

VU Research Portal

Effects of plant-mediated differences in host quality on the development of two related endoparasitoids with different host-utilization strategies

Harvey, Jeffrey A.; Gols, Rieta

published in

Journal of Insect Physiology
2018

DOI (link to publisher)

[10.1016/j.jinsphys.2018.03.006](https://doi.org/10.1016/j.jinsphys.2018.03.006)

document version

Publisher's PDF, also known as Version of record

document license

Article 25fa Dutch Copyright Act

[Link to publication in VU Research Portal](#)

citation for published version (APA)

Harvey, J. A., & Gols, R. (2018). Effects of plant-mediated differences in host quality on the development of two related endoparasitoids with different host-utilization strategies. *Journal of Insect Physiology*, 107, 110-115. <https://doi.org/10.1016/j.jinsphys.2018.03.006>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl



Effects of plant-mediated differences in host quality on the development of two related endoparasitoids with different host-utilization strategies

Jeffrey A. Harvey^{a,b,*}, Rieta Gols^c

^a Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6700 EH Wageningen, The Netherlands

^b Department of Ecological Sciences – Animal Ecology, VU University Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, The Netherlands

^c Laboratory of Entomology, Wageningen University, Droevendaalsesteeg 4, 6708 PB Wageningen, The Netherlands

ARTICLE INFO

Keywords:

Brassica oleracea

Cotesia vestalis

Dolichogenidea sicaria

Host quality

Life-history

Plutella xylostella

ABSTRACT

Among parasitoids that develop inside the bodies of feeding, growing hosts (so-called 'koinobiont' endoparasitoids), two strategies have evolved to dispose of host resources. The larvae of one group consumes most host tissues before pupation, whereas in the other the parasitoid larvae consume only host hemolymph and fat body and at maturity emerge through the host cuticle to pupate externally. Here we compared development and survival (to adult emergence) of two related larval endoparasitoids (Braconidae: Microgasterinae) of the diamondback moth, *Plutella xylostella*. Larvae of *Dolichogenidea sicaria* are tissue feeders whereas larvae of *Cotesia vestalis* are hemolymph feeders. Here, development of *P. xylostella* and the two parasitoids was compared on three populations (one cultivar [Cyrus], two wild, [Winspit and Kimmeridge]) of cabbage that have been shown to vary in direct defense and hence quality. Survival of *P. xylostella* and *C. vestalis* (to adult eclosion) did not vary with cabbage population, but did so in *D. sicaria*, where survival was lower when reared on the wild populations than on the cultivar. Furthermore, adult herbivore mass was significantly higher and development was significantly shorter in moths reared on the cultivar. The tissue-feeding *D. sicaria* was larger but took longer to develop than the hemolymph-feeder *C. vestalis*. The performance of both parasitoids was better on the cabbage cultivar than on the wild populations, although the effects were less apparent than in the host. Our results show that (1) differences in plant quality are diffused up the food chain, and (2) the effects of host quality are reflected on the development of both parasitoids.

1. Introduction

In nature, multitrophic interactions are abundant and ubiquitous, making them excellent subject for studying a range of ecological questions. For instance, plants may be attacked by a wide range of insect herbivores, and these herbivores also act as prey or hosts for many species of predators and parasitoids. In particular, specialist-feeding herbivores and parasitoid wasps make excellent subjects for ecophysiological studies. The vast majority of herbivores are specialists (Bernays and Graham, 1988; Cornell and Hawkins, 2003; Loxdale and Harvey, 2016) attacking a limited number of plants that have phylogenetically conserved chemical defenses. Similarly many species of endoparasitoid wasps attack only one or a few species of closely related hosts in nature that have phylogenetically conserved immune responses (Godfray, 1994).

In both cases involving plant-herbivore or herbivore-parasitoid interactions, the co-evolutionary arms race is characterized by selection for traits in the resource that resist attack by consumers and select for

traits in the consumers that enhance the ability to exploit the resource. In plants, resistance traits can be chemical, morphological, or physiological and are either constitutively expressed (i.e. present throughout the life of the organism) or are induced after feeding damage is inflicted by the consumer (e.g. increased after attack). There may also be considerable genetic variation in the expression of these defense traits in plants (Gols et al., 2008; Mooney and Agrawal, 2008; Whitham et al., 2012). Chemical plant defenses based on the production of secondary metabolites (allelochemicals) have been shown to negatively affect the growth, development and survival of many insect herbivores (Schoonhoven et al., 2005; Iason et al., 2012).

However, most insect herbivores have evolved various counter-adaptations that enable them to more effectively exploit plants. For example, specialist-feeding herbivores may often use secondary metabolites in plant tissue as feeding or oviposition cues and stimulants or even sequester them into their own body tissues as a putative defense against their own natural enemies (Renwick, 2002; Després et al., 2007; Opitz and Müller, 2009). Still other herbivores may detoxify and

* Corresponding author at: Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6700 EH Wageningen, The Netherlands.
E-mail address: j.harvey@nioo.knaw.nl (J.A. Harvey).

excrete the toxic by-products of plant allelochemicals. For example, many herbivores produce enzymes such as cytochrome P450 monooxygenases that detoxify various types of secondary plant metabolites which are then excreted with frass (Schuler, 1996; Feyereisen, 1999). Larvae of the small cabbage white butterfly, *Pieris rapae*, produce a nitrile-specifier protein that prevents the formation of toxic mustard oils from their food plants and which are excreted as harmless nitriles (Wittstock et al., 2004). Despite this, it is well established that inter- and intraspecific differences in plant quality can profoundly affect the development and reproduction of insect herbivores (Awmack and Leather, 2002; Schoonhoven et al., 2005).

