Entomologia Generalis, Vol. 38 (2018), Issue 1, 47–59 **Article**
Published online July 2018, published in print October 2018

Host plants of the polyphagous grapevine moth *Lobesia botrana* during larval stage modulate moth egg quality and subsequent parasitism by the parasitoid *Trichogramma cacoeciae*

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With 3 figures

Abstract: The European grapevine moth *Lobesia botrana* is the main pest in viticulture, and recently extended its area to South and North America. Biological control by egg parasitoids is a current issue, which may help achieving pesticide use reduction in grapes. We hypothesized that the host plant bearing the larvae of this polyphagous moth species could affect the egg quality produced by the adults with consequences on the egg parasitism by the egg parasitoid *Trichogramma cacoeciae* Marchal. Larval food of agar based supplemented with different host berries or flowers has been proposed to *L. botrana* larvae. Berries of two grape cultivars, Cabernet Franc and Sauvignon, and flowers of three host plants of *L. botrana*, Olive tree (*Olea europea*), privet (*Ligustrum vulgare*) and tansy (*Tanacetum vulgare*), have been offered to larvae during their entire development, and eggs laid were exposed to *T. cacoeciae* females under laboratory controlled conditions. Results indicated an influence of the food offered to *L. botrana* larvae on the parasitism rate of their eggs by *T. cacoeciae* females. The rearing medium containing Sauvignon berries led to host eggs significantly less parasitized than those produced by *L. botrana* females raised on the other plants. Moreover, the percentage of aborted *L. botrana* eggs also differed and was the highest with the media containing Sauvignon berries. Our results suggest that host plant compounds ingested by the larvae could be stored in the eggs and affect their quality or viability. Finally, we observed that the presence of *T. cacoeciae* females significantly increased by two fold the percentage of aborted eggs compared to eggs with no female in the control treatment. Implications of these results in the biological control of *L. botrana* by *Trichogramma species* are discussed, especially for vineyards planted with different grape cultivars or surrounded by different vegetation.

www.schweizerbart.de
DOI: 10.1127/entomologia/2018/0675 0171-8177/18/0675 $ 3.25

Keywords: European grapevine moth, behaviour, host egg quality, parasitism, larval food, tritrophic interactions, Sauvignon, Cabernet-Franc, Olive, Privet, Transy

1 Introduction

Trichogramma (Hymenoptera: Trichogrammatidae) parasitoids are used worldwide for biological control of major Lepidopteran pests, notably using inundative releases (Schmidt, 1994, Desneux et al. 2010, Chailleux et al. 2013). However, factors related to egg quality such as age, shape, volume, chorion thickness, biochemical composition, but also kairomones, are well known to affect parasitism by such egg parasitoids (Vinson 1985, Schmidt 1994, Yang et al. 2016, Du et al. 2018, Hou et al. 2018). In phytophagous insects, the host plant also affects fitness parameters including egg attractiveness to parasitoids or predators (Stamp 2001, Singer & Stireman 2003). Factors driving and maintaining polyphagy in the European grapevine moth *Lobesia botrana* Den. & Schiff. (Lepidoptera, Tortricidae) have been investigated in relation to host-plant, showing that larval food quality is important for the reproductive performance of this insect (Torres Vila et al. 1999, Torres Vila & Molina 2002, Thiéry & Moreau 2005, Moreau et al. 2006a, b). The survival and efficiency of parasitoids or predators attacking different instars of this species also contributes to the progeny survival and may also be affected.

