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PLANT ANIMAL INTERACTIONS

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Relative performance of European grapevine moth (*Lobesia botrana*) on grapes and other hosts

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Abstract The European grapevine moth, *Lobesia botrana* is a major grapevine pest, but despite the abundance of vineyards it is a generalist and uses either grapes or alternative species. Given the abundance and predictability of grape, *L. botrana* could be expected to have evolved towards monophagy. In order to understand why this species remains polyphagous, we hypothesized that larvae reared on rare wild host plants should have higher fitness than those reared on the more abundant grape host. For this, we compared larval performance and several life history traits on three alternative host plants (*Daphne gnidium*, *Olea europaea*, *Tanacetum vulgare*) and three Vitaceae (*Vitis vinifera*), two cultivars and one wild species (*Ampelopsis brevipedunculata*), and two control groups raised on either a low or a high nutritive value medium. Alternative hosts are more suitable than Vitaceae for the reproductive performance of *L. botrana*: larval mortality and development time was reduced, while pupal weight, growth rate, female longevity, female fecundity, duration of laying and mating success were increased. High quality food ingested by larvae promotes higher adult body weight and enhances female reproductive output. This suggests that alternative hosts provide greater nutritional value for *L. botrana* than Vitaceae. The use of alternative host plants could thus be maintained in the host range because they offer *L. botrana* a better fitness than on the Vitaceae. This could typically represent an advantage for moths behaving in plant diversity grape landscapes.

Keywords *Lobesia botrana* · Polyphagy · Insect plant relationships · Life history traits

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Introduction

The European grapevine moth, *Lobesia botrana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae) is a major grapevine pest in the paleartic region (Bovey 1966; Roehrich and Boller 1991). Its adaptation to grapes is considered to be relatively recent, as intense damage in vineyards started getting noticed during the beginning of the twentieth century (Marchal 1912; Balachowsky and Mesnil 1935). Despite the abundance of vineyards across Europe this insect is still a generalist, females being attracted and able to oviposit on alternative plants like rosemary (Roditakis 1988) or *Daphne gnidium* (Maher et al. 2000) and larvae completing their development on more than 20 species (Stoeva 1982; Thiéry 2005). In addition, natural populations of *L. botrana* were observed on several different plants of Mediterranean origin such as flowering olive trees (Savopoulou-Soultani et al. 1990), rosemary, sea squill *Urginea maritima* (Liliaceae) or raspberries (Roditakis 1988), and two Thymeleaceae, *Passerina hirsutum* and the flax-leaved daphne (*D. gnidium*), which is for several authors (Balachowsky and Mesnil 1935; Bovey 1966; Stoeva 1982) and ourselves, the presumed native host plant of *L. botrana*.

Natural populations of *L. botrana* face two main alternatives: they can either use a very predictable resource, i.e. almost all the varieties of cultivated grapes; or they can use alternative species most of which are chemically protected and quite rare, or have rather strict ecological requirements. Given the abundance and predictability of vineyards, *L. botrana* could represent a good candidate for specialization on grapes since specialized species generally use predictable, abundant, and easily found plants (Dethier 1970; Southwood 1972; Strong et al. 1984). Indeed, the probability that females encounter suitable hosts is the critical factor that determines host range and thus polyphagy (Jaenike 1978; Rausher 1985; Courtney et al. 1989; West and Cunningham 2002). Therefore, *L. botrana* could have evolved towards monophagy on grapes, and the fact that this species remains polyphagous raises an interesting question. This question is relevant since specialization appears to be associated with measurable and significant advantages; the much larger numbers of relative specialists supports the idea that specialization offers greater overall advantages than polyphagy (Barbosa 1988; Bernays and Graham 1988).

Most adaptative functions of diet breadth in phytophagous insects focus on adult fecundity and offspring performance as a function of host plant (Jaenike 1990). Specialization is expected to evolve towards an optimal exploitation of the host in order to maximize the expected fitness of individuals, and most authors have concentrated on the importance of plant chemistry in driving evolution of monophagy by improving the specialization for dealing with particular toxins (see for example Ehrlich and Raven 1964; Feeny 1976; Swain 1977; Cates 1980; Schultz 1988). As a result, species which overcome these defences are more efficient at exploiting the plants in terms of foraging performance (Bernays and Wcislo 1994) or synchrony with their host plants (Slansky 1976).

Generalist natural enemies of herbivores also act as a selection pressure for restricted host plant range. Indeed, predation (by predators or parasitoids) might select for specialization since specialists may be better protected from predators and parasitoids by, for example, better camouflage (Bernays and Graham 1988; Bernays 1989; Camara 1997; Keese 1997).

Considering this, there are undoubtedly costs of being a generalist like the costs of being able to develop and maintain the ability to exploit the different alternative host plants (Dall and Cuthill 1997). If one insect species maintains its ability to use several host plants and continues to use them despite the abundant occurrence of one of them, presumable benefits of polyphagy will outweigh costs for that species. If this hypothesis is true, alternative wild or rare host plants should increase offspring quality (e.g. better larval survival and growth and better resistance to parasitism or better adult fecundity) above that produced on the more abundant but less suitable plants, as suggested by West and Cunningham (2002). Here, in order to understand why polyphagy is maintained in *L. botrana*, we decided to test the hypothesis suggested by these authors by evaluating several fitness traits on different host plants. We compared the larval performance and several traits related to fitness on different alternative host plants and compared them to those obtained on two cultivars of grapes. Particularly, we focused on how host plants affect growth and development from neonate larvae to the adult stage by measuring the growth and development duration of individuals, the timing of adult hatching and the achieved female fecundity.

Materials and methods

Study system, moths, their origin and maintenance

For this study, we used *L. botrana* individuals collected in a Bordeaux vineyard (cultivar white sauvignon) which were maintained without diapause for about ten generations on a semi artificial diet at 23 ± 1°C, 60 ± 10% r.h. with a photoperiod of L15:D8 + 1 h of dusk. Light intensities were: $L = 1{,}000$ lux; dusk = less than 25 lux. All tests were performed in a climatic chamber.

