

Grape variety affects female but also male reproductive success in wild European grapevine moths

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Abstract. 1. For insect herbivores the quality of the larval host plant is a key determinant of their fitness. Only little attention, however, has been given to the effects of plants on mating success of males and its consequence for the reproductive output of their mates. In addition, almost all the studies that have investigated the influence of host plants on herbivore fitness components have been done in the laboratory, and less is known of these effects in natural conditions.

2. Using the phytophagous European grapevine moth (*Lobesia botrana* Den. & Schiff., Lepidoptera: Tortricidae), we tested the influence of grape cultivars as larval food on the probability of acquiring a mate for both sexes, and on the reproductive output of females and males.

3. Results from this study stress the importance of larval host plants on the reproductive success of both sexes. Larval diet differentially affected mating success and reproductive output of male and female moths. Fecundity, egg size, and egg hatchability were significantly different when larvae were fed on particular grape cultivars.

4. A given cultivar that is of poor quality for females is generally also of poor quality for males. A cultivar, however, could be suitable for females but not for males and vice-versa. Apparently, the nutrients required for adult reproduction are not necessarily the same for males and females.

5. The important conclusion from this study is that evaluating the differential effect of host-plant species on traits associated with reproductive success of herbivores requires that the effects on both sexes be taken into account.

Key words. Female reproductive output, grapevine, host plant, *Lobesia botrana*, male reproductive output.

Introduction

The abundance of phytophagous insects is determined by numerous interacting biotic and abiotic factors. Lifetime reproductive success of individuals within a given population is determined by the cumulative effects of critical factors experienced during larval development and adult life. Factors such as,

adult mass (Dixon, 1987; Lavoie & Oberhauser, 2004), temperature (Ratte, 1985; Leather, 1995), larval food quality (Scriber & Slansky, 1981), and adult food quality (Leather, 1995), the last two being variable among host-plant species (Leather, 1994), have been shown to influence adult reproductive success.

For most capital breeder insects, for which their reproductive potential is limited by the nutrition ingested during the larval stages, larval food quality is one of the most important factors in explaining female reproductive output (Awmack & Leather, 2002). Several studies have shown the influence of plant quality on larval development, larval survival, and female reproductive output (see Awmack & Leather, 2002 for a review, or Thiéry & Moreau, 2005 for an example). In general, high quality larval

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food results in larger females and, as a consequence, in increased fecundity, longevity and survival (Awmack & Leather, 2002).

Host-plant quality, however, is not the only factor that can explain the female reproductive output. There are several well-documented cases for Lepidoptera that show an effect of male nutrition on the reproductive output of the female with which they mate. In such cases, males may acquire some resources during larval stages (Dussourd *et al.*, 1991; Takakura, 2004) or during adult life (Pivnick & McNeil, 1987; Lederhouse *et al.*, 1990) that are transferred to the female during mating and increase female reproductive output (Boogs & Gilbert, 1979). Females mated with males reared on low-quality larval diet will produce fewer viable progeny than those mated with males feeding on high-quality food. Most evidence for this has been obtained by supplementing male diet with sodium and/or other electrolytes in laboratory conditions (e.g. Pivnick & McNeil, 1987; Lederhouse *et al.*, 1990). Despite this well-established knowledge on the male effect, only very few studies have examined the influence of host plants consumed by males during their larval development and its consequence on the reproductive output of females that mate with them (Royer & McNeill, 1993; Delisle & Bouchard, 1995; Delisle & Hardy, 1997). For example, in the polyphagous Tortricid *Choristoneura rosaceana* (Lepidoptera: Tortricidae, Harris), lab-reared females showed differential fecundity and fertility when they were mated with males that as larvae had fed on different host-plant species (Delisle & Bouchard, 1995).

The question of the relative role of the larval diet on female reproductive success and on the contribution that males can have on this success, for example by providing the female with nutrients while mating, is particularly important for phytophagous insects. Such a lack of information may bias our understanding of the natural variation in reproductive success of phytophagous insects. Herbivores may use a range of host-plant species or varieties within the same plant species with varying nutritional quality. The effects of a poor larval diet on the reproductive success of an adult female may be compensated for by resources donated by the male during mating. Very few studies have examined the combined effects of larval diet on the reproductive output of both sexes and no study has examined this question under natural conditions.