The performance of natural enemies may also be affected by prey or host quality mediated directly or indirectly through the plant (Hunter, 2003; Harvey, 2005; Ode, 2006). Numerous studies have shown, for example, that the development of parasitoids is strongly affected by host traits such as the age, size and growth potential of the host (Godfray, 1994; Harvey, 2005). This is in turn often correlated with the nutritional status of the host and is often based on the quality of its food plant (Turlings and Benrey, 1998; Harvey, 2005; Ode, 2006; Gols et al., 2008). The effects of the plant on the parasitoid mediated through the herbivore host can be direct or indirect. Direct exposure to toxic allelochemicals has been shown to deleteriously affect parasitoid growth, development and survival (Barbosa et al., 1986, 1991; Ode et al., 2004). Gauld et al. (1992) even argued that the lower diversity of many parasitoid lineages in tropical biomes may be the result of the much more toxic diets of their herbivore hosts. However, indirect effects of plant quality on host performance can also affect parasitoid development, even in the absence of direct exposure to allelochemicals (Ode, 2006).

One area that has received little attention thus far is the effect of trait-mediated variations in parasitoids in response to differences in plant quality, as mediated through their host. Many parasitoids are koinobionts that allow their hosts to continue feeding and growing during parasitism (Godfray, 1994; Harvey, 2005). Koinobionts are further subdivided into species that obligatorily consume virtually the entire host before pupation and species that feed only on hemolymph and fat body and whose larvae emerge through the cuticle of the still-living host to pupate externally (Shaw and Huddleston, 1991; Harvey et al., 2000; Harvey and Strand, 2002; Quicke, 2015; Harvey and Malcicka, 2016). The hemolymph-feeding strategy is apparently only represented by species in a small number of subfamilies in the Braconidae such as the Microgastrinae. In microgastrines, species in the genera *Apanteles*, *Microgaster* and *Dolichogenidea* are represented by species whose larvae are tissue-feeders, whereas larvae of species in the genera *Cotesia* and *Microplitis* are hemolymph feeders (Gauld and Bolton, 1988; Quicke, 2015). Some advantages of the hemolymph-feeding over the tissue-feeding habit have recently been discussed by Harvey and Malcicka (2016). However, thus far no studies have directly compared the development of related tissue- and hemolymph-feeding parasitoids in the same host species.

In this study we examine the development and survival of the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) when reared on a cultivar and two wild populations of cabbage, *Brassica oleracea* (L.) (Brassicales: Brassicaceae) that have previously been shown to differ in foliar concentrations of glucosinolates (GS) secondary metabolites characteristic for Brassicaceae (Moyes et al., 2000; Gols et al., 2008; Newton et al., 2009, 2010; Harvey et al., 2011; reviewed by Hopkins et al., 2009). GS function as defensive compounds and they have been shown to directly or indirectly affect the performance of insect herbivores and their parasitoids (Gols and Harvey, 2009; Hopkins et al., 2009).

We then compare and contrast the development and survival of two related solitary endoparasitoids that utilize host resources differently when reared on second instars (hereafter L2) of *P. xylostella* reared on the different cabbage populations. *Dolichogenidea sicaria* (Marshall) (Hymenoptera: Braconidae) and *Cotesia vestalis* (Haliday)

(Hymenoptera: Braconidae) are in the same subfamily, Microgastrinae, which contains species that are all endoparasitic koinobionts of larval Lepidoptera. Both parasitoids are native to Eurasia where they occur sympatrically, although they are more common in warmer regions or southern Europe and North Africa (Sarfranz et al., 2005; Seven et al., 2005; Stefanescu et al., 2012; Furlong et al., 2013; Papp, 2014; Malcicka and Harvey, 2015). The group is well studied because many species are important natural enemies of crop pests such as the diamondback moth. However, there is a strong divergence in host usage strategies among the older larvae of parasitoids in this group. In both strategies young larvae feed exclusively on host hemolymph; however, older larvae of *D. sicaria* consume virtually the entire host before pupation (tissue-feeding strategy), whereas *C. vestalis* consume only a small fraction of the host and emerge from the still-living host by perforating the cuticle with their mandibles to pupate externally (hemolymph-feeding strategy) (Gauld and Bolton, 1988; Harvey and Strand, 2002; Harvey and Malcicka, 2016).

We hypothesize that (1) performance of *P. xylostella* will be better on the cultivated population of cabbage than on the wild populations because the latter are better defended chemically, (2) development and survival of both parasitoids will reflect host quality, and (3) development of the tissue-feeder (*D. sicaria*) will be more negatively affected than development of the hemolymph feeder (*C. vestalis*) because larvae of the latter species can more effectively adjust how much of the host they consume in accordance with differences in host size.

2. Methods and materials

2.1. Plants

Seeds of the wild cabbages were originally collected from plants naturally growing in two locations along the Dorset coastline of Great Britain at Kimmeridge (KIM) and Winspit (WIN). Brussel sprout plants var. Gemmifera, cv. Cyrus (CYR) were grown from seeds obtained from (Cyngenta Crop Protection B.V, Bergen op Zoom, The Netherlands). This cultivar is also used as host plant by *P. xylostella* for colony maintenance. These same plant populations have been used in prior studies e.g. Gols et al. (2008), Harvey et al. (2011).

Seeds of the three cabbage populations were germinated and seedlings were subsequently transferred to 1.1-L pots containing peat soil ('Lentse potgrond' no. 4; lent, The Netherlands). Plants were grown in a greenhouse at 21 ± 2 °C (day) and 16 ± 2 °C (night), 50% r.h., with a photoperiod not less than 16 h. When the light dropped below 225 μmol photons/m²/s over the 16-h photoperiod, supplementary illumination was applied by sodium lamps. Plants were watered twice a week over the first 3 weeks of growth after which time they were watered once daily. When they were 3 weeks old, the plants were fertilized once per week with Hoagland solution which was directly applied to the soil. Watering and fertilization continued during the course of the experiment. This fertilization regime compensates for the use of nutrients by the plants during their early growth.

