Deformed Wing Virus

Comprehensive Findings Review

Synthesised from the abstracts and full texts of the most-cited and representative papers within a harvested corpus of 1,482 records (1,206 open access). This is a curated review of landmark findings, not an exhaustive catalogue of every study. Generated 2026-06-12.

Executive Summary

Deformed wing virus (DWV) is a positive-sense, single-stranded RNA virus of the family **Iflaviridae** and is now the most prevalent and intensively studied viral pathogen of the honey bee (*Apis mellifera*). For most of the 20th century DWV was an obscure, largely harmless covert infection. Its transformation into a global killer was driven almost entirely by one event: the host switch and worldwide spread of the ectoparasitic mite **Varroa destructor**, which transmits DWV directly into developing bee pupae and amplifies it to lethal titres (Martin 2012; Wilfert 2016). DWV is the leading viral factor in overwintering colony losses, occurs in at least three genotypes (DWV-A, DWV-B, DWV-C) that recombine readily, suppresses bee immunity in a mutualistic loop with the mite, and has spilled over into bumblebees, wasps and dozens of other arthropods. Unlike most bee viruses, its causal pathology — wing deformity, shortened abdomen, early death — is experimentally established. This document synthesises the published findings by theme and then catalogues the landmark studies.

Family / genus	Iflaviridae / Iflavirus; positive-sense ssRNA (Lanzi 2006; Valles 2017)
Genome	10,140 nt, single ORF → 328-kDa polyprotein; VP1/VP2/VP3 capsid + helicase/protease/RdRp
Genotypes	DWV-A, DWV-B (more virulent), DWV-C; extensive recombination (McMahon 2016; Mordecai 2016)
Vector	Varroa destructor — biological vector; replicates in mite to 10^{10}–10^{12} copies (Gisder 2009)
Hallmark effect	Varroa raises prevalence ~10%→100%, titre ×10^6, diversity collapse (Martin 2012)
Global prevalence	≥55% of colonies across 32 countries; 65 arthropod host species (Martin 2019)
Pathology	Deformed wings, bloated abdomen, early death; OID50 ≈ 2,500 genome eq. (Möckel 2011)

Taxonomy, Genome and Virion

DWV is a member of the genus *Iflavirus*, family **Iflaviridae** — small, non-enveloped viruses with a monopartite, positive-sense RNA genome of ~9–11 kb that infect arthropods, mostly insects (Valles 2017). The DWV genome is 10,140 nucleotides with a single large open reading frame encoding a ~328-kDa polyprotein, flanked by a 1,144-nt 5′ leader and a 317-nt 3′ region with a poly(A) tail (Lanzi 2006). The polyprotein yields three major capsid proteins (VP1 ~44 kDa, VP2 ~32 kDa, VP3 ~28 kDa) at its N-terminus and the non-structural enzymes — an RNA helicase, a chymotrypsin-like 3C protease and an RNA-dependent RNA polymerase — at its C-terminus (Lanzi 2006). Because it is positive-sense, the genome functions directly as mRNA. Its close relatives include Kakugo virus and Varroa destructor virus-1 (VDV-1, now recognised as DWV-B), which share ~84% genome identity and replicate in the mite (Ongus 2004).

The Varroa Transmission Revolution

In the absence of *Varroa*, DWV persists as a low-level covert infection that causes no visible symptoms and little measurable harm (de Miranda 2010). The arrival of *Varroa destructor* changed everything: the mite is not merely a mechanical carrier but a **biological vector** in which DWV

replicates before being injected into pupae (Bowen-Walker 1999; Gisder 2009). The clearest evidence is a natural experiment in Hawaii, where *Varroa*'s arrival raised DWV prevalence from ~10% to 100% of bees, drove a millionfold increase in viral titre, and collapsed DWV genetic diversity to a single dominant strain (Martin 2012). At the global scale, phylogeographic analysis shows DWV is a recent, human-driven pandemic spreading from European *A. mellifera* via trade and colony movement, with *Varroa* providing the direct transmission route (Wilfert 2016). Mites capable of inducing overt, deformed-wing infections carry 10^{10}–10^{12} viral genome equivalents, versus a maximum of ~10^{8} in mites that cannot (Gisder 2009).

Pathology: Covert Infection to Overt Disease

DWV is unusual among bee viruses in having an experimentally demonstrated causal pathology. When the mite transmits DWV to pupae, infected bees emerge with shrivelled, deformed wings, a bloated and shortened abdomen, and discolouration; they are non-viable and die soon after emergence (de Miranda 2010). Deformed bees carry roughly 10^{6} times more virus than mite-parasitised but normal-winged bees (Yang 2005), and in crippled bees the virus is present throughout the body including the head, whereas asymptomatic bees show it only in thorax/abdomen (Yue 2005). The route and dose of infection determine the outcome: injecting pupae produces overt, deformed-wing disease with an overt-infection dose around 2,500 genome equivalents, and injecting adults with >10^{7} equivalents also yields overt infection, whereas the same dose fed orally produces only covert infection (Möckel 2011). This dose- and route-dependence explains why mite vectoring — which delivers virus directly to the haemocoel — is so much more pathogenic than natural oral/food-borne transmission.

