubular petals (*Chamaecrista sp.*) that might act as extensions of the anther and facilitate pollen placement on bees.

How do buzz properties affect pollen release?

Floral vibrations differ in properties such as frequency, duration and amplitude. These properties can affect how much pollen these buzzes release. In experiments in which flowers are vibrated and the pollen released measured, it has been found that high velocity and high acceleration buzzes released the most pollen from anthers. Bees could therefore release more pollen during floral vibrations by producing high velocity and acceleration vibrations. Indeed, the floral vibrations produced by buff-tailed bumblebees, *Bombus terrestris,* have higher velocities and accelerations than vibrations produced during flight or defence. The transmission of vibrations from the bee's thorax to the anthers is mediated by characteristics of the bee, the flower being vibrated, and the coupling between bee and flower. Floral traits such as anther mass relative to the bee, anther geometry and architecture, and its material properties might influence how bee vibrations translate into pollen release. Furthermore, the amount of pollen released for a given buzz can also change over time. Older virgin *Primula conjugens* (Primulaceae) flowers release more pollen than younger virgin flowers when buzzed at frequencies similar to those used by bees (less than 400Hz). The ecological interaction between plants and bees through their biomechanics and behaviour, make buzz pollination an excellent system to investigate the mechanical ecology of plant-animal interactions.

Can bees modify their buzzes?

The buzz a bee produces differs among bee species and, in some cases, between larger and smaller members of the same species. In some species, individual bees can also modify the vibrations they generate, producing longer or shorter buzzes or buzzes at higher or lower frequencies depending on the plant species they are visiting. In other species, including other bumblebees, there is very little difference in the buzzes bees produce on different flowers, with most variation in vibration properties being caused by how plants transmit vibrations rather than bees producing different vibrations. While foraging on a flower, bees can modify their buzzes based on how much pollen they are extracting. When a flower does not release pollen, bees may change the properties of their buzz, increasing the frequency or amplitude. Evidence for bees learning to produce buzzes with particular properties is mixed. Although bees seem to get better at buzzing flowers, collecting more pollen with experience, we are not sure why this is. Different studies have found changes in the frequency, duration, and amplitude of buzzes as bees gain experience, but attempts to train bees to buzz at higher or lower frequencies, showed no signs of bees learning the "best" frequency. Instead, bees continued to use the same heuristics they would use in other situations, increasing their buzzing frequency when flowers are not rewarding them with pollen.

Why does buzz pollination evolve?

The relationship between pollen-foraging bees and flowers goes back to the origins of bees in the early Cretaceous over 120 million years ago. While many plant species use nectar, oils, scents and other rewards to attract pollinators, buzz-pollinated plants are usually nectarless and almost exclusively rely on pollen. Pollen consumption leads to a potential conflict between plants and their pollinators. Poricidal anthers and other specialised floral morphologies of buzz-pollinated plants may have evolved to restrict pollen access by greedy and/or inefficient pollinators. These floral modifications may have in turn shaped the evolution of floral buzzing by bees. Flower buzzing has evolved over 45 times in bees and likely preceded the evolution of buzz-pollinated flower as a method to improve pollen collection efficiency. However, restricting pollen access may have encouraged further evolution of this behaviour, resulting in an arms race between plants and bees and causing further evolution in buzz-pollinated flowers.

Is buzz pollination an evolutionary dead end?