2.2. Insects

All insects were reared at 22 ± 2 °C with a photoperiod of 16:8h light-dark regime. *Plutella xylostella* is native to the Mediterranean and North Africa but now a major pest of mustards and collards over many parts of the world (Furlong et al., 2013). It passes through four larval instars before pupation. Individuals were obtained from an insect culture maintained at the Laboratory of Entomology of Wageningen University, (WU) the Netherlands. *C. vestalis* is widespread throughout most of the Palearctic, although it is most common in more southerly regions (Sarfranz et al., 2005). It is a major parasitoid of *P. xylostella* but apparently has a fairly broad host range (Hiroyoshi et al., 2017). *C. vestalis* was obtained from the culture at the Laboratory of Entomology at WU and was originally collected from *P. xylostella* in cabbages in

fields near the university. *Dolichogenidea sicaria* has been little studied but has been previously recorded as a parasitoid of *P. xylostella* in the Mediterranean region (Avcı and Özbek, 1990) as well as in Paleractic populations of the Painted lady butterfly, *Vanessa cardui* (Stefanescu et al., 2012). Given that *P. xylostella* and *V. cardui* are not closely related, this suggests that *D. sicaria* is a generalist in terms of host range in the Lepidoptera. Other studies suggest that it is common in southern Europe and North Africa (İnanç and Beyarslan, 2001; Seven et al., 2005; Papp, 2014). It was recovered from larvae of *P. xylostella* in cabbage fields close to WU and thereafter reared on this host at NIOO (Malcicka and Harvey, 2015).

2.3. Experimental protocol

2.3.1. Determination of herbivore and parasitoid survival, size and development time

To measure different fitness-related traits in *P. xylostella*, cohorts of 20 early L2 caterpillars were taken from the culture where they were being reared on the cultivar (CYR) and gently placed with a brush onto the surface of middle leaves of the cabbage plants (CYR, KIM or WIN). These plants were placed inside of meshed cages (40 × 40 × 60 cm, Vermandel, Hulst, The Netherlands) with three other cabbage plants of the same population.

For each cabbage population there were 5 cages (= biological replicates) each with 20 *P. xylostella* larvae population. Caterpillars were allowed to move freely about on the plants until pupation. Pupae were then carefully removed from plant leaves, stems, cage mesh or pot trays and were transferred to Petri dishes (12 cm). At eclosion, the moths were sexed, anesthetized using CO₂, and weighed on a Mettler microbalance (accuracy ± 1 µg) to determine their fresh body masses. Development time was determined as the number of days between being placed onto the plants and adult eclosion. Pupae were checked at least 5 times each day for adult eclosion.

In parasitized groups, second instar caterpillars of *P. xylostella* were presented individually on the end of a brush to mated females of *D. sicaria* or *C. vestalis* in small glass vials. After successful stinging, which was verified by the insertion and removal of the parasitoid ovipositor into the host, parasitized caterpillars were placed onto leaves of cabbages from one of the three populations inside of cages containing three other plants of the same population. Twenty parasitized larvae were placed into each cage with 7 replicates (= cages) for each plant population (= 140 parasitized caterpillars per population). Parasitized larvae were allowed to feed and grow until the parasitoid emerged from them and constructed cocoons on the plants, cages or pot trays at which point they were collected and maintained in Petri dishes. Newly emerged adult wasps were sexed, anesthetized using CO₂ and then weighed to determine their fresh body masses. The development time were measured as the number of days between parasitism and adult emergence. Cocoons were checked at least 5 times each day for adult eclosion.

2.3.2. Statistical analyses

The effect of cabbage population on the development time and adult mass of the insects was analyzed using a general linear mixed model with plant population and sex as fixed factors. As response variable we used the mean values calculated for males and females per cage. In this analysis the data were analyzed for each species separately (herbivore and the two parasitoid species). To reveal how differences in host exploitation between the two parasitoid species affected adult mass and development, we compared these variables for the two parasitoid species ignoring the effect of plant population. In this second analysis parasitoid species and sex were entered as fixed factors. Assumptions of normality and homoscedasticity were met, based on visual inspection of the residuals. If any of the fixed factors were significant, pairwise differences among factor levels were determined using Tukey-Kramer-corrected LSD tests.

Survival to adult eclosion was analyzed using a generalized linear model with a binomial distribution and a logit link function. Data obtained for each cage served as biological replicate. For *P. xylostella*, we also analyzed survival to pupation (there was no pupal mortality in the parasitoids). All data were analyzed in SAS version 9.3 (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Determination of herbivore and parasitoid survival, size and development time

3.1.1. *Plutella xylostella*

Larval survival of *P. xylostella* to pupation and adult egression did not vary significantly across the different cabbage populations (pupation: $\chi^2_2 = 0.34$, $P = 0.84$; adult egression: $\chi^2_2 = 0.89$, $P = 0.64$). On average 69.7 ± 4.3% of *P. xylostella* caterpillars successfully pupated and from the initially released caterpillars 57.7 ± 5.4% emerged as adults. Development time varied significantly depending on the cabbage population on which *P. xylostella* was reared ($F_{2,24} = 4.21$, $P = 0.02$), but did not vary with offspring sex ($F_{1,24} = 0.21$, $P = 0.64$), neither was the interaction between these parameters significant ($F_{2,24} = 0.03$, $P = 0.96$; Fig. 1a). Development was approximately 1 day faster on the cultivar (CYR) than on WIN plants. Adult body mass of moths did also vary significantly with cabbage population ($F_{2,24} = 43.3$, $P < 0.001$), offspring sex ($F_{1,24} = 243$, $P < 0.001$) with the interaction between these parameters also being significant ($F_{2,24} = 8.98$, $P = 0.001$). Female moths were much larger than males and individuals developing on the cultivar were significantly larger