The goal of the present study was to determine in natural populations of *Lobesia botrana* (Lepidoptera: Tortricidae, Denis & Schiffermueller), an important pest of grapes in Europe, North Africa and West Asia (Roehrich & Boller, 1991; Thiéry, 2005) the influence of larval diet on male and female reproductive output. This pest insect appears an ideal candidate for such a study because previous laboratory studies have shown that female reproductive output is strongly related to the host plants on which they fed as larvae (Savapoulou-Soultani & Tzanakakis, 1987; Savapoulou-Soultani *et al.*, 1990; Torres-Vila *et al.*, 1999; Thiéry & Moreau, 2005, Moreau *et al.*, 2006b,c). In addition, Torres-Vila *et al.* (1999) found that the number of spermatophores produced by males depends upon cultivars on which they fed. Until now, the outcome of mating with such males on female reproductive output had not been considered.

Materials and methods

Field Sampling

This study was designed as a comparison among different grape varieties of different quality in a local population of *L. botrana* in the field. To avoid potential confounding effects due to environmental variation in temperature, light exposure, humidity, and parasitism, we chose to sample larvae inside a single vineyard where the different grape varieties were subjected to identical viticulture conditions. The following criteria were taken into consideration: (i) significant population density; (ii) several grape varieties, which differ in their suitability as food for this insect species; and (iii) no insecticide treatments. Larvae were collected during the spring of 2003 (in June corresponding to the first generation of the year), in Switzerland on the following grape varieties: *V. vinifera* cv 'Chasselas', 'Gammay', 'Gewurztraminer', 'Pinot', and 'Riesling'. A control was designed in order to compare two geographically different populations on the same cultivar. A second group of larvae was thus sampled from 'Chasselas' in Alsace (France).

We sampled a large number of vine stocks (more than 1000 for each grape species). Late larval instars (L4–L5) of *L. botrana* were collected in young flower buds called 'nests' (phenology 17–25, Baillod & Baggiolini, 1993). Nests contain only one larva but may be empty. On each variety, occupied nests were extensively collected independently of their size. Larvae of *L. botrana* almost never move from one bunch to another, each collected larva was therefore considered as having accomplished its whole development on this bunch (Torres-Vila *et al.*, 1997). Larvae were maintained in small polyethylene boxes (18 × 12 cm, height 6 cm) and fed *ad libitum* on bunches collected in the same locality (*L. botrana* larvae almost exclusively feed on bunches and rarely on leaves), at 24 ± 1 °C, 60 ± 10% RH at natural photoperiod until the end of their development. Larvae were checked daily until pupation, upon which pupae were carefully removed from the flower buds, weighed to the nearest 0.01 mg and placed individually in glass tubes (70 × 9 mm diameter) stopper with cotton plugs, labelled, and stored at 23 °C under natural photoperiod. Adults were sexed immediately after emergence. We recorded: (i) pupal mass, and (ii) the emergence rate from all pupae collected (therefore corresponding to pupal mortality). Emerged adults resulting from the different grape varieties were used to evaluate the reproductive output of females and males.

Origin of laboratory male and female *Lobesia botrana*

We used a strain of *L. botrana* (INRA Bordeaux) originating from individuals collected in a French Sauternes vineyard (cultivar white Sauvignon). The stock colony is maintained without diapause on a semi-artificial diet (as described in Thiéry & 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 Nipagine, and 0.2 g Iprodione, at 24 ± 1 °C, 60 ± 10% RH with a photoperiod of light/dark (LD) 15: 8 h +1 of dusk. The first

15 photophase hours were at 1000 lux luminosity and the last one (dusk) at 25 lux.

In order to get standardised males and females, we placed 100 males and 100 females in a large cage, and large bands of waxed paper (15 × 2 cm) were hanged for oviposition support. Oviposition usually starts one or two nights after mating and once the paper received sufficient number of eggs, it was placed in a plastic box (18 × 12 cm, h 6 cm) for 1 week until the eggs hatched. Eggs were daily checked until hatching. Neonate larvae (age < 24 h) were then placed using a fine brush on a semi-artificial diet as described in previous studies (Thiéry & Moreau, 2005; Moreau *et al.*, 2006a,c). Larvae were checked daily until pupation, and the same procedure as described before was followed.

