

Current Opinion in Insect Science

Influence of parasitoid-associated viral symbionts on plant-insect interactions and biological control --Manuscript Draft--

Short Title:	Parasitoid viruses and plant-insect interactions
Keywords:	polydnviruses; parasitoid microbes; extended phenotype; plant-insect-microbe interactions
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Abstract:	Insect parasitoids have evolved symbiotic interactions with several viruses and thousands of parasitoid species have established mutualistic associations with polydnviruses (PDVs). While PDVs have often been described as virulence factors allowing development of immature parasitoids inside their herbivore hosts, there is increasing awareness that PDVs can affect plant-insect interactions. We review recent literature showing that PDVs alter not only host physiology, but also feeding patterns and composition of herbivore's oral secretions. In turn PDV-induced changes in herbivore phenotype affect plant responses to herbivory with consequences ranging from differential expression of plant defense-related genes to wider ecological effects across multiple trophic levels. In this opinion paper we also highlight important missing gaps to fully understand the role of PDVs and other parasitoid-associated viral symbionts in a plant-insect interaction perspective. Because PDVs negatively impact performance and survival of herbivore pests, we conclude arguing that PDV genomes offer potential opportunities for biological control
Author Comments:	we have no additional comments

Dear Dr. Feng Zhu,

Please, find submitted our invited contribution for Current Opinion in Insect Science entitled
“Influence of parasitoid-associated viral symbionts on plant-insect interactions and biological control”

As suggested referees we list the following experts

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Best regards

Antonino Cusumano, also on the behalf of Anne-Nathalie Volkoff



Influence of parasitoid-associated viral symbionts on plant-insect interactions and biological control

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Abstract

Insect parasitoids have evolved symbiotic interactions with several viruses and thousands of parasitoid species have established mutualistic associations with polydnviruses (PDVs). While PDVs have often been described as virulence factors allowing development of immature parasitoids inside their herbivore hosts, there is increasing awareness that PDVs can affect plant-insect interactions. We review recent literature showing that PDVs alter not only host physiology, but also feeding patterns and composition of herbivore's oral secretions. In turn PDV-induced changes in herbivore phenotype affect plant responses to herbivory with consequences ranging from differential expression of plant defense-related genes to wider ecological effects across multiple trophic levels. In this opinion paper we also highlight important missing gaps to fully understand the role of PDVs and other parasitoid-associated viral symbionts in a plant-insect interaction perspective. Because PDVs negatively impact performance and survival of herbivore pests, we conclude arguing that PDV genomes offer potential opportunities for biological control

Keywords: polydnviruses; parasitoid microbes; extended phenotype; plant-insect-microbe interactions

23 **1. Introduction**

24 In nature plants and insects do not interact alone because microbial symbionts can act as “hidden players”
25 modulating the strength of plant responses against insect herbivory. The role of microbial mutualistic
26 symbioses is receiving increasing attention to unravel the arms races between plants and herbivores, yet the
27 focus has been almost exclusively towards understanding the role played by plant-associated and herbivore-
28 associated microbes [1-3]. Carnivore insects such as endoparasitoid wasps also harbor microbial symbionts but
29 their role in plant-based food webs is largely unexplored. Since the seminal paper by Price et al. [4], it has
30 become evident that integrating the third-trophic level in plant-insect investigations is crucial because plant
31 traits may enhance herbivore suppression by recruiting natural enemies. The emerging view is that parasitoid-
32 associated symbionts should be taken into account in plant-based multitrophic interactions, to fully understand
33 their complexity [5,6]

34 Evidence that parasitoid-associated symbionts can affect plant-based trophic webs comes from a handful of
35 recent studies on Polydnaviruses (PDVs) [7-9]. PDVs are the most abundant viral symbionts of parasitoids which
36 are divided in two genera, bracoviruses and ichnoviruses, each associated with one parasitoid family, the
37 braconids and the ichneumonids respectively. These viral symbionts represent the best-known example of the
38 intricate relationship between parasitoids and viruses. Polydnaviruses are endogenous viral elements
39 integrated in the wasp chromosomes and vertically transmitted through the wasp germline. Viral particles are
40 produced exclusively in the parasitoid female ovaries and injected into the herbivore host along with the eggs
41 during parasitism. Once within the parasitized host, viral particles infect the different tissues, the polydnavirus
42 genes are expressed and then induce profound physiological changes in the host which are essential for
43 successful parasitoid larval development [10-12]. Because PDVs alter the herbivore’s phenotype, in turn they
44 can affect the way the herbivore interacts with its food plant and with other members of the plant-associated
45 community.

