Grape variety affects larval performance and also female reproductive performance of the European grapevine moth *Lobesia botrana* (Lepidoptera: Tortricidae)

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Abstract

For insect herbivores, the quality of the larval host plant is a key determinant of fitness. Therefore, insect populations are supposed to be positively correlated with the nutritional quality of their host plant. This study aimed to determine if and how different varieties of grapes (including the wild grape Lambrusque) affect both larval and adult performance of the polyphagous European grapevine moth *Lobesia botrana* (Denis & Schiffermüller). Significant differences were found in larval development time, but not in pupal mass, adult emergence rate, or sex ratio. Although the fecundity of females is not different among varieties, females fed on some varieties produced eggs of different sizes which are correlated to their fertility. Thus, females adapt resource allocation to eggs depending on their diet as larvae. Using a fitness index, the average reproductive output was found to be highest for females reared on cv. Chardonnay. Females reared on wild grape produced a fitness index identical to the cultivated grapes. However, Lambrusque and Gewurztraminer separate themselves from the cultivated varieties according to our discriminant analyses. It is emphasized, through this study, that cultivars fed on by larvae should be considered in the population dynamics of *L. botrana* and that egg number is insufficient to determine host plant quality.

Keywords: female reproductive output, fitness, host plant selection, insect–plant relationships, larval food

Introduction

The demography of phytophagous insect populations is determined by critical factors, such as abiotic environmental variables (Leather & Dixon, 1982; Ratte, 1985; Leather, 1995), adult weight (Dixon, 1987) and larval and adult food supply

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(Scriber & Slansky, 1981; Leather, 1995) being directly related with the nutritional quality of the host plant. In nature, the nutritional quality of plants varies naturally among plant species and also among varieties within cultivated species (Van Emden, 1987). This variation influences both larval performance and female reproductive output of herbivorous insects (see Awmack & Leather, 2002 for a review or Kaspi *et al.*, 2002 for an example). Particularly, for most herbivorous insects that are considered capital breeders (species with non-feeding adults) host plant quality is a key determinant of their fitness since they have a reproductive potential limited by the resources accumulated during their larval stages (Slansky & Rodriguez, 1987; Awmack & Leather, 2002). Therefore, the density of insect populations

is supposed to be positively correlated with the nutritional quality of their host plant as larvae.

As a model phytophagous insect we used the European grapevine moth *Lobesia botrana* (Denis & Schiffermueller) (Lepidoptera: Tortricidae), the most harmful pest of grapes in Europe, North Africa and West Asia, and it can develop on *c.* 30 host plants including grapes (Bovey, 1966; Roehrich & Boller, 1991; Thiéry, 2005). In regions of wine production, some cultivars suffer more damage than others. A differential susceptibility of grape cultivars to *L. botrana* has been reported (Marchal, 1912; Stellwaag, 1928) and recent studies have attributed this variable susceptibility either to differences in larval settlement (Gabel & Roehrich, 1995; Fermaud, 1998) or to oviposition preferences for certain varieties (Thiéry & Gabel, 2000; Maher *et al.*, 2001; Maher & Thiéry, 2004). In the particular case of the ancestor of European cultivated grapevines (*Vitis vinifera sylvestris*, Gmelin, called 'Lambrusque') (Scossiroli, 1988; Heywood & Zohary, 1995), found in several Mediterranean regions and in south west of France, we never observed any damage by *L. botrana*. This observation is supported by the low levels of injury caused by insect pests on wild grapes in general (Ocete *et al.*, 1997; Arnold, 1999; J. Moreau, personal observation).

In order to explain why some cultivars suffer more damage by *L. botrana* than others, we tested if different cultivars of grapes affect the reproductive strategy of this pest. We also tested whether Lambrusque (wild grape) is less suitable for *L. botrana* than cultivated grape, explaining why *L. botrana* larvae are never found on this wild grape. Performance on four cultivated grape varieties (Chardonnay, Chasselas, Gewurztraminer and Grenache) and the wild ancestor of grapes (Lambrusque) were examined by measuring the complete suite of life history traits of *L. botrana*, from egg hatching to individual death in order to calculate the fitness of females fed as larvae on these different varieties. Pupal mass, larval development time and larval survival were recorded, and the influence of plant quality on reproductive success was also determmined, by measuring mating success fecundity, egg size, egg hatchability and adult longevity.