Genotypes, Quasispecies and Recombination

DWV exists as a quasispecies — a swarm of related variants — resolved into master variants. DWV-A was the originally described genotype; DWV-B (formerly VDV-1) is more virulent in adult bees and has been increasing in prevalence in Europe and North America (McMahon 2016). A third master variant, DWV-C, was identified by deep sequencing and estimated to have diverged from the others roughly three centuries ago (Mordecai 2016). The genotypes recombine extensively in vivo, and DWV/VDV-1 recombinants can accumulate to higher levels than either parent in both bees and mites — the genome appears modular, with the 5′-UTR, capsid and non-structural regions evolving semi-independently (Moore 2011; McMahon 2016). Critically, *Varroa*-mediated or in-vitro transmission selects for a near-clonal, virulent DWV variant out of the diverse covert population, whereas oral exposure preserves diversity (Ryabov 2014). This selection for virulent, transmissible variants is central to DWV's emergence.

Immune Suppression and Synergistic Stressors

DWV interacts with the bee immune system and with other stressors in ways that amplify its impact. *Varroa* parasitism suppresses bee immunity — down-regulating antimicrobial peptides and immune enzymes — which activates latent DWV replication (Yang 2005; Shen 2005). At the molecular level this is mediated by suppression of NF-κB immune signalling, converting a cryptic, vertically transmitted virus into a rapidly replicating killer late in the season (Nazzi 2012). The relationship between mite and virus is mutualistic: DWV's immunosuppression of the bee actually enhances *Varroa* reproduction, creating a reciprocal loop with escalating damage to colony health (Di Prisco 2016). External stressors feed in: the neonicotinoid insecticide clothianidin (and imidacloprid) suppresses NF-κB-controlled antiviral defences and promotes DWV replication in bees carrying covert infections (Di Prisco 2013), and poor nutrition raises viral loads (DeGrandi-Hoffman 2010).

Transmission Routes

DWV uses multiple, well-characterised transmission routes. **Vector transmission** by *Varroa* into pupae is the most pathogenic (Bowen-Walker 1999). **Vertical transmission** occurs from both

queens and drones to offspring through eggs and DWV-positive semen — true covert infection maintained across generations (Chen 2006; Yue 2007). **Oral/food-borne transmission** occurs via virus-contaminated larval food, pollen and honey; viruses in pollen pellets are infective and can establish infection when fed to virus-free colonies (Singh 2010; Yue 2005). **Horizontal transmission** among adults occurs through phoretic mites and through nurse bees cannibalising infected pupae (Möckel 2011). The interplay of these routes lets DWV persist covertly in the absence of *Varroa* and erupt into overt disease in its presence.

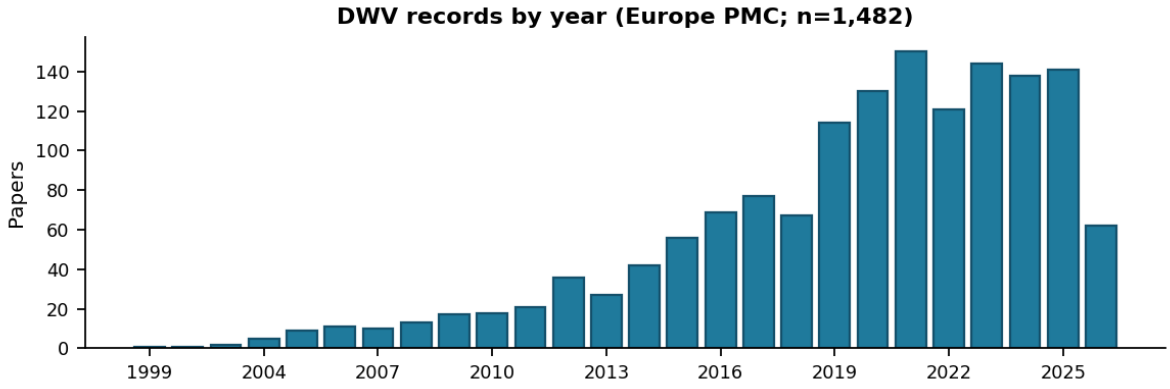
Host Range and Pollinator Spillover

Although named for honey bees, DWV is a multi-host pathogen. Field and experimental data show honey bees are the likely source of DWV spillover into wild bumblebees, which share the same DWV strains and can develop the same wing deformities (Fürst 2014; Genersch 2006). DWV prevalence in honey bees predicts prevalence in sympatric bumblebees (McMahon 2015). It has been detected — with evidence of active replication — in numerous non-*Apis* species: at least six in one survey (Levitt 2013), and about a third of sampled bumblebees and wasps in another (Evison 2012), though notably not in all pollinator groups, so it is not a universal pollinator parasite. The most recent review records DWV in 65 arthropod species spanning eight insect orders and three orders of Arachnida (Martin 2019), making it one of the most host-versatile insect viruses known and a recognised threat to wild pollinator conservation.