The European grapevine moth is one of the major insect pests of vineyards worldwide (Thiéry et al. 2018), notably owing to its recent geographical extension to South and North America (Gilligan et al. 2011). This economically important pest of grapes can be controlled either by different insecticides, but by also biotechnical methods like Bt or mating disruption and by biological control mainly by several species of parasitoids (see Thiéry et al. 2018 and Lucchi et al. 2018 for recent reviews). It generally completes two to five generations per year according to the latitude, beginning in April-May after a winter facultative diapause. *L. botrana* females lay their eggs on several plants, including wild or cultivated grapes, privet as berries or flowers, olive as berries, gooseberry, strawberry tree, plums, and a wild Thymeleaceae, *Daphne gnidium* (Maher & Thiéry 2006). Larvae can develop easily on these different plants (Marchal 1912, Thiéry & Moreau 2005, Maher & Thiéry 2006, Thiéry 2007). In this species, larval dispersal is space-limited and selection of oviposition sites is performed by the adult females (Torres Vila et al. 1997, Thiéry 2005, Maher & Thiéry 2006). Occasionally, *L. botrana* larvae can develop on food plants like raisins, dates, pears and also leaves of few plant species. Several fungi may also improve larval food quality, e.g., the grey mold *Botrytis cinerea*, which attack grapes mostly in Summer/Autumn, is known to improve several adult life-history traits of *L. botrana* (Savopoulou Soultani & Tsanakakis 1988, Mondy & Corio-Costet 2000). Eggs *L. botrana* are naturally parasitized by several species of hymenopterous egg parasitoids of the genus *Trichogramma* (Barnay et al. 1999, El Wakeil et al. 2010, Pizzol et al. 2012), or predated by egg predators from which *Orius* species are common (Thiéry et al. 2011, 2018). For these different reasons, *L. botrana* represents an interesting biological model to test the variation of egg quality for *Trichogramma* species and a previous work already established such effect on *Trichogramma evanescens* Westwood (Moreau et al. 2009). Different host plants have been compared for their effects on the reproductive success of the adult moth (Stavridis & Savoupoulou Soultani 1998, Thiéry & Moreau 2005, Moreau et al. 2006a, b), but the impact of the larval food of *L. botrana* on parasitism of further generation was bee addressed only by Moreau et al. 2009 on *T. evanescens*, and by Xuéreb & Thiéry (2006) who compared preferences of wild larval parasitoids for *L. botrana* larvae raised on five different grape cultivars.

Several *Trichogramma* species were found in vineyards worldwide (Barnay et al. 2001, Reda, 2004, Paull & Austin, 2007). Although *Trichogramma* spp. were early noticed as grape moth eggs parasitoids in ancient literature under the name *Oophtora* sp. (Marchall & Feytaud 1911), their natural control efficiency is still debated (Marchesini & Dalla Monta 1994, Thiéry 2018). Recent large scales release programmes are however currently attempted, for example in French vineyards (see Thiéry et al. 2018). A survey in Switzerland suggested that native populations of *Trichogramma* may be low, few individuals being caught in traps and 10,600 eggs of *L. botrana* exposed in vineyards yielding no *Trichogramma* (Genini 2000). The situation was similar in the Bordeaux area (Thiéry, D., unpublished data). Such low occurrence of native *Trichogramma* in vineyards are consistent with results from Barnay et al. (2001) who exposed eggs cards in different vineyards and recorded between 0% and 3.3% parasitism by four species (*Trichogramma cacoeciae* Vogelé, *Trichogramma daumalae* Dugast & Vogelé, *T. evanescens* and *Trichogramma principium* Sugonyaev & Sorokina), *T. cacoeciae* being the most commonly found. Biological control based on *Trichogramma* species releases is also poorly developed in Europe in vineyards. This is partly due to the great level of variation observed in efficiency of the various biological control release programmes tested so far. For example, several years of release in Alsace, Champagne and Burgundy areas in France led to contrasted parasitism rates, varying from 13 to 100% (Barnay 1999, Pizzol 2004). Several factors related to the vineyard agrosystem itself (e.g. routine phytosanitary measures potentially affecting natural enemies, see Desneux et al. 2007 for a thorough review of possible side effects), as well as both availability and quality of hosts, may account for such variations.

The present work aimed at testing if larval food has an influence on the susceptibility of the eggs to an egg parasitoid species. This was tested under controlled conditions by offering to *L. botrana* larvae different host plants in similar feeding substrate (i.e., dried food material incorporated to a larval feeding substrate as in Thiéry & Moreau 2005). After complete development, the egg production of mated females were exposed to *T. cacoeciae* (Hymenoptera, Trichogrammatidae). This species was found in several European vineyards either on the European grape vine moth (*L. botrana*) or the grape berry moth (*Eupoecilia ambiguella* Hübner) (Babi 1990, Wajnberg & Hassan 1994, Barnay et al. 2001, Pizzol 2004), and several biological control programs were attempted against the grape moths with that species (Barnay et al. 1999). *Trichogramma. cacoeciae* is a generalist egg parasitoid first described by Marchal (1936) on the Tortricid moth *Archips rosana* L. It can parasitize eggs of several Tortricid species like the oriental fruit moth *Cydia molesta* Busck, the codling moths *Cydia pomonella* L. and *Cydia Funebrana* Treitschke, and *Ostrinia nubilalis* Hübner for example (Stengel et al. 1977).

