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ORIGINAL PAPER

Larval food influences temporal oviposition and egg quality traits in females of *Lobesia botrana*

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Abstract Many phytophagous insects are agricultural pests, and control methods require accurate monitoring and decisions based on the determination of population age structure. The reproductive output (fecundity, egg size and percent egg hatch) is a central life history trait because it determines the offspring number, and temporal oviposition patterns are of primary importance in conditioning larval hatching and the occurrence of later larval instars in time. In turn, these phenomena determine the window for natural enemy attack and thus impact the context of biological control programmes. In addition, for most phytophagous insects, the quality of the host plants that larvae consume determines the insects' reproductive output. The purpose of the present study was to determine whether the number of eggs laid, egg size and egg hatch percentage vary with female age and the cultivar on which females develop as larvae, as well as the temporal effects of these parameters. This determination was performed in laboratory experiments where larvae were reared on artificial diets based on dried fruits of seven cultivars. Our results showed that the cultivars had a significant effect on female temporal oviposition. Independent of the food tested, the numbers of oviposited eggs, their size and percent egg hatch decreased with daily oviposition rank. Such temporal patterns must be incorporated in age-structured mathematical models used in the design of control strategies. Temporal oviposition and variation in egg quality traits will also be useful in biological control programmes, especially when based on egg or larval parasitoids, which is thus discussed.

Keywords *Lobesia botrana* · Fecundity · Egg size · Percent egg hatch · Cultivars · Female age

Key message

- In insects, temporal oviposition and hatching success are critical to reproductive success and in determining population age structure and the windows in which juvenile and other instars are available to parasitoids.
- We hypothesized that variability in larval food would influence the temporal characteristics of female oviposition and several egg quality traits of *Lobesia botrana*.
- We found a significant effect of grape cultivar on the temporal oviposition and egg quality traits.
- These results could be useful for adjusting the release of the natural enemies of eggs in biological control strategies and for age structure population temporal models.

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Introduction

The abundance of phytophagous insects and the optimal regulation of their interactions with their trophic resources are determined by numerous interacting biotic and abiotic factors. Consequently, substantial literature on phytophagous insects has been devoted to understanding the factors that govern female reproductive output because this output determines the potential number of offspring produced. The female reproductive output depends on at least three determinant life history traits: fecundity, egg size and percent egg hatch. The number of eggs laid by a female is clearly important to determine their reproductive potential, but egg size (often correlated to percent egg hatch) is also considered a crucial reproductive parameter. Numerous studies have examined the relationship between egg size and fitness components of the progeny. Such studies often demonstrate that, within a species, small eggs are less likely to hatch (Fox and Czesak 2000 and references therein), and hatching individuals from larger eggs have higher fitness than those from smaller eggs (Karlsson 1989; Fox and Czesak 2000; Roff 2002; Torres-Vila and Rodriguez-Molina 2002).

Many insect species are pests and are responsible for huge annual losses in global crop production (Thacker 2002). Most of the control methods currently used to increase crop production rely on accurate monitoring and decisions, which require precise information on the biology and the ecology of the pest (Tammaru and Javois 2000). In capital breeder insects (whose individual reproductive potential is limited by the nutrition ingested during the larval stages), larval food quality is one of the most important factors that determine female reproductive output (Awmack and Leather 2002). Several studies have shown the influence of plant quality on larval development, larval survival and female reproductive output (Awmack and Leather 2002; Thiéry and Moreau 2005; Moreau et al. 2006a, b, 2007). However, most studies have considered the effect of the host plant on fecundity, egg size and percent egg hatch without considering the temporal effect on these life history traits. This information is lacking because for the same fecundity, the temporal oviposition pattern could be dramatically different. For instance, all eggs could be laid in a single session, or an equal number of eggs could be laid each day throughout the life of the female. These different temporal oviposition patterns can lead to differences in population growth rate and the timing of further larval instars. They can also influence biological control management by modifying the optimal windows of attack for natural enemies (e.g. egg parasitoids or predators and larval parasitoids). Information on temporal oviposition is needed for progress in the study of pest population age structure determination and the construction of basic life tables (Carey 2001 for a review; Ainseba et al. 2011; Farahani et al. 2012). To our knowledge, only a few studies have examined the effect of the host plant on temporal oviposition (see Hafiz 2006; Samih and Izadi 2006), and no studies have examined the egg size and percent egg hatch throughout the oviposition period, which are necessary for a complete understanding of the variation in insect oviposition and integration into life history tables.