Colony Losses, Prevalence and Control

DWV is a leading viral driver of overwintering colony mortality. It is among the few pathogens that independently predict colony loss: DWV load and prevalence correlate with overwintering failure even in mite-controlled colonies (Highfield 2009), and DWV (with *Varroa*) shortens the lifespan of winter bees, providing a proximate mechanism for collapse (Dainat 2012). Prevalence is high and global — DWV was found in 97% of French apiaries in an early survey (Tentcheva 2004), and a recent review reports a minimum average of 55% of colonies/apiaries infected across 32 countries (Martin 2019). Control remains difficult and indirect: managing *Varroa* is the primary lever, alongside breeding tolerant bees and RNA-interference (RNAi) approaches. A notable advance engineered the bee gut symbiont *Snodgrassella alvi* to produce double-stranded RNA that activates the bee's RNAi defence and can also kill *Varroa* (Leonard 2020), pointing toward future symbiont-mediated therapeutics.

Research Activity



DWV is the most-studied bee virus: publication volume has grown steadily, passing 100 papers/year from 2019 onward, reflecting its central role in honey bee health research.

Landmark Study Catalogue

Selected from 1,482 records by citation impact and thematic importance.

Core studies — central DWV findings:

Martin 2012 — Global honey bee viral landscape altered by a parasitic mite (2012, Science; cited 430)

Used Varroa's arrival in Hawaii as a natural experiment to track DWV prevalence, load and diversity.

- Varroa raised DWV prevalence from ~10% to 100% of bees within populations.
- Accompanied by a millionfold increase in viral titre.
- Caused a massive collapse of DWV strain diversity to a single dominant variant.
- Concluded the global spread of Varroa selected DWV variants that made it one of the most widespread, contagious insect viruses on Earth.

None · doi:10.1126/science.1220941

Wilfert 2016 — Deformed wing virus is a recent global epidemic in honeybees driven by Varroa mites (2016, Science; cited 320)

Phylogeographic reconstruction of DWV's global spread and the role of Varroa and trade.

- DWV is globally distributed and recently spread from a common source, European Apis mellifera.
- Shows epidemic growth driven by European and North American honey bee movement and trade.
- Varroa provides the direct transmission route fuelling a worldwide, man-made epidemic.

None · doi:10.1126/science.aac9976

Lanzi 2006 — Molecular and biological characterization of deformed wing virus of honeybees (2006, Journal of Virology; cited 233)

Cloned and sequenced the DWV genome and mapped its proteins.

- Genome is 10,140 nt with a single ORF encoding a 328-kDa polyprotein, plus a 1,144-nt 5′ leader and 317-nt 3′ region with poly(A) tail.
- Identified three capsid proteins VP1 (44 kDa), VP2 (32 kDa), VP3 (28 kDa) at the polyprotein N-terminus.
- C-terminal non-structural region contains an RNA helicase, 3C-like protease and RdRp.
- Genome organization and capsid place DWV in the genus Iflavirus.

PMC1472076 · doi:10.1128/jvi.80.10.4998-5009.2006

de Miranda 2010 — Deformed wing virus (review) (2010, J. Invertebrate Pathology; cited 360)

Foundational review of DWV genetics, pathobiology and transmission.

- Without Varroa, DWV causes no visible symptoms or apparent fitness cost.
- Varroa-mediated transmission to pupae causes pupal death and adults with deformed wings, bloated shortened abdomens and discolouration; such bees die soon after emergence.
- Framed DWV within RNA-virus concepts of genetic variability, virulence evolution and disease-symptom development.

None · doi:10.1016/j.jip.2009.06.012

Bowen-Walker 1999 — The transmission of deformed wing virus between honeybees by the ectoparasitic mite Varroa (1999, J. Invertebrate Pathology; cited 241)

Established Varroa as a DWV vector under field conditions.

- Varroa mites are highly effective vectors of DWV between bees.
- Mites carried virus titres far in excess of their hosts', suggesting DWV may replicate within the mite.
- DWV-positive bees showed wing deformity and/or died during pupation; a positive relationship between mite numbers and deformity/death.
- Proposed a threshold concentration of DWV in pupae is required to cause pathology.