46 The purpose of this work is to highlight recent findings in PDV-mediated plant-insect interactions focusing on
47 what still needs to be investigated, in our opinion, to advance the understanding of the role played by
48 parasitoid viral symbionts in a multitrophic perspective. Our aim is to augment the emerging framework
49 outlined by previous reviews [5-6]. We restrict our attention to PDVs because virtually nothing is known on
50 other viral symbionts of parasitoids (BOX 1) in a plant-insect perspective. We structure our review by
51 addressing: 1) the impact of PDVs on the phenotype of the herbivore host; 2) the extended phenotype of PDVs
52 in plant-based multitrophic interactions and, 3) the potential of using PDVs in biological control.

53

54 **2. Impact of polydnaviruses on herbivore insects**

55 Once in the parasitized herbivore, PDVs rapidly infect host cells (Figure 1). There is expression of the virulence
56 genes - encoded by the viral segments transferred through the particles - but no replication in this insect host.
57 Expression of PDV genes in the parasitized herbivore occurs as soon as 2 hours post-parasitization [13-14].
58 Then, PDV transcripts can be detected during all the duration of parasitism, although time-course expression
59 pattern depends of the gene considered [15]. Based on the available data, ichnovirus genes are generally quite
60 continuously expressed over parasitism, whereas bracovirus genes can more frequently be expressed
61 preferentially at certain time of the parasitism, thus suggesting different regulation mechanisms in the two
62 genera. Spatial patterns of expression also differ between PDV segment genes. Available studies (Table 1)
63 indicate that most of the PDV genes are expressed ubiquitously in various tissues of the parasitized herbivore;
64 however, some can be preferentially expressed in particular host cells or tissues [15]. Hemocytes (the insect
65 blood cells) and fat body are usually the tissues where polydnavirus genes are the most transcribed. One
66 reason could be that these two tissues are more readily available for the viral particles present in the hemocoele
67 of the parasitized insect; in addition, these two tissues are crucial in insect physiology (immune defense and
68 general metabolism, respectively). However, other tissues as midgut, salivary glands, or nervous system, can
69 also be targeted (Table 1). For instance, one protein tyrosine phosphatase (*PTP*) from the *Cotesia congregata*

70 bracovirus (CcBV) is selectively expressed in the nervous system[16]. Also, several transcripts from the *Cotesia*
71 *glomerata* bracovirus (CgBV) were detected in the *Pieris brassicae* salivary gland transcriptome [9]. This is
72 remarkable given the fact that salivary glands produce several elicitors that plants use to recognize herbivore
73 attack and tailor their defenses accordingly [17-18]. The extreme variability observed in the expression
74 patterns of PDV genes, in particular amongst members of the largest and conserved gene families (*PTPs*,
75 *vanks*), led to the hypothesis that individual gene family members may have specialized function in
76 particular host cells or tissues [15].

77 In most of the studied models, the expression of polydnavirus genes protects the parasitoid offspring by
78 inhibiting the host encapsulation response [12,19]. The most frequently described phenotypes are a drastic
79 decrease of the number of circulating hemocytes and induction of cell apoptosis. Another crucial effect of
80 polydnavirus infection on the parasitized herbivore, is alteration of the host development [11,20] or
81 metabolism [21]. From a plant-insect perspective, the most interesting phenotype described so far is the
82 alteration of caterpillar oral secretions, including a reduced activity of elicitors such as glucose oxidase [8] and
83 β -glucosidase [9]. The emerging pattern is that PDVs do not only manipulate the herbivore phenotype but also
84 plant responses to herbivory (see next section).

85

86 **3. Effects of polydnaviruses on plants**

87 The first hint that parasitoid-associated symbionts could play a role in plant-insect interactions was the finding
88 that plant responses to herbivory depend on the parasitism status of the attacking herbivore [22-27].
89 Subsequently it was shown that PDVs-injected caterpillars can mimic the response of plants induced by
90 parasitized herbivores therefore the parasitoid progeny itself seems to have a negligible role [7-9]. This is
91 fascinating given the fact that PDVs do not come in contact with plant tissues, yet they are capable of affecting
92 plant responses via the phenotypic changes on the infected herbivore.

