





How can a pathogen subvert honey bee social behaviors to increase its success?

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Honey bees are extremely important pollinators. Understanding the way bees manage infections can help us protect them. In this study, we show how the Israeli acute paralysis virus can change bees' social behavior to increase infection rates.



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Honey bees are important pollinators. However, like us, they can become hosts to many pathogens. As a social species living in enormous colonies, honey bees have evolved many behavioral defenses to deal with disease, for example changes in social contact. However, as new pathogens continue to arise, some have the potential to subvert these defenses for their own benefit.

We explored how one pathogen, a bee virus called Israeli acute paralysis virus (IAPV), affects honey bee behavior to improve its transmission. To do this, we used two types of "sick bees": "infected bees" that were fed the live IAPV and "immune-stimulated bees" that were fed only a piece of viral genetic code, that stimulated their immune systems without actually infecting them. By using both, we could see which changes in bee behavior were specific to IAPV and which were caused by triggering the immune system. We also used two different methods to observe these behaviors: automated monitoring with a computer and manual monitoring by a human observer.

Using the computer system, we tracked the social interactions of infected bees inside special experimental colonies. We focused particularly on food sharing behavior, called trophallaxis, where individual bees 'spit' food to each other. They normally do this as a way to efficiently share food between different members of the colony. Since trophallaxis involves sharing body fluids, it can also





play an important role in spreading diseases. In parallel, a human observer monitored the behavior of small groups of infected and immune-stimulated bees at a finer scale. The computer observations found that infected bees reduced social contacts with other bees in their colony; human observations found that both infected and immune-stimulated bees showed these reduced social contacts. Because we saw this in both types of "sick" bees, this is likely a general immune response meant to help reduce disease transmission within the colony. We might think of this like a fever - it's a non-specific response to many pathogens.

Since beekeepers often manage multiple adjacent hives, we also need to consider how diseases spread between colonies. Honey bees spend their early lives totally inside their nest; as they get older, they start leaving the colony to forage for food to bring back to the colony. Other researchers have shown that stressed bees start leaving the colony at a younger age and are more likely to get lost. Bees also sometimes "drift", or return to the wrong colony; if this happens with sick bees, they could spread diseases! To defend themselves, bee colonies have "guard" bees, who prevent intruders from other colonies from entering.

We explored how guard bees might receive a sick bee mistakenly wandering into their colony by watching how guards interacted with normal, infected, or immune-stimulated bees from other colonies. We found that, while both infected and immune-stimulated bees appear to be isolated in their home colony, infected bees may be more warmly received by other colonies! While immunestimulated bees experienced many aggressive behaviors (like stinging and biting) from guards, bees infected with a real virus were much less likely to be attacked, even compared to healthy bees. Instead of attacking, guard bees actually shared food with the infected bees, and ultimately allowed them to enter the new colony.

How could the virus trigger this change in behavior? Ordinarily, guards distinguish the smell of arriving bees, and only let in those that match the colony odor. When we measured chemical signatures of these odors, we found that sick, immune-stimulated, and normal bees each had distinct odors, but shared many similarities. This suggests that stimulation of the immune system causes odor differences (allowing other bees to identify sick bees), but that IAPV causes further changes that may disguise the sickness.

Why is this strategy of the virus so successful? Why don't bees have better defenses against it? For millions of years, natural honey bee colonies have lived very far apart from each other and drifting honey bees were probably rare. However, in most modern beekeeping operations, bee colonies often live in close proximity to dozens, even hundreds of other colonies! This means it's more likely for drifting to happen and for pathogens to be spread this way. Since viruses are typically much quicker to adapt to new environmental conditions than their hosts, they are more likely to quickly evolve new ways to exploit the environment than honey bees are likely to adapt to deal with new virus behavior. We need to consider how human actions can modify the delicate balances established among organisms in nature. This is especially important in respect to honey bees that we all rely on for our well-being!