None · doi:10.1006/jipa.1998.4807

Gisder 2009 — Deformed wing virus: replication and viral load in mites (Varroa destructor) (2009, J. General Virology; cited 172)

Tested whether DWV replication in the mite determines overt disease.

- Mites able to induce overt (deformed-wing) infection contained 10^{10}–10^{12} DWV genome equivalents per mite.
- Mites unable to induce crippled wings contained at most ~10^{8} equivalents.
- Overt disease depends not just on transmission but on DWV replication and titre within the vectoring mite.

None · doi:10.1099/vir.0.005579-0

Yang 2005 — Impact of an ectoparasite on immunity and pathology: host immunosuppression and viral amplification (2005, PNAS; cited 328)

Tested the mechanism by which Varroa harms bees, via immunity and DWV replication.

- Varroa parasitism significantly suppressed expression of immunity-related genes (antimicrobial peptides and enzymes).
- DWV titres were negatively correlated with immune-enzyme expression.
- Deformed-wing bees carried ~10^{6} times more DWV than mite-infested but normal-winged bees.
- Immune challenge dramatically boosted DWV titres, indicating immunosuppression activates latent infection.

PMC1140434 · doi:10.1073/pnas.0501860102

Nazzi 2012 — Synergistic parasite-pathogen interactions mediated by host immunity can drive colony collapse (2012, PLoS Pathogens; cited 294)

Integrated population and molecular analysis of Varroa-infested collapsing colonies.

- Varroa de-stabilises within-host DWV dynamics, turning a cryptic vertically transmitted virus into a rapidly replicating killer that peaks late in the season.
- De-stabilisation is linked to immunosuppression via strong down-regulation of NF-κB.
- Proposed NF-κB as a 'common currency' underlying multifactorial colony collapse.

PMC3375299 · doi:10.1371/journal.ppat.1002735

Di Prisco 2013 — Neonicotinoid clothianidin adversely affects insect immunity and promotes viral replication (2013, PNAS; cited 422)

Tested whether neonicotinoid exposure undermines antiviral immunity and promotes DWV.

- Clothianidin negatively modulates NF-κB immune signalling in insects.
- It up-regulates a leucine-rich-repeat inhibitor of NF-κB, reducing antiviral defences.
- This promotes replication of DWV in bees bearing covert infections; imidacloprid does the same, chlorpyriphos does not.
- Effect occurs at sublethal, field-relevant doses — implications for pesticide risk assessment.

PMC3831983 · doi:10.1073/pnas.1314923110

Di Prisco 2016 — A mutualistic symbiosis between a parasitic mite and a pathogenic virus undermines bee immunity (2016, PNAS; cited 180)

Tested the mechanistic and evolutionary basis of the Varroa-DWV association.

- DWV vectored by Varroa suppresses humoral and cellular immunity by interfering with NF-κB signalling.
- This immunosuppression enhances Varroa reproduction.
- Identified an unrecognised mutualistic symbiosis: a reciprocal loop with escalating negative effects on bee immunity and health.

PMC4812730 · doi:10.1073/pnas.1523515113

Ryabov 2014 — A virulent strain of DWV prevails after Varroa-mediated, or in vitro, transmission (2014, PLoS Pathogens; cited 250)

Tested whether Varroa amplifies/selects virulent DWV strains or suppresses host immunity.

- Varroa-free pupae carried low levels of a highly diverse DWV population.
- Varroa-associated pupae either had low diverse DWV or high levels of a near-clonal virulent variant.
- Varroa-mediated and in-vitro transmission selected the virulent variant from the diverse population.
- All tested mites contained a diverse replicating DWV population implying the virulent variant.

PMC4072795 · doi:10.1371/journal.ppat.1004230

McMahon 2016 — Elevated virulence of an emerging viral genotype as a driver of honeybee loss (2016, Proc. Royal Society B; cited 153)

Compared virulence of DWV genotypes A and B via lab experiments and field survey.

- DWV-B is more virulent than the established DWV-A and is widespread in the landscape.
- Modelling showed colonies infected with DWV-B collapse sooner than those with DWV-A.
- Revealed extensive genome-wide recombination between genotypes in vivo.
- Emergence of DWV-B, including via recombination with DWV-A, has major ecological/economic implications.

PMC4936039 · doi:10.1098/rspb.2016.0811

Mordecai 2016 — First report of a third master variant of the DWV quasispecies (2016, The ISME Journal; cited 134)

Next-generation sequencing of the DWV quasispecies in an overwintering-loss apiary.

- The DWV species complex comprises three master variants.
- Identified a new Type C variant distinct from Types A and B; together they form a clade within Iflaviridae.
- Molecular-clock estimate: Type C diverged from the others ~319 years ago.
- Has implications for correctly identifying the true pathogen across global bee populations.