2 Material and methods

2.1 Plants and larval rearing media

Four host-plant species of *L. botrana* were compared: (1) grapevine berries of Cabernet Franc and Sauvignon at stage 31 according to Eichorn & Loren (1977) scale, i.e., when berries are small bunches begin to hang, (2) *Ligustrum vulgare* (Oleaceae) flowers, (3) *Olea europea* (Oleacea) flowers and (4) *Tanacetum vulgarae* (Asteracea) flowers. Tansy has several well studied chemotypes (or chemical races) (Holopainen et al. 1987, Keskitalo et al. 2001) and we used tansy from the β chemotype (see Gabel & Thiéry 1994 for a description). The influence of each plant was assayed by breeding *L. botrana* larvae individually on semi-artificial media enriched with freeze-dried flowers or berries of the different plants as described in Thiéry & Moreau (2005). A similar procedure has been used in other studies (Mondy & Corio-Costet 2000, Moreau et al. 2006b). This procedure allows offering either flowers or berries as foods of similar texture and amounts to the larvae (see Thiéry & Moreau 2005, for a detailed explanation).

The basal rearing medium we used constituted of corn oil and no other plant material except cellulose. On it, larvae were raised individually in Eppendorf tubes following the same procedure as described elsewhere (Thiéry & Moreau 2005). Proportions per 1.5 ml water were: 0.05 g of agar, 0.07 g of casein, 0.06 g of cellulose, 0.035 g of glucose, 0.0008 g of cholesterol, 0.02 g of different mineral salts, 0.04 g of vitamin-free casein, 0.001 g of nipagine (methyl hydroxyl-benzoate), 0.0025 g of benzoic acid, 0.001 g of corn oil and 70 µg of tetracycline. All plants were harvested from our experimental vineyards or from its edges and then deep-frozen (-18°C) until use for experiments. Frozen plant materials (berries or flowers) were then crushed using a blender, freeze-dried, blended as a fine powder and incorporated in the basal medium (except for the control). For each Eppendorf tube we used 1.35 g of berries of Cabernet Franc or Sauvignon or 0.30 g of flowers of tansy, privet or olive.

2.2 Insects

Neonate larvae of *L. botrana* were obtained from our stock culture reared at 22 ± 1°C, 65 ± 5% r.h., 16L:8D on the artificial medium (as described above). The strain of *L. botrana* (INRA Bordeaux) used for this study originated from individuals > 5,000 larvae collected the year before in a French Sauternes vineyard. Larvae used in the experiments came from this stock culture and were breed individually in 2.5 ml Eppendorf tubes containing rearing medium and kept in climatic chambers under the same conditions. Emerging males and females were caged in groups of 40–50 couples (males and females same plant origin) in mesh cylindrical cages (21 cm diam., 39 cm length). Oviposition was only possible on wax paper sheets (egg laying surrogate well accepted by most ovipositing moths) harvested daily. Small pieces of papers with one day old eggs were thus cut off and exposed to *T. cacoeciae* (thelytokous strain collected in 1987 and 1989 in Alsatian vineyards reared in our laboratory on an alternative host (*Ephestia kuehniella* Zeller) and provided by INRA Sophia-Antipolis). After expected parasitism the eggs of *L. botrana* were maintained in a climatic chamber under the same conditions as described above.

2.3 Bioassays

Pieces of waxed paper containing 25 eggs issued from one rearing medium were introduced in a small glass tube (1 × 7 cm) and were then offered for 24 hours to one-to-two-day-old isolated females of *T. cacoeciae* (Pizzol et al. 2012) and never exposed to *L. botrana* eggs before. Two variables were measured: the percent of parasitized (black) *L. botrana* eggs, and the percent of aborted eggs from which no *T. cacoeciae* or *L. botrana* developed. Twenty nine female *T. cacoeciae* were used per treatment except in Cabernet Franc (31). The effect of *T. cacoeciae* on egg abortion was evaluated by comparing the control eggs exposed to *T. cacoeciae* females to eggs laid and handled under the same conditions but not exposed to *T. cacoeciae*.