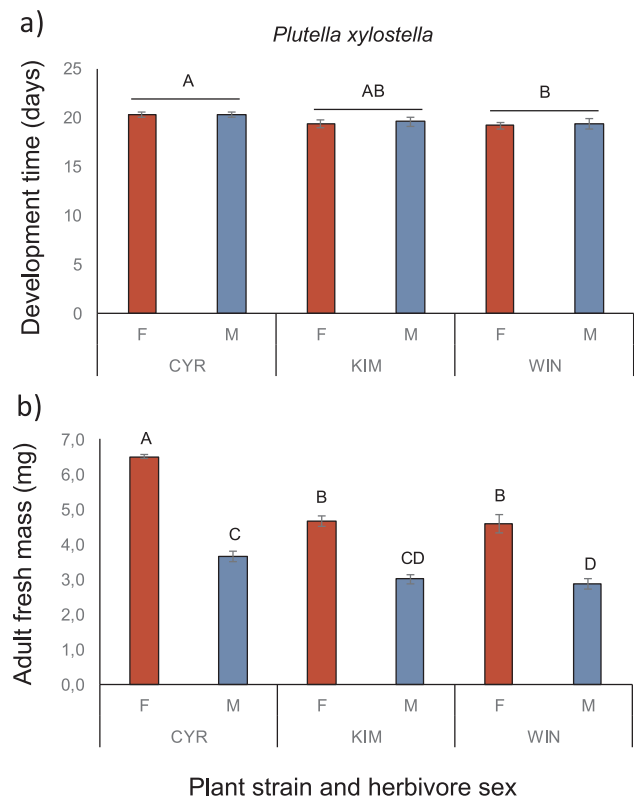


Fig. 1. Development time (a) and adult fresh mass (b) of *Plutella xylostella* females (red bars) and males (blue bars) when reared on either CYR, KIM or WIN plants. Bars present means ± SE (n = 5 cages per plant population with 20 early L2 caterpillars being initially released in each cage). Bars with different letters denote significant difference between means (Tukey-Kramer tests, $P < 0.05$). Plant population affected development time of males and females similarly, which is depicted by the lines over the bars. Statistics on main effects of sex are given in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

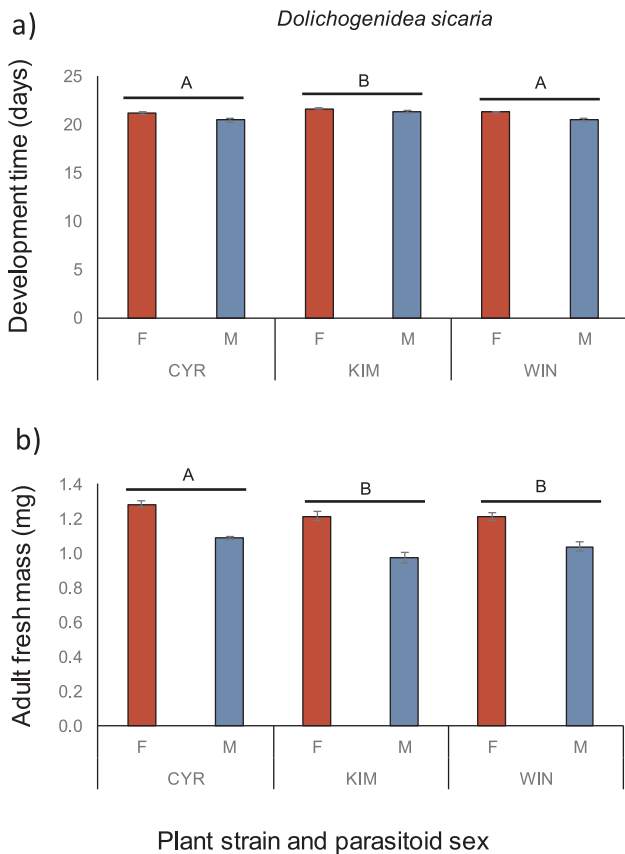


Fig. 2. Development time (a) and adult fresh mass (b) of *Dolichogenidea sicaria* females (red bars) and males (blue bars) when reared on either CYR, KIM or WIN plants. Bars present means \pm SE ($n = 7$ cages per plant population with 20 parasitized caterpillars being initially released in each cage). Bars with different letters denote significant difference between means (Tukey-Kramer tests, $P < 0.05$). Plant line affected males and females similarly, which is depicted by the lines over the bars. Statistics on main effects of sex are given in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

than those developing on the wild populations (KIM and WIN; Fig. 1b). Plant population affected the females stronger than the males (Fig. 1b). Female moths were approximately 75% heavier than males when they were reared on CYR plants, whereas females were 50% heavier than males on the wild cabbage plants.