PMC5029213 · doi:10.1038/ismej.2015.178

Moore 2011 — Recombinants between DWV and VDV-1 may prevail in Varroa-infested colonies (2011, J. General Virology; cited 132)

Illumina sequencing to characterise DWV/VDV-1 recombinants in bees and mites.

- Identified novel DWV/VDV-1 recombinants accumulating to higher levels than DWV in both bees and mites.
- Crossovers occur between the 5′-UTR and the structural/non-structural regions — implying a modular genome.
- A recombinant with DWV-derived 5′-UTR/non-structural regions flanking a VDV-1 capsid appears best adapted to mite-bee transmission.

None · doi:10.1099/vir.0.025965-0

Fürst 2014 — Disease associations between honeybees and bumblebees as a threat to wild pollinators (2014, Nature; cited 411)

Infection experiments + landscape-scale field data on DWV spillover to bumblebees.

- DWV prevalence in honey bees and bumblebees is linked; sympatric individuals share the same DWV strains.
- Honey bees have higher DWV prevalence, identifying Apis as the likely source of this emerging disease in wild pollinators.
- Highlights the need for pathogen control in managed bees to protect declining wild pollinators.

PMC3985068 · doi:10.1038/nature12977

Genersch 2006 — Detection of DWV in bumble bees with wing deformities (2006, J. Invertebrate Pathology; cited 134)

Investigated wing-deformed bumblebees for DWV.

- First report of Bombus terrestris and B. pascuorum with wing deformities resembling DWV-infected honey bees.
- RT-PCR and sequencing confirmed the bumblebees were infected with DWV.
- Because deformed bumblebees are non-viable, DWV may pose a serious threat to bumblebee populations.

None · doi:10.1016/j.jip.2005.10.002

Martin 2019 — Deformed Wing Virus in Honeybees and Other Insects (review) (2019, Annual Review of Virology; cited 149)

Comprehensive review of DWV epidemiology, host range, structure and evolution.

- DWV is the most prevalent honey bee virus: a minimum average 55% of colonies/apiaries infected across 32 countries.
- Detected in 65 arthropod species spanning eight insect orders and three orders of Arachnida.
- Reviews progress on capsid structure, expanding host range, genome evolution and recombination.
- Sets goals: identify tissues where variants replicate and understand DWV impact in non-honeybee hosts.

None · doi:10.1146/annurev-virology-092818-015700

Möckel 2011 — Horizontal transmission of DWV: pathology depends on the transmission route (2011, J. General Virology; cited 122)

Lab infection assays to link transmission route/dose to deformed-wing disease.

- Pupae injected with DWV develop dose-dependent overt infections with deformed wings — direct causal evidence for the deformed-wing syndrome.
- Overt-infection dose (OID50) was ~2,500 genome equivalents in pupae.
- Adults injected with $>10^7$ equivalents developed overt infection; the same dose fed orally gave only covert infection.
- Phoretic-mite infection and nurse-bee cannibalism of infected pupae are plausible horizontal routes.

None · doi:10.1099/vir.0.025940-0

Yue 2007 — Vertical-transmission routes for deformed wing virus (2007, J. General Virology; cited 123)

Tested vertical transmission via eggs and semen using inseminated queens.

- Demonstrated vertical transmission of DWV from queens and drones to offspring via unfertilised and fertilised eggs.
- Viral sequences detected in the ovary of a DWV-positive queen and transmissible via DWV-positive semen.
- Confirms DWV maintains true covert infections through vertical transmission in the absence of overt disease.

None · doi:10.1099/vir.0.83101-0

Chen 2006 — Prevalence and transmission of honeybee viruses (2006, Applied & Environmental Microbiology; cited 165)

Examined queen tissues/feces and offspring for viruses including DWV.

- DWV (and other viruses) detected in queen feces and tissues including ovaries and spermatheca.
- Viruses present in queens were detected in their eggs, larvae and adult workers — first evidence of vertical transmission in honey bee colonies.

PMC1352288 · doi:10.1128/aem.72.1.606-611.2006

Highfield 2009 — Deformed wing virus implicated in overwintering honeybee colony losses (2009, Applied & Environmental Microbiology; cited 196)

Year-long qPCR monitoring of DWV/ABPV/BQCV in mite-controlled colonies.

- Despite Varroa control, a significant correlation existed only between DWV load and overwintering colony loss.
- Suggests DWV can act independently of heavy mite infestation to cause colony losses.
- Positions DWV as a potentially major factor in overwintering mortality.

PMC2786540 · doi:10.1128/aem.02227-09

Dainat 2012 — Dead or alive: DWV and Varroa reduce the life span of winter honeybees (2012, Applied & Environmental Microbiology; cited 219)

6-month colony monitoring linking pathogens to winter-bee longevity.