Materials and methods

Study system: moths, their origin and maintenance

A strain of *L. botrana* (INRA Bordeaux) originating from individuals collected in a French Sauternes vineyard (cultivar White Sauvignon) was used. The stock colony is maintained without diapause for about 20 generations on a semi-artificial diet at $24 \pm 1°C$, $60 \pm 10\%$ r.h. with a photoperiod of L15:D8+1h of dusk. The first 15 photophase hours were at 1000 lux luminosity and the last one (dusk) at 25 lux. All tests were performed under these same conditions.

Larval diet treatments and general procedure

All the cultivars were compared using a standardized procedure similar to that described elsewhere (Thiéry & Moreau, 2005). This procedure is on artificial Lepidoptera medium in which freeze-dried powder of plant material is incorporated. This presents at least three main advantages: (i) feeding larvae in isolation thus preventing biases due to competition and subsequent food deprivation; (ii)

preventing differences in bunch compactness, which has an effect on larval feeding behaviour (our unpublished observations); and (iii) preventing incidences of infections by fungi which naturally grow on harvested bunches and can modify larval fitness (Savopoulou-Soultani & Tzanakakis, 1988; Mondy & Corio-Costet, 2000). Larvae were raised individually to pupation in Eppendorf tubes filled with 1.5 ml of a medium composed of: 150 ml water, 5 g agar, 6 g cellulose powder, 7 g casein, 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 nipagine, 0.007 g tetracycline and 12 g freeze-dried plant powder. The plant powder was obtained from bunches of *V. vinifera* cv. Chasselas, Chardonnay, Gewurztraminer, Grenache or Lambrusque, wild grape, which were all harvested from the gene bank collection 'Domaine de la Grande Ferrade', at INRA Bordeaux. The bunches were collected at the beginning of the growing season (beginning of May 2003), all at phenological stages 23–27 (Eichhorn & Lorenz, 1977), which correspond to the grape phenology when the first generation of *L. botrana* occurs in the year.

The Eppendorf lids were pierced to allow air circulation. Using a fine brush, an individual newly-hatched larva (age < 24 h) was transferred to each of 100 Eppendorfs per grape variety diet.

Growth and development

Larvae were monitored daily until pupation; pupae were then gently removed from the diet and weighed to the nearest 0.1 mg. The weight of live pupae was used as an index of body size. Pupae were placed individually in glass tubes (70 mm × 9 mm diameter), which were sealed with a cotton plug and stored in the test room until emergence. Adults were sexed upon emergence. The following variables were recorded: (i) total survival (larval and pupal) (= percentage adult emergence); (ii) pupal mass; (iii) total development time (larval and pupal); and (iv) adult sex-ratio.

Reproductive life history traits

Adults resulting from the five larval diets were used to evaluate the reproductive output of females. Newly emerged (less than 1-day-old) females were individually confined in 0.5 l transparent cellophane bags as mating and oviposition chambers and 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, the period of sexual activity (Bovey, 1966). Within a treatment, males were considered equivalent and thus were randomly assigned to females. Pairs were caged in these bags until the death of both sexes. At the end of the experiment, eggs on the cellophane bags were counted and measured with an ocular micrometer. Their surface (estimated as an elliptic surface, $S = \pi \times a \times b$ (mm²), where *a* and *b* are the ellipse semiaxes) was used as an index of egg size. Mean egg size was estimated for each female from a randomly chosen sample of 15 eggs from her total egg production. To determine fertility, all eggs were incubated at 22°C for 10 days until hatching, and the number of hatched eggs was counted.

Seven variables were considered: (i) percentage of mated female (female mating success) assessed by production of at

Table 1. Developmental life history traits of *Lobesia botrana* raised on different grape cultivars.

Grape cultivar	% of emergence (=larval survival)	Sex-ratio (% of females)	Development time (days) mean ± S.E.M.		Pupal mass (mg) mean ± S.E.M.	
			Males	Females	Males	Females
Chardonnay	91	57.14	27.92 ± 0.45BC	29.63 ± 0.23B	9.94 ± 0.21	14.24 ± 0.33
Chasselas	90	51.11	28.36 ± 0.34B	30.43 ± 0.23B	9.59 ± 0.29	13.92 ± 0.36
Gewurztraminer	87	49.42	29.64 ± 0.28A	32.23 ± 0.31A	9.98 ± 0.25	15.06 ± 0.36
Grenache	86	44.18	26.92 ± 0.18C	29.89 ± 0.23B	10.13 ± 0.17	13.89 ± 0.34
Lambrusque	84	53.57	27.00 ± 0.34C	29.27 ± 0.33C	9.80 ± 0.31	14.06 ± 0.29
χ^2_4	3.05[a]	3.28[a]	54.07[b]	55.91[b]	0.64[b]	5.26[b]
P	0.55	0.51	<0.0001	<0.0001	0.96	0.26