93 PDVs may indirectly influence plant responses to herbivory through their effects on herbivore feeding and
94 physiology (Figure 1). It is known that PDVs impact herbivore traits such as developmental time and feeding
95 rates: for PDVs associated with solitary parasitoids, manipulations generally result in a reduction of growing
96 rates and early developmental arrest leading to less damage inflicted to plants compared to healthy herbivores.
97 Yet, the opposite pattern can occur for PDVs associated with gregarious parasitoids when manipulation leads
98 to an extension of developmental time in herbivores which can translate in more damage inflicted to plants.
99 Nonetheless by using caterpillar oral secretions in plant induction experiments – thus controlling for the
100 amount of inflicted damage –, it was shown that PDVs mainly interact via qualitative rather than quantitative
101 effects. In fact, it has been suggested that the PDV-mediated effects on elicitor activity (e.g. glucose oxidase, β -
102 glucosidase) lead to a reduction of plant chemical defenses [7,8]. This finding could indicate that viral-induced
103 manipulations increase the nutritional value of the food plant for the benefit of the parasitoid developing into
104 the herbivore [8].

105 In turn the plant phenotypic changes induced by PDV-infected caterpillars have consequences for the other
106 members associated with the plant community across multiple trophic levels [7,9]. What remains to be
107 investigated are the consequences for plant fitness: if there is a trade-off between defense and growth, the
108 fact that the plants invest less in defenses when attacked by PDV-infected caterpillars could lead to positive
109 effects in reproduction. *Sinapis arvensis* plants produced more seeds when attacked by *Pieris brassicae*
110 caterpillars parasitized by *Hyposoter ebeninus* or *Cotesia glomerata* when compared to conspecific plants
111 attacked by healthy herbivores [28]. Furthermore, induction of tomato plants with saliva from *Helicoverpa zea*
112 caterpillars hosting *Microplitis croceipes* larvae is associated with an increase in flower number and fruit weight
113 [29]. Considering that *H. ebeninus*, *C. glomerata* and *M. croceipes* carry PDVs, it would be intriguing to explore
114 whether such symbionts can mediate the plant fitness effects shown in the above-mentioned studies.
115 Nonetheless, the net effect of the plant fitness cannot be evaluated in isolation but under a community
116 perspective. PDV-mediated effects could potentially impose ecological costs for the plants: for example the

117 value of HIPVs recruiting primary parasitoids (i.e. indirect plant defenses) can be attenuated when 4th trophic
118 level organisms exploit plant volatiles induced by PDV-infected caterpillars [9,30]. An additional cost can occur
119 when unparasitized herbivores feeding alongside parasitized ones can increase their performances by taking
120 advantage of the PDV-induced plant-mediated reduction of chemical defenses, a hypothesis that needs to be
121 yet investigated.

122

123 **4. Can we exploit polydnaviruses to improve biological control of agricultural pests?**

124 PDV packaged genomes offer an incredible opportunity to identify a number of novel compounds targeting
125 different insect pests: they encode hundreds of genes that are all potentially expressed in the parasitized
126 herbivore and involved in alterations of herbivore physiological and ecological traits. Because viral genes are
127 especially active against Lepidoptera, one of the most economically important insect groups worldwide, PDVs
128 represent an underexploited source of active molecules that could be used to control agricultural pests. There
129 are three main ways this could be achieved: using directly the viral effectors, using the polydnaviruses in
130 combination with other biological control agents, or using their diversity to select parasitoid strains that are
131 more efficient as biological control agents.

132 Attempts to use parasitoid viral symbionts in a crop protection perspective have been made by generating
133 genetically transformed plants expressing PDV genes (a secreted ichnovirus cys-motif protein [31], or a
134 bracovirus viral ankyrin [32] which induced developmental delays in caterpillars feeding on such plants.
135 However, the use of PDV proteins as bioinsecticides has been limited till now due to the great challenges raised
136 by the complexity of the biological model. In fact, the majority of viral genes and gene families - where
137 members may have redundant function - still have to be functionally characterized. Another main challenge is
138 the delivery of the PDV proteins we want to use as a bioinsecticide. The “natural” way of delivery is injection of
139 viral particles by the female wasp directly into the pest hemocoel. To reproduce this delivery system,

140 biotechnologies allowing the molecules of interest to cross either the cuticle (for molecules intended to be
141 delivered by contact) or the midgut (for molecules intended to be delivered by oral ingestion) barriers need to
142 be developed [33] Note that to circumvent this challenge, oral activity of recombinant PDV proteins have been
143 tested in the past, with some interesting results. For instance, oral intake of a Cys-motif gene family member of
144 *C. sonorensis* ichnovirus (CslV) resulted in a marked reduction of larval growth and a quite large number of
145 nonviable pupae [34].