3.1.2. *Dolichogenidea sicaria*

Larval survival of *D. sicaria* to adult eclosion varied significantly with cabbage population ($\chi^2_2 = 8.61$, $P = 0.014$). Whereas on average $76.4 \pm 2.6\%$ of wasps emerged from hosts developing on CYR plants, only 61.4 ± 5.3 and $63.6 \pm 4.0\%$ successfully developed on WIN and KIM plants, respectively. Development time was also significantly affected by the population of cabbage on which the *P. xylostella* hosts were reared ($F_{2,36} = 15.0$, $P < 0.001$). Development time differed also and with offspring sex ($F_{1,36} = 37.3$, $P < 0.001$). The interaction between plant population and sex was not significant ($F_{2,36} = 1.84$, $P = 0.17$; Fig. 2a). Males developed faster (10–20 h) than females, and both sexes developed (on average 14 h) slower on KIM plants than on plants of the other two cabbage populations (Fig. 2a). Also, adult body mass of parasitoids varied significantly with cabbage population ($F_{2,36} = 8.46$, $P = 0.001$) and offspring sex ($F_{1,36} = 118$, $P < 0.001$) with the interaction between these parameters not being significant ($F_{2,36} = 1.15$, $P = 0.32$). Female parasitoids were approximately 20% heavier than males and individuals developing on the cultivar (CYR) were 5 to 8% larger than those developing on the wild populations (KIM and WIN; Fig. 2b).

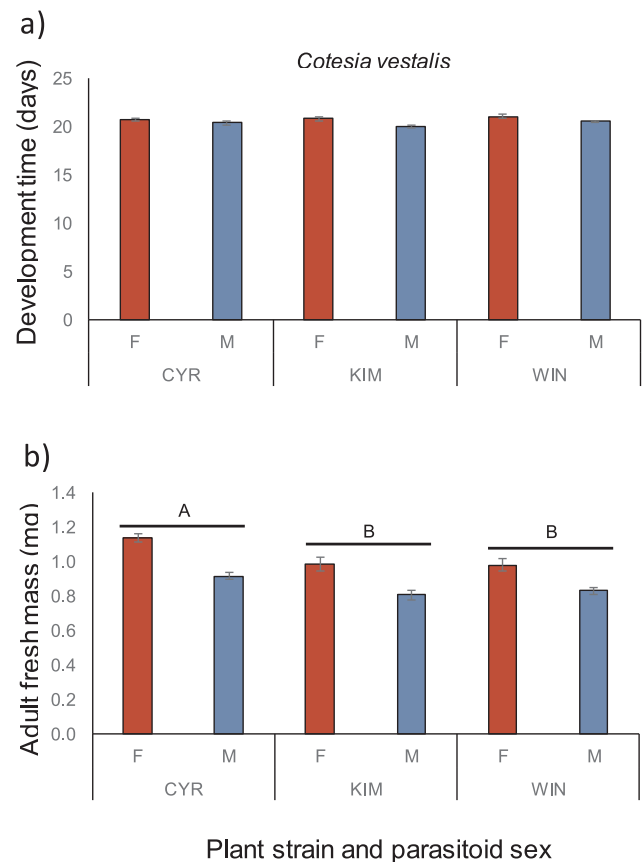


Fig. 3. Development time (a) and adult fresh mass (b) of *Cotesia vestalis* females (red bars) and males (blue bars) when reared on either CYR, KIM or WIN plants. Bars present means \pm SE ($n = 7$ cages per plant population with 20 parasitized caterpillars being initially released in each cage). Bars with different letters denote significant difference between means (Tukey-Kramer tests, $P < 0.05$). Plant line affected fresh mass of males and females similarly, which is depicted by the lines over the bars. Statistics on main effects of sex are given in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1.3. *Cotesia vestalis*

Survival of *C. vestalis* to adult eclosion was similar on the three plant populations ($\chi^2_2 = 0.42$, $P = 0.81$). On average $64.3 \pm 3.0\%$ of the parasitized larvae that were placed on the plants developed into adults. Plant population had a significant effect on adult mass of *C. vestalis* ($F_{2,20.4} = 15.8$, $P < 0.001$), but not on development time ($F_{2,36} = 2.17$, $P = 0.12$). As was found for healthy *P. xylostella*, these parasitoids grew heavier (by c. 15%) on CYR plants than on KIM and WIN plants (Fig. 3a). Female *C. vestalis* were approximately 20% heavier ($F_{1,36} = 59.7$, $P < 0.001$), but developed slower (10–20 h) than their male conspecifics ($F_{1,36} = 13.5$, $P < 0.001$; Fig. 3b). The interaction between plant population and sex was not significant for both parasitoid development time ($F_{2,36} = 0.60$, $P = 0.55$) and adult mass ($F_{2,36} = 0.7$, $P = 0.50$).

3.2. Comparing development of *Dolichogenidea sicaria* and *Cotesia vestalis*

When adult mass and development time of the two parasitoid species was compared, ignoring the effect of plant population, *D. sicaria* were approximately 20% heavier than *C. vestalis* wasps ($F_{1,80} = 110$, $P < 0.001$), but *D. sicaria* also took longer than *C. vestalis* to develop into adults ($F_{1,80} = 16.9$, $P < 0.001$). The development time of *D. sicaria* was extended by approximately half a day. In terms of adult mass and development time, females were heavier but developed more slowly than males (mass: $F_{1,80} = 109$, $P < 0.001$; development time: $F_{1,80} = 33.4$, $P < 0.001$), and this was similar in the two species, as the

interaction terms between species and sex were not significant (mass: $F_{1,80} = 0.32$, $P = 0.57$; development time: $F_{1,80} = 0.20$, $P = 0.65$).