100 larvae per cultivar. Values (mean ± S.E.M.) in each column with the same letter are not significantly different ($P > 0.05$) after a non–parametric PLSD test.
[a]Pearson χ^2; [b]Kruskal-Wallis test.

least five fertile eggs during her lifetime (non-mated females are able to lay some infertile eggs at the end of their life); (ii) delay before the first egg laid (days); (iii) total achieved fecundity (mean number of eggs laid); (iv) duration of laying (days); (v) mean egg size; (vi) total number of viable eggs (=female fertility); and (vii) longevity of mated females.

Statistical analysis

The statistical tests were performed using the JMP software (Version 3.2.2, SAS Institute Inc.). A stepwise analysis (backward procedure) was used to remove non-significant effects and interactions (at $P > 0.05$) and only the resulting models are presented here. Kruskal-Wallis or Wilcoxon Rank Sum non-parametric tests were used when data did not meet normality (Shapiro-Wilk's test) or homogeneity of variances assumptions (Levene's test) and when attempts to fit data to normal distributions failed. Two-tailed tests of significance were used throughout. A discriminant analysis was used to select the core variables that are pertinent to describe the interrelationships. A stepwise discriminant analysis was carried out using a 'forward' procedure, which begins with no variables in the model and adds the variables with the greatest discriminating power (see Legendre & Legendre, 1998 for statistical details). This analysis selects the variables that describe differentiation among cultivars. The input parameters for the discriminant analysis were group variables (Chardonnay, Chasselas, Gewurztraminer, Grenache and Lambrusque) and continuous independent variables (all continuous life history traits measured during experiments).

Results

Growth and development

The percentage of moths that emerged (equivalent to larval survival) from the five cultivars was not significantly different (almost 90% of larvae reached the adult stage) and there was no effect of diet on the sex ratio of the emerging adults (table 1). Among the emerging adults, the developmental time of males was significantly shorter than that of females, and developmental time of both sexes varied slightly but significantly among the cultivars on which larvae were fed (two-way ANOVA: general model: $F_{5,437} = 52.81$, $P < 0.0001$; effect of cultivar: $F_{4,437} = 28.45$, $P < 0.0001$; effect of sex: $F_{1,437} = 151.89$, $P < 0.0001$). Although differences were found in developmental time among larvae fed on different cultivars, the resulting pupae (male and female) exhibited similar weight (table 1). However, females were always heavier than males, independent of cultivars and the pupal mass of both sexes was independent with their development duration (three-way ANOVA: general model: $F_{6,437} = 91.83$, $P < 0.0001$; effect of sex: $F_{1,437} = 457.38$, $P < 0.0001$; effect of cultivar: $F_{4,437} = 1.21$, $P = 0.13$; effect of duration of larval development: $F_{1,437} = 1.45$, $P = 0.10$).

Reproduction

Female mating success, measured as the number of females that produced viable eggs, ranged from 70% to 84%, and was not significantly different among cultivars (table 2). Among mated females, the delay between encountering a mate and the first egg laid was around 4 days and was also

Table 2. Reproductive life history traits of adult female *Lobesia botrana* according to the grape cultivar on which the larvae developed.

Grape cultivar	No. of female tested	% of mated females	Delay before the first egg (days)	Duration of laying (days)	Longevity of mated females (days)
Chardonnay	50	84.00	4.81 ± 0.46	5.40 ± 0.33	10.21 ± 0.30
Chasselas	45	73.33	4.94 ± 0.43	5.39 ± 0.31	10.33 ± 0.36
Gewurztraminer	40	70.00	4.25 ± 0.46	4.93 ± 0.23	9.18 ± 0.43
Grenache	36	72.22	4.42 ± 0.44	5.77 ± 0.38	10.19 ± 0.38
Lambrusque	45	77.78	4.32 ± 0.33	5.82 ± 0.19	10.00 ± 0.35
χ^2_4		3.07[a]	2.00[b]	7.71[b]	8.98[b]
P		0.55	0.74	0.10	0.06