The European grapevine moth, *Lobesia botrana* (Denis and Schiffermuller, Lepidoptera: Tortricidae), is certainly the most harmful grape pest in Europe, north Africa and west Asia (Bovey 1966; Roehrich and Boller 1991; Ioriatti et al. 2011; Thiéry et al. 2014), and its recent introduction to Chilean and California vineyards highlights the problem of pest management (Gutierrez et al. 2012; Varela et al. 2013). *Lobesia botrana* may cause serious damage to the grape directly by consuming flower clusters and fruits, or by facilitating infection by pathogenic fungi such as grey mould disease, *Botrytis cinerea* (Persoon, Helotiales: Sclerotiniaceae), or black mould, *Aspergillus* spp. (Micheli, Eurotiales: Trichocomaceae) (Cozzi et al. 2006; Thiéry 2008; Delbac and Thiéry 2015). It may also facilitate attack by secondary pests, including fruit flies (Barata et al. 2012) such as *Drosophila melanogaster* (Meigen, Diptera: Drosophilidae) (Gravot et al. 2001) and *D. suzukii* (Matsumura, Diptera: Drosophilidae) (Rouzes et al. 2012). Therefore, *L. borana* is a highly problematic pest in vineyards and requires permanent monitoring and control (Thiéry 2008, 2011; Ortega-Lopez et al. 2014). This pest is an ideal candidate for testing the effect of the host plant on temporal oviposition because (i) previous studies have shown strong effects of cultivars where larvae feed on both larval developmental and reproductive life history traits (Moreau et al. 2006a, b, c, 2007; Thiéry et al. 2014) and (ii) information on temporal oviposition is needed for advancements in grape pest mathematical models (Ainseba et al. 2011).

The present work focuses on the temporal oviposition of the main pest of European vineyards and on how the host plant can affect this temporal pattern. Therefore, we determine whether the cultivar on which the females fed as larvae affect the number of eggs laid, egg size and egg hatch percentage, as well as the temporal patterns of these three life history traits. To examine this dependence, we conducted laboratory experiments by rearing larvae on artificial diets derived from seven different cultivars (Chardonnay, Chasselas, Gewurztraminer, Grenache, Merlot, Pinot and Riesling). We then measured individual female oviposition based on time, egg size and percent egg hatch.

Materials and Methods

Study system, origin and maintenance of moths

The strain of *L. botrana* (INRA-Bordeaux) used for this study originated from individuals collected in a French Sauternes vineyard (cultivar Semillon) in 1997, to which wild adults are periodically added. This rearing line is maintained with a substantial number of caged adults (several thousand a week) to avoid genetic drift. This laboratory strain has conserved genetic variability because considerable variation is found in the larval and adult behaviours and in larval immune parameters (Vogelweith et al. 2011). The stock colony is maintained without diapause on a semi-artificial diet (as described in Thiéry and Moreau 2005), with the following composition: 150 ml water, 3 g agar, 9 g maize flour, 11 g wheat germ, 9 g yeast, 0.9 g ascorbic acid, 0.3 g benzoic acid, 0.3 ml maize oil, 0.3 g nipagin and 0.2 g iprodione, at 24 ± 1 °C, 60 ± 10 % RH with a photoperiod of 15: 8 h light/-dark + 1 of dusk. The first 15 photophase hours were at 1000 lux luminosity, and the last hour (dusk) was at 25 lux. All tests were performed under these conditions.

Larval diet treatments and general procedure

The influence of different grape cultivars on *L. botrana* was tested using a standardized procedure (Thiéry and Moreau 2005; Moreau et al. 2006a, b). Compared to direct feeding on bunches in the laboratory or in the field, this procedure has at least three main advantages: (a) feeding isolated larvae prevents competition and subsequent food deprivation; (b) it prevents differences in grape bunch compactness, which impact larval feeding behaviour (our unpublished observations) and the climatic environment (temperature and insolation) of the larvae (Pieri and Fermaud 2005); and (c) it prevents infections by fungi on grapes, which may affect larval fitness as shown by Savopoulou-Soultani and Tzanakakis (1988) and Mondy and Corio-Costet (2000).