4. Discussion

The performance of *P. xylostella* on the three cabbage populations was also partially reflected on the performance of the *D. sicaria* and *C. vestalis*, showing some congruity in plant and host quality up the food chain. Here, both sexes of the herbivore and its parasitoids achieved much larger adult body mass when reared on the cabbage cultivar than on the wild populations. This difference was most pronounced in *P. xylostella*, where females were significantly heavier when reared on the cultivar (CYR) than on the wild type plants. Both parasitoids were also much smaller when developing on herbivores reared on KIM and WIN plants. Development time was less variable in response to plant quality and differed primarily with offspring sex. In both parasitoid species males egressed as adults approximately 10–20 h before the females. Only for *D. sicaria*, did plant population on which the host developed affect survival and development time of the parasitoid. Survival to adult eclosion in *D. sicaria* was higher on the cabbage cultivar than on the wild populations. On KIM plants, both body mass and development time of *D. sicaria* were negatively affected, whereas adult wasps were smaller on WIN plants. Perhaps unsurprisingly, adult parasitoid body mass of *D. sicaria* was larger, and development time longer, than in *C. vestalis*.

Previous work with other macro-lepidopteran herbivores and their parasitoids that were reared on CYR, KIM and WIN plants reported negative effects of the wild populations on the development and survival of generalists (e.g. *Mamestra brassicae* and its parasitoid *Microplitis mediator*) and specialists (e.g. *Pieris rapae* and *P. brassicae*, and their respective parasitoids *Cotesia rubecula* and *C. glomerata*) (Gols et al., 2008; Harvey et al., 2011). However, the negative effects of the wild cabbage populations on insect performance are less pronounced in specialists compared to generalists and mainly affected secondary fitness correlates such as development time and biomass, whereas in generalists survival was also strongly affected (Gols et al., 2008). The effects on insect performance have been attributed to variable plant quality, with the wild cabbage plants possessing producing significantly higher concentrations of GS than cultivars, because wild plants have evolved under natural selection in response to attack from pathogens and herbivores whereas cultivars have often been artificially selected to emphasize traits, such as taste, that may be incompatible with defense (Gols et al., 2008; Chen et al., 2015). *Plutella xylostella* does not sequester GS, but produces a sulfatase enzyme that prevents the formation of toxic hydrolysis products (Ratzka et al., 2002). Thus, the effects of plant quality on parasitoid performance were probably not based on direct larval exposure to allelochemicals but on indirect effects of the cabbage populations on host quality.

Our results provide only partial support for our hypothesis that hemolymph feeding benefitted *C. vestalis* in terms of overcoming plant-related differences in host quality. Development – in particular survival of the hemolymph-feeder *C. vestalis* – was less negatively affected by plant/host-mediated variation in host quality than development of the tissue-feeder *D. sicaria*. Although the sample size is of course very low ($n = 1$ species for each developmental strategy), other benefits of the hemolymph-feeding over the tissue-feeding habit have been previously demonstrated. For example, some species of hemolymph-feeders are able to parasitize and exploit a much broader range of host sizes than tissue-feeders of approximately similar adult mass (Harvey and Strand, 2002). This is because the larvae of solitary tissue-feeders become occasionally trapped within the integument of larger hosts and are unable to emerge from them (Beckage and Templeton, 1985; Harvey, 1996). The larvae of some hemolymph feeders, by contrast, often develop rasping jaws in their final instar that enable them to perforate the host cuticle through which they emerge to pupate successfully (Nakamatsu et al., 2006).

The cocoons of tissue- and hemolymph-feeding parasitoids are themselves often prey or hosts for predators and hyperparasitoids respectively, and selection therefore has resulted in the expression of different strategies to reduce enemy-induced mortality. After egressing from the host, the cocoons of some tissue-feeding species protect themselves by resembling bird droppings or by using the spiny host cuticle as a kind of ‘shroud’ (Gross, 1993). However, the cocoons of parasitoids cannot ‘fight back’ once they are discovered by an enemy. Hemolymph feeders have evolved two ingenious strategies involving the host to reduce enemy-induced mortality. Some hemolymph feeders have evolved manipulative strategies whereby the dying hosts are used as more attractive prey for passing predators (Harvey et al., 2013). Alternatively, these dying hosts may also be employed as ‘bodyguards’ and aggressively defend parasitoid cocoons against attackers (Brodeur and Vet, 1994; Grosman et al., 2008; Harvey et al., 2008; Maure et al., 2011). These adaptive benefits of using still-living hosts are clearly unavailable for tissue feeders (Harvey and Malcicka, 2016). Most parasitized hosts die after their alternate prey/bodyguard function is no longer required (but see Maure et al., 2011).

In the two parasitoid species studied here, we envisaged no benefits of the hemolymph-feeding habit over the tissue feeding habit for two reasons. First of all, *P. xylostella* is a very small host relative to the adult size of both parasitoids and larvae of the tissue-feeding *D. sicaria* can easily consume fully grown L4 larvae. The advantages of hemolymph feeding in other associations have been primarily restricted to parasitoids attacking macro-lepidopteran hosts with a significant growth potential (Harvey and Strand, 2002). Second, after egression of the *C. vestalis* larva from the host, the exhausted *P. xylostella* caterpillar generally falls from the food plant and dies within 24 h or less. Therefore it has no utility as a ‘bodyguard’ as has been demonstrated in several other associations. Given that both parasitoids also were affected by differences in host quality and that *C. vestalis* did not gain some competitive edge on the basis of its feeding strategy, our results thus suggest that the benefits of hemolymph feeding, if any, are highly association-specific.

Acknowledgments

The authors wish to thank Leon Westerd and Andre Gidding for originally collecting cocoons of both parasitoid species in fields near WU, and for supplying the culture of *Plutella xylostella*.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.jinsphys.2018.03.006>.