Plants, larval diets and general procedure

The effect of host plant species on the development rate and female reproductive output of *L. botrana* was tested on individual larvae with equivalent amounts of food. Larvae were raised individually to pupation in small eppendorf tubes filled with 1.5 ml of a medium made of Agar with plant material added from the different species. This protocol presents at least three main advantages: (a) preventing unwanted noise induced by growing potted alternative plants in climatic chambers and all sorts of variation due to microhabitats effects, (b) feeding larvae in isolation thus preventing biases due to competition and subsequent food deprivations and (c) preventing incidences of infections by fungi which naturally grow on harvested plants and can modify larval fitness (Savopoulou-Soultani and Tzanakakis 1988; Mondy and Corio-Costet 2000).

We tested six different plants which present suitable hosts during the first generation (mainly June) of *L. botrana*. We tested three different species of Vitaceae, two cultivars and one wild species. The grapes of *V. vinifera* cv. 'cabernet-sauvignon' and of red Bacco (Vitaceae) were harvested in our experimental vineyard. We collected young grape bunches (at the beginning of the growing season, stage 27, Eichhorn and Lorenz 1977) and of *Ampelopsis brevipedunculata* (Porcelain Berry Vine) (Vitaceae), flowers of the remaining plants: *D. gnidium* (Thymeleaceae), *Olea europaea* (Oleaceae) (commercial variety) and Tansy (β thujone chemotype, Gabel and Thiéry 1994) (*Tanacetum vulgare*, Asteraceae). Tansy was not considered to be a host (Gabel 1995) because it was described as toxic to the larvae (Lustner 1914) and deterrent to oviposition (Gabel and Thiéry 1994). However, we have observed eggs on tansy and have obtained larval development on flowers. Therefore we now consider tansy as a possible host of *L. botrana*.

All plant materials were immediately deep frozen after collection and then freeze dried. A fine powder of each material was added in the following medium: for

100 eppendorfs, 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 de nipagine (methyl hydroxyl-benzoate), 0.007 g tetracycline and 4 g of freeze-dried plant powder. A control group of larvae was reared on this medium with no plant material (called basic medium, BM). A complementary larval rearing programme was conducted on semi-synthetic diet (called augmented medium, AM) under the rearing conditions described above, to compare this diet to others. These two media provide respectively low and high nutritive value to the larvae. Its composition for 100 eppendorfs was as follows: 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. Ascorbic, benzoic acid, nipagine and Iprodione are classically used and were tested for non-noxious effects against *L. botrana*.

Eppendorfs were filled with the diet and neonate larvae (age < 24 h) were transferred individually using a fine brush in each eppendorf, 100 larvae were examined per diet.

Larval performance

Forty larvae were monitored daily until pupation to follow the duration of each instar. The loss of the cephalic capsule was the criterion used to determine the moult. Pupae were extracted from the diet and weighed to the nearest 0.1 mg as an index of the adult body size, and sex ratio was calculated based from these 40 larvae.

Pupae were then placed individually in glass tubes (70 mm×9 mm diameter) covered with a cotton plug and stored in the test room until emergence. We recorded the following variables: (1) duration of each larval instar, (2) total larval development duration defined here as the number of days from hatching out of the egg until pupation, (3) pupal mass, (4) the growth rate (pupal weight in mg/development time in days), (5) larval survival and therefore the emergence rate and (6) adult sex ratio.

Reproductive life history traits

Sixty additional larvae per feeding treatment (not monitored daily) were used to produce the adults needed to test the reproductive output of females. Newly emerged females (< 1 day old) were individually confined in 0.5 l cellophane bags both for mating and oviposition with a water source provided. One 1–2 day old virgin male originating from the same diet as the female was added to each caged virgin female, 1 h before dusk. Males were randomly assigned to females. Males and females were caged in these bags until the death of both sexes. Females could oviposit inside the cellophane bag and eggs were checked each morning through the cellophane until death of the female. Egg fertility was checked by the hatching larvae.

We considered four variables: (1) female mating success assessed by production of fertile eggs, (2) total fecundity (number of eggs laid), (3) duration of laying and (4) longevity of mated females.

Statistical analysis

All 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 ($P > 0.05$) effects and interactions. Only the resulting models are presented here. In cases where no factor had a significant effect in the global model, only the factor of interest is presented. 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). Two-tailed tests of significance were used throughout. To evaluate the effects of larval diet on development duration until emergence of the moths, we used a non-parametric survival analysis (proportional hazards test) since the assumption for Weibull distribution was always violated. In order to examine the effect of plants (alternative host plants vs Vitaceae) on different life history traits, we group the three species of Vitaceae and the three species of alternative host plants to form two groups.

Results

Growth and development

Overall, the development duration of males was significantly shorter than that of females and development duration of both sexes varied significantly according to the plants on which larvae were fed (Fig. 1a, Table 1a). The significant interaction indicates that on some plants (AM, Daphne, Olive, Red Bacco and Tansy) males emerged sooner than females, whereas in other plants the time lag disappeared (Ampelopsis, BM and Cabernet-Sauvignon) (Fig. 1a). Interestingly, late male emergence occurred only in the diets which promoted a long larval duration. Females and males developed faster when reared on an alternative host plant than on Vitaceae and also compared to those reared on AM (Fig. 1a, Kruskal–Wallis test for male: $\chi^2_3 = 78.10$, $P < 0.0001$; for female $\chi^2_3 = 30.29$, $P < 0.0001$).

The development duration of each larval instar varied significantly according to the diet (Table 2). Each larval instar developed faster on alternative host plants than on Vitaceae, except for the first instar where duration on alternative host was the same as on Vitaceae (Table 3). The only significant difference in larval instar duration due to sex appeared in the fifth instar (females needed more time to develop than males) (Table 2).