To avoid immature competition, larvae were reared individually to pupation in Eppendorf tubes filled with 1.5 ml of a medium containing the following (for 100 Eppendorfs): 150 ml water, 5 g agar, 6 g cellulose powder, 4 g vitamin-free casein, 3.5 g glucose, 2 g mineral salt, 0.12 g cholesterol, 0.12 g maize oil, 0.25 g benzoic acid, 0.1 g nipagin and 12 g freeze-dried grape fruit powder. Freeze-dried material was obtained from freshly collected grape flower clusters within 12 h of collection using a Christ alpha 1–4 LD plus device. This classic procedure preserves fresh foods (Rati 2001) and is typically used for secondary metabolites conservation in grapes (see Michalczyk et al. 2009). The grape cultivar-dried powders were obtained from grape flower clusters of *V. vinifera* cv. Chardonnay, Chasselas, Gewurztraminer, Grenache, Merlot, Pinot and Riesling, all of which were harvested from our gene collection of grape plants "Domaine de la Grande Ferrade", INRA-Bordeaux. The insecticide-free grape flower clusters were collected at the beginning of the growing season (beginning of May 2003) at phenological stages 23–27 (Eichhorn and Lorenz 1977), which correspond to the grape phenology on which the first annual generation of *L. botrana* larvae feeds.

The Eppendorf lids were pierced to allow air circulation. Using a fine brush, newly hatched larvae (age < 8 h) were transferred individually to the diets in each Eppendorf, with 100 larvae per diet (cultivar). Neonate larvae from eggs produced by thousands of caged females were randomly chosen and assigned to the different diets. Eppendorf tubes were randomized in the Eppendorf racks, which were moved within the climatic chamber every 3 days to minimize the effect of possible climatic gradients.

The larvae from each diet were monitored daily until pupation. Two-day-old pupae were then carefully removed from the diet and weighed to the nearest 0.1 mg. Because it is difficult to weigh adult moths with sufficient accuracy, we used the mass of living pupae as an index of adult body size. Pupae were then placed individually in glass tubes (70 mm × 9 mm diameter) covered with cotton plugs and stored in the test room until emergence under the same conditions previously described. Adults were sexed after emergence by checking their ventral abdominal extremity (Thiéry 2008).

All newly emerged female adults resulting from the eight larval diets were used to evaluate the temporal effect of (1) egg laying, (2) egg size and (3) larval hatching. Because it has been reported that the cultivars on which larvae develop can modify the female oviposition preferences (Moreau et al. 2008), we decided not to run the oviposition experiments on one specific cultivar, which may have interfered with the temporal oviposition. Thus, we used an inert substrate (i.e. considered equal for all females) where females could deposit their eggs. Newly emerged females (less than 1 day old) were individually confined to 0.5 litre transparent cellophane bags as mating and oviposition chambers, and they were provided with water ad libitum through a soaked cotton dental wick. One- or two-day-old virgin males originating from the same diet were added to each caged virgin female 1 h before dusk, which is just before their sexual activity (Bovey 1966). Only one male was randomly assigned to each female. Pairs were caged in these bags until the death of both sexes.

Females could behave and oviposit freely inside the cellophane bags until death. Each morning, the cellophane bags were checked, and new eggs laid during the previous night were marked with a specific colour outside the bags.

For the analyses, only females that laid a sufficient number of eggs (>7 eggs) during their lifetime (because non-mated females can lay only a few eggs) and that began to lay at the beginning of her life were considered to obtain a representative picture of the temporal oviposition in this species. We thus obtained the temporal oviposition for a variable number of females that depended on the sex ratio, larval survival and mating success: Chardonnay $n = 33$, Chasselas $n = 24$, Gewurztraminer $n = 24$, Grenache $n = 20$, Merlot $n = 35$, Pinot $n = 34$ and Riesling $n = 29$.

At the end of the experiment (i.e. when the females were found dead in the bags), we randomly selected a sample of females that had laid a sufficient number of eggs each day in each cultivar to assess egg size and percent egg hatch: Chardonnay $n = 14$, Chasselas $n = 9$, Gewurztraminer $n = 12$, Grenache $n = 9$, Merlot $n = 17$, Pinot $n = 15$ and Riesling $n = 10$. For each selected female, three eggs from the walls of the cellophane bags were randomly selected per oviposition day, when possible. Indeed, some females sometimes laid less than three eggs per day, particularly at the end of life. Previous studies we have done (results not shown in this paper) showed that measuring three eggs per oviposition day and per female gives the same results than if we measured more eggs whatever the oviposition rank. Each egg was then measured with an ocular micrometre. The egg surface (estimated as an elliptic surface, $S = \pi \times a \times b$ in mm^2, where a and b are the ellipse semi-axes) was used as an index of egg size. The mean egg size per day was estimated for each female from this sample. To estimate daily fertility (i.e. hatching success), the measured eggs were incubated at 22 °C for 10 days until hatching.