Values (mean ± S.E.M.) in each column with the same letter are not significantly different ($P > 0.05$) after a non–parametric PLSD test.
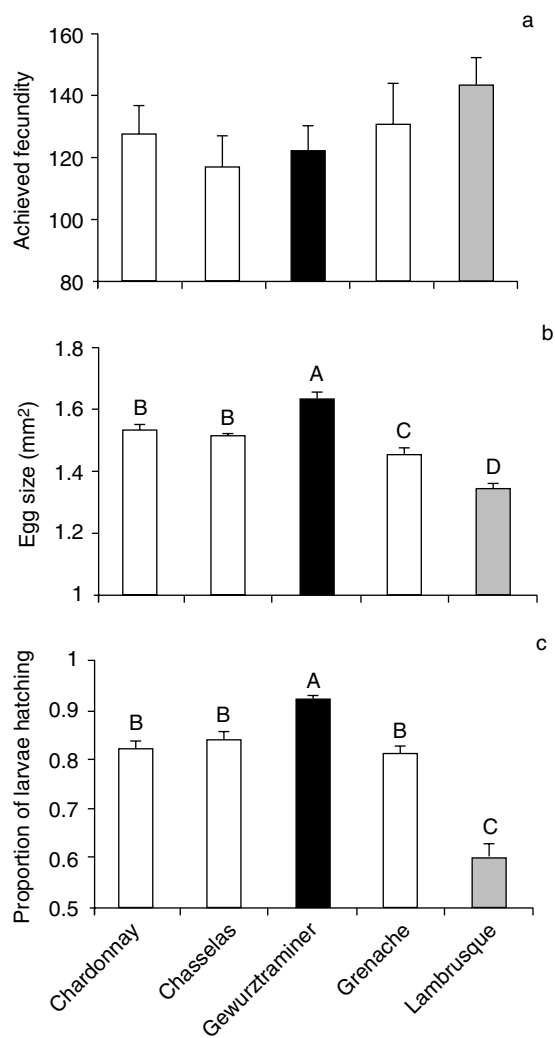[a]Pearson χ^2, [b]Kruskal-Wallis test.

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Fig. 1. (a) Achieved fecundity (mean ± S.E.M.), (b) size of eggs laid (mean ± S.E.M.) and, (c) proportion of larvae hatching from *Lobesia botrana* females, reared on different grape cultivars. The colour of columns is arranged according to the groups defined by the female development time in table 1: ■, cultivars that promote a slow larval development; ▨, cultivars that promote a fast larval development; □, cultivars that promote an intermediate larval development. Columns with the same capital letter are not significantly different (*P* > 0.05) after a non-parametric PLSD test.

not influenced by larval food (table 2). The total number of eggs laid per female was not affected by the origin of females (fig. 1a, Kruskal-Wallis test, $\chi^2_4 = 4.83$, $P = 0.31$). The number of eggs laid by a given female was positively correlated with her pupal mass and negatively correlated with the delay before the first egg laid, but there was no correlation with egg-laying duration (three-way ANOVA: general model: $F_{3,162} = 111.20$, $P < 0.0001$; effect of pupal weight: $F_{1,162} = 43.52$, $P < 0.0001$; effect of duration of egg laying: $F_{1,162} = 0.52$, $P = 0.47$; effect of delay: $F_{1,162} = 171.89$, $P < 0.0001$) (table 2). In contrast to fecundity, egg size and the proportion of larvae hatching were strongly affected by the cultivars on which females fed as larvae (fig. 1b, Kruskal-Wallis test, $\chi^2_4 = 73.81$, $P < 0.0001$; fig. 1c, Kruskal-Wallis test, $\chi^2_4 = 68.23$, $P < 0.0001$). Interestingly, egg size was correlated with the duration of the female's development (linear regression: $F_{1,163} = 13.26$, $P = 0.0004$, $r^2 = 0.58$). In other words, the longer the female's larval and pupal stages were, the bigger were her eggs. Fertility was also positively correlated with egg size and development time (two-way ANOVA: general model: $F_{2,163} = 32.51$, $P < 0.0001$; effect of egg size: $F_{1,163} = 39.44$, $P < 0.0001$; effect of larval development time: $F_{1,163} = 9.83$, $P = 0.002$). Thus, females raised on Gewurztraminer (which promoted a long larval development) laid the largest and most viable eggs, whereas females raised on Lambrusque (which promoted fast larval development) laid the smallest and least viable eggs (fig. 1b,c). The three other cultivars were relatively similar. Finally, the longevity of mated females was not different among cultivars (table 2).