References

- Avci, U., Özbek, H., 1990. Lepidopterous cabbage pests and their parasitoids in Erzurum. In: Proceedings of the Second Turkish National Congress of Biological Control. Ege Üniversitesi, İzmir, Turkey, pp. 319–330.
- Awmack, C.S., Leather, S.R., 2002. Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Entomol.* 47, 817–844.
- Barbosa, P., Saunders, J.A., Kemper, J., Trumbule, R., Olechno, J., Martinat, P., 1986. Plant allelochemicals and insect parasitoids effects of nicotine on *Cotesia congregata* (say) (Hymenoptera: Braconidae) and *Hyposoter annulipes* (Cresson) (Hymenoptera: Ichneumonidae). *J. Chem. Ecol.* 12, 1319–1328.
- Barbosa, P., Gross, P., Kemper, J., 1991. Influence of plant allelochemicals on the tobacco hornworm and its parasitoid, *Cotesia congregata*. *Ecology* 72, 1567–1575.
- Beckage, N.E., Templeton, T.J., 1985. Temporal synchronization of emergence of *Hyposoter exiguae* and *Hyposoter fugitivus* (Hymenoptera, Ichneumonidae) with apolysis preceding larval molting in *Manduca sexta* (Lepidoptera, Sphingidae). *Ann. Entomol. Soc. Am.* 78, 775–782.
- Bernays, E., Graham, M., 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* 69, 886–892.
- Brodeur, J., Vet, L.E.M., 1994. Usurpation of host behavior by a parasitic wasp. *Anim. Behav.* 48, 187–192.
- Chen, Y.H., Gols, R., Benrey, B., 2015. Crop domestication and its impact on naturally selected trophic interactions. *Annu. Rev. Entomol.* 60, 35–58.
- Cornell, H.V., Hawkins, B.A., 2003. Herbivore responses to plant secondary compounds: a