146 Another way to use PDVs in biological control is to include the gene of interest in the genome of an
147 entomopathogenic virus. This strategy has been implemented by expressing ichnovirus or bracovirus proteins
148 using recombinant baculoviruses. It was for example shown that expression of the *Cotesia rubecula* bracovirus
149 CrV 1 protein enhanced the insecticidal toxicity of AcMNPV baculovirus against lepidopteran pests [35,36].
150 Alternatively, PDV particles can be injected into herbivores to enhance susceptibility to baculovirus infection
151 [37,38 but see 39]. Complementarity between PDVs and entomopathogenic fungi is less explored. However, it
152 was recently shown that parasitism by the ichneumonid *Hyposoter didymator* promoted infection with the
153 fungus *Metarhizium brunneum* in *Spodoptera littoralis* larvae [40].

154 Finally, knowledge on how PDVs impact the behavioral and physiological adaptive traits to host and habitat of
155 parasitoids could be used to select more efficient parasitoid strains against agricultural pests. Indeed, it has
156 been shown that the braconid *Cotesia sesamiae* comprises different populations specialized on different
157 lepidopteran hosts, and that this intraspecific specialization is related with polymorphism of its associated
158 bracovirus [41,42]. We can thus imagine that studies on population genetics of PDV-associated parasitoids
159 could help in the identification of parasitoid populations or strains that will be more adapted to a particular
160 pest species or biotype.

161

162 5. Conclusions

163 Studies on plant-insect interaction should take into considerations that third-trophic levels symbionts such as
164 PDVs can affect plant responses to herbivore attack. There is increasing awareness that PDVs do not only serve
165 as delivery of virulence genes to suppress host immunity, but they have an extended phenotype capable of
166 affecting the interaction of the infected herbivore with its food plant. If phenotypes associated with PDV
167 infection have been largely described in hemocytes and fat bodies, information on other tissues relevant for
168 plant-insect interactions such as midgut and salivary glands is very limited. The present scarcity of functional
169 studies is further complicated by the fact that most of the PDV genes have little similarities with proteins of
170 known functions in other organisms. In addition, PDVs encode a very high number of genes, that may have
171 complementary or redundant function, and which act in concert to manipulate herbivore physiology.

172 Considering that many of the parasitoid species associated with PDVs attack lepidopteran pests, these viral
173 symbionts have potential application for biological pest control. Yet research in this field is still at its infancy
174 and, although promising approaches have been developed, there are still many challenges that must be solved
175 before considering practical applications.

176 We are just starting to unravel the ecological role played by parasitoid associated symbionts. In addition to
177 PDVs, parasitoids have established association with fungi, bacteria and a wide array of viruses (BOX 1) whose
178 role beyond host-parasitoid regulation is largely unknown. Future research should investigate whether
179 parasitoid-associated symbionts other than PDVs possess an extended phenotype that can affect plant
180 multitrophic interactions.

181

182 **Acknowledgements**

183 We thank Dr. Feng Zhu for the invitation to write this manuscript. This work was not supported by specific
184 funding