Statistical analysis

For all analyses, mixed effects models were performed, including the identity of the females as a random effect. The pupal mass of the females was also included to control for its potential effect. The number of eggs laid by day and cultivar was compared using negative binomial generalized linear mixed effects model (GLMM) accounting for zero-inflated data. The statistical significance of each parameter was tested with χ^2 statistics for unbalanced design (Fox and Weisberg 2011). The proportion of hatching eggs was arcsine square root transformed to normalize. However, the transformed variable was not normally distributed and did not meet the assumption of homoscedasticity, as was the case for the size of eggs laid. Therefore, the proportion of hatched eggs and their size were compared among cultivars and days using a linear mixed effects model based on rank transformation (as a more powerful alternative to the classical non-parametric Friedman test, Baguley 2012). The statistical significance of each parameter was tested with Wald χ^2 statistics for unbalanced design. In each case, pairwise Wilcoxon multiple comparison post hoc tests were performed (P values were adjusted for multiple comparisons using the Benjamini–Yekutieli step-up procedure; Benjamini and Yekutieli 2001). The same procedure was used to analyse differences in egg size.

All statistical analyses were performed using R software (v. 3.1.1, R Development Core Team 2014) and implemented using the following packages: *lme4* (linear mixed effects models), *glmmADMB* (negative binomial generalized linear mixed effects model with zero-inflated data) and *car* (deviance analysis for unbalanced design).

Results

Number of eggs laid throughout the oviposition period

The total number of eggs laid did not differ among females fed on the different cultivar diets (GLMM: $\chi^2 = 4.07$, df $= 6$, $P = 0.67$) but varied positively according to the mass of the pupae ($\chi^2 = 18.77$, df $= 1$, $P < 0.0001$). The number of eggs laid decreased with oviposition day (female age) with the maximum of eggs laid in the first day of oviposition and with only few eggs laid at the end of the oviposition period ($\chi^2 = 231.57$, df $= 6$, $P < 0.0001$, Fig. 1). A significant interaction between cultivar and day was found (interaction cultivar × day, $\chi^2 = 62.51$,

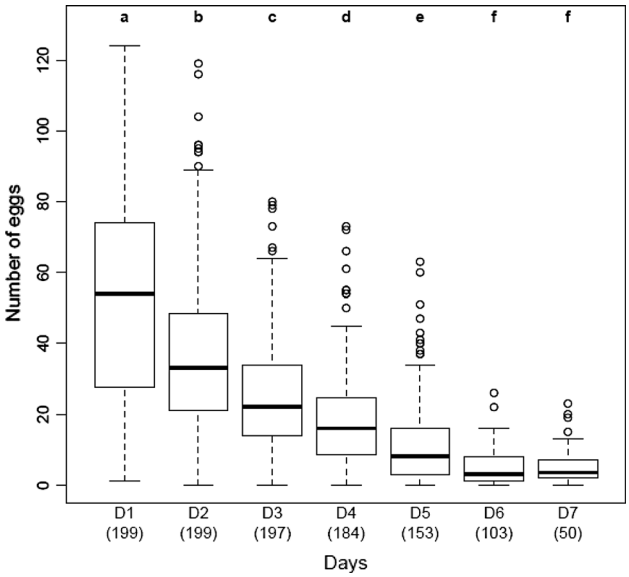

Fig. 1 Number of eggs laid by a *Lobesia botrana* female according to the day of oviposition for all cultivars. *Bold line* median; *box*: *middle two quartiles*; *dashed lines*: 1.5 × interquartile range; *open circle*: extreme value. The numbers inside the parentheses indicate the number of females. Columns with the same letter are not significantly different ($P > 0.05$) based on pairwise Wilcoxon multiple comparison post hoc tests