2.4 Statistical analysis

Percent parasitized and aborted eggs were analysed, after being first arcsin-transformed, with a one-way ANOVA, eventually followed by a Duncan post-hoc test to compare average values among rearing media. All computations were done using SAS (SAS Institute 1988). Correlations between individual rates of parasitism and egg abortion were tested using the non-parametric Spearman's rank correlation. Results are expressed in both text and figures as mean ± SD.

3 Results

3.1 Influence of larval food on egg parasitism

One hundred and seventy-five *T. cacoeciae* females were tested in this work. Considering all the experimental treatments (4,375 eggs), the total parasitism rate reached slightly more than half of the eggs (mean ± SD 50.7 ± 1.1 %) and a 100 % parasitism of the egg batches offered to each female was never observed. It varied from 80 % for two *T. caccoeciae* females to no parasitism in two females which were found alive after the experiment. The parasitism rate by *T. cacoeciae* varied according to the rearing medium offered to *L. botrana* larvae ($F_{5, 172} = 2.96$, $P = 0.014$) (Fig. 1).

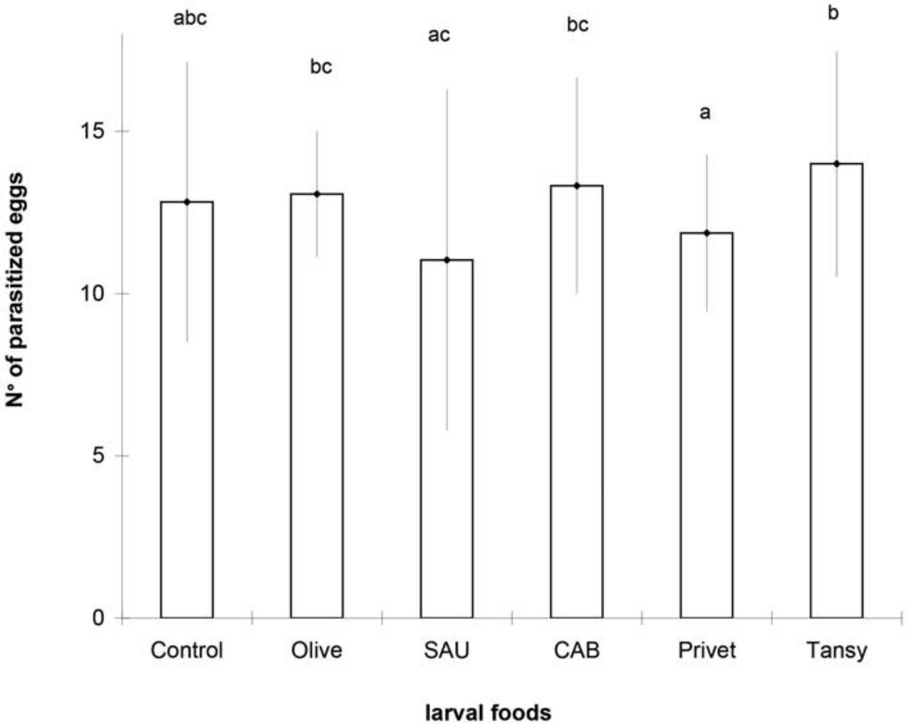

Fig. 1. Mean (± SE) number parasitized eggs by *Trichogramma cacoeciae* for the different rearing media offered to *Lobesia botrana* as a larva. SAU = Sauvignon, CAB = Cabernet Franc. Bars with similar letters are not statistically different ($p > 0.05$).

In the control, 359 out of 700 eggs were parasitized (mean ± SD: 51.3 ± 17.2 %). Tansy induced the highest proportion of parasitized eggs (56 ± 13.8 %) and the lowest were obtained with the Sauvignon (45.6 ± 21.2%) and the privet medium (47.8 ± 9.6 %). Replicates with no parasitism were observed only in three individuals in the Sauvignon treatment. Sauvignon differed statistically from the other treatments and specifically from the other grape treatment (Cabernet-Franc) (Fig. 1).