185

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Annotated references

- *Cusumano et al 2018. This work shows that PDVs can affect plant-mediated species interactions between herbivores. Herbivory by *Pieris brassicae* caterpillars, previously injected with venom and PDVs from *Cotesia glomerata* wasps, induces phenotypic changes in wild *Brassica oleracea* plants which affect oviposition decisions of the diamondback moth *Plutella xylostella*, a later herbivore colonizer associated with the same plant.
- **Zhu et al 2018. This study is the first evidence showing an ecological cost imposed by PDVs on their parasitoid partners through complex four-trophic level interactions. Injection of venom and PDVs from *Cotesia glomerata* females into *Pieris brassicae* caterpillars feeding on wild *Brassica oleracea* plants triggers changes in herbivore induced plant volatiles that recruit *Lysibia nana*, a hyperparasitoid of *C. glomerata*
- **Tan et al 2018. This study provides the first evidence showing that PDVs do not only benefit their parasitoid partners via manipulation of herbivore immunity but also provide additional advantages at the plant-insect interface. Injection of PDVs from *Microplitis croceipes* into *Helicoverpa zea* caterpillars feeding on tomato plants suppresses plant chemical defenses allowing parasitized caterpillars to grow faster eventually benefitting the performance of parasitoid larvae
- *Strand 2012:139-147. This article extensively reviews past works conducted on PDV expression patterns in the parasitized herbivore. It highlights the wide range of expression sites and the diversity of expression patterns observed among PDV genes depending on the parasitoid/PDV association or on the gene considered.
- **Di Lelio et al 2014. This work is one of the few that addresses the use of PDV proteins as potential bioinsecticides to control agriculture pests. It describes the effect of a PDV protein (a viral ankyrin) on herbivore development when the protein is delivered through transgenic tobacco plants. The authors show that the observed developmental delay is actually related to the accumulation of the viral ankyrin inside the herbivore midgut, emphasizing that PDV proteins could be used as bioinsecticides even if not directly delivered into the herbivore hemocele.

BOX 1 Parasitoid-associated viral symbionts: not only Polydnaviruses

Several DNA and RNA viruses have been described in association with parasitoids with the nature of the symbiotic relationship ranging from parasitism to mutualism. Amongst the pathogenic viruses, a picorna-like RNA virus described in the endoparasitic wasp *Pteromalus puparum* has been shown to deteriorate the venom apparatus of infected females [43]. *P. puparum* may also harbor a vertically transmitted RNA virus (PpNSRV-1), which affects the parasitoid sex ratio by reducing female offspring [44]. On the other side, most of the reports concerning viruses have positive effects for the parasitoid, although the underlying mechanisms of the benefit for the wasp remain often unknown. For instance, an entomopoxvirus vertically transmitted in the opiine wasp *Diachasmimorpha longicaudata* improves parasitism success in fruit fly hosts [45]. Similarly, a vertically transmitted double-stranded RNA virus associated with the figitid wasp *Leptopilina boulardi* is injected by the wasp into *Drosophila* hosts where it enhances the survival of developing parasitoid larvae [46]. Other examples of association with viruses beneficial to parasitoids involve manipulation of host's behavior or physiology. The braconid wasp *Dinocampus coccinellae* manipulates the behavior of its host (*Coleomegilla maculata*), by injecting an iflavirus, named *D. coccinellae* Paralysis Virus (DcPV). The proposed mechanism is that replication of DcPV in cerebral ganglia of parasitized lady beetle induces behavioral changes that eventually transform the parasitized insect into a "bodyguard" for the developing parasitoid [47]. A number of viruses are reported to favor parasitoid development by affecting host immune defenses. For instance, the ichneumonid wasp *Diadromus pulchellus* possesses an ascovirus (named DpAV-4a), which replicates in the host (*Acrolepiopsis assectella* pupa) where it causes immune suppression [48,49]. *D. pulchellus* also occasionally carry a cypovirus (DpRV-2), which can contribute to parasitism success [50].

Although the viral associations described so far consist of free viruses that usually replicate in both the parasitoid and its herbivore host, there is an increasing number of reports for integrated viral sequences retained in parasitoid genomes because of the benefits they bring to the wasp. Indeed, endogenous viral elements (EVEs) mostly derive from the integration, during parasitoid evolution, of arthropod-infecting dsDNA

409 viruses [51]. EVEs found in parasitoid genomes consist in a series of viral genes constituting machineries that
410 allow production of virus particles, containing DNA, or virus-like particles (VLPs), devoid of DNA, in the
411 parasitoid female genital tract. These particles are then injected in the parasitoid's host upon oviposition
412 inducing host immunosuppression to support parasitoid offspring development. Polydnviruses are a well-
413 known example of EVEs leading to production of particles that carry DNA molecules. VLPs produced in the
414 wasp ovaries by a viral machinery have been reported in the braconid *Fopius arisanus* [52] and the
415 ichneumonid wasp *Venturia canescens* [53]. VLPs are also produced in the venom glands of *L. boulardi*, or of
416 the braconid wasps *Biosteres longicaudatus* [54] and *Meteorus pulchricornis* [55], however their viral nature
417 has not been demonstrated yet.