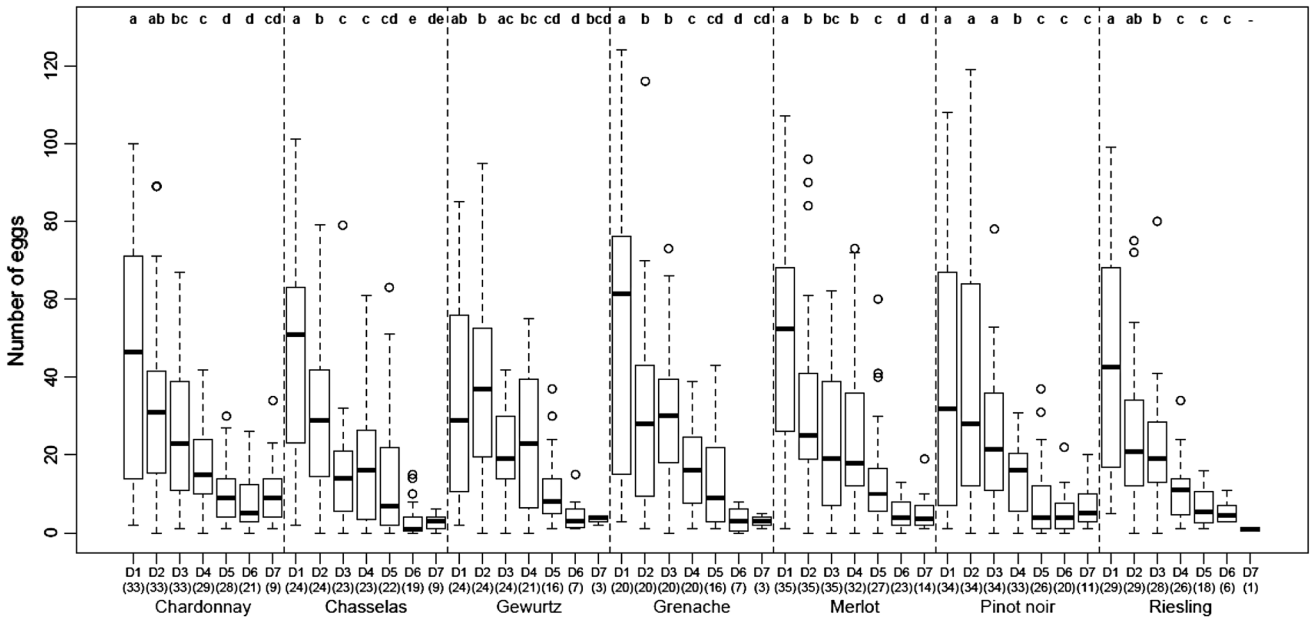

Fig. 2 Number of eggs laid by *Lobesia botrana* female according to the day of oviposition and for each cultivar where the female came from. *Bold line*: median; *box*: *middle two quartiles*; *dashed lines*: 1.5 × interquartile range; *open circle*: extreme value. The numbers inside the parentheses indicate the number of females. Columns with the same letter are not significantly different ($P > 0.05$) based on pairwise Wilcoxon multiple comparison post hoc tests

df = 36, $P < 0.01$, Fig. 2), indicating that larval diets with different grape cultivars had an effect on female temporal oviposition. For some cultivars, such as Gewürztraminer and Pinot noir, the number of eggs laid remained stable for the first 4 days of oviposition and decreased for the remaining oviposition days, whereas for other cultivars, such as Chardonnay, the numbers of eggs laid decreased linearly with oviposition days (Fig. 2).

Egg size variation throughout the oviposition period

The size of the eggs laid by females fed with different cultivars during their larval period did not differ (linear mixed effect model: $\chi^2 = 11.45$, df = 6, $P = 0.08$) and did not vary with female pupal mass ($\chi^2 = 0.62$, df = 1, $P = 0.43$). However, the size of eggs decreased with increasing days ($\chi^2 = 340.92$, df = 6, $P < 0.0001$, Fig. 3). There was also a significant interaction between day and cultivar ($\chi^2 = 132.26$, df = 36, $P < 0.0001$): for some cultivars, such as Chardonnay or Riesling, the size of eggs laid remained stable for the first 4 days of oviposition and then decreased, whereas for other cultivars, such as Pinot noir, the size of eggs laid decreased progressively (Fig. 4).

Percent egg hatch throughout the oviposition period

The percent of hatching eggs did not vary according to the female mass (linear mixed effects model: $\chi^2 = 0.40$,

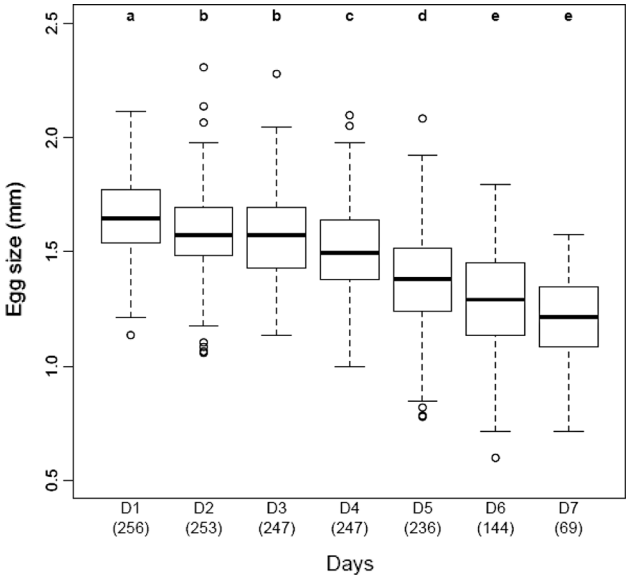

Fig. 3 Egg size according to the day of oviposition for all cultivars. *Bold line*: median; *box*: *middle two quartiles*; *dashed lines*: 1.5 × interquartile range; *open circle*: extreme value. The numbers inside the parentheses indicate the number of measured eggs. Columns with the same letter are not significantly different ($P > 0.05$) based on pairwise Wilcoxon multiple comparison post hoc tests