Mating success and reproductive output of field collected females from different cultivars

One 1-day-old virgin female reared on one of the five grape varieties, was caged 1–2 h before dusk with one 1-day-old virgin standardised male, in transparent cellophane bags serving as mating and oviposition chambers (cylinders: 15 cm length, 8 cm diameter), closed at one extremity with a soaked cotton dental wick. Pairs were caged in these bags until death of both sexes and the bags were checked every morning for oviposition. The surface of eggs was used as an index of egg size [estimated as an elliptic surface, $S = \pi \times a \times b$ (mm²), where *a* and *b* are the ellipse semi-axes]. Egg size was measured using a binocular micrometer on a randomly chosen sample of 15 eggs laid by each female. Fertility corresponds to the proportion of hatched eggs (counted from the batch of measured eggs) after 10 days at 22 °C, 60 ± 10% RH with a photoperiod of LD 15: 8 h + 1 of dusk.

We recorded: (i) the percentage of mated females, as determined by the production of at least one fertile egg during female lifetime (non-mated females are able to lay some infertile eggs at the end of their life); (ii) delay before the first egg is laid (in days) by checking the bags every morning to note the day of appearance of the first eggs (as the mating occurs during the night); (iii) total achieved fecundity (mean number of eggs laid per female); (iv) overall mean egg size; and (v) female fertility (percentage of hatched eggs). All life-history traits were recorded blind (origin of the cultivar or the female unknown by the experimenter).

Body mass of standardised males paired with field females did not significantly differ among the five grape varieties (Kruskal–Wallis, $\chi_4^2 = 1.13$, $P = 0.98$). In addition, the mass of standardised males that successfully mated (indicated by fertile eggs laid by the female) was not significantly different (Kruskal–Wallis, $\chi_4^2 = 1.10$, $P = 0.97$). Therefore, any observed differences in female reproductive life-history traits could not be attributed to male mass or male origin.

Mating success of field males and effect on reproductive output of their mate

One 1-day-old virgin male originating from each variety was caged with one 1-day-old virgin standardised female originating

from the culture population. We used the same procedure as the one described in the section above. Thus, all females paired with field males could be considered having the same origin. The mass of standardised females offered to field males (Kruskal–Wallis, $\chi_4^2 = 3.17$, $P = 0.65$), as well as the mass of mated females (Kruskal–Wallis, $\chi_4^2 = 2.19$, $P = 0.92$) were not significantly different among male origin. Therefore, potential occurrence of male mating success and the reproductive output of females paired to these males cannot be attributed to the female mass or their origin. The same life-history traits were assessed as described in the above section.

Control treatment: reproductive output of individuals reared on semi-synthetic diet

In order to compare the performance of field individuals with the performance of stock culture individuals raised on a diet of high nutritional value (Thiéry & Moreau, 2005; Moreau *et al.*, 2006a), we conducted the following experiment. One 1-day-old virgin male originating from the semi-synthetic diet was caged with one 1-day-old virgin female originating from the semi-synthetic diet. The variation of male mass (mean ± SEM: 9.92 ± 0.18) or female mass (mean ± SEM: 11.32 ± 0.20) was very low among different pairs formed, mainly due to rearing conditions. The same life-history traits were assessed as described in the above section.

Statistical analysis

All statistical tests were performed using JMP software (Version 3.2.2, SAS Institute, 1995). A stepwise analysis (backward procedure) was used to remove non-significant ($P > 0.05$) effects and interactions. Only the resulting models are presented here. The effect of female and male origin on life-history traits was analysed using ANOVA (or ANCOVA), or non-parametric tests (Kruskal–Wallis or Wilcoxon Rank Sum non-parametric tests), when data did not meet normality (Shapiro–Wilk's test) or homogeneity of variance assumptions (Levene's test), and when attempts to fit data to normal distributions or to meet homogeneity of variances failed. Two-tailed tests of significance were used throughout. Experimental groups are named further according to their diet origin (e.g. Riesling larvae, Riesling females). Results are presented for each life-history trait considered for both sexes.

Results

Effect of larval diet on pupal performance

Rate of emergence. The percentage of moths that emerged was significantly different among the different larval diets (Table 1), and was positively correlated to pupal mass, i.e. dead pupae were lighter than the living ones (both sexes pooled: 7.21 mg ± 0.16 vs. 7.73 mg ± 0.06) (Logistic regression: general model: Wald $\chi_7^2 = 55.2$, $P < 0.0001$; effect of cultivars: Wald

Table 1. Pupal performance of *Lobesia botrana* on different grape cultivars. The numbers in brackets represent sample size.