Evaluation of fitness in L. botrana

The life history traits assessed during this study allowed us to estimate the fitness of *L. botrana* females. By using the fecundity and hatching rate, the mean number of larvae produced per mated female was calculated. From this, the number of females emerged was calculated by using larval and pupal mortality and the sex ratio. Finally, from the mating success, the number of mated females that contributed to the production of the next generation was calculated. This estimation was then used as an overall measure of fitness (= Fitness Index). The estimates for females that were reared on Chardonnay were higher than for those reared on the four other cultivars (Kruskall-Wallis Test, $\chi^2_4 = 15.85$, $P = 0.003$). Interestingly, the fitness index of females reared on Lambrusque (wild grapes) was very similar to three other cultivars (table 3).

Table 3. Number of estimated females (mean ± S.E.M.) participating in reproduction in the next generation of *Lobesia botrana* according to the grape cultivar on which the larvae developed and according to the life history traits assessed.

Grape cultivar	No. of larvae produced for all females mated (fecundity × hatch rate used)	No. of adults emerging (% of emergence used)	No. of females (sex-ratio used)	No. of females participating to the reproduction (mating success used) = Fitness Index	PLSD Test after Kruskall-Wallis tests on Fitness Index
Chardonnay	104.95 ± 8.06	95.50 ± 7.34	54.44 ± 4.18	45.73 ± 3.51	A
Chasselas	98.40 ± 9.25	88.56 ± 8.33	45.16 ± 4.25	32.97 ± 3.10	B
Gewurztraminer	111.83 ± 8.46	97.29 ± 6.37	47.67 ± 3.61	33.37 ± 2.52	B
Grenache	103.61 ± 10.09	89.11 ± 8.68	39.21 ± 3.82	28.23 ± 2.75	B
Lambrusque	87.52 ± 7.03	73.51 ± 5.98	38.96 ± 3.13	30.00 ± 2.41	B

Table 4. Power of discrimination of life history traits driving the discrimination of the five grape cultivars, considered individually and at the end of the analysis.

Life history traits	Exact *F* at last step	*P*
Egg size	17.16	< 0.001
Fertility	12.22	< 0.001
Development time	5.83	< 0.001
Duration of laying	1.75	0.14
Longevity	1.61	0.17
Fecundity	1.19	0.31
Delay of laying	0.62	0.65
Pupal mass	0.15	0.96

Discriminant analysis

A significant discriminant model was obtained when using egg size, fertility, and development time to distinguish among five cultivars (table 4). The graphical representations of the cultivars in the plane defined by the first two canonical functions (fig. 2) shows that Lambrusque (wild grapes) are clearly separated from other cultivars, whereas among cultivated grapes, Gewurztraminer separates itself. In other words, the individuals raised on wild grape exhibited life history traits different to those raised on cultivated grapes (faster development time, smaller eggs and lower proportion of larvae hatching). In addition, among individuals raised on

different cultivated grapes differences also exist. Individuals raised on Gewurztraminer exhibited longer development time, larger eggs and a higher proportion of larvae hatching as compared to those raised on the three other cultivars.

Discussion

In the present study, the different grape varieties used as larval food sources strongly affected development and reproductive life history traits in *L. botrana*. Females reared on Chasselas, Chardonnay and Grenache exhibited a similar pattern of life history traits as revealed by our discriminant analysis. The two other varieties (Lambrusque and Gewurztraminer) are well separated mainly due to differences in their patterns of egg size, egg hatchability and development time.