df = 1, $P = 0.53$) or among cultivars ($\chi^2 = 10.44$, df = 6, $P = 0.11$). However, the percent of hatched eggs decreased with increasing oviposition days ($\chi^2 = 93.77$,

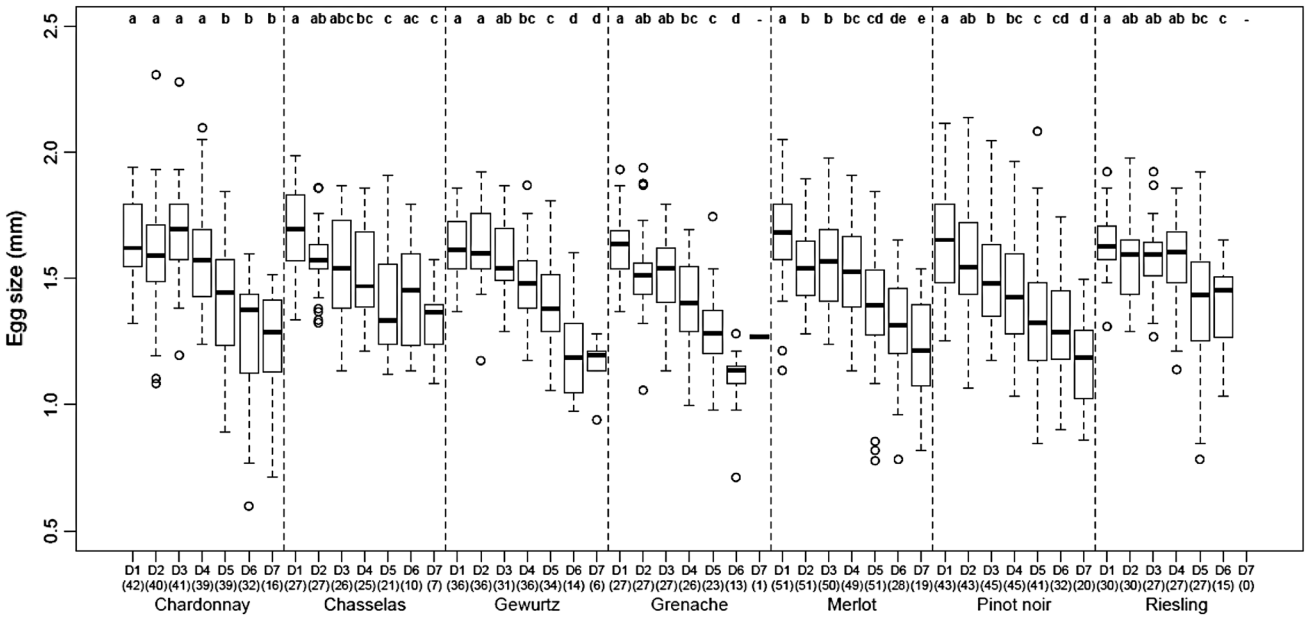

Fig. 4 Egg size according to the day of oviposition and for each cultivar where the female comes from. *Bold line*: median; *box*: *middle two quartiles*; *dashed lines*: 1.5 × interquartile range; *open circle*: extreme value. The numbers inside the parentheses indicate the number of measured eggs. Columns with the same letter are not significantly different ($P > 0.05$) based on pairwise Wilcoxon multiple comparison post hoc tests