418

419 **Table 1:** Examples of studies where expression of polydnavirus genes has been analyzed in parasitized or
 420 polydnavirus-infected caterpillar host tissues (by RT-PCR, RT-qPCR or RNA-seq)

PDV	PDV gene(s)	Host tissue	Lepidopteran host	Comment	Reference
CcBV	<i>PTPs</i>	NS, M, MT, FB, H	<i>Manduca sexta</i>	Some genes with ubiquitous expression profile, others restricted to subsets of tissues	16
CcBV	<i>vanks</i>	H, NC, FB, M, MT	<i>Manduca sexta</i>	Some genes are preferentially transcribed in given tissues	56
CcBV	several	H, FB, NS, G, MT	<i>Manduca sexta</i>	Expressed in all tissues (more in H and FB globally)	57
CgBV	<i>several</i>	SG	<i>Pieris brassicae</i>	RNAseq of SG reveals transcripts from several gene families	9
CpBV	<i>several</i>	H, FB, M	<i>Plutella xylostella</i>	Expressed in all tissues (similar)	58
CvBV	<i>CvBV202 (PTP)</i>	B, M, H	<i>Plutella xylostella</i>	Expressed in all tissues	59
GiBV	<i>PDVPTP (PTP)</i>	H, B, FB	<i>Lymantria dispar</i>	Expressed in all tissues	60
GiBV	<i>PTPs, vanks</i>	FB, NS, H, M	<i>Lymantria dispar</i>	Tissue-specific patterns of PTP expression	61
MdBV	<i>PTPs, vanks, glcs, orphans</i>	H, FB, M, NS, SG	<i>Pseudoplusia includens (MdBV injected)</i>	Some genes preferentially transcribed in particular tissues	62
CsIV	<i>reps</i>	FB, L, T, H, NS, M, MT, Ep	<i>Heliothis virescens</i>	Expressed in all tissues	63
CsIV	<i>vanks</i>	FB, H, NC, Ep, DT	<i>Heliothis virescens</i>	Some preferentially in H, others in FB	64
TrIV	<i>reps</i>	FB, H, M, C	<i>Choristoneura fumiferana</i>	Differences in their tissue specificity	65
HdIV	<i>vanks</i>	H, FB, NC, M	<i>Spodoptera spp</i>	Higher level in H & FB compared to NC & M	66

421 H: hemocytes; FB: fat body; NC: nerve cord; B: brain; NS: nervous system (NC+B); M: midgut; SG: salivary gland;
 422 MT: Malpighian tubules; Ep: epiderm (include muscles, trachea & epidermis); DT: digestive tract (M+MT); C:
 423 cuticular epithelium; L: labial glands; T: testes

424 **Bracoviruses:** CcBV, *Cotesia congregata* BV; CgBV, *Cotesia glomerata* BV; CpBV, *Cotesia plutellae* BV; CvBV,
 425 *Cotesia vestalis* BV; GiBV, *Glyptapanteles indiensis* BV; MdBV, *Microplitis demolitor* BV; **Ichnoviruses:** CsIV,
 426 *Campoletis sonorensis* IV; HdIV, *Hyposoter didymator* IV; TrIV, *Tranosema rostrale* IV.

427 Genes: *glc*, glycosylated central domain containing protein; *PTP*, protein tyrosine phosphatase; *rep*, repeat
 428 element gene; *vank*, viral ankyrin.