Larval development time varied among the five grape varieties, whereas larval mortality, sex ratio and pupal weight were not significantly different among cultivars. Gewurztraminer induced a slower larval development than other cultivars suggesting that this cultivar is of lower nutritional value for larvae of *L. botrana*. Interestingly, although total development time clearly varied among cultivars, the resulting pupae had similar weights indicating no fitness penalty to speed up the larval development. The classic relationship between size and development time appears in general to be less strict in butterflies than in some other animals due to plasticity in growth rate (Wiklund *et al.*,
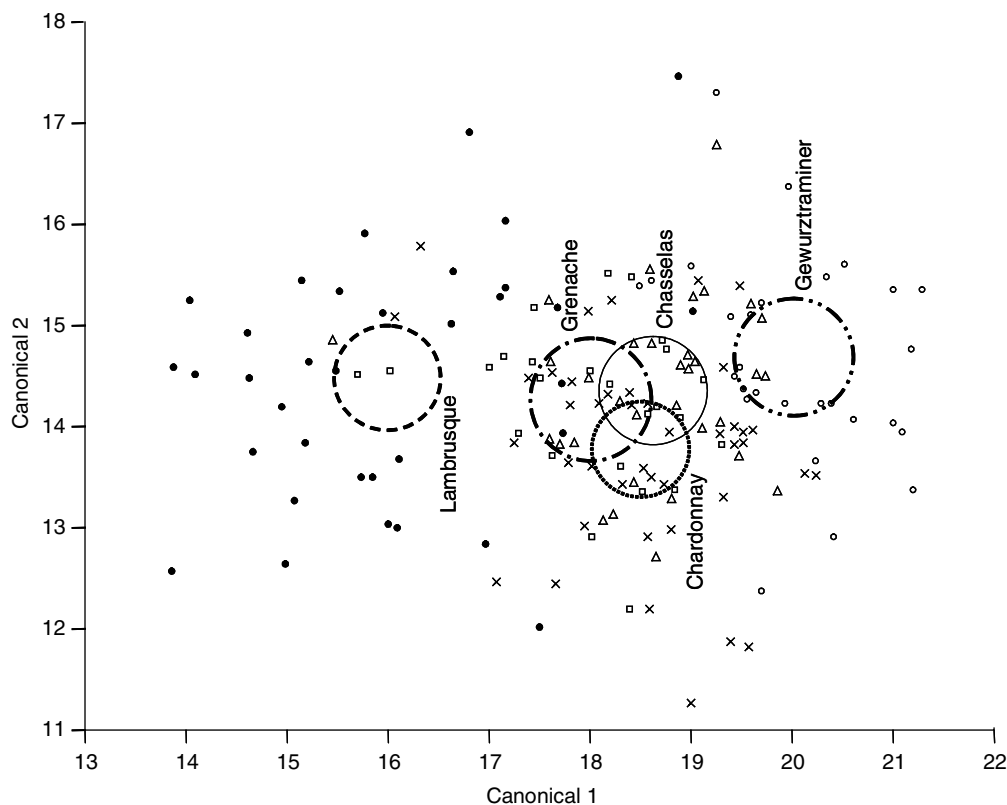

Fig. 2. Visual representation of the results of the stepwise discriminant analysis: position of five cultivars (x, Chardonnnay; △, Chasselas; ○, Gewurztraminer; □, Grenache; ●, Lambrusque) on the plane defined by the canonical variables 1 and 2. The size of the circle corresponds to a 95% confidence limit for the mean. Groups that are significantly different have non-intersecting circles.

1991). Here, prolonged larval development time in Gewurz-traminer enabled larvae to compensate for a low consumption rate or for food of poor quality and to finally reach the same weight as larvae that were reared on cultivars that promoted a faster larval development. However, a prolonged development time could be a potentially important component of fitness in nature because it may increase larval exposure to predators and parasites (Weseloh *et al.*, 1983; Benrey & Denno, 1997; Parry *et al.*, 1998). Females of *L. botrana* are often heavier and larger than males, a trait that is mainly attributed to the storage of nutrients used for egg production (Raven, 1961; Slansky & Scriber, 1985). Female larvae certainly achieve a greater size by feeding and developing for a longer period of time (Mackey, 1978; Lederhouse *et al.*, 1982) as observed during the present experiments.

For all grape varieties, the development time of males was significantly shorter than that of females, probably due to different nutritional larval requirements. Consequently, males started to emerge before females, this protandry is commonly found in fruit tortricids and several other Lepidoptera (Rodriguez-del-Bosque *et al.*, 1989; Roehrich & Boller, 1991; Wiklund *et al.*, 1993). It presents at least two advantages, by maximizing copulation opportunities for a male (reviewed in Wiklund & Fagerström, 1977; Bulmer, 1983), and minimizing the pre-reproductive period of females so they emerge when most males are available (Fagerström & Wiklund, 1982). Torres-Vila *et al.* (1995) showed that three-day-old *Lobesia* males are the most efficient at mating. Thus, the two days of protandry observed during our experiments represents a potential advantage for the emerging females by minimizing the risk of emergence when no males are present (Fagerström & Wiklund, 1982).