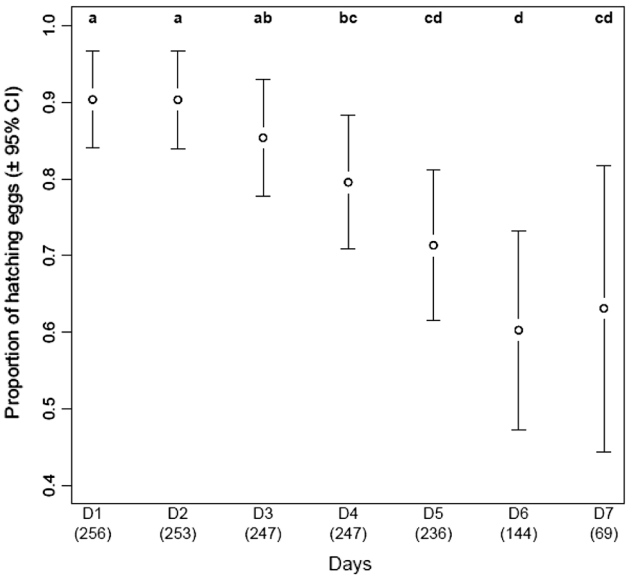

Fig. 5 Proportion of hatching eggs according to the day of oviposition for all cultivars. *Bold line*: median; *box*: *middle two quartiles*; *dashed lines*: 1.5 × interquartile range; *open circle*: extreme value. The numbers inside the parentheses indicate the number of eggs checked for percent egg hatch. Columns with the same letter are not significantly different ($P > 0.05$) based on pairwise Wilcoxon multiple comparison post hoc tests

df = 6, $P < 0.0001$, Fig. 5), with no interaction with cultivar (interaction cultivar × day, $\chi^2 = 38.80$, df = 35, $P = 0.30$). At the beginning of the oviposition period, approximately 90 % of eggs hatched, whereas only approximately 60 % of eggs hatched at the end of the oviposition period.

Discussion

One of the goals of the present study was to assess the temporal effect on three major life history reproductive traits of *L. botrana* (fecundity, egg size and percent egg hatch). Our results show that all three parameters decreased over time. The second goal of this study was to determine whether larval feeding on diets containing different cultivars had an effect on the temporal oviposition patterns and on egg size and percent egg hatch throughout the oviposition period. Our results clearly showed that the cultivar on which females developed as larvae had a significant effect on the temporal oviposition and egg size. However, no effect on percent egg hatch was detected. This result indicates that food characteristics associated with the immature stages affect how adult females distribute eggs over time. This phenomenon, combined with the effect of cultivars on the larval growth rates, may explain how the distribution of the next adult generation varies over time (Thiéry et al. 2014).

In the context of our study, the distinction between income and capital breeding insects is important. Income breeder females mature their eggs throughout their adult

life, whereas capital breeders emerge with a nearly fixed number of ovocytes (Papaj 2000). *Lobesia botrana* is considered a capital breeder (species with non-feeding adults); its female reproductive potential is thus limited by the resources accumulated during the larval stage (Slansky and Rodriguez 1987; Awmack and Leather 2002). In our experimental design, females lacked access to any additional food except clear water, so the resources mobilized for the egg production were derived from reserves accumulated during the larval stage (Awmack and Leather 2002). Previous studies showed that pupal mass is a good predictor of fecundity in *L. botrana* (Moreau et al. 2007). Egg-laying activity is under physiological pressure from the oogenesis process and oocyte formation (McDonald and Borden 1995; Chapman et al. 2013). Females used in the present study had an average egg load of 144.6 ± 37.8 eggs and laid approximately 60 % of its eggs in the two first days of the laying period. Subsequently, the number of eggs laid decreased daily until the death of the female. The large number of eggs laid during the first night could be adaptive because under natural conditions *L. botrana* adults have a relatively short life expectancy (ca. 1 week according to the climatic conditions) (Moreau et al. 2006a, b; Thiéry 2008). In addition, the predation risk for a moth is high because nocturnal insectivores often prey on moths; these predators include bats, species of owls and other species of birds (Arlettaz et al. 2000). Given that there is a delay between encountering a mate and the first egg laid of approximately 4 days for a female from our rearing strain (Moreau et al. 2006a) or in the field (Moreau et al. 2007), females have only a few days to lay eggs. In that case, laying a maximum number of eggs as quickly as possible could be adaptive. This phenomenon was observed, for example, in *Dryas iulia* (Fabricius, Lepidoptera: Nymphalidae), whose females laid the greatest number of eggs at the beginning of the laying sequence (Dunlap-Pianka et al. 1977).

