Following an enquiry about Australian Finger Limes and Desert Limes, we were astonished to find that caffeine is not only present in coffee, chocolate and tea, but also in Citrus!

In 1985, Ivan Stewart from the Citrus Research and Education Centre of the University of Florida, accidentally discovered the presence of caffeine when he was extracting hormones (cytokinins) from flower buds of oranges. He recorded the highest levels of caffeine in fully open flower buds of Valencia oranges; young leaves contained much less. You can relax at this point, he didn’t find caffeine in Valencia orange juice, so it’s still fine for the kids to drink. However, it begs the question, do lime leaves add more than a citrus flavour?

Methylxanthines, such as caffeine, occur naturally in coffee, tea and chocolate. Not only do they inhibit insectivory but they are quite effective as insecticides. Stewart speculated that the caffeine in Citrus buds and flowers might protect them against herbivores.
The highest caffeine concentrations in *Citrus* flowers are in the stamens, where levels in the pollen-bearing anthers at the very tip of the stamens can be as high as 0.9% dry weight; this is very close to concentrations in Arabica coffee beans. Maybe not surprisingly, caffeine has been found in honey from orange orchards.

Prior to the work with *Citrus*, there were numerous studies on the effect of caffeine on honey bees. At very low levels caffeine is not toxic to bees, although given a choice they prefer sugar solutions without the caffeine. When no alternative was offered, the caffeinated version was acceptable!

So, could a low dose of caffeine confer a benefit to bees as it is purported to do in humans? In 1999, research by two Swiss biologists found that it not only boosted egg production of young queen bees, but worker bees became more active, including becoming better able to defend the hive from hornets. Curiously, hornets fed with caffeine, reacted entirely in the opposite way, becoming less active in the field. Caffeine is known to be toxic to a predatory mite, *Euseius mesembrinus*, so the researchers suggested that levels not harmful to honeybees might control the ectoparasitic mite, *Varroa jacobsoni*, whose impacts are much feared by bee keepers world-wide.

More recently, in 2013, researchers compared the responses of honey bees to caffeine-laced sugar (sucrose) rewards (similar to that found in nectar from both coffee and *Citrus* plants), to rewards based solely on sugar. Not surprisingly to coffee drinkers, honey bees rewarded with caffeine were more likely to remember the source than those rewarded just with sugar. Caffeine in high concentrations on its own is bitter, and unappealing to bees, but the levels of caffeine in nectar in flowers of coffee and *Citrus* apparently don’t exceed the bees’ tolerance for bitterness. So perhaps like many of us who enjoy their coffee with added sugar, bees are attracted to nectar with levels of caffeine that don’t act as deterrents. When foraging bees preferentially visit caffeine-laden flowers, plants benefit from increased pollination and ultimately, reproduce and secure their genetics.

So, once again, like us, it seems that, high doses of caffeine are lethal to bees, but low doses are rewarding and enhance cognitive performance and memory retention.
However, things are not always as they seem. Later studies (2015) have shown that caffeine in flowers can trick honey bees into over-estimating both the quantity and quality of nectar available to them, resulting in bees ‘over-investing’ in foraging from flowers with caffeine, and caffeinated plants needing to make less nectar than they might otherwise. The bees that had foraged on caffeinated flowers put far more energy into waggle dancing as a signal to their fellow worker bees, reflecting the trickery that caffeine can induce.

So, the relationship between plants and honey bees can be mutually beneficial but like all mutualisms, can be exploitative, especially by the plants. However, there is little doubt that caffeine improves the memory of both bees and people. To quote Ian Musgrave, Senior Lecturer in Pharmacology from the University of Adelaide on The Conversation:

*If you are out hiding Easter eggs for the Easter egg hunt, maybe you should have a good cup of espresso first, so you can remember where you hid them the next morning.*

**Alison Downing, Brian Atwell, Kevin Downing**  
Department of Biological Sciences


Choose your coffee!
A display board in a café in Puerto Natales, southern Chile.