Larval diet	Number of pupae	Rate of emergence	Pupal mass (mg) mean \pm SE	
			Males	Females
Chasselas 1	180	86.11	6.20 \pm 0.09 (65) B	8.28 \pm 0.14 (90) B
Chasselas 2	214	86.92	5.78 \pm 0.16 (48) C	7.32 \pm 0.07 (138) C
Gammay	62	87.10	6.38 \pm 0.19 (18) B	8.34 \pm 0.20 (36) B
Gewurztraminer	158	90.51	5.72 \pm 0.14 (39) C	7.34 \pm 0.12 (104) C
Pinot	113	80.53	5.95 \pm 0.12 (42) BC	7.48 \pm 0.13 (49) C
Riesling	165	74.55	5.87 \pm 0.15 (41) BC	8.28 \pm 0.17 (82) B
Control	250	78.80	8.52 \pm 0.11 (101) A	11.45 \pm 0.15 (96) A
Statistical test	—	$\chi^2_6 = 22.67$	$\chi^2_6 = 113.79$	$\chi^2_6 = 259.20$
	—	$P < 0.001^*$	$P < 0.0001^\dagger$	$P < 0.0001^\dagger$

*Pearson χ^2 , \dagger Kruskal–Wallis test. The same letter in one column is not significantly different ($P > 0.05$).

$\chi^2_6 = 41.83$, $P < 0.0001$; effect of pupal mass: Wald $\chi^2_1 = 30.28$, $P < 0.0001$).

Pupal mass. Pupal mass varied significantly according to origin and sex of the moths, with females being significantly heavier than males independently of diet (two-way ANOVA: general model: $F_{13,948} = 133.90$, $P < 0.0001$, effect of diet: $F_{6,948} = 193.20$, $P < 0.0001$, effect of sex: $F_{1,948} = 546.19$, $P < 0.0001$, effect of their interaction: $F_{6,948} = 7.76$, $P < 0.0001$) (Table 1). The significant interaction indicates that several larval diets induced important differences between the mass of the two sexes (e.g. larval semi-synthetic diet and Riesling) while in the others the differences were lower (e.g. Pinot).

Effect of larval diet on mating success of males and females

Field female mating success ranged from 22 to 78%. Field male mating success ranged from 40 to 100%. There was a significant effect of larval diet on the mating success of both field females (Pearson χ^2 , $\chi^2_6 = 78.25$, $P < 0.0001$) (Fig. 1, black bars) and field males (Pearson χ^2 , $\chi^2_6 = 40.81$, $P < 0.0001$) (Fig. 1, white bars), respectively. In particular, field females and field males raised on Riesling were less successful at mating than individuals from the other cultivars. Mating success of control individuals was higher than almost all the field individuals except for field males raised on Gammay.

The delay between encountering a mate and the first egg laid for a field female (Fig. 2, black bars, Kruskal–Wallis test, $\chi^2_6 = 15.23$, $P = 0.02$) and for a field male (Fig. 2, white bars, Kruskal–Wallis test, $\chi^2_6 = 18.96$, $P < 0.001$), was influenced by the larval diet. Particularly, the longest delay before the first eggs laid was observed for females and males fed on Riesling.

Effect of larval diet on female reproductive output

Female achieved fecundity. Fecundity of field females varied among larval diets and was positively correlated to pupal mass and negatively correlated to the delay before laying the first egg (Fig. 3a, black bars, three-way ANOVA: general model: $F_{8,207} = 69.24$, $P < 0.0001$; effect of diet: $F_{6,207} = 10.50$, $P < 0.0001$;

effect of pupal mass: $F_{1,207} = 50.56$, $P < 0.0001$; effect of delay: $F_{1,207} = 32.62$, $P < 0.0001$). Overall, females raised on artificial diet were more fecund than females that were from larvae collected in the vineyards. Among field females, Gammay females were the most fecund, while Riesling females showed the lowest fecundity. Fecundity of lab females mated with field males varied as a function of male origin and was negatively correlated with the delay in laying (as the delay got longer, fewer eggs were laid) (Fig. 3a, white bars, ANCOVA: general model: $F_{7,141} = 11.68$, $P < 0.0001$; effect of diet: $F_{6,141} = 2.72$, $P = 0.02$; effect of delay: $F_{1,141} = 51.97$, $P < 0.0001$). Particularly, females mated with Riesling males and Gammay males were less fecund than females mated with males from other cultivars.