We showed that eggs laid on the first day of oviposition are larger than eggs laid on the subsequent days. This size decrease is consistent with previous results performed in the same species (Moreau et al. 2009). Lepidoptera ovaries' structure and morphological aspects of oogenesis are well known (see Swever et al. 2005 for a review or Chapman et al. 2012 for a book). Briefly, oocytes are produced in the germarium and begin to move down the ovariole, enlarging as they pass through the vitellarium, where yolk containing both protein and lipids is deposited on them (vitellogenesis). The fat body is the principal site of production of the major yolk protein precursor (YPP), which is vitellogenin (Vg) in most insects (Swever et al. 2005). In many butterflies and moths, ovaries contain only previtellogenic oocytes and vitellogenesis starts at eclosion. Therefore, their ovarioles usually contain a series of oocytes in successive stages of development. In *L. botrana*, we found a delay of approximately 4 days between encountering a mate and the first egg laid (Moreau et al. 2006a, 2007). During this time, the first eggs have time to mature and enlarge with yolk. The only reason for the differential size is thus the amount of yolk, which is related to the decreased synthesis by the fat body or its depletion.

The proportion of larvae that hatched from eggs was strongly dependent on the oviposition days; fewer eggs hatched at the end of the life of females independently of the cultivars, which is consistent with the amount of yolk in the egg. This decline can be interpreted as a result of the egg size decrease, which was clearly associated with the egg size in that species (Moreau et al. 2006a, 2007), most likely because larger eggs have the largest nutritional provisions inside, as already shown in other species (Berrigan 1991; Fox and Czesak 2000). This decrease is not due to a decrease in sperm numbers because we showed that in *L. botrana*, one male ejaculate contains much more spermatozoids than necessary to fertilize all female eggs (Muller et al. 2015).

Our results show that the effect of the cultivar on which females developed as larvae had a significant effect on the temporal oviposition and egg size. For some cultivars, the number and the size of eggs laid remained stable for the first 4 days of oviposition and decreased for the remaining oviposition days, whereas for other cultivars the numbers of eggs laid or the size of eggs decreased through oviposition days. However, no effect of cultivar was detected for percent egg hatch. This effect is very weak in comparison to the profound effect of cultivar on total number of eggs laid, total mean egg size and mean percent egg hatch that we have previously demonstrated (Moreau et al. 2006a, b, 2007).

We found here that time within the oviposition period affects the number of eggs laid and the probability that an egg hatches. These individual temporal effects also influence the population scale. The data provided here on time-dependent offspring production in *L. botrana* could also be useful for the development of age-structured mathematical models of vineyard infestation such as that developed by Ainseba et al. (2011). Therefore, we also believe that this feature needs to be incorporated in future *L. botrana* population age-structured mathematical models. These effects of time would also influence biological control management based on egg parasitoids, predators and larval parasitoids to determine the optimal windows in which natural enemies should be released. As an example, several species of *Trichogramma* can be used in inundative biological control programmes in a variety of crops against numerous

pests (Morrison 1985; Reda Abd el-Monsef 2004; Agamy 2010; Andrade et al. 2011) including *L. botrana* with irregular results (Barnay 1999; Hommay et al. 2002; El-Wakeil et al. 2010). Parasitism efficiency in *Trichogramma* parasitoids is, of course, influenced by environmental factors (Calvin et al. 1984; Pizzol et al. 2010) and by intrinsic factors (Schmidt 1994; Pizzol et al. 2012) such as egg size, quality and age (Roriz et al. 2006; Moreau et al. 2009; Pizzol et al. 2012). Indeed, large and numerous eggs are often more conspicuous for the searching females and more suitable for the subsequent development of their progeny (Van Huis and De Rooy 1998; Moreau et al. 2009; Pizzol et al. 2012). With our results, the optimal window for parasitoids or predator release must occur when the first eggs are laid (bigger eggs and more eggs). This optimal window could be calculated because we showed that for each grape variety, the emergence of *L. botrana* females occurred as a single wave after approximately 10 days (Thiéry et al. 2014). In addition, considering the cultivar effect on temporal oviposition could be useful when monitoring eggs in vineyards. Insecticides against the larvae (growth regulators or *Bt*) are mostly applied at a typical egg stage called 'black head', which corresponds to 2/3 of the egg incubation period. Shorter or longer oviposition periods as a function of previous-generation food (i.e. the cultivar on which the female fed as larva) would thus cause, at the population and the vineyard scales, important variation in these typically monitored stages. We strongly believe that this information concerning temporal oviposition is needed to advance our knowledge of pest ecology with the aim of better biological control.

Author contribution

Conceived and designed the experiments: JM and DT. Performed the experiments: JM and DT. Analysed the data: KM and JM. Contributed reagents/materials/analysis tools: JM, DT and KM. Wrote the paper: JM, KM and DT.

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Compliance with ethical standards

Conflict interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Informed consent This article does not contain any studies with human participants performed by any of the authors.

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