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Insect virus transmission: different routes to persistence

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Transmission is a fundamental process in disease ecology; however, the factors that modulate transmission and the dynamical and evolutionary consequences of these factors in host populations are difficult to study in natural settings. Much of our current knowledge comes from a limited number of virus groups and few ecological studies. Alternatively, progress has been made in the detection of new viruses and in probing the molecular basis of behavioural manipulation of hosts that might influence virus transmission. An expanding theoretical framework provides guidelines on the conditions under which particular transmission strategies might evolve, and their dynamical consequences, but empirical tests are lacking.

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Introduction

Transmission to new hosts is a fundamental process in disease ecology as it determines the long-term persistence of a pathogen within its host population. Pathogen transmission can be divided into two broad categories: vertical transmission, the transfer of a pathogen between parent and offspring and horizontal transmission, the passage of virus among individuals who are not parent and offspring (Figure 1). Viruses have a range of strategies to locate and invade new hosts. Pathogen transmission strategies and their impacts on disease dynamics and virulence levels are active areas of empirical and theoretical research.

Research on the roles and impacts of different transmission strategies in insect pathogens is still sparse although a good theoretical framework has been developed to explore the factors which modulate the role pathogens play in insect dynamics. Long-term data collected under realistic conditions are required however to test these models. Progress has also been made in the development and application of tools to probe insect populations for viruses, and in understanding the molecular basis of virus-induced changes in host behaviour that facilitate virus transmission. A particular challenge is understanding the process of vertical transmission and the means by which viruses can form asymptomatic, covert infections, although molecular evidence now provides potential mechanisms for the switch between latency and active virus replication (see also Asgari, this issue). These areas are the focus of this review.

Insect viruses — new viruses and cryptic communities

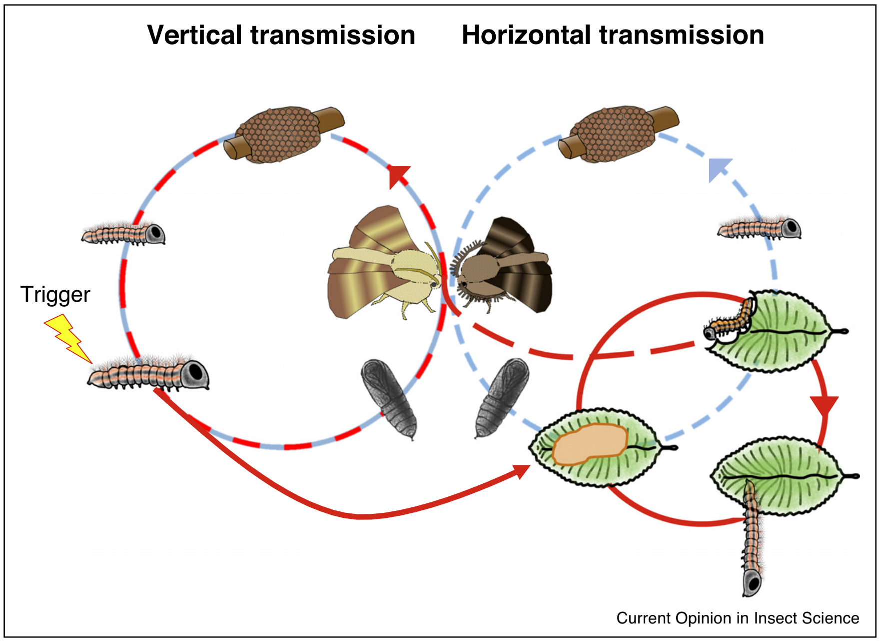
Insects host a huge diversity of viruses; however, few have been studied in detail. The origins of insect virology lie in the investigation of diseases of species of commercial interest, primarily the silkworm and more recently bees, and in the development of viruses (primarily baculoviruses) as biological control agents for insect pests. Much of what we know about insect virus ecology is based on baculoviruses [1,2]. However, information on this group of DNA viruses, which is somewhat unusual in that they produce occlusion bodies that can persist outside the host, is unlikely to be representative of many other virus groups lacking this adaptation. There is a dearth of data on the ecology of most other virus groups, particularly RNA viruses, which often cause chronic infections. The exception is research on the RNA viruses that infect *Drosophila*, particularly Sigma viruses, which were identified over 60 years ago due to the characteristic CO_2 sensitivity that infection induced [3].