Egg size. Larval diet significantly affected the size of eggs laid by field females (Fig. 3b, black bars, Kruskal–Wallis test, $\chi^2_6 = 99.11$, $P < 0.0001$). Females raised on artificial diet laid larger eggs than females collected in nature. Among these females, Riesling females and Pinot females laid the smallest eggs. Similarly, the larval food of field males significantly

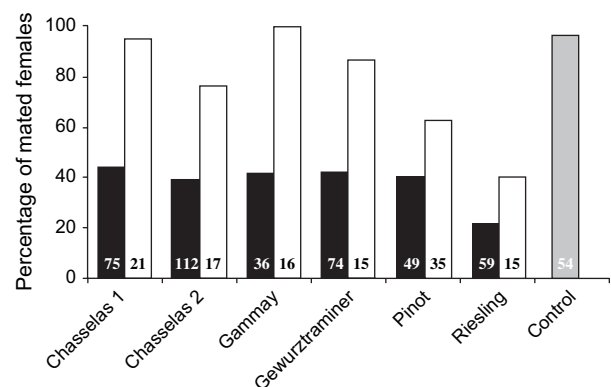


Fig. 1. Mating success (number of females mated) of *L. botrana* females fed on different cultivars in nature or on larval diet. Black bars represent mating success of field females. White bars represent mating success of field males. Grey bar represent control. The number at the bottom in each bar represents the number of pairs.

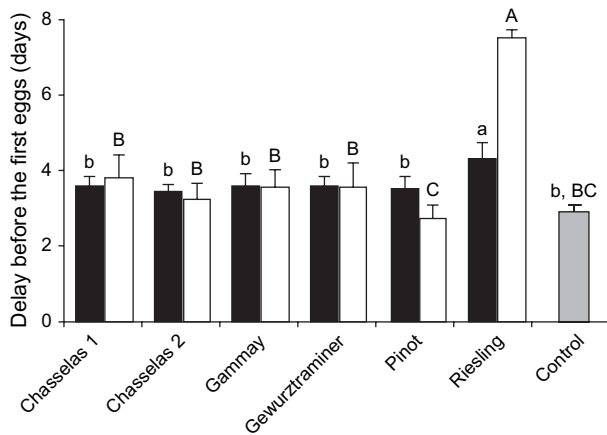


Fig. 2. Delay before laying of the first eggs (mean \pm SE) of *L. botrana* females fed on different cultivars in nature or on larval diet. Black bars represent the delay for field females. White bars represent the delay for field males. Grey bar represent control. The same letters in bar are not significantly different ($P > 0.05$) after a non-parametric PLSD test, capital letters for field males or small letters for field females.

affected the size of the eggs laid by their mate (Kruskal–Wallis test, $\chi^2 = 20.50$, $P = 0.002$) (Fig. 2b, white bars). Lab females mated with Riesling males laid smaller eggs than females from the other grape cultivars.

Female fertility. The proportion of larvae that hatched from eggs on the different cultivars strongly depended on the cultivar ingested during the mother's larval development, and was positively correlated to egg size (larger eggs resulted in higher hatchability) (Fig. 3c, black bars, ANCOVA: general model: $F_{7,207} = 143.76$, $P < 0.0001$; effect of diet: $F_{6,207} = 76.40$, $P < 0.0001$, effect of egg size: $F_{1,207} = 103.16$, $P < 0.0001$). Control females were more fertile than females from natural populations and among these, females from Riesling and Pinot had the lowest fertility. Similarly, for field males, the proportion of hatched eggs was affected by grape cultivar and also positively correlated to egg size (Fig. 3c, white bars, ANCOVA: general model: $F_{7,141} = 76.24$, $P < 0.0001$; effect of diet: $F_{6,141} = 69.72$, $P < 0.0001$, effect of egg size: $F_{1,141} = 14.29$, $P = 0.0002$). Females mated with males collected from Riesling and Gammay were the less fertile.