Pupal mass varied significantly according to the diet, and sex (females were heavier than males) but was not related to the development duration (Fig. 1b, Table 2b). The significant interaction indicates that in most diets the difference between two sexes was huge while in other diets the differences were smaller (e.g. Ampelopsis and BM). The weights of female and male pupae differed significantly across the four groups of diets (Kruskal–Wallis test for female: $\chi^2_3=24.61$, $P<0.0001$; for male: $\chi^2_3=14.55$, $P<0.001$). Female pupae reared on alternative host plants exhibited similar weight to those raised on AM but were heavier than those reared on Vitaceae, although no difference was observed for males between alternative host plant and Vitaceae (Fig. 1b).

The growth rate differed significantly between sexes (females had a higher growth rate than males) and between individuals reared on different hosts (Fig. 1c, Table 1c). The growth rate of females and males were significantly different according to the four groups of diets (Kruskal–Wallis test for female: $\chi^2_3=37.84$, $P<0.0001$; for male: $\chi^2_3=56.37$, $P<0.001$). Whatever sex, larvae reared on alternative host plants exhibited the same growth rate as larvae reared on AM, but much higher than those reared on Vitaceae or on BM (Fig. 1c).

The proportion of larvae dying differed among plants (Pearson $\chi^2_7=16.15$, $P=0.02$) (Table 4). Particularly, the highest rates of larval mortality were observed on the three Vitaceae as the same level of those raised on BM (around 20%) whereas the larval mortality for alternative host plants was very low (Table 4).

There was a significant effect of diet on sex ratio of the emerging adults (Pearson $\chi^2_7=19.07$, $P=0.008$) (Table 4). However, globally there is no difference among four groups of diets.

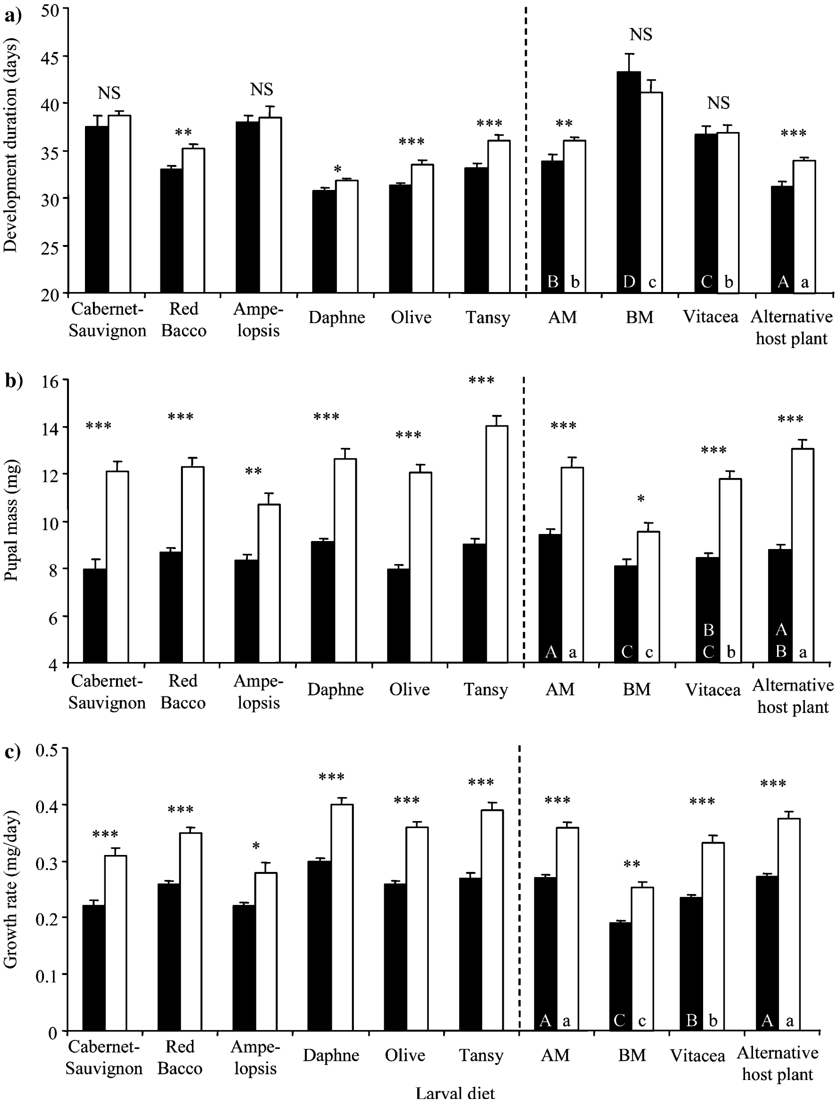

Fig. 1 **a** Development duration, **b** Pupal mass and **c** Growth rate (pupal weight$_{mg}$/development time$_{days}$) of *L. botrana* females (*white columns*) and males (*black columns*) reared on eight larval diets (mean ± SEM). Comparisons between males and females was done with a Kruskal–Wallis tests, *NS* $P>0.05$, *single asterisk* $P<0.05$, *double asterisks* $P<0.01$, *triple asterisks* $P<0.0001$. A stastical comparison was performed only on the four groups of diets (AM, BM, alternative host plant and Vitaceae). Columns sharing the same letter are not significantly different ($P>0.05$) after a non-parametric PLSD test (*capital letters* for male and *small letters* for female). For detail on statistical analysis see Table 1

Table 1 Statistical details for the analyses of the different effects on total development duration (non-parametric survival analysis), pupal mass (ANOVA), growth rate (ANOVA) and total fecundity as the number of eggs laid (ANOVA)

Analysis	Source	DF	Sum of squares	F ratio	*P*
(a) Total development duration	General model	15	–	204.23	< 0.0001
	Plants	7	–	170.76	< 0.0001
	Sex	1	–	16.08	< 0.0001
	Plants × sex	7	–	13.52	0.04
(b) Pupal mass	General model	16	1104.5	41.53	< 0.0001
	Plants	7	92.8	7.97	< 0.0001
	Duration of larval development	1	0.1	0.04	0.85
	Sex	1	689.9	415.08	< 0.0001
	Plants × sex	7	37.0	3.18	0.003
	Error	236	392.3		
	Total	252	1496.7		
(c) Growth rate	General model	15	0.9	40.00	< 0.0001
	Plants	7	0.3	30.55	< 0.0001
	Sex	1	0.4	283.37	< 0.0001
	Plants × sex	7	< 0.1	1.56	0.15
	Error	237	0.4		
	Total	252	1.3		
(d) Total fecundity (number of eggs laid)	General model	9	78415.3	15.39	< 0.0001
	Pupal weight	1	6427.8	11.35	0.0013
	Duration of egg laying	1	10744.9	18.98	< 0.0001
	Plant	7	14484.1	3.65	0.0023
	Error	63	35673.5		
	Total	72	114088.8		

