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Larval intraspecific competition for food in the European grapevine moth *Lobesia botrana*

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Abstract

Effective pest management with lower amounts of pesticides relies on accurate prediction of insect pest growth rates. Knowledge of the factors governing this trait and the resulting fitness of individuals is thus necessary to refine predictions and make suitable decisions in crop protection. The European grapevine moth, *Lobesia botrana*, the major pest of grapes in Europe, is responsible for huge economic losses. Larvae very rarely leave the grape bunch on which they were oviposited and thus cannot avoid intraspecific competition. In this study, we determined the impact of intraspecific competition during the larval stage on development and adult fitness in this species. This was tested by rearing different numbers of larvae on an artificial diet and measuring developmental and reproductive life history traits. We found that intraspecific competition during larval development has a slight impact on the fitness of *L. botrana*. The principal finding of this work is that larval density has little effect on the life history traits of survivors. Thus, the timing of eclosion, duration of subsequent oviposition, fecundity appears to be more uniform in *L. botrana* than in other species. The main effect of larval crowding was a strong increase of larval mortality at high densities whereas the probability of emergence, sex ratio, pupal mass, fecundity and longevity of mated females were not affected by larval crowding. Owing to increased larval mortality at high larval densities, we hypothesized that mortality of larvae at high densities provided better access to food for the survivors with the result that more food was available *per capita* and there were no effect on fitness of survivors. From our results, larval crowding alters the reproductive capacity of this pest less than expected but this single factor should now be tested in interaction with limited resources in the wild.

Keywords: larval crowding, intraspecific competition, growth rate, life history traits, compensatory mortality, Lepidoptera

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Introduction

Identifying the factors that are responsible for variation in size of population is a central goal in theoretical and applied ecology, and has important implications for pest management. Among these factors, density-dependent intra-specific competition is considered to be one of the main factors governing population size, mainly due to its effect on life history traits. Numerous studies have shown that intraspecific competition can negatively affect insect development and life history traits (see Applebaum & Heifetz, 1999 for a review). Juvenile crowding when resources (i.e., water, carbohydrates, mineral nutrients and so on) are limited, causes competition and often results in longer larval development periods, higher larval mortality, and lower pupal masses (Mercer, 1999; Tammaru *et al.*, 2000; Gibbs *et al.*, 2004). In addition, larval crowding can profoundly affect female reproduction, especially in capital breeders in which the potential reproductive output is determined by the food quality and quantity during the larval development (Awmack & Leather, 2002). Therefore, competition for food among larvae can negatively affect female fecundity and survival to adulthood (see Fantinou *et al.*, 2008; Frouz *et al.*, 2009; Reiskind & Lounibos, 2009; Tsurim *et al.*, 2013 for examples). Thus, intraspecific competition during the larval period has the potential to reduce the overall fitness of insects.

Many insect species are pests and are responsible for huge annual losses in global crop production (Thacker, 2002). Today, a great arsenal is available to control insect pests but to be effective, substances should target the most susceptible stage to maximize effectiveness and thus minimize the number of applications (Thacker, 2002; Van Driesche *et al.*, 2008). Accurate prediction of the insect growth rate and timings of emergence is therefore essential for developing effective pest management strategies and mathematical models greatly help in determining insect emergence dates and population size in order to construct optimal treatment schedules (Li *et al.*, 2004; Yonow *et al.*, 2004; Moravie *et al.*, 2006; Georgescu & Morosanu, 2007; Zhang *et al.*, 2008; Jiao *et al.*, 2009; Ainseba *et al.*, 2011; Baumann *et al.*, 2013). Models sometimes fail to provide useful predictions for pest management due to the lack of basic knowledge of pest ecology (Shaffer & Gold, 1985; Ainseba *et al.*, 2011). One of the main challenges of applied ecology is to define the factors that would refine predictions. Hence, current models often neglect some important factors related to juvenile growth because of a lack of data. By considering such factors models could give a better estimate of the period of appearance of the pest and allow determination of an optimal window of treatment. As intraspecific larval competition has the potential to impact the duration of larval development, mortality rate and female fecundity, a better understanding of this effect on pest life history traits might be incorporated into mathematical models to improve our predictive capability.