Discussion

Results from this study reveal the importance of larval food plant of both sexes on the reproductive success of pairs of the European grapevine moth. The rate of emergence, pupal mass, and reproductive life-history traits were strongly affected by grape varieties in the wild for both sexes as has been already demonstrated in several laboratory studies (Savapoulou-Soultani *et al.*, 1999; Torres-Vila *et al.*, 1999; Thiéry & Moreau, 2005; Moreau *et al.*, 2006b,c). In addition, the reproductive output of females reared on semi-artificial diet was higher than that of females raised on grapes in vineyards, which indicates that grapes represent a poorer resource for these moths (Torres-Vila *et al.*, 1999). Finally, the effect of cultivars on life-history traits

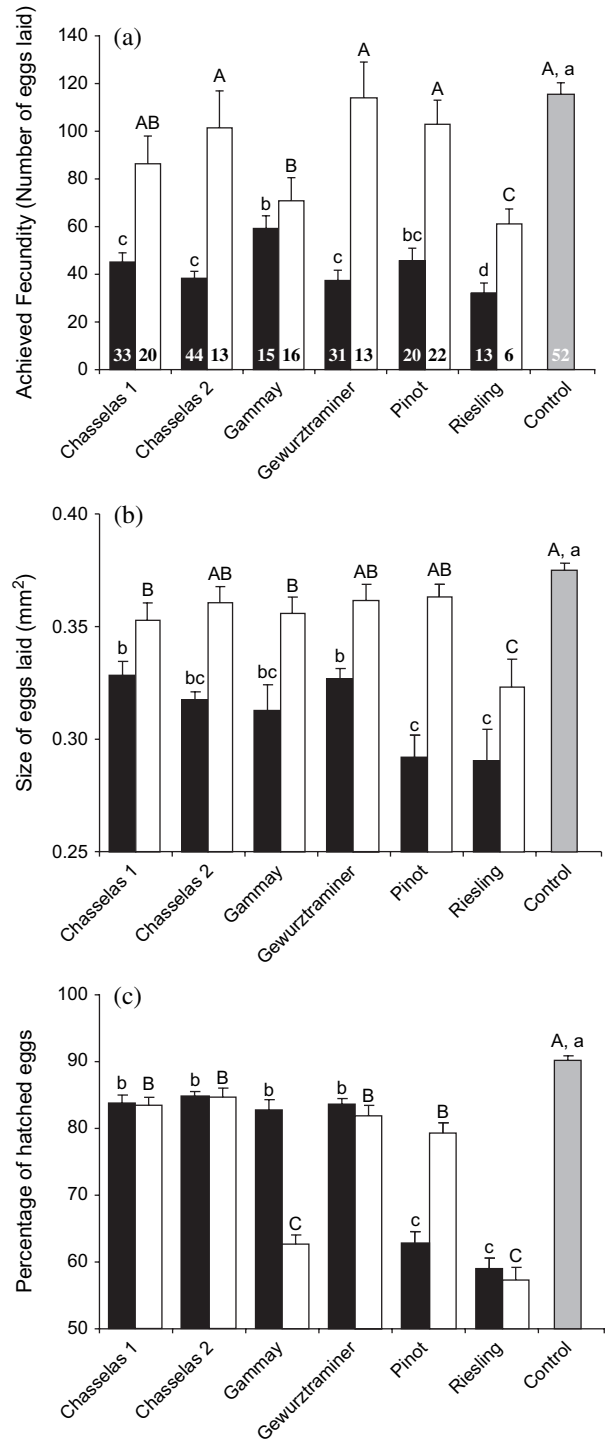


Fig. 3. (a) Achieved fecundity (mean \pm SE), (b) size of eggs laid (mean \pm SE), and (c) proportion of eggs that hatched (mean \pm SE), of *L. botrana* females fed on different cultivars in nature or on larval diet. Black bars represent field females. White bars represent field males. Grey bar represent control. The number at the bottom in each bar in (a) represents the number of females that laid eggs. For (b) and (c), the same letter in bars are not significantly different ($P > 0.05$), capital letters for field males or small letters for field females.

appears to be relatively stronger. Indeed, we did not observe any difference on life-history traits between Chasselas individuals from our two different sampling locations, except for pupal mass. Additional natural populations of larvae grown on the same cultivars, however, would be needed to strengthen this conclusion.

Larval food affected pupal mass, suggesting differential nutritional value among cultivars for larvae of *L. botrana*. Overall, female pupae were heavier than male pupae. In this species, females are heavier and larger than males, a trait that in many lepidopteran species has been attributed to the storage of nutrients used for egg production (Raven, 1961; Slansky & Scriber, 1985). One way in which females may attain this larger size is by feeding during a longer period of time, which in turn results in a slower development time (Thiéry & Moreau, 2005; Moreau *et al.*, 2006a,c).