Effect of larval diet on reproductive life history traits

Female mating success (number of females mated), ranged from 97.1% to 70.4%. A significant difference was due to plants (Pearson $\chi^2_7 = 20.04$, $P = 0.0055$) (Table 4). Particularly, females raised on Vitaceae presented the same mating success than those raised on AM but less than on alternative host (Table 4).

Total fecundity was positively correlated with both female pupal weight and the duration of laying, but it strongly varied among plants (Fig. 2, Table 1d). Indeed, the duration of egg laying varied among diets (Kruskal–Wallis test, $\chi^2_7 = 64.66$, $P < 0.0001$) (Table 4). Overall, females raised on AM exhibited the highest fecundity whereas those raised on BM exhibited the lowest fecundity. Females that had been reared on alternative host plants were more fecund than those that had been reared on Vitaceae (Fig. 2) and laid eggs for a longer period (Table 4).

For fertilized females, the plant on which they had developed influenced their longevity (Kruskal–Wallis test, $\chi^2_7 = 66.70$, $P < 0.0001$) (Table 4). Particularly, females raised on the Vitaceae lived for a shorter period than females from alternative host plants and females raised on AM lived the longest (Table 4).

Discussion

We demonstrate an impact of diet on several life history traits of *L. botrana*. These experiments were done on our lab strain raised for ten successive generations. The lower performance on AM than on several host plant addition mediums implies that even after ten generations of selection on this medium there has been no adaptation to it. Globally, alternative host plants are more suitable than Vitaceae for the individual performance of *L. botrana*: larval mortality was reduced and development time of the larvae was shortened, while pupal weight, growth rate, female longevity, female fecundity, laying duration and mating success were increased.

Larval development time varied among plant species. Species of alternative host plant induced faster larval development than the species of Vitaceae. This result fits the observations from natural populations found in Greece where larvae develop between 2–3 days faster on olive flowers than on grapes (Savopoulou-Soultani et al. 1990). Development time is potentially an important component of fitness in the field because it determines how long larvae are exposed to predators and parasites. For example, the effectiveness of several parasitoid species depends on host larval growth rates: parasitism increases when host growth is slowed (Weseloh et al. 1983). Thus, the shortening of larval stages with alternative hosts may provide an important selective advantage under pressure from natural enemies, as demonstrated by several authors (Häggström and Larsson 1995; Benrey and Denno 1997; Parry et al. 1998). The two most efficient and widely distributed larval parasitoids of *L. botrana* (*Dibrachys cavus* and *Campoplex capitator*) attack the fifth and the second to third larval instars, respectively (Thiéry et al. 2001; Thiéry and Xuéreb 2003). A reduction in these instar durations could hence represent a serious advantage to the moth by reducing its apparency to the parasitoids. The shortening of several

Table 2 Duration of each development instar of *L. botrana* according to the diet on which the larvae developed followed by a non-parametric survival analysis (Proportional hazards)

Larval diet	Sex	Duration of each instar in days (mean ± SEM)					
		First instar	Second instar	Third instar	Fourth instar	Fifth instar	Pupae
Red Bacco	Male (17)	4.30 ± 0.11	3.53 ± 0.17	3.71 ± 0.19	4.47 ± 0.24	9.41 ± 0.32	7.59 ± 0.30
	Female (18)	4.44 ± 0.14	3.50 ± 0.12	3.56 ± 0.17	4.44 ± 0.20	9.67 ± 0.40	9.56 ± 0.46
Cabernet-Sauvignon	Male (16)	6.25 ± 0.38	4.81 ± 0.31	4.31 ± 0.28	4.62 ± 0.26	6.69 ± 0.51	10.81 ± 0.31
	Female (12)	6.00 ± 0.30	4.75 ± 0.25	4.42 ± 0.40	4.50 ± 0.45	8.00 ± 0.51	11.00 ± 0 .21
Ampelopsis	Male (23)	6.22 ± 0.38	4.35 ± 0.25	4.39 ± 0.34	4.48 ± 0.26	7.26 ± 0.35	11.26 ± 0.16
	Female (7)	5.43 ± 0.30	4.14 ± 0.26	4.29 ± 0.29	5.00 ± 0.62	8.43 ± 0.53	11.14 ± 0.26
Daphne	Male (24)	4.58 ± 0.12	2.96 ± 0.20	2.71 ± 0.09	3.21 ± 0.21	6.67 ± 0.24	10.54 ± 0.17
	Female (12)	4.83 ± 0.11	2.92 ± 0.08	2.58 ± 0.15	3.75 ± 0.33	7.08 ± 0.34	10.67 ± 0.14
Olive	Male (22)	5.09 ± 0.23	3.32 ± 0.15	3.00 ± 0.13	3.59 ± 0.16	6.14 ± 0.14	10.14 ± 0.15
	Female (13)	5.15 ± 0.27	3.62 ± 0.18	3.38 ± 0.33	3.46 ± 0.31	7.15 ± 0.36	10.77 ± 0.20
Tansy	Male (12)	5.58 ± 0.26	3.08 ± 0.19	3.33 ± 0.14	4.17 ± 0.39	6.83 ± 0.41	10.08 ± 0.08
	Female (24)	5.92 ± 0.17	3.29 ± 0.24	3.21 ± 0.15	4.12 ± 0.26	8.62 ± 0.49	10.87 ± 0.16
AM	Male (19)	5.05 ± 0.12	3.58 ± 0.14	3.00 ± 0.13	3.74 ± 0.23	7.16 ± 0.51	11.37 ± 0.23
	Female (12)	5.33 ± 0.14	3.33 ± 0.14	2.92 ± 0.15	4.17 ± 0.44	8.83 ± 0.56	11.42 ± 0.19
BM	Male (12)	6.58 ± 0.40	5.50 ± 0.57	5.75 ± 0.60	4.33 ± 0.40	7.42 ± 0.54	13.67 ± 1.71
	Female (10)	6.10 ± 0.53	4.90 ± 0.41	5.50 ± 0.31	5.40 ± 0.45	8.20 ± 0.46	11.00 ± 0.26
Non-parametric survival analysis	Whole model	$\chi^2_{15} = 65.22^{***}$	$\chi^2_{15} = 66.31^{***}$	$\chi^2_{15} = 89.75^{***}$	$\chi^2_{15} = 30.22^{**}$	$\chi^2_{15} = 69.84^{***}$	$\chi^2_{15} = 73.67^{***}$
	Larval diet	$\chi^2_7 = 56.89^{***}$	$\chi^2_7 = 60.87^{***}$	$\chi^2_7 = 83.01^{***}$	$\chi^2_7 = 23.61^{***}$	$\chi^2_7 = 48.39^{***}$	$\chi^2_7 = 56.62^{***}$
	Sex	$\chi^2_1 = 0.01^{NS}$	$\chi^2_1 = 0.48^{NS}$	$\chi^2_1 = 0.04^{NS}$	$\chi^2_1 = 1.68^{NS}$	$\chi^2_1 = 12.40^{***}$	$\chi^2_1 = 6.06^{*}$
	Interaction	$\chi^2_7 = 3.50^{NS}$	$\chi^2_7 = 2.21^{NS}$	$\chi^2_7 = 3.11^{NS}$	$\chi^2_7 = 2.33^{NS}$	$\chi^2_7 = 6.92^{NS}$	$\chi^2_7 = 27.29^{***}$

