

The Case for Pathogen Spillover from Managed Honey Bees to Wild Pollinators

By Dr Rachel Down, Invertebrate Biologist, Fera Science Ltd.

Pathogen spillover is the term used to describe the transmission of infections among species; the pathogen is transmitted from a reservoir host species to a recipient host species in a shared environment. Pathogen spillover from managed bees is increasingly thought to be a contributory factor in pollinator decline. This article reviews the current knowledge of pathogen spillover from managed western honey bees, *Apis mellifera*, to other species, particularly focussing on spillover of honey bee viruses to wild bee populations.

Transmission routes

Apis mellifera is known to harbour many pathogens, providing potential for it to act as a reservoir host species. Coupled with its global distribution, this creates opportunity for spillover events to occur, especially as many of the pathogens associated with the western honey bee have followed its spread across the world. Furthermore, many of the pathogens associated with honey bees are now known not to be host-specific, and are capable of infecting other species of bees, wasps and hoverflies, as well as species, such as small hive beetle and wax moth, that come into close contact with honey bees.¹

Transmission of pathogens between pollinating species can occur through direct contact or indirect routes. Direct contact between different species might occur, for instance, when wild bee species rob infected honey bee colonies² or when wasps predate on infected honey bees.³ Indirect routes include via vectors or the sharing of floral resources during which oral-faecal transmission can occur and contaminated food resources, such as pollen and nectar, can be collected.¹ Managed bees and wild pollinator species interact when they share the same floral resources, meaning that flowers are a likely site for the transmission of pathogens.⁴

Detection of pathogens

In recent years there has been an increasing number of publications documenting the detection of honey bee pathogens in other species.³ Nanetti and colleagues found 81 articles published between 1960 to 2021 relating to spillover of honey bee pathogens, in its broadest sense, to wild or other managed arthropods, predominantly reporting work conducted in North and South America, Europe and New Zealand.³ According to these authors, the most frequently reported pathogens in spillover events from honey bees are: deformed wing virus (DWV), Kashmir bee virus (KBV) and Israeli acute paralysis virus (IAPV), all vectored by the *Varroa* mite, *Varroa destructor*; black queen cell virus (BQCV), sacbrood virus (SBV), and the microsporidian pathogen, *Nosema ceranae*. Nanetti also reports that these five viruses have been found naturally occurring in several different species of arthropods, including other species of bees, as well as other species of Hymenoptera, i.e. wasps and ants.³ DWV, BQCV and SBV are also found in other pollinator species, e.g. hoverflies, and in species that live in close contact with honey bees, e.g. wax moth and small hive beetle, and even species that you might not necessarily expect to have direct contact with honey bees such as earwigs and spiders.³ The microsporidium, *Nosema ceranae*, has been detected



Mixed bathing! A variety of insects visiting the same flower crop could provide a source of pathogen transmission. Photo: Chris Knott.

in some other bee species, including *Bombus* spp. as well as small hive beetle.³ However, spillover and the direction of it, is difficult to prove, and Tehel and colleagues (2016)³ suggest that there is the possibility that some honey bee viruses are generalists shared between a number of species. Furthermore, the mechanism of pathogen transmission to the reported recipient hosts is often not known, also making it difficult to prove that a spillover has occurred.

The detection of a pathogen using molecular diagnostics does not, by itself, prove that the pathogen is infective and replicating within a specimen. Relatively few articles investigate and demonstrate replication of virus or pathogenicity within recipient host species. In the case of positive-strand RNA viruses, detection of the negative strand within a host is indicative of viral replication. Some reviews^{2,3} provide information on studies where replicating virus has been detected or pathogenicity of virus has been demonstrated in species other than honey bees. They include DWV in: the bees *Andrena haemorrhoa*, *Osmia cornuta* and several species of *Bombus* (*B. bimaculatus*, *B. huntii*, *B. impatiens*, *B. lapidarius*, *B. lucorum*, *B. moniticola*, *B. terrestris* and *B. vagans*), the hornets *Vespa crabro* and *V. velutina nigrithorax*, the wasps *Vespula germanica* and *V. vulgaris*, the ant *Linepithema humile*, small hive beetle *Aethina tumida*, and a cockroach *Celatoblatta* spp. Similarly, BQCV has been reported as

replicating and/or pathogenic in *B. bimaculatus*, *B. huntii*, *B. soroensis*, *B. terrestris*, *B. vagans* and *B. vestalis*, and *V. velutina nigrithorax*; IAPV has been found replicating and/or pathogenic in the bees *B. impatiens* and *B. terrestris* and in *V. velutina nigrithorax*; KBV in *V. velutina nigrithorax*, the wasp *V. vulgaris*, the ant *L. humile*, small hive beetle and a cricket (*Bobilla* spp.); CBPV has been found replicating and/or pathogenic in the ants *Camponotus vagus* and *Formica rufa*; ABPV has been shown infective in the bees *B. hortorum*, *B. agrorum*, *B. lucorum*, *B. pascuorum*, *B. ruderaius* and *B. terrestris*; LSV in the bee *O. cornuta*; and Moku virus has been shown replicating in the wasps *Polistes chinensis*, *V. germanica*, *V. vulgaris*, the ant *L. humile*, and the spider *Steatoda capensis*.