- Workers in colonies that failed to overwinter had reduced lifespan, were more likely DWV-infected and carried higher DWV loads.
- Varroa infestation and individual DWV infection were associated with reduced life expectancy.
- Nosema ceranae and ABPV were NOT correlated with longevity — singling out Varroa+DWV as the parsimonious mechanism for colony loss.

PMC3273028 · doi:10.1128/aem.06537-11

Mondet 2014 — Quantitative virus dynamics along a new Varroa expansion front (New Zealand) (2014, PLoS Pathogens; cited 169)

Tracked viral landscapes as Varroa spread across New Zealand over a decade.

- DWV titres in bees kept increasing with Varroa-infestation history even as infestation rates dropped.
- Linked to rising DWV titres in the mites themselves.
- Suggests DWV levels in mites, boosted by replication, maintain the DWV epidemic after initial establishment.

PMC4140857 · doi:10.1371/journal.ppat.1004323

Ongus 2004 — Complete sequence of a picorna-like virus (VDV-1) replicating in Varroa destructor (2004, J. General Virology; cited 201)

Characterised VDV-1, the DWV relative now recognised as DWV-B.

- Described 27-nm virus-like particles replicating in mite tissue.
- VDV-1 genome is 10,112 nt, ~84% identity to DWV and Kakugo virus, one large ORF (2,893-aa polyprotein).
- Negative-strand RT-PCR confirmed VDV-1 and DWV both replicate in the mite.

None · doi:10.1099/vir.0.80470-0

Leonard 2020 — Engineered symbionts activate honey bee immunity and limit pathogens (2020, Science; cited 168)

Engineered the bee gut symbiont Snodgrassella alvi to deliver RNAi.

- Engineered S. alvi stably recolonised bees and produced dsRNA to trigger host RNAi.
- Improved bee survival after viral challenge.
- The same approach killed parasitic Varroa mites by triggering the mite's RNAi response — a route toward symbiont-mediated DWV/Varroa control.

PMC7556694 · doi:10.1126/science.aax9039

Supporting studies — prevalence, transmission and host-range evidence:

Valles 2017 — ICTV Virus Taxonomy Profile: Iflaviridae (2017, J. General Virology; cited 121)

Official ICTV taxonomy summary for the family containing DWV.

- Iflaviridae: small non-enveloped viruses, monopartite positive-strand RNA ~9–11 kb, infecting arthropods.
- Infections range from symptomless to developmental abnormalities — DWV is the named example of the latter.
- Most common infection route is ingestion of contaminated food.

PMC5657024 · doi:10.1099/jgv.0.000757

Tentcheva 2004 — Prevalence and seasonal variations of six bee viruses in France (2004, Applied & Environmental Microbiology; cited 285)

Large-scale PCR survey of six viruses across 36 French apiaries.

- DWV detected at least once in 97% of apiaries (adult bees) and 94% (pupae) — the most prevalent virus surveyed.
- DWV found in 100% of Varroa samples, supporting the mite's role in transmission.
- Infections persisted without clinical signs, implying environmental triggers activate replication.

PMC535170 · doi:10.1128/aem.70.12.7185-7191.2004

Yue 2005 — RT-PCR analysis of DWV in honeybees and mites (2005, J. General Virology; cited 214)

Mapped DWV distribution in symptomatic vs asymptomatic bees and mites.

- 100% of both crippled and asymptomatic bees were DWV-positive, but in crippled bees all body parts (incl. head) were strongly positive.
- DWV replicated in some but not all mites; replication in mites correlated with wing deformity.
- Detected DWV in larval food, indicating food-borne transmission alongside Varroa.

None · doi:10.1099/vir.0.81401-0

Singh 2010 — RNA viruses in hymenopteran pollinators: inter-taxa transmission via pollen (2010, PLoS ONE; cited 283)

Surveyed viruses in honey bees, pollen loads and non-Apis pollinators.

- First detection of DWV (and SBV, BQCV) in pollen pellets collected from forager bees.
- Pollen- and honey-borne viruses were infective: queens became infected and laid infected eggs after virus-contaminated food.
- DWV detected in 11 non-Apis hymenopteran species, expanding the host range.

PMC3008715 · doi:10.1371/journal.pone.0014357

McMahon 2015 — A sting in the spit: widespread cross-infection of RNA viruses across wild and managed bees (2015, J. Animal Ecology; cited 209)

National survey of RNA-virus prevalence in co-occurring honey bees and bumblebees.

- Multiple honey bee RNA viruses including DWV are widespread in sympatric wild bumblebees.
- Virus prevalence in honey bees significantly predicts prevalence in bumblebees.
- Bumblebee pathogen loads can be high, indicating real cross-species disease pressure.

PMC4832299 · doi:10.1111/1365-2656.12345

Levitt 2013 — Cross-species transmission of honey bee viruses in associated arthropods (2013, Virus Research; cited 120)

Screened arthropods around apiaries for five bee viruses and replication.