3.2 Percentage of aborted eggs and contribution by *T. cacoeciae*

The percent aborted eggs also varied significantly according to the moth larval food from 15.7 ± 2.5% for the control to 26.5 ± 2.6% for Sauvignon ($F_{5, 172} = 4.27$: $P = 0.0011$). Actually, only the Sauvignon medium differed from the other media (Fig. 2). The presence of *T. cacoeciae* clearly increased the number of aborted control eggs in these experiments, almost two times more aborted eggs were found in the presence of the parasitoids (16.3 ± 2.5% vs. 8.3 ± 1.2%, $F_{1, 54} = 9.5$, $p = 0.0032$).

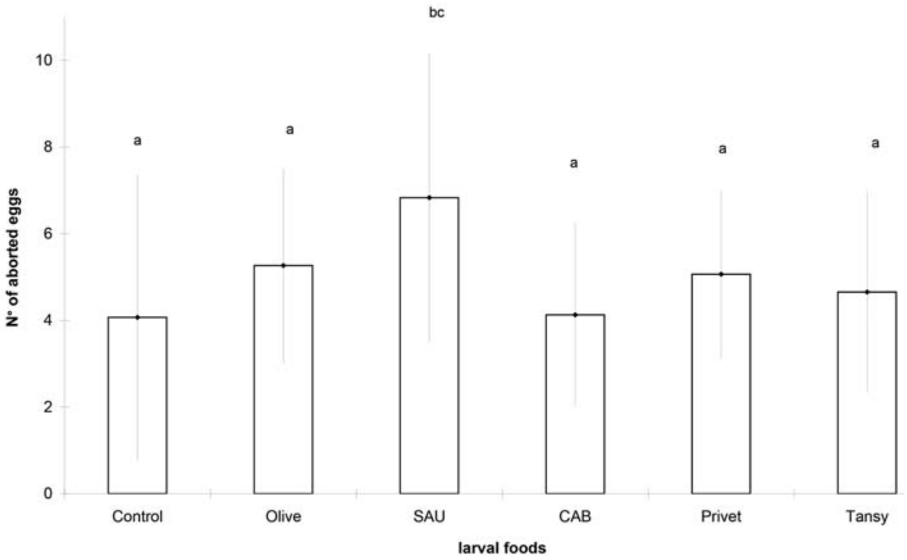

Fig. 2. Mean (± SE) number of aborted eggs (*Trichogramma cacoeciae* present) according to the rearing media offered to *Lobesia botrana* as a larva. SAU = Sauvignon, CAB = Cabernet Franc. Bars with similar letters are not statistically different ($p > 0.05$).

3.3 Relationship between rate of parasitism and percentage of aborted eggs

As shown Fig. 3, the two variables were negatively correlated in three treatments: tansy ($\rho = -0.438$, $p = 0.017$), sauvignon ($\rho = -0.502$, $p = 0.005$) and control ($\rho = -0.477$, $p = 0.010$). This indicates that the higher the parasitism rate, the lower the rate of aborted eggs. There was no significant correlation in the other treatments.

4 Discussion

The present work examined some variation factors and especially how the food plant consumed by the moth larvae may contribute to explain such variation. In a previous work, Moreau et al. 2009 found for *T. evanescens* that the grape cultivar on which the *L. botrana* larva developed affected the parasitism of eggs produced subsequently by such larva as adults. We demonstrate in the present study, by focussing on alternative host plants that egg acceptance by *T. cacoeciae* females can also be modified substantially by the type of food consumed by the host during its larval development. This result is in line with results from Moreau et al., 2009. The advantages and disadvantages of the experimental procedure used here have been discussed elsewhere (Thiéry & Moreau 2005, Moreau et al. 2006c).