Direction of spillover

It is all too tempting to use prevalence of a virus alone to infer spillover events. However, caution should be exercised when interpreting data based on viral prevalence alone, as virulence must also be considered.^{2,5} Furthermore, it is advisable to investigate prevalence and pathogen load at multiple sites in both managed honey bees and wild bees to infer spillover. This should be done in conjunction with providing proof that the pathogen in the managed and wild species is the same variant,³ but even so, this may not necessarily prove direction of spillover. Such investigations have been reported.^{5,6,7}

Fürst and colleagues investigated prevalence and viral load of DWV in honey bee and *Bombus* species at multiple sites and found that prevalence of DWV to be greater in the managed bees.⁷ They also demonstrated that DWV was replicating in a proportion of the sampled *Bombus*, and that the shared DWV was the same variant, suggesting spillover from managed to wild bees.⁷

In 2015, McMahon and colleagues published the results of their large-scale study investigating the prevalence of several RNA honey bee viruses within managed honey bees and wild populations of *Bombus* species at 26 sites across the UK.⁵ Five viruses: BQCV, DWV, ABPV, SBPV and SBV, were detected in both honey bee and *Bombus* species suggesting that widespread transmission of these viruses was occurring between populations of managed and wild bees. While viral loads of DWV were far greater in honey bees compared to *Bombus* species, viral loads of BQCV did not differ between the honey bees and *Bombus* species and were indicative of low-level infection. ABPV, on the other hand, was more prevalent in wild *Bombus*. While the results may suggest that DWV could spill over from honey bees to wild bees, ABPV is more common in bumblebees and could indicate spillover from bumblebees to honey bees.



A honey bee showing signs of deformed wing virus (DWV) infection; photo courtesy of theapiarist.org. Inset: the culprit responsible for DWV transmission, the *Varroa* mite (adult, female shown); photo courtesy of the Animal and Plant Health Agency (APHA), Crown copyright.

“The detection of a pathogen using molecular diagnostics does not, by itself, prove that the pathogen is infective and replicating within a specimen.”

In 2019, Manley demonstrated a higher prevalence and detection of DWV in bumblebees in areas where *Varroa*-infested honey bees are present compared with sites where honey bees are free of the mite. The same viral genotypes were detected in the honey bees and bumblebees.⁸ These findings led Manley to conclude that higher levels of DWV in bumblebees were driven by the presence of the mite, despite the fact that it does not infest bumblebees, because the mite was responsible for increasing prevalence within the honey bees, and this in turn led to spillover into the wild bumblebee population.⁸

Meanwhile, Dalmon also reported the same viral isolate of DWV in honey bees and *Bombus* foraging on the same floral resource.⁶ However, Dalmon did not detect any temporal patterns with viral prevalence to further corroborate spillover.⁶ These authors also looked at prevalence of SBV, BQCV, ABPV and IAPV and found them to be widespread in managed honey bees as well as wild pollinating species. They could not find any evidence for frequent spillover events, and suggest that wild bees may actually provide reservoirs for some of these viruses.

Despite the data obtained in the above studies, and the evidence obtained indicating that the prevalence of DWV in managed and wild bees is linked, the authors all remain cautious about speculating the direction of transmission.

Floral surfaces and resources have long been implicated in the transmission of bee pathogens.⁹ The first study to demonstrate that viruses could be transmitted between bee species via foraging on the same floral resources was conducted by Singh and colleagues¹⁰ back in 2010. They provided evidence of potential spillover of IAPV from honey bees to wild bees, as IAPV was detected in wild bees collected at sites where honey bee colonies infected with IAPV were present, but not at sites where honey bee colonies were not infected with IAPV. These authors set up a greenhouse study, which appeared to demonstrate that IAPV could be transmitted, in both directions, between honey bees and commercial bumblebees foraging on the same flowers.