For bees, buzzing is one of several behavioural tools to extract rewards. Many buzz pollinating bees, like bumblebees (*Bombus spp.*), are generalists and will seek pollen on buzz-pollinated and non-buzz-pollinated flowers. Other bees rely more strongly on buzz-pollinated flowers. Several mining bees in the subfamily Oxeinae strongly prefer buzz-pollinated flowers for pollen collection. As buzz-pollinated flowers are often nectarless, few bees can rely exclusively on buzz-pollinated plants as they have to find nectar sources elsewhere. An exception might be those bees specialising in nectariferous buzz-pollinated flowers, such as the anthophorid (digger) bee *Habropoda laboriosa,* a blueberry specialist. It has yet to be seen if these bees possess specific adaptations for buzz-pollination. For plants the story may be slightly different as buzz-pollinated plants may rely heavily on visitation by buzzing bees for reproduction, leading to functional specialisation. It has been suggested that the morphological adaptations associated with buzz-pollination may have trapped these plants in an adaptive peak. Despite this, there are examples of plant species that have evolved other modes of pollination derived from buzz-pollinated ancestors. For example, a few species of Melastomataceae have evolved flowers with modified anthers that act as bellows to release pollen. When a pollinator collects floral perfumes (non-buzzing male orchid bees in *Solanum*) or remove the sugar-rich structures at the base of modified stamens (birds in Melastomataceae), the flexible anther is squeezed, producing a puff of air, which fires pollen onto the pollinator’s body. Having lost their need for buzz pollinators, these flowers demonstrate the diversity of ways in which plants evolve to disperse their pollen.

Where can I find out more?

Buchmann, S. L. (1983). Buzz Pollination in Angiosperms. In *Handbook of Experimental Pollination Biology* (pp. 73–113). Van Nostrand Reinhold Company. New York, NY

Danforth, B. N., Minckley, R. L., Neff, J. L., & Fawcett, F. (2019). *The Solitary Bees: Biology, Evolution, Conservation*. Princeton University Press. Princeton, NJ

Dellinger, A. S., Chartier, M., Fernández-Fernández, D., Penneys, D. S., Alvear, M., Almeda, F., Michelangeli, F. A., Staedler, Y., Armbruster, W. S., & Schönenberger, J. (2019). Beyond buzz-pollination–departures from an adaptive plateau lead to new pollination syndromes. *New Phytologist*, 221, 1136–1149. https://doi.org/10.1111/nph.15468

De Luca, P.A., Bussière, L.F., Souto-Vilaros, D., Goulson, D., Mason, A.C., and Vallejo-Marín, M. (2013). Variability in bumblebee pollination buzzes affects the quantity of pollen released from flowers*. Oecologia 172*, 805–816.

Harder, L. D., & Barclay, R. M. R. (1994). The functional significance of poricidal anthers and buzz pollination: controlled pollen removal from *Dodecatheon*. *Functional Ecology*, *8*, 509-517. https://doi.org/10.2307/2390076

King, M. J., Buchmann, S. L., & Spangler, H. (1996). Activity of asynchronous flight muscle from two bee families during sonication (buzzing). *Journal of Experimental Biology*, *199*, 2317–2321.

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. *Journal of the Kansas Entomological Society*, *76*, 295–305.

Switzer, C. M., Russell, A. L., Papaj, D. R., Combes, S. A., & Hopkins, R. (2019). Sonicating bees demonstrate flexible pollen extraction without instrumental learning. *Current Zoology*, *65*, 425–436. https://doi.org/10.1093/cz/zoz013

Whitehorn, P. R., Wallace, C., & Vallejo-Marin, M. (2017). Neonicotinoid pesticide limits improvement in buzz pollination by bumblebees. *Scientific Reports*, *7*, 15562. https://doi.org/10.1038/s41598-017-14660-x

Vallejo-Marín, M. (2019). Buzz pollination: studying bee vibrations on flowers. *New Phytologist, 224*, 1068-1074. https://doi.org/10.1111/nph.15666

Acknowledgements

This work was supported by a research grant from The Leverhulme Trust (RPG-2018-235) to MVM.

Figure

Figure 1. Examples of bees visiting buzz-pollinated flowers. Clockwise from top left: Sweat bee (possibly *Augochlora* or *Augochloropsis,* Halictidae) on *Tibouchina sp.* (Melastomataceae) in Brazil; carpenter bee (*Xylocopa sp.*) on *Tibouchina sp.* in Brazil; unidentified bee on *Solanum houstonii* (Solanaceae) in Mexico; bumblebee (*Bombus sp.,* Apidae) on *Senna alata* (Fabaceae). Photo credits: Douglas Moore (*Solanum houstonii*), Carlos Eduardo Pereira Nunes (*Senna alata*), and Mario Vallejo-Marín (*Tibouchina sp.*).