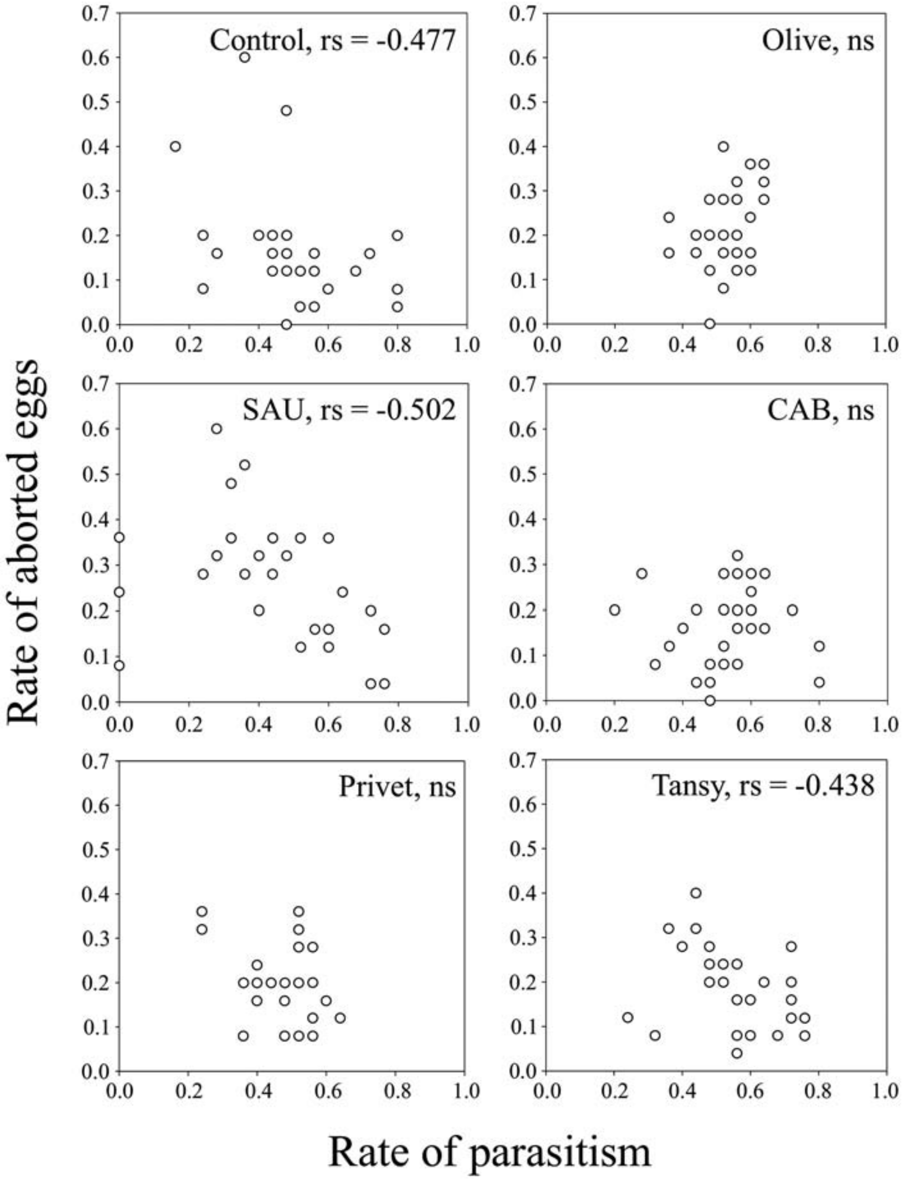

Fig. 3. Relationships between individual rate of parasitism and rate on aborted egg (axis are similar for 6 graphs). rs-values are Spearman rank correlations. SAU = sauvignon, CAB = Cabernet Franc.

Significant differences were observed between the different larval foods. Tansy significantly differed from Privet and Sauvignon, which led to eggs producing the lowest amounts of parasitoids, while olive, control, and Cabernet Franc led to similar results. Eggs contain a wide variety of natural products that act against their natural enemies (Hilker & Meiners 2002), and plant metabolites that are ingested by an herbivore can be incorporated during oocyte production and may affect the host acceptance by parasitoids (Blum & Hilker 2002, Hilker & Meiners 2002). Host acceptance by egg parasitoids is known to depend upon different characteristics of the egg from which size and chemical information provided by the egg shell mucus and by the egg quality itself. The egg size was not measured in this work, but using a similar approach with a similar larval food Moreau et al. (2009) found that grape cultivars offered to larvae had no significant differences in egg size. Assuming that egg quality is related to egg viability and thus mortality, the significant negative correlations between parasitism and egg mortality rates found in the control and with tansy and Sauvignon as food sources is instructive. They suggest that *T. cacoeciae* perceived information related to egg quality and would mostly parasitize good quality eggs, and that parasitism is lowered in replicates where eggs are less viable.