- Negative-strand RT-PCR indicated active DWV replication in at least six non-Apis species.
- Phylogenetics showed DWV freely disseminating across sampled species.
- Bee viruses are not specific to pollinators — other arthropods may participate in transmission.

None · doi:10.1016/j.virusres.2013.06.013

Evison 2012 — Pervasiveness of parasites in pollinators (2012, PLoS ONE; cited 113)

Screened diverse UK pollinators for viruses and other parasites.

- About a third of sampled bumblebees (B. pascuorum, B. terrestris) and wasps (Vespula vulgaris) were DWV-positive, as were all honey bees.
- DWV was absent from other pollinator types — it is not a general pollinator parasite but interacts with specific bumblebee and wasp species.

PMC3273957 · doi:10.1371/journal.pone.0030641

DeGrandi-Hoffman 2010 — Effect of diet on protein, hypopharyngeal glands and virus load in worker bees (2010, J. Insect Physiology; cited 147)

Tested how diet quality affects DWV titre.

- DWV concentrations increased as bees aged and were highest in sugar-syrup-fed bees, lowest in pollen-fed bees.
- Links nutrition and protein status to antiviral capacity — supplemental feeding may reduce DWV-related losses.

None · doi:10.1016/j.jinsphys.2010.03.017

Genersch 2010 — Emerging and re-emerging viruses of the honey bee (review) (2010, Veterinary Research; cited 164)

Reviewed how Varroa transformed previously harmless bee viruses.

- DWV outbreaks are tied to Varroa acting as both mechanical and biological vector.
- Replication in mites before vectoring into pupae appears necessary and sufficient for overt infection in non-viable deformed bees.
- DWV is now a key player in final colony collapse; control options (tolerant bees, RNAi, biosecurity) are limited short-term.

PMC2883145 · doi:10.1051/vetres/2010027

Scope note: studies excluded as off-topic

- **Vanengelsdorp 2009 / Cornman 2012 / Johnson 2009**: Colony Collapse Disorder descriptive/pathogen-web studies — DWV is one of many pathogens measured, not the focus.
- **Pisa 2015 / Wood 2017 / Fairbrother 2014 / Sandrock 2014**: Neonicotinoid risk reviews/experiments — relevant to bee health but not DWV-specific (cf. Di Prisco for the DWV link).
- **Hunter 2010 / Chen 2014 (IAPV)**: Israeli acute paralysis virus RNAi/epidemiology — different virus.
- **Zheng 2018 / Moran 2015 / Motta 2024**: Honey bee gut-microbiome reviews — DWV peripheral (except via the Leonard 2020 symbiont-RNAi link, which is included).
- **Metsky 2017 (Zika) / Donaldson 2010 (bat virome) / Ferreira 2014 (Drosophila Toll) / Luke 2008 (2A peptides)**: Non-bee or general virology that surfaced via shared methods/citations; no DWV-specific findings.
- **Dussaubat 2012 / Gisder 2010 / Aufauvre 2014 (Nosema)**: Nosema ceranae pathology/epidemiology — different pathogen.

References

Bowen-Walker 1999. *The transmission of deformed wing virus between honeybees by the ectoparasitic mite Varroa.* J. Invertebrate Pathology (1999). doi:10.1006/jipa.1998.4807

Ongus 2004. *Complete sequence of a picorna-like virus (VDV-1) replicating in Varroa destructor.* J. General Virology (2004). doi:10.1099/vir.0.80470-0

Tentcheva 2004. *Prevalence and seasonal variations of six bee viruses in France.* Applied & Environmental Microbiology (2004). doi:10.1128/aem.70.12.7185-7191.2004 · PMC535170

Yang 2005. *Impact of an ectoparasite on immunity and pathology: host immunosuppression and viral amplification.* PNAS (2005). doi:10.1073/pnas.0501860102 · PMC1140434

Yue 2005. *RT-PCR analysis of DWV in honeybees and mites.* J. General Virology (2005). doi:10.1099/vir.0.81401-0

Chen 2006. *Prevalence and transmission of honeybee viruses.* Applied & Environmental Microbiology (2006). doi:10.1128/aem.72.1.606-611.2006 · PMC1352288

Genersch 2006. *Detection of DWV in bumble bees with wing deformities.* J. Invertebrate Pathology (2006). doi:10.1016/j.jip.2005.10.002

Lanzi 2006. *Molecular and biological characterization of deformed wing virus of honeybees.* Journal of Virology (2006). doi:10.1128/jvi.80.10.4998-5009.2006 · PMC1472076

Yue 2007. *Vertical-transmission routes for deformed wing virus.* J. General Virology (2007). doi:10.1099/vir.0.83101-0