A recent article by Alger¹¹ also provides compelling evidence for the spillover of DWV and BQCV into wild populations of bumblebees. They reported active infections of DWV were prevalent in bumblebees collected near apiaries and in areas where honey bees had a high level of infection, but was not detected in bumblebees in areas where no apiaries were present. Actively replicating BQCV was also detected in bumblebees at a higher prevalence in specimens collected from near apiaries. These authors went on to demonstrate the presence of both viruses on flowers collected at their test sites where honey bees were present. Thus, their work also provides evidence that flowers present an important route for virus spillover, particularly for DWV, from honey bees to wild bumblebees, and also to a lesser extent for BQCV. However, in controlled experiments also conducted by Alger,¹² although the authors demonstrated that honey bees did indeed deposit DWV and BQCV onto flowers, differences in floral

traits influenced the likelihood of deposition. The 2019(b) study also failed to demonstrate transmission of virus to bumblebees from flowers previously visited by honey bees.¹²

Results of a laboratory study conducted by Gusachenko and co-workers¹³ were also interpreted as not supportive of transmission of DWV from honey bees to bumblebees, *B. terrestris*, via oral acquisition from a contaminated environment. These authors were able to demonstrate that DWV can replicate in adult bumblebees if injected. However, although they could detect replication of DWV following oral administration, they were unable to demonstrate detectable replication or infection. Gusachenko concluded that oral acquisition of DWV was unlikely to be an effective transmission route between the honey bee and bumblebee.¹³ They could offer no other

plausible route of transmission and went as far as suggesting that detection of DWV in bumblebees present in areas where managed honey bees exist could simply be indicative of environmental contamination due to large populations of honey bees rather than replication of DWV within *Bombus* populations.

Future questions and thoughts

The decline in pollinators has serious consequences for food security, as well as ecosystems and biodiversity. The literature provides a strong indication of the need for careful management of honey bees to reduce the introduction and spread of pathogens both between honey bees themselves and between honey bees and wild pollinators. Manley⁸ suggests the *Varroa* mite must also be effectively managed to minimise prevalence of viruses, such as DWV, that are vectored by this mite, to protect the health of wild

pollinator populations by reducing spillover from managed honey bees. Despite the currently available knowledge on the potentially broad host ranges for a number of honey bee pathogens, surprisingly little is known of their epidemiology, their potential impact on other pollinating species and on other arthropod species in general, and the potential consequences on ecosystems and pollinating services. Modes of transmission are still undetermined. Tehel² and others, suggest that a better understanding of these factors are critical to enable better management of both managed honey bees and wild bee species, for the protection of wild bee populations, biodiversity, ecosystems and pollinator services.

References

1. Manley R, Boots M, Wilfert L. Emerging viral disease risk to pollinating insects: ecological, evolutionary and anthropogenic factors. *Journal of Applied Ecology* 2015; 52: 331–40.
2. Tehel A, Brown MJF, Paxton RJ. Impact of managed honey bee viruses on wild bees. *Current Opinion in Virology* 2016; 19: 16–22.
3. Nanetti A, Bortolotti L, Cilia G. Pathogens spillover from honey bees to other arthropods. *Pathogens* 2021; 10: 1044.
4. Goulson D, Hughes WHO. Mitigating the anthropogenic spread of bee parasites to protect wild pollinators. *Biological Conservation* 2015; 191: 10–19.
5. McMahon DP, Fürst MA, Caspar J *et al.* A sting in the spit: Widespread cross-infection of multiple RNA viruses across wild and managed bees. *Journal of Animal Ecology* 2015; 84: 615–24.
6. Dalmon A, Diévar V, Thomasson M *et al.* Possible spillover of pathogens between bee communities foraging on the same floral resource. *Insects* 2021; 12: 122.
7. Fürst MA, McMahon DP, Osborne JL *et al.* Disease associations between honeybees and bumblebees as a threat to wild pollinators. *Nature* 2014; 506: 364–6.
8. Manley R, Temperton B, Doyle T *et al.* Knock-on community impacts of a novel vector: Spillover of emerging DWV-B from *Varroa*-infested honeybees to wild bumblebees. *Ecology Letters* 22: 2019; 1306–15.
9. McArt SH, Koch H, Irwin RE, Adler LS. Arranging the bouquet of disease: floral traits and the transmission of plant and animal pathogens. *Ecology Letters* 2014; 17: 624–636.
10. Singh R, Levitt AL, Rajotte EG *et al.* RNA viruses in hymenopteran pollinators: Evidence of inter-taxa virus transmission via pollen and potential impact on non-*Apis* hymenopteran species. *PLoS ONE* 2010; 5(12): e14357.
11. Alger SA, Burnham PA, Boncristiani HF, Brody AK. RNA virus spillover from managed honey bees (*Apis mellifera*) to wild bumblebees (*Bombus* spp.). *PLoS ONE* 2019a; 14(6): e0217822.
12. Alger SA, Burnham PA, Brody AK. Flowers as viral hot spots: Honey bees (*Apis mellifera*) unevenly deposit viruses across plant species. *PLoS ONE* 2019b; 14(9): e0221800.
13. Gusachenko ON, Woodford L, Balbirnie-Cumming K *et al.* Evidence for and against deformed wing virus spillover from honey bees to bumble bees: a reverse genetic analysis. *Nature* 2020; 10: 16847.