Trichogramma are known to be attracted by, and to locate host eggs at short distance (Bruins et al. 1994, Wajnberg & Colazza 1998) and several studies reported reduced parasitism due to egg rejection during the preliminary sequences leading to oviposition (Song et al. 1997, Babendreier et al. 2003). Cues can include fatty acids and their derivatives present on the egg surface (Frenoy et al. 1992, Gabel & Thiéry 1996). However, because *T. cacoeciae* were kept near the eggs for 24 h, it seems unlikely that a difference in egg attractiveness can explain our results. Indeed, variation in host acceptance when probing before ovipositing is more likely to have occurred in this study. *Trichogramma* wasps can evaluate the size of the eggs in which they oviposit (Waage & Ming 1984, Bai et al. 1992, Schmidt 1994) and to adjust their reproductive strategy accordingly. Differences in egg size may thus contribute to differences in parasitism, but this factor was not considered to be important here since we exposed to *T. cacoeciae* eggs laid by females during their first period of oviposition (three days). It was also found that *L. botrana* larvae developed on different grape cultivars produced eggs varying from 1.45 to 1.62 mm^2 which was considered to be a small level of variation (less than 12% variation in size) (Moreau et al. 2006a). Such a range of variation is small compared to those proposed in studies where clear-cut effects of host size were observed. For example, Nurindah et al. (1999) exposed eggs of different sizes to *T. australicum* in non-choice experiments and found that 0.50 mm diameter eggs of *Heliothis armigera* were less parasitized than 0.75 mm ones. Therefore, we believe that, in the present study, egg size, but not this factor alone, might have possibly contributed to the differences observed.

An interesting result of the present work concerns differences in the viability of non-parasitized eggs which may explain differences in host acceptance by *T. cacoeciae*. This is related to the fact that *Trichogramma* females are known to probe eggs before accepting or rejecting them as hosts. By simply considering control treatments, we show that the presence of a *T. cacoeciae* female doubles the host egg mortality. Female *Trichogramma* are known to probe their host eggs by inserting the ovipositor (Le Ralec & Wajnberg 1990) not necessarily followed by oviposition. Such behaviour along with repeated walking activity and the possible injection of venom might lead to egg mortality as found in *T. australicum* (Jarjees & Merritt 2004). However, further behavioural observations elucidating the causes of egg mortality by *Trichogramma* are needed to test this hypothesis.

Our results report a parasitism rate slightly above 50% of the eggs offered to *T. cacoeciae* females. Such a limited host attack rate, which never exceed 80% in confined exposure procedure and under favourable climatic conditions, raises the question of the potential efficiency of *T. cacoeciae* in vineyards, even if the strain we used originated from vineyards. Sauvignon and Cabernet Franc led to differences in egg parasitism and differences in reproductive traits of *L. botrana* were previously observed using different cultivars following a similar experimental approach (Moreau et al. 2006a, Moreau et al. 2007). However, van Bergeijk et al., 1989 also found unexpected low rate of parasitism in *T. maidis* and they attributed this result to the continuously rearing on a factitious host (*E. kuehniella* eggs). The host rearing origin of the *Trichogramma* wasps should thus be investigated in more details. Results presented here suggest that differential sensitivity to egg parasitism may be linked to the grape cultivars consumed by the host. This should encourage further studies considering such partial resistances to egg parasitoids acquired through the food ingested by the host larvae. A survey of *Trichogramma* parasitism rates in vineyards with Cabernet Franc and Sauvignon would be instructive.

Although the different plants studied in this work explain no more than 20% difference in rates of egg parasitism, this could contribute like other interacting factors to reduce or increase the efficiency of *Trichogramma* as biological control agents in vineyards against *L. botrana*. Therefore, more attention should be paid to vineyards with small patches of different grape cultivars or with important plant diversity, which could thus explain varying parasitism rates by *Trichogramma* parasitoids.

Acknowledgements: We thank Dr. Eric Wajnberg for very helpful comments on the manuscript, Julien Pfister, Jeanine Pizzol and Arlette Marconi for their technical support during different steps of this work.

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Manuscript received: 10 April 2018
Revision required: 22 May 2018
Revised version received: 15 June 2018
Accepted: 18 June 2018