The numbers in brackets represent the sample size
$^{NS}P > 0.05$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.0001$

larval stages of this species was already observed as a result of larval food when larvae were raised on grapes or apples infected by *Botrytis cinereae* (Savopoulou-Soultani and Tzanakakis 1988).

The emergence of males always occurred before females, but its time difference varied according to the plant tested. This phenomenon, termed 'protandric emergence', is common in many Lepidoptera (Wiklund et al. 1993; Savopoulou-Soultani et al. 1994; Thomas 1989). It presents at least two advantages, by maximizing copulation opportunities for a male (reviewed in Wiklund and Fagerström 1977; Bulmer 1983), and minimizing the prereproductive period of females because they emerge when most males are available (Fagerström and Wiklund 1982). Torres-Vila et al. (1995) showed that *Lobesia* 3-day-old males are the most efficient at mating. Thus, 2 days of protandry represents a potential advantage for the first emerging females by minimizing the risk to emerge with no male (Fagerström and Wiklund 1982). In this context, the absence of protandry observed on the plants that promote a long development time (two species of Vitaceae and BM) could be a clear disadvantage for adults that emerge from these plants and could impair their mating success and overall fitness.

Another advantage for *L. botrana* to develop on alternative host plants concerns their pupal mass and larval mortality. The larvae raised on alternative host plants suffered lower mortality and produced heavier pupae than those on Vitaceae. The results indicate that high quality food promotes higher adult body weight as well as a faster larval development, which indicates that no fitness penalty is paid for fast development.

As a consequence of the variation in larval development duration and pupal mass, growth rates were higher on alternative host plants than on Vitaceae species. In addition, the growth rate of females was higher than that of males. The fact that female growth rate is higher than that of males is classic in capital breeders (species with non feeding adults) since male body weight is not as directly coupled with fitness as it is for females (Haukioja and Neuvonen 1985). As a general rule within a species, female moth fecundity is correlated with their size whereas male body weight is not related to their mating potential, as shown in *L. botrana* (Torres-Vila et al. 1995). These authors could neither correlate male size with the number of matings performed nor with the size of spermatophores transferred, but this does not necessarily mean that no female choice exists. There seems no strong selection for males to spend longer time as larvae in order to become bigger. However our experimental procedure based only on couples could not test that. We could however, postulate that in males selection for speed of development is of greater advantage than that for size. If protandry provides a fitness advantage, it can also act as a selective factor against maximal body weight (Singer 1982; Nylin et al. 1993), but this was not tested here.

Our results illustrate that the larval feeding plant affects adult reproductive success. Host plants can play an important role in mating success in at least two ways: either in the production and release of pheromones in some phytophagous insects (including moths) through the acquisition of chemical precursors of pheromones from plant material (see Landolt and

Table 3 Development duration in days (mean ± SEM) of each larval instars of *L. botrana* according to the group of diet on which the larvae developed

Larval instar	Larval diet		Kruskal–Wallis test	
	Vitaceae	Alternative host plant	χ^2_1	P
First	5.44 ± 0.15	5.19 ± 0.09	0.32	0.57
Second	4.15 ± 0.11	3.19 ± 0.08	60.63	< 0.0001
Third	4.09 ± 0.12	3.03 ± 0.07	49.08	< 0.0001
Fourth	4.54 ± 0.12	3.68 ± 0.11	30.54	< 0.0001
Fifth	8.20 ± 0.21	7.12 ± 0.17	17.19	< 0.0001

Table 4 Performance of *L. botrana* according to the diet or to the group of diets on which the larvae developed