- test of phytochemical coevolution theory. *Am. Nat.* 161, 507–522.
- Després, L., David, J.P., Gallet, C., 2007. The evolutionary ecology of insect resistance to plant chemicals. *Trends Ecol. Evol.* 22, 298–307.
- Feyereisen, R., 1999. Insect P450 enzymes. *Annu. Rev. Entomol.* 44, 507–533.
- Furlong, M.J., Wright, D.J., Dossdall, L.M., 2013. Diamondback moth ecology and management: problems, progress, and prospects. *Annu. Rev. Entomol.* 58, 517–541.
- Gauld, I.D., Bolton, B., 1988. *The Hymenoptera*. Oxford University Press / The Natural History Museum, London, Oxford.
- Gauld, I.D., Gaston, K.J., Janzen, D.H., 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the “nasty” host hypothesis. *Oikos* 65, 353–357.
- Godfray, H.C.J., 1994. *Parasitoids*. Behavioral and Evolutionary Ecology. Princeton University Press, Princeton, New Jersey.
- Gols, R., Wagenaar, R., Bukovinsky, T., van Dam, N.M., Dicke, M., Bullock, J.M., Harvey, J.A., 2008. Genetic variation in defense chemistry in wild cabbages affects herbivores and their endoparasitoids. *Ecology* 89, 1616–1626.
- Gols, R., Harvey, J.A., 2009. Plant-mediated effects in the Brassicaceae on the performance and behaviour of parasitoids. *Phytochem. Rev.* 8, 187–206.
- Grosman, A.H., Janssen, A., de Brito, E.F., Cordeiro, E.G., Colares, F., Fonseca, J.O., Lima, E.R., Pallini, A., Sabelis, M.W., 2008. Parasitoid increases survival of its pupae by inducing hosts to fight predators. *PLoS One* 3, e2276.
- Gross, P., 1993. Insect behavioral and morphological defenses against parasitoids. *Ann. Rev. Entomol.* 38, 251–273.
- Harvey, J.A., 1996. *Venturia canescens* parasitizing *Galleria mellonella* and *Anagasta kuehniella*: is the parasitoid a conformer or regulator? *J. Insect Physiol.* 42, 1017–1025.
- Harvey, J.A., Kadash, K., Strand, M.R., 2000. Differences in larval feeding behavior correlate with altered developmental strategies in two parasitic wasps: implications for the size-fitness hypothesis. *Oikos* 88, 621–629.
- Harvey, J.A., Strand, M.R., 2002. The developmental strategies of endoparasitoid wasps vary with host feeding ecology. *Ecology* 83, 2439–2451.
- Harvey, J.A., 2005. Factors affecting the evolution of development strategies in parasitoid wasps: the importance of functional conpopulations and incorporating complexity. *Entomol. Exp. Appl.* 117, 1–13.
- Harvey, J.A., Kos, M., Nakamatsu, Y., Tanaka, T., Dicke, M., Vet, L.E.M., Brodeur, J., Bezemer, T.M., 2008. Do parasitized caterpillars protect their parasitoids from hyperparasitoids? a test of the ‘usurpation hypothesis’. *Anim. Behav.* 76, 701–708.
- Harvey, J.A., van Dam, N.M., Raaijmakers, C.E., Bullock, J.M., Gols, R., 2011. Tri-trophic effects of inter- and intra-population variation in defence chemistry of wild cabbage (*Brassica oleracea*). *Oecologia* 166, 421–431.
- Harvey, J.A., Weber, D., De Clercq, P., Gols, R., 2013. A bodyguard or a tastier meal? Dying caterpillar indirectly protects parasitoid cocoons by offering alternate prey to a generalist predator. *Entomol. Exp. Appl.* 149, 219–228.
- Harvey, J.A., Malcicka, M., 2016. Nutritional integration between insect hosts and koinobiont parasitoids in an evolutionary framework. *Entomol. Exp. Appl.* 159, 181–188.
- Hiroyoshi, S., Harvey, J.A., Nakamatsu, Y., Nemoto, H., Mitsuhashi, J., Mitsunaga, T., Tanaka, T., 2017. Potential host range of the larval endoparasitoid *Cotesia vestalis* (= *plutellae*)(Hymenoptera: Braconidae). *Int. J. Insect Sci.* 9 1179543317715623.
- Hopkins, R.J., van Dam, N.M., van Loon, J.J.A., 2009. Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Annu. Rev. Entomol.* 54, 57–83.
- Hunter, M.D., 2003. Effects of plant quality on the population ecology of parasitoids. *Agric. Forest Entomol.* 5, 1–8.
- Iason, G.R., Dicke, M., Hartley, S.E., 2012. *The Ecology of Plant Secondary Metabolites: From Genes to Global Processes*. Cambridge University Press, Cambridge.
- İnanç, F., Beyarslan, A., 2001. A study on Microgastrinae (Hymenoptera: Braconidae) species in Gökçeada and Bozcaada. *Turk. J. Zool.* 25, 287–296.
- Loxdale, H.D., Harvey, J.A., 2016. The ‘generalism’ debate: misinterpreting the term in the empirical literature focusing on dietary breadth in insects. *Biol. J. Linn. Soc.* 119, 265–282.
- Malcicka, M., Harvey, J.A., 2015. Development of two related endoparasitoids in larvae of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). *Biocontrol* 60, 149–155.
- Maure, F., Brodeur, J., Ponlet, N., Doyon, J., Firliej, A., Elguero, É., Thomas, F., 2011. The cost of a bodyguard. *Biol. Lett.* 7, 843–846.
- Mooney, K.A., Agrawal, A.A., 2008. Plant genotype shapes ant-aphid interactions: Implications for community structure and indirect plant defense. *Am. Nat.* 171, E195–E205.
- Moyes, C.L., Collin, H.A., Britton, G., Raybould, A.E., 2000. Glucosinolates and differential herbivory in wild populations of *Brassica oleracea*. *J. Chem. Ecol.* 26, 2625–2641.
- Nakamatsu, Y., Tanaka, T., Harvey, J.A., 2006. The mechanism of the emergence of *Cotesia kariyai* (Hymenoptera: Braconidae) larvae from the host. *Eur. J. Entomol.* 103, 355–360.
- Newton, E.L., Bullock, J.M., Hodgson, D.J., 2009. Glucosinolate polymorphism in wild cabbage (*Brassica oleracea*) influences the structure of herbivore communities. *Oecologia* 160, 63–76.
- Newton, E., Bullock, J.M., Hodgson, D., 2010. Temporal consistency in herbivore responses to glucosinolate polymorphism in populations of wild cabbage (*Brassica oleracea*). *Oecologia* 164, 689–699.
- Ode, P.J., Berenbaum, M.R., Zangerl, A.R., Hardy, I.C.W., 2004. Host plant, host plant chemistry and the polyembryonic parasitoid *Copidosoma sosares*: indirect effects in a tritrophic interaction. *Oikos* 104, 388–400.
- Ode, P.J., 2006. Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions. *Annu. Rev. Entomol.* 51, 163–185.
- Opitz, S.E., Müller, C., 2009. Plant chemistry and insect sequestration. *Chemoecology* 19, 117–154.
- Papp, J., 2014. Braconidae (Hymenoptera) from Tunisia, 4. Fourteen subfamilies. *Folia Entomol. Hungarica* 75, 143–166.
- Quicke, D.L., 2015. *Phylogeny and Systematics of the Ichneumonidae. The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology*. Wiley and Sons, New York.
- Ratzka, A., Vogel, H., Kliebenstein, D.J., Mitchell-Olds, T., Kroymann, J., 2002. Disarming the mustard oil bomb. *Proc. Natl. Acad. Sci.* 99, 11223–11228.
- Renwick, J.A.A., 2002. The chemical world of crucifers: lures, treats and traps. *Entomol. Exp. Appl.* 104, 35–42.
- Sarfraz, M., Keddie, A.B., Dossdall, L.M., 2005. Biological control of the diamondback moth, *Plutella xylostella*: a review. *Biocontrol Sci. Tech.* 15, 763–789.
- Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., 2005. *Insect-Plant Biology*, 2nd ed. Oxford University Press.
- Schuler, M.A., 1996. The role of cytochrome P450 monooxygenases in plant-insect interactions. *Plant Physiol.* 112, 1411–1419.
- Shaw, M.R., Huddleston, T. 1991. *Classification and biology of braconid wasps. Handbooks for the Identification of British Insects* 7.
- Seven, S., Özdemir, M., Özdemir, Y., Bozkurt, V., 2005. On the species of *Rhyacionia Hübner* [1825] (Lepidoptera: Tortricidae) in Turkey. *Phytoparasitica* 33, 123–128.
- Stefanescu, C., Askew, R., Corbera, J., Shaw, M., 2012. Parasitism and migration in southern Palaearctic populations of the painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae). *Eur. J. Entomol.* 109, 85–94.
- Turlings, T.C., Benrey, B., 1998. Effects of plant metabolites on the behavior and development of parasitic wasps. *Ecoscience* 5, 321–333.
- Whitham, T.G., Gehring, C.A., Lamit, L.J., Wojtowicz, T., Evans, L.M., Keith, A.R., Smith, D.S., 2012. Community specificity: life and afterlife effects of genes. *Trends Plant Sci.* 17, 271–281.
- Wittstock, U., Agerbirk, N., Stauber, E.J., Olsen, C.E., Hippler, M., Mitchell-Olds, T., Gershenson, J., Vogel, H., 2004. Successful herbivore attack due to metabolic diversion of a plant chemical defense. *Proc. Natl. Acad. Sci.* 101, 4859–4864.