The recent upsurge in genomic technologies and deep sequencing has lead to a burgeoning in viral sequence data from a range of insect species and includes a large number of RNA viruses, such as viruses belonging to the families *Ilfaviridae* and *Dicistroviridae* in the Order Picornavirales (e.g. [4–6], see also Liu *et al.*, this issue). The application of sequencing methodologies, combined with PCR-based techniques, now allows the identification of cryptic virus infections, including multi-pathogen infections (e.g. [7]). This paves the way for more detailed ecological studies of virus communities in natural populations (e.g. [8]), as well as providing methods to investigate the persistence and transmission strategies adopted by a broad range of viruses.

Horizontal transmission — moderating factors and tritrophic effects

Horizontal transmission in insect viruses often occurs through the ingestion of contaminated food via the susceptible feeding stages of insects, although examples of

Figure 1



Vertical and horizontal routes of baculovirus transmission. In horizontal transmission the larva ingests the virus while feeding or moving around in the environment. This initiates a productive infection and the larva eventually dies, releasing virus occlusion bodies on the host plant which are then ingested by other, susceptible larvae, thereby producing one or more cycles of infection (solid red line). In vertical transmission the covert virus infection passes continuously from parents (probably via both sexes) to offspring without expression of disease symptoms (dashed red line). This cycle can continue until some point when a trigger, either internal or external, switches the virus from a covert form to an overt productive infection. This virus then joins the horizontal infection cycle. It is likely that covert infection is initiated when an insect survives a sublethal virus challenge. The host life cycle is shown in blue.

cannibalism, sexual transmission and even vectoring occur. Factors that can potentially influence horizontal transmission of nucleopolyhedrovirus (NPV) and its impact on host dynamics have been explored with small-scale experiments and mathematical models, particularly in the gypsy moth-NPV system (e.g. [9,10]). But field observations and tests of influences at the population level are lacking. Horizontal transmission can be modulated by a variety of environmental factors, one of which is host plant [2]. Baculoviruses, and other pathogens that must be ingested, have an intimate relationship with their host plant [11]. Host plants can impact transmission by interacting directly with the virus, altering the resistance of the host or even interacting with the gut biota (e.g. [12,13,14•]). Host plant effects can be based, *inter alia*, on different chemical compositions or, less well understood, the presence of an induced response as a result of insect damage (e.g. [15]). These plant-mediated interactions could clearly impact biological control using baculoviruses, but whether these laboratory studies can be extrapolated to the dynamics of natural populations is less clear. However, a recent experimental and modelling study of gypsy moth–NPV interaction has implicated variation in induced defences as one possible explanation for complex patterns seen in gypsy moth dynamics [16]. Thus host plant–virus interactions could have a more significant impact on host dynamics than had been previously envisaged.

Pathogen-induced changes in transmission behaviour

One of the fascinating features of many parasites is that they can alter host behaviour after infection, in order to increase the likelihood of their transmission (see also Pinheiro *et al.*, this issue for plant virus modulation of vector behaviour). Such behavioural changes have been shown in insect viruses, primarily baculoviruses. For example, NPV infected larvae in some species have increased activity and climb up the plant to die, which increases dissemination of virus occlusion bodies to the leaves below [17]. This has recently been shown to be a positive phototactic response [18]. Behavioural modifications have also been recorded in sexually transmitted insect viruses. Insects infected with *Helicoverpa zea* nudivirus 2 are sterilized [19]; however, continued mating is vital for virus transmission and infected females have enhanced sexual behaviour, that increases transmission [20]. A more recent discovery of an iridovirus infection in crickets, demonstrated that infection prolonged sexual behaviour, and thus virus transmission, by reducing, among other things, the time males took to start courting females [21].