Larval diet	Larval performance ($n = 40$ larvae)		Female performance		
	Larval mortality (%)	Sex-ratio (% of females)	Mating success (%)	Duration of laying in days	Longevity of mated females in days
Red Bacco	12.5	51.4	70.4 (27)	6.00 ± 0.36 (19)	10.57 ± 0.54 (19)
Cabernet-Sauvignon	27.5	41.4	86.7 (30)	4.69 ± 0.31 (26)	6.88 ± 0.32 (26)
Ampelopsis	22.5	22.6	75.0 (20)	6.00 ± 0.41 (15)	7.66 ± 0.45 (24)
Daphne	7.5	32.4	97.1 (35)	6.06 ± 0.29 (34)	9.94 ± 0.34 (34)
Olive	7.5	35.1	96.8 (31)	7.07 ± 0.25 (30)	9.60 ± 0.35 (30)
Tansy	7.5	67.6	88.9 (27)	5.33 ± 0.24 (24)	7.95 ± 0.27 (35)
AM	7.5 A	40.5	88.5 (26) B	8.13 ± 0.42 (23) A	10.83 ± 0.41 (23) A
BM	22.5 B	51.6	78.3 (23) C	4.00 ± 0.40 (18) D	8.89 ± 0.76 (18) B
Alternative host plant	7.5 A	45.0	94.7 A	6.20 ± 0.17 B	9.28 ± 0.21 B
Vitaceae	20.8 B	38.9	86.1 B	5.43 ± 0.21 C	8.25 ± 0.32 C
χ^2	$\chi^2_3 = 12.36$	$\chi^2_3 = 1.85$	$\chi^2_3 = 7.58$	$\chi^2_3 = 43.92$	$\chi^2_3 = 25.10$
P	$< 0.01^a$	0.60^a	$< 0.05^a$	$< 0.0001^b$	$< 0.0001^b$

The numbers in brackets represent the sample size.

Statistical tests were performed only on the four groups of diets (AM, BM, Alternative Host Plant and Vitaceae). Values 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

Phillips 1997 for a review), or through physiological effects such as the quality of spermatophores transferred by males (Torres-Vila et al. 1999) or a deficiency in oocyte production (Ringo 1996; Kaspi et al. 2002).

Larval diet also strongly influenced female fecundity (via pupal weight and the duration of egg laying) as well as their longevity. Females reared on alternative host plants laid more eggs (around 23% more) and lived longer (around 1 day more) than females reared on Vitacea.

The assessment of all life history traits suggests that alternative host plants are of greater nutritional value for larvae or are more phagostimulant than Vitaceae. A high quality food ingested by larvae promoting higher adult body weight enhances female reproductive output.

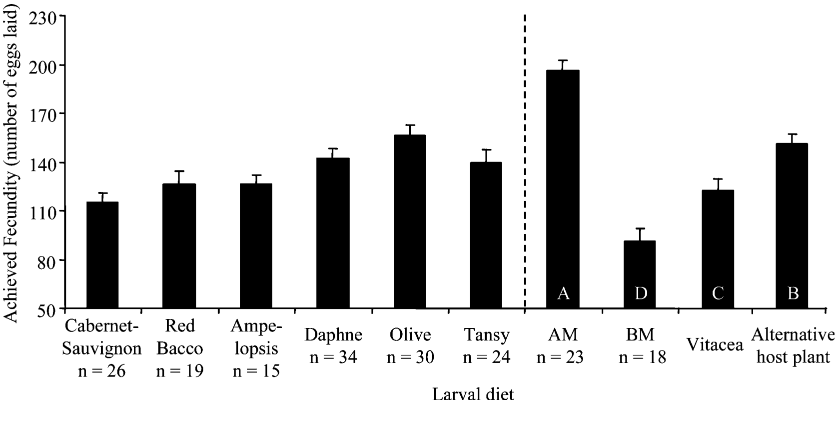

Fig. 2 Achieved fecundity as the number of eggs laid (mean ± SEM) by *L. botrana* females reared on different larval diet. The numbers represent the sample size. A statistical comparison was performed only on the four groups of diets (AM, BM, alternative host plant and Vitaceae). Columns sharing the same letter are not significantly different ($P > 0.05$) after a non-parametric PLSD test. For detail on statistical analysis see Table 1

Our study confirms the results of others who found that larvae that developed on plums (*Prunus avium*) and olive trees (*O. europaea*) resulted in larger adults than those developing on grapevine (*V. vinifera*) with overall female fecundity increasing with adult size (Stoeva 1982; Savopoulou-Soultani and Tzanakakis 1987; Savopoulou-Soultani et al. 1990). The comparison of alternative host plants and artificial diet (AM) on most life history traits suggests that they provide a similar quality of diet.

The use of alternative host plants could be maintained in the host range of *L. botrana* because the fitness of females using alternative host plants is higher than of those raised on Vitaceae. Then, the principal question raised is why *L. botrana* so frequently uses grapes since its performance is better on alternative host plants? The model for host plant selection in insects developed by West and Cunningam (2002) considers this point. The rate at which suitable hosts can be found by ovipositing females is probably the most important factor favouring polyphagy. More specifically, the model predicts that when the more favourable hosts are rare or absent, females are selected to broaden the range of species on which they oviposit. This statement is mainly true if the insect species is short-lived or has a poor dispersal capacity (as is the case for *L. botrana*). Therefore, such insects cannot afford to be very selective in host plant choice, especially if plant resources are scarce or unpredictable (Jaenike 1990). Except in traditional Mediterranean vineyards or those with a diversity of wild species, plants favourable to this species (e.g. *D. gnidium*, olive trees or sea squills) are quite rare. On the other hand, in their habitat, vineyards are locally abundant covering large geographic areas and representing a very predictable resource in space and time. Indeed, grapes are widely distributed and almost all grape cultivars are more or less suitable for this species (Gabel and Roehrich 1995). Consequently, despite the relative advantage of alternative host plants on life history traits of *L. botrana*, the abundance and predictability of grapes may counterbalance their nutritional disadvantage.

This study only considered the influence of physiological and biochemical factors on the performance of *L. botrana*. As noted by Janzen (1985) and Bernays and Graham (1988), the host plant is not merely something fed on, it is something lived on. Thus plant chemistry is not the sole driving force in determining a phytophagous host plant range, and it is argued that generalist enemies may be one of the dominant factors in the evolution of narrow host range. Insects may prefer nutritionally suboptimal host plants because they are ‘enemy-free spaces’ (Ohsaki and Sato 1994). A nice example is given by pyralid caterpillars: protection is dominant over nutritional factors as caterpillars consistently prefers the older leaves because they are more suitable as shelter, even though younger leaves provide better food (Damman 1987).