429

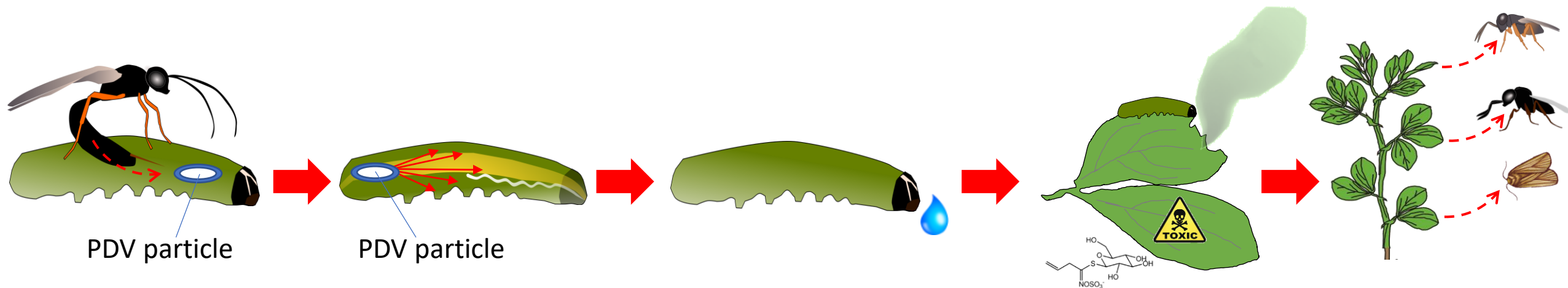
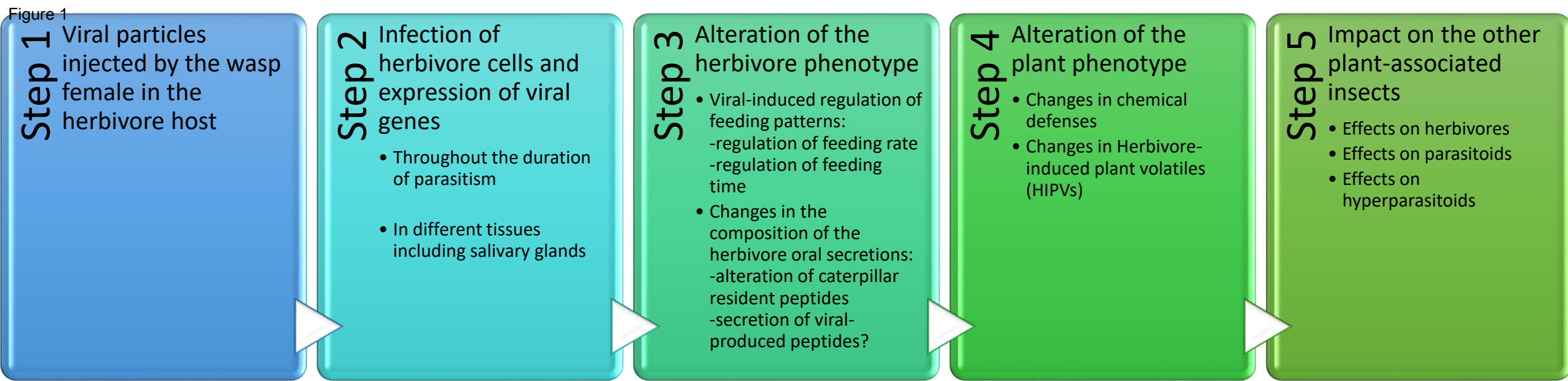
430 **Figure 1 caption**

431 **Step 1/**The polydnavirus (PDV) particles produced in the ovaries of the parasitoid wasp are injected inside the
432 herbivore host during parasitism. **Step 2/** Once in the hemocoel of the herbivore, PDVs infect the host cells
433 where viral genes are expressed. PDV expression lasts throughout the duration of parasitism and transcripts are
434 detected in mostly all the tissues of the parasitized insect (hemocytes, fat body, epithelia, nervous system,
435 midgut, salivary glands). **Step 3/** PDV infection leads to major physiological changes in the parasitized herbivore
436 that affect its development and food intake. PDV infection also leads to variations in herbivore's gene
437 expression and in production of viral proteins. It has been shown that PDVs affect the composition of
438 caterpillar resident proteins, but because viral genes are also expressed in salivary glands, viral encoded
439 proteins can be potentially produced in this tissue and secreted in the external environment. **Step 4/** Changes
440 regarding the feeding rate and oral secretions' content (elicitors) in PDV-infected herbivores alter chemical
441 defenses and emission of volatiles in the attacked plants. **Step 5/** Plant phenotypic changes induced by feeding
442 activity of PDV-infected herbivores lead to cascading effects on members of the insect community associated
443 with the same plant (other herbivores, parasitoids, hyperparasitoids).

Conflict of interest

The authors declare that the content of this manuscript was not affected by any financial, commercial, legal, or professional interest.

Figure 1



Highlights

- The best-known viral symbionts of endoparasitic wasps are polydnviruses (PDVs)
- There is increasing awareness that PDVs can affect plant-insect interactions
- PDVs alter the feeding patterns and composition of oral secretions in herbivores
- PDV-induced phenotypic changes in herbivores affect plant responses to herbivory
- PDV packaged genomes offer potential opportunities for biological pest control