Gisder 2009. *Deformed wing virus: replication and viral load in mites (Varroa destructor).* J. General Virology (2009). doi:10.1099/vir.0.005579-0

Highfield 2009. *Deformed wing virus implicated in overwintering honeybee colony losses.* Applied & Environmental Microbiology (2009). doi:10.1128/aem.02227-09 · PMC2786540

DeGrandi-Hoffman 2010. *Effect of diet on protein, hypopharyngeal glands and virus load in worker bees.* J. Insect Physiology (2010). doi:10.1016/j.jinsphys.2010.03.017

Genersch 2010. *Emerging and re-emerging viruses of the honey bee (review).* Veterinary Research (2010). doi:10.1051/vetres/2010027 · PMC2883145

Singh 2010. *RNA viruses in hymenopteran pollinators: inter-taxa transmission via pollen.* PLoS ONE (2010). doi:10.1371/journal.pone.0014357 · PMC3008715

de Miranda 2010. *Deformed wing virus (review).* J. Invertebrate Pathology (2010). doi:10.1016/j.jip.2009.06.012

Moore 2011. *Recombinants between DWV and VDV-1 may prevail in Varroa-infested colonies.* J. General Virology (2011). doi:10.1099/vir.0.025965-0

Möckel 2011. *Horizontal transmission of DWV: pathology depends on the transmission route.* J. General Virology (2011). doi:10.1099/vir.0.025940-0

Dainat 2012. *Dead or alive: DWV and Varroa reduce the life span of winter honeybees.* Applied & Environmental Microbiology (2012). doi:10.1128/aem.06537-11 · PMC3273028

Evison 2012. *Pervasiveness of parasites in pollinators.* PLoS ONE (2012). doi:10.1371/journal.pone.0030641 · PMC3273957

Martin 2012. *Global honey bee viral landscape altered by a parasitic mite.* Science (2012). doi:10.1126/science.1220941

Nazzi 2012. *Synergistic parasite-pathogen interactions mediated by host immunity can drive colony collapse.* PLoS Pathogens (2012). doi:10.1371/journal.ppat.1002735 · PMC3375299

Di Prisco 2013. *Neonicotinoid clothianidin adversely affects insect immunity and promotes viral replication.* PNAS (2013). doi:10.1073/pnas.1314923110 · PMC3831983

Levitt 2013. *Cross-species transmission of honey bee viruses in associated arthropods.* Virus Research (2013). doi:10.1016/j.virusres.2013.06.013

Fürst 2014. *Disease associations between honeybees and bumblebees as a threat to wild pollinators.* Nature (2014). doi:10.1038/nature12977 · PMC3985068

Mondet 2014. *Quantitative virus dynamics along a new Varroa expansion front (New Zealand).* PLoS Pathogens (2014). doi:10.1371/journal.ppat.1004323 · PMC4140857

Ryabov 2014. *A virulent strain of DWV prevails after Varroa-mediated, or in vitro, transmission.* PLoS Pathogens (2014). doi:10.1371/journal.ppat.1004230 · PMC4072795

McMahon 2015. *A sting in the spit: widespread cross-infection of RNA viruses across wild and managed bees.* J. Animal Ecology (2015). doi:10.1111/1365-2656.12345 · PMC4832299

Di Prisco 2016. *A mutualistic symbiosis between a parasitic mite and a pathogenic virus undermines bee immunity.* PNAS (2016). doi:10.1073/pnas.1523515113 · PMC4812730

McMahon 2016. *Elevated virulence of an emerging viral genotype as a driver of honeybee loss.* Proc. Royal Society B (2016). doi:10.1098/rspb.2016.0811 · PMC4936039

Mordecai 2016. *First report of a third master variant of the DWV quasispecies.* The ISME Journal (2016). doi:10.1038/ismej.2015.178 · PMC5029213

Wilfert 2016. *Deformed wing virus is a recent global epidemic in honeybees driven by Varroa mites.* Science (2016). doi:10.1126/science.aac9976

Valles 2017. *ICTV Virus Taxonomy Profile: Iflaviridae.* J. General Virology (2017). doi:10.1099/jgv.0.000757 · PMC5657024

Martin 2019. *Deformed Wing Virus in Honeybees and Other Insects (review).* Annual Review of Virology (2019). doi:10.1146/annurev-virology-092818-015700

Leonard 2020. *Engineered symbionts activate honey bee immunity and limit pathogens.* Science (2020). doi:10.1126/science.aax9039 · PMC7556694

Provenance & caveat. This is a curated synthesis of landmark and representative DWV studies drawn from a harvested corpus of 1,482 records (1,206 open access); it is not exhaustive. Findings are extracted from the cited papers' abstracts and full texts; quantitative values are as reported by the original authors. Not peer-reviewed — verify specific figures against the cited DOIs. VDV-1 is now recognised as DWV-B.