Finally, the simplest but perhaps more common reason why certain plants are not preferred by a given herbivore may be related to an asynchrony of phenologies. For example, larvae of the Virginia white, *Pieris virginiensis*, are restricted to *Dentaria* plants, partly because of habitat selection and synchronisation to the phenology of the plants. Such restricted host use occurs even though, in the laboratory, adults will oviposit and larvae will feed and develop normally on plants in other genera (Slansky 1976). On the most common plant (grapes), *L. botrana* can accomplish between two and four generations a year between May and October whereas alternative plants like olive trees, privets, raspberries, rosemary, sea squills or flax-leaved-daphne can barely host more than one or two generations (Balachowsky and Mesnil 1935; Roditakis 1988; D. Thiéry unpublished observation).

Despite the few disadvantages due to alternative host plants on the ecology of *L. botrana*, we can attribute a relatively important function to them. All alternative host plants tested in this study have the potential to serve as reservoirs for populations of *L. botrana*, especially early in spring. Females are active about a month before the blooming of Vitacea and may thus lay some or all of their eggs on alternative host plants, such as olives when found adjacent to Vineyards (Savopoulou-Soultani et al. 1990). Also, little is known quantitatively about the movements of *L. botrana* adults between patches of vegetation and we do not know if migrations can occur between sites with different plant diversity. In this context, we can imagine that alternative host plants may serve as reservoirs for *L. botrana* that disperse from one vineyard to another. If the dispersal capacity of *L. botrana* is limited as we assumed, it would be difficult for some adults to reach another vineyard area from their vineyard of origins. In this way, alternative host plants could be a stepping stone breeding one or several generation during a colonisation process. Data concerning the dispersal capacities of females will be needed to elucidate further their ability to disperse to areas with different plant diversity.

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References

Balachowsky A, Mesnil L (1935) Les Insectes Nuisibles à la vigne, *Polychrosis botrana* Schiff. (Lepid. Tortricidae) In: Les insectes nuisibles aux plantes Cultivées, leurs mœurs, leur destruction, vol 1, Paris, pp 677–686

Barbosa P (1988) Some thoughts on the evolution of host range. Ecology 69:912–915

Benrey B, Denno RF (1997) The slow growth-high mortality hypothesis: a test using the cabbage butterfly. Ecology 78:987–999

Bernays EA (1989) Host range in phytophagous insects: the potential role of generalist predators. Evol Ecol 3:299–311

Bernays EA, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892

Bernays EA, Wcislo WT (1994) Sensory capabilities, information processing, and resource specialization. Q Rev Biol 69:187–204

Bovey P (1966) Super-famille des Tortricoidea. In: Balachowsky AS (ed) Entomologie Appliquée à l'Agriculture. Vol 2 Lépidoptères, Masson et Cie, Paris, pp 456–893

Bulmer MG (1983) Models for the evolution of protandry in insects. J Theor Biol 35:195–206

Camara MD (1997) A recent host range expansion in *Junonia coenia* Hubner (Nymphalidae): oviposition preference, survival, growth, and chemical defense. Evolution 51:873–884

Cates RG (1980) Feeding patterns of monophagous, oligophagous, and polyphagous insect herbivores: the effect of resource abundance and plant chemistry. Oecologia 46:22–31

Courtney SP, Chen GK, Gardner A (1989) A general model for individual host selection. Oikos 55:55–65

Dall SRX, Cuthill IC (1997) The information costs of generalism. Oikos 80:197–202

Damman H (1987) Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology 68:88–97

Dethier VG (1970) Chemical interactions between plants and insects. In: Sondheimer E, Simeone JB (eds) Chemical ecology. Academic, New York, pp 83–102

Ehrlich PR, Raven PH (1964) Butterflies and plants: a study in coevolution. Evolution 18:586–608

Eichhorn KW, Lorenz DH (1977) Phonologische Entwicklumggsstadien der Rebe Nachrichtenbl. Pflanzenschutzd (Braunschweig) 29:119–120

Fagerström T, Wiklund C (1982) Why do males emerge before females? Protandry as a mating strategy in male and female butterflies. Oecologia 52:164–166

Feeny P (1976) Plant apparency and chemical defense. In: Wallace JW, Mansell RL (eds) Biochemical interactions between plants and insects. Recent Advances in Phytochemistry. Plenum, New York, pp 1–40

Gabel B (1995) Tansy flowers attract European grapevine moth females, *Lobesia botrana* den. & Schiff. (Lep. Tortricidae). J Appl Entomol 113:153–158

Gabel B, Roehrich R (1995) Sensitivity of grapevine phenological stages to larvae of European grapevine moth, *Lobesia botrana* Den. et Schiff. (Lep., Tortricidae). J Appl Entomol 119:127–130

Gabel B, Thiéry D (1994) Non-host plant odor (*Tanacetum vulgare*; Asteracea) affects the reproductive behaviour of *Lobesia botrana* Den. et Schiff. (Lepidoptera Tortricidae). J Insect Behav 7:149–157

Häggström H, Larsson S (1995) Slow larval growth on a suboptimal willow results in high predation mortality in the leaf beetle *Galerucella lineola*. Oecologia 104:308–315

Haukioja E, Neuvonen S (1985) Induced long-term resistance of birch foliage against defoliators: defensive or incidental? Ecology 66:1303–1308

Jaenike J (1978) On optimal oviposition behaviour in phytophagous insects. Theor Popul Biol 14:350–356

Jaenike J (1990) Host specialization in phytophagous insects. Annu Rev Ecol Syst 21:243–273

Janzen DH (1985) A host is more than its chemistry. Illinois Nat Hist Surv Bull 33:141–175

Kaspi R, Mossinson S, Drezner T, Kamensky B, Yuval B (2002) Effects of larval diet on development rates and reproductive maturation of male and female Mediterranean fruit flies. Physiol Entomol 27:29–38