The results confirm the importance of the larval host-plant for the adult reproductive success and it can be expected that grape variety will affect survival and numbers of *L. botrana* in vineyards. Indeed, although fecundity and the mating success of the resulting adult was not affected by the origin of females, the size of eggs laid, as well their probability of hatching varied among cultivars, supporting the hypothesis that larval food quality is of primary importance for the reproductive performance of this generalist herbivore. The females raised on Gewurztraminer laid larger eggs than others and had a higher fertility. Since females are unfed during the adult stage, the amino acids in egg protein of female moths derive exclusively from the larval diet, as demonstrated by O'Brien *et al.* (2002) in hawkmoth. Therefore, the availability of essential amino acids in the diet of larvae poses a significant constraint in egg manufacture. On Gewurztraminer, it is possible that females allocate more lipids and proteins to their eggs (consequently, increasing the probability of hatching) than females from other cultivars, which could explain why egg hatchability was positively correlated with egg size. This contradicts a previous study that found no relationships between these two traits in *L. botrana* (Torres-Vila & Rodriguez-Molina, 2002) and in other insects (Wiklund & Persson, 1983; Karlsson & Wiklund, 1984, 1985). The present study supports the assumption that larger eggs are associated with more nutritional provisions (Berrigan, 1991; Fox & Czesak, 2000). Further biochemical analyses of egg contents would be necessary, but were not carried out in the present work. Interestingly, the highest fertility was found on the

variety where the larvae exhibited the slowest development time. This suggests the existence of plasticity on reproductive strategies associated with immature development duration. It is thus possible that larvae are able to assess the quality of their host-plant as an environmental quality indicator, and then anticipate the food available to the next generation. By doing this, females that encounter, as larvae, a poor-quality host plant (indicated by a prolonged development time), provision their eggs with a large amount of vitellus to enhance larval survival in this adverse environment. In some insects, this phenotypic plasticity is maternally induced: mothers that experience a predictive environmental cue can change their progeny size and quality so that it is best suited to the conditions predicted by that cue (examples reviewed in Mousseau & Fox, 1998). For example, in the seed beetle *Stator limbatus* Horn (Coleoptera: Bruchidae), females change the size of the eggs produced in response to host stimuli, so that their progeny are prepared for the host plant upon which they will develop (Fox *et al.*, 1997). However, to produce big eggs may represent a disadvantage when exposed to egg parasitoids (e.g. *Trichogramma*) or egg predators like pirate bugs or ants. Also faster development may allow larvae to escape parasitism, which would compensate for the trade-off between small eggs and lower fertility.

Despite the fact that the wild grape (Lambrusque) is well separated from other cultivated varieties (mainly due to the pattern of egg size, egg hatchability and development time being different from that on other cultivars), as shown by the discriminant analysis, the present data did not support the prediction that wild grape is less suitable for the performance of *L. botrana* than cultivated grapes, in contrast to what has been reported for other cultivated crops and associated insect herbivores (Evans, 1993; Idris & Grafius, 1996; Benrey *et al.*, 1998; Chen & Welter, 2003). Performance, survival and the fitness index of *L. botrana* were quite similar on the wild variety and the cultivars. Food quality therefore does not explain why wild grape plants carry no or few insect pests (Ocete *et al.*, 1997; Arnold, 1999).

Due to the variation in life-history traits, whether this results from phenotypic plasticity or not, Chardonnay seems the most suitable of the varieties for the performance of *L. botrana*, as indicated by the fitness index. Quality of cultivars as larval food should be taken into account as a factor affecting the population dynamics of *L. botrana*. Another key message from the outcome of the present study is that investigations into host-plant quality should extend to the reproductive output of the resulting offspring, whereby not only egg number, but also egg viability should be measured to obtain a more precise estimate of fitness.

In this study we have only considered the direct effects of the host-plant. For an even more complete assessment, further studies should also investigate indirect effects of host plants like its susceptibility to natural enemies, such as predators, parasitoids and pathogens.

Marc-Etienne Toulouse and Anne Xuéreb (INRA Bordeaux) for experimental contributions and Louis Bordenave (INRA Bordeaux) for free access to bunches of grapes collected in the INRA cultivar bank.

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