A bumble bee (*Bombus terrestris*) worker is poised to damage a leaf to spur flowering, which suggests a phenological synchrony between plants and pollinators.

ECOLOGY

The secret lives of bees as horticulturists?

Pollen-starved bumble bees may manipulate plants to fast-forward flowering

By **Lars Chittka**

The symbiotic relationship between insect pollinators and flowers is as tight as it is fragile. Plants provide nutrition for flower visitors in exchange for pollination services. However, timing is critical in this exchange: If pollinators are out of sync with the blooming times of their favorite flowers, then the plants might display their beautiful sex organs in vain, and pollinators and their offspring might starve (*1, 2*). Now, on page 881 of this issue, Pashalidou *et al.* report that bumble bees are not passive players in this relationship. Rather, the bees have developed a way to hasten flowering specifically under conditions in which bees are food-deprived early in the season (*3*).

Climate change threatens the long-established synchronization of seasonal pollinator activity and flowering time. Temperature strongly affects the emergence of pollinating insects after hibernation (*4*). By contrast, flowering relies heavily on the time of exposure to light (the photoperiod), which is not subject to climate change (*5*). Thus, pollinators might find themselves critically short of nutrition early in the season.

In contrast to hypothesis-driven research, scientific discovery often springs from careful observation of natural phenomena. Pashalidou *et al.* noticed a previously unreported natural behavior: Using their mouth parts, bumble bees deliberately damaged leaves of a variety of plant species (see the figure). The authors suspected that this behavior might be related to a shortage of pollen, the bees' sole source of protein. Therefore, the researchers compared the leaf-damaging behavior exhibited by experimental pollen-starved colonies of bumble bees with that of worker bees from well-fed nests. The results were consistent across years and experimental situations (laboratory settings as well as free-flying colonies): Pollen-starved workers made considerable efforts to puncture holes in the leaves of flowerless plants, whereas workers from well-fed colonies rarely did so.

But why? Pashalidou *et al.* then discovered a dramatic effect of the leaf-damaging behavior on flowering phenology. When exposed to leaf-biting bees, the black mustard plant

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(*Brassica nigra*) flowered 2 weeks earlier and tomato plants (*Solanum lycopersicum*) came into flower a month sooner than would normally be expected. Thus, bumble bees appear to perform a low-cost, but highly efficient, trick to accelerate flowering in plants around their nest under conditions when flower pollen resources are most urgently needed for colony growth.

Many intriguing questions surround the evolution of leaf-biting behavior as well as its adaptive importance. How might this behavior have arisen? One possibility is that individual bees figured out that leaf-biting results in future rewards, and that these bees remember the very plants they have damaged and return to them weeks later to reap the benefits of their efforts. This is perhaps not wholly implausible, given that bumble bees have developed other impressively innovative solutions to access rewards (*6*), and their spatial memories can last a lifetime (*7, 8*). However, it is unlikely that bees can learn that a link exists between an action and a reward that occurs a month later. Also, worker bees in the wild rarely survive longer than 1 month (*7*).

An alternative explanation for how leaf-biting first arose is that individual bees receive an immediate benefit in addition to the more long-term one for colony fitness. For example, bees might extract a substitute protein source from leaf-biting, such as plant sap. However, Pashalidou *et al.* rejected this possibility because most leaf-damaging interactions seemed too brief for bees to imbibe plant juices in appreciable quantities.

Perhaps pollen-starved bees just bite plant parts indiscriminately in the hope that these might conceal some pollen. This too is unlikely, because even entirely inexperienced bees can tell flowers from vegetative parts (*9*). Bumble bees sometimes extract nectar from hard-to-access flowers by puncturing floral structures, a technique called nectar robbing. Inexperienced workers attempt this at various flower parts, until they figure out the reward location (*10*).

One might also wonder why bees would bite holes in vegetative parts of plants that do not even have flowers, instead of searching for plants that do. Unselective perforation of leaves in a bee colony's flight range will not confer much profit. For example, spreading the perforation treatment too far from the native nest might be more likely to benefit competing bees with nearby nests. In addition, many plants, such as mosses or ferns, will never provide any useful pollen for bees, nor will it be beneficial to bite the leaves of plants that are past the blooming stage. Perhaps bumble bees can use flower buds as cues that flowering is on the horizon. Thus, the bees would know that these plants are worth their effort to further speed up flowering (*11*). Future studies should develop a plausible evolutionary scenario for how the first mutant bees that began leaf-biting might have conferred a sufficient selective colony-fitness advantage for this trait to spread through a population.

Turning to plants, there are many equally fascinating questions relating to why an adequate response to bee-driven leaf damage would be to accelerate flower development. One possibility is that such damage is interpreted by the plants as an ongoing herbivore attack; annual plants, therefore, might force an earlier flowering period before the plant's untimely demise. Plants are known to speed up their flowering as a response to various stressors, but there are no known examples of such a response to herbivory (*4*). An adaptive explanation might be that plants "want" to respond to bees that are signaling a dearth of food, because this also means there might be an excess of pollination services available. However, there will also be an opposing selective pressure to synchronize flowering with potential mates within plant species (*12*), which would be a disadvantage to individual plants that move their flowering forward.

A further reason why plants might fast-track flowering is that they are simply manipulated into doing so against their own advantage, but to the benefit of bumble bees. Mechanical damage made with metal forceps and razors does not have the same effect on flowering times as does perforation by bees. Thus, it remains possible that bees inject chemicals into the plants to promote flowering. If so, scientists might realize a horticulturist's dream by deciphering the molecular pathways through which flowering can be accelerated by a full month. An encouraging interpretation of the new findings is that behavioral adaptations of flower visitors can provide pollination systems with more plasticity and resilience to cope with climate change than hitherto suspected. ■

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METROLOGY

Synchronized to an optical atomic clock

Microwave generation using optical frequency comb technology hits new milestones

By **E. Anne Curtis**

Metrology, the science of measurement, is at the heart of all scientific endeavors. Of all parameters, frequency is the most accurately measurable quantity in the scientific portfolio. Tabletop experiments can generate highly accurate and stable frequencies that are being used to challenge the tenets of fundamental physics (*1*) as well as for specific applications such as the synchronization of large-scale radio telescope arrays (*2*). Optical atomic frequency standards have the intrinsic capacity to attain higher levels of stability and accuracy than microwave-based standards. Microwave technology, used in every sector of society, would benefit greatly from similar performance. On page 889 of this issue, Nakamura *et al.* introduce an experimental system with the ability to transfer the precise phase and accuracy of optical clock signals into the electronic domain, while demonstrating a fractional frequency instability of one part in 10^{18} (*3*). This result brings the superior performance of an optical frequency standard into the microwave regime.

The innovation of the femtosecond optical frequency comb (OFC) was a major breakthrough in the pursuit of improved frequency standards based on optical transitions (*4*). Although optical signals oscillate much too quickly for their frequencies to be counted electronically, an OFC can phase-coherently link optical frequencies to much slower microwave frequencies. The OFC is best described as a pulsed-laser device whose output is a series of very short-lived light pulses, produced at a repetition rate in the microwave regime. The output can also be observed in the frequency domain, where it looks like a comb of evenly spaced fre-

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