Keese MC (1997) Does escape to enemy-free space explain host specialization in two closely related leaf-feeding beetles (Coleoptera: Chrysomelidae)? Oecologia. DOI 10.1007/s004420050286

Landolt PJ, Phillips TW (1997) Host plant influences on sex pheromone behaviour of phytophagous insects. Annu Rev Entomol 42:371–391

Lustner G (1914) Das Verhalten der Raupen des ein-und zweibindingen Traubenwicklers zu den Weinbergskraüten und anderen Pflanzen. Z Weinbau Weinbehandl 1:3–35

Maher N, Toulouse ME, Jolivet J, Thiéry D (2000) Oviposition preference of the European grape vine moth, *Lobesia botrana* (Lepidoptera: Tortricidae) for host and non host plants present in Bordeaux area. IOBC/wprs Bull 23(4):131–134

Marchal P (1912) Mission d'étude de la Cochylis et de l'Eudemis pendant l'année 1911. Librairie Polytechnique. Paris

Nylin S, Wiklund C, Wickman PO, Garcia-Barros E (1993) Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. Ecology 74:1414–1427

Ohsaki N, Sato Y (1994) Food plant choice of Pieris butterflies as a trade-off between parasitoids avoidance and quality of plants. Ecology 75:59–68

Parry D, Spence JR, Volney WJA (1998) Budbreak phenology and natural enemies mediate survival of first-instar forest tent caterpillar (Lepidoptera: Lasiocampidae). Environ Entomol 27:1368–1374

Rausher MD (1985) Variability for host preference in insect populations: mechanistic and evolutionary models. J Insect Physiol 31:873–889

Ringo J (1996) Sexual receptivity in insects. Annu Rev Entomol 41:473–494

Roditakis NE (1988) Factors affecting population size of grapes berry moth *Lobesia botrana* Den. & Schiff. in Crete. In: Cavalloro R (ed) Influence of environmental factors on the control of grape pests diseases and weeds. ECC publications, Balkema, Amsterdam, pp 69–76

Roehrich R, Boller E (1991) Tortricids in vineyards. In: Van der Gesst LPS, Evenhuis HH (eds) Tortricid pests, their biology natural enemies and control. Amsterdam, Elsevier, pp 507–514

Savopoulou-Soultani M, Tzanakakis ME (1987) Comparison of olive flowers with vine flowers and leaves as food for larva of *Lobesia botrana*. In: Cavalloro R (ed) Influence of environmental factors on the control of grape pest diseases and weeds. Commision of the European Communities, Rotterdam, pp 63–67

Savopoulou-Soultani M, Tzanakakis ME (1988) Development of *Lobesia botrana* (Lepidoptera: Tortricidae) on grapes and apples infected with the fungus *Botrytis cinerea*. Environ Entomol 17:1–6

Savopoulou-Soultani M, Stavridis DG, Tzanakakis ME (1990) Development and reproduction of *Lobesia botrana* on vine and olive inflorescences. Entomologia Hellenica 8:29–35

Savopoulou-Soultani M, Stavridis DG, Vassiliou A, Stafilidis JE, Iraklidis I (1994) Response of *Lobesia botrana* (Lepidoptera: Tortricidae) to levels of sugar and protein in artificial diets. J Econ Entomol 87:84–90

Schultz JC (1988) Many factors influence the evolution of herbivore diets, but plant chemistry is central. Ecology 69:896–897

Singer MC (1982) Sexual selection for small size in male butterflies. Am Nat 119:440–443

Slansky F (1976) Phagism relationship among butterflies. J N Y Entomol S 84:91–105

Southwood TRE (1972) The insect/plant relationship—an evolutionary perspective. Symp R Entomol Soc Lond 6:3–30

Stoeva R (1982) Les hôtes de la teigne bariolée des vignes *Lobesia botrana* Schiff en Bulgarie. Horticult Viticult Sci 19:83–89

Strong DL, Lawton JH, Southwood R (1984) Insects on plants. Harvard University Press, Cambridge

Swain T (1977) Secondary plant compounds as protective agents. Annu Rev Plant Physiol 42:55–302

Thiéry D (2005) Les vers de la grappe. Guide Pratique, Vigne & Vins Publ. Int. (in press)

Thiéry D, Xuéreb A (2003) Relative abundance of several larval parasitoids of *Lobesia botrana* on different varieties of grapes. IOBC/wprs Bull 26:135–139

Thiéry D, Xuéreb A, Villemant C, Sentenac G, Delbac L, Kuntzman P (2001) Larval parasites of vineyards tortricids: a brief overview from 3 french vine growing areas. IOBC/wprs bull 24:13–142

Thomas AW (1989) Food consumption and utilization by 6th-instar larvae of spruce budworm, *Choristoneura fumiferana*: a comparison on three *Picea* (spruce) species. Entomol Exp Appl 52:205–214

Torres-Vila LM, Stockel J, Roehrich R (1995) Le potentiel reproducteur et ses variable biotiques associées chez le mâle de l'Eudémis de la vigne *Lobesia botrana*. Entomol Exp Appl 77:105–119

Torres-Vila LM, Rodriguez-Molina MC, Roehrich R, Stockel J (1999) Vine phenological stage during larval feeding affects male and female reproductive output of *Lobesia botrana* (Lepidoptera: Tortricidae). Bull Entomol Res 89:549–556

Weseloh RM, Andreadis TG, Moore REB, Andersson JF, Dubois NR, Lewis FB (1983) Field confirmation of a mechanism causing synergism between *Bacillus thuringiensis* and the gypsy moth parasitoid, *Apanteles melanoscelus*. J Invertebr Pathol 41:99–103

West SA, Cunningham JP (2002) A general model for host plant selection in phytophagous insects. J Theor Biol 214:499–513

Wiklund C, Fagerström T (1977) Why do males emerge before females? Oecologia 31:153–158

Wiklund C, Kaitala A, Lindfors V, Abenius J (1993) Polyandry and its effect on female reproduction in the green-veined white butterfly (*Pieris napi* L.). Behav Ecol Sociobiol 33:25–33