The results also show that larval food influenced the ability of males and females to mate. Interestingly, a strong decrease in mating success occurred for females and males that emerged from Riesling cultivars, confirming previous results obtained from lab insects reared on food supplemented with Riesling (Moreau *et al.*, 2006c). The reason for this reduced mating success remains to be explained. Host plants may play an important role in the production and release of pheromones in some phytophagous insects including moths (see Landolt & Phillips, 1997 for a review). We cannot exclude that some cultivars may have affected the quality of the pheromones released by the females resulting in low acceptance by the males.

Larval diet also affected reproductive output in terms of fecundity, egg size, and egg hatchability for field females. Again, females that emerged from Riesling laid fewer eggs and had a lower fertility than females from other cultivars. This finding contrasts with results from a previous study showing that in laboratory conditions a decrease in fecundity for Riesling females was balanced by an increase in egg size and egg hatchability (Moreau *et al.*, 2006c). Furthermore, egg hatchability (or fertility) was positively correlated with egg size (Moreau *et al.*, 2006c). Torres-Vila and Rodríguez-Molina (2002) did not find a relationship between these two traits. For other insect species, it has been shown that the plant species on which the larvae develop can influence the amount of nutrients allocated to their eggs (Berrigan, 1991; Fox & Czesak, 2000). A larger amount of nutrients may result in larger eggs with an increased capacity to hatch. In our study, the relationship between egg size and egg hatchability appears to be stronger for field females than for lab females mated with field males. Indeed, females that emerged from Pinot and Riesling laid small eggs and exhibited low fertility (Fig. 2b,c), whereas lab females mated with males from Gammay had the lowest fertility, even though the size of their eggs did not differ from those of females mated with males from other cultivars. Thus, in this case, egg size is not a reliable predictor of fertility.

The outcome of this study implies that different host-plant cultivars also affect male reproductive output. Females mated with males that emerged from Riesling and Gammay had poor reproductive performance. Previous studies on Lepidoptera demonstrated that material from ejaculates is incorporated into female soma and eggs and females use male-derived

nutrients to boost reproductive performance and longevity (Boggs & Gilbert, 1979; Pivnick & McNeil, 1987; Oberhauser, 1989). In this context, the observed male mating deficiency may be due to spermatophores of low quality offered to the females. This is the case for *Colias eurytheme* (Lepidoptera: Pieridae, Boisduval), in which females paired with males producing small spermatophores laid fewer eggs per day and had a shorter life span (Rutowski *et al.*, 1987). Therefore, we propose that some varieties of grapes (such as Riesling or Gammay) are not of sufficient quality to allow males to produce good quality ejaculate. The results reported by Torres-Vila *et al.* (1999) support this hypothesis. They showed that the volume of spermatophore transferred by males of *L. botrana* was larval-diet-dependent (i.e. males reared on ripe berries produced significantly larger ones than those of raised on inflorescences). The idea that this could decrease female fecundity and fertility has yet to be examined with a comparative analysis of male ejaculates for nutrients such as hydrocarbons and lipids of individuals reared on different larval diets (Marshall & McNeil, 1989).

Our findings uncover an exciting importance of male quality for female reproductive output. In this context, one would expect that females of *L. botrana* capable of being selective in their choice of a partner would have an advantage. The same would be true for males, as female quality varied significantly among cultivars. It would be interesting to find out whether females and males are able to discriminate between the different origins of individuals and whether they choose to mate with the partner of better quality when the opportunity to do so occurs. *Lobesia botrana* provides an excellent experimental system to examine such mate choice behaviour in males and females.

Finally, the results revealed that a cultivar can be favourable for females, but not for males and vice-versa. The only exception was Riesling, which resulted in a poor resource for both sexes. For example, females reared on Gammay exhibited high fecundity and fertility, whereas the opposite was found for males reared on this cultivar. Similarly, Pinot females exhibited a poor egg hatch in comparison with females from other cultivars, whereas couples involving Pinot males produced high percentages of hatched eggs. Globally these results suggest that nutrients required for the optimal reproduction are probably not the same for males and females, or female and male larvae differed in their ability to assimilate nutrients obtained from their diet. Thus, when addressing questions on the influence of host plants on life-history traits associated with reproductive success in phytophagous insects it is crucial to consider both sexes.

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