The European grapevine moth *Lobesia botrana* (Denis & Schiffermueller) (Lepidoptera: Tortricidae) is the major pest of grapes in Europe, north Africa and west Asia (Bovey, 1966; Roehrich & Boller, 1991; Thiéry, 2008) owing to its wide geographical distribution and the great damage it can cause to vineyards. *L. botrana* is a multivoltine tortricid in which wild females can mate several times and lay up to ca. 100 eggs singly on flower buds or berries during their 1–2 weeks lifespan. This polyphagous species is an interesting model to study competition since larvae may experience overcrowding in bunches. For example, up to 25–35 larvae per bunch have been observed in the wild (Thiéry *et al.*, 2014; Thiéry & Chuche, unpublished data). Except in pergola training systems, most growers keep limited numbers of bunches on vines and larvae rarely move between bunches so they may have to deal with intraspecific competition (Torres-Vila *et al.*, 1995). *Lobesia botrana* may cause serious damage to bunches either by quantitative or qualitative losses especially by facilitating the infection of pathogenic fungi such as the grey mold disease *Botrytis cinerea* Persoon: Fries (Leotiales: Sclerotiniaceae, Roehrich & Boller, 1991) or black mold *Aspergillus* spp. (Thiéry, 2008). Therefore, important economic losses are due to *L. botrana* and associated fungi (Thiéry, 2008, 2011). In insect, pest management programmes aimed at controlling *L. botrana*, pesticides are used extensively, even though techniques such as mating disruption allow a reduction in their use (Ioriatti *et al.*, 2011). For most of the current techniques (mating disruption, Bt or growth regulators), knowledge of population dynamics of the adults or the structure in age of the juvenile instars is fundamental (Ainseba *et al.*, 2011). Thus, prediction of larval development and size of population become critical and mathematical models are extensively used (Briolini *et al.*, 1997; Milonas *et al.*, 2001; Moravie *et al.*, 2006; Ainseba *et al.*, 2011; Amo-Salas *et al.*, 2011; Baumann *et al.*, 2013).

The purpose of the present study was to determine whether intraspecific competition occurs during the larval stage in this species and if so, whether larval crowding can impact development rates and adult fitness of *L. botrana*. With this knowledge, we are able to determine whether intraspecific competition should be incorporated into mathematical models to improve the predictive capability of models. To examine the effect of larval crowding on both developmental and reproductive life history traits, we compared different amounts of larvae on the same food quantity and quality and measured a series of developmental and reproductive traits.

Materials and methods

Study system: moths, their origin and maintenance

The strain of *L. botrana* (INRA Bordeaux) used for this study originated from over 5000 larvae collected in a French Sauternes vineyard (cultivar sauvignon). This rearing line was based on large numbers of caged adults (several thousands a week) in order to avoid genetic drifts. The stock colony was 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 light:dark cycle of 16 h light and 8 h of dark. The first 15-photophase hours were at 1000 lux luminosity and the last one (dusk) at 25 lux. All tests were performed under the same conditions.

Larval diet treatments and general procedure

The influence of different levels of larval competition in *L. botrana* was tested by rearing larvae at four different densities (1, 5, 10 and 20 larvae) on 10 ml of artificial diet (see composition above) in small plastic cups (3.2 cm height, Ø 4 cm) with an aerated cover, treatments referred further as

Table 1. Survival of *L. botrana* to pupation (larva > pupae), adult eclosion (pupae > adult) and adult sex ratios for larvae reared at different densities on artificial diet. Treatments (larval density) with the same letter are not significantly different ($P > 0.05$) based on 95% CI overlap.

Treatments (larval density)	Groups	*N* larvae	Larva > pupae		Pupae > adult		Adult sex ratio
			N pupae	*P* survival[1] [95% CI]	*N* adults	*P* survival[2] [95% CI]	F/M
D1	72	72	67	0.93 [0.87–0.99][a]	56	0.84 [0.75–0.92][a]	27/29
D5	16	80	65	0.81 [0.73–0.90][ab]	61	0.92 [0.86–0.99][a]	31/30
D10	18	180	136	0.76 [0.69–0.82][b]	127	0.93 [0.89–0.98][a]	67/60
D20	11	220	130	0.59 [0.53–0.66][c]	110	0.85 [0.78–0.91][a]	54/56

[1] *N* pupae/*N* larvae.
[2] *N* adults/*N* pupae.

D1, D5, D10 and D20. As compared to grape bunches, artificial food presents the advantage of reducing the chance of secondary effects due to fungal contamination (by *B. cinerea* and *Aspergillus carbonarius* or *niger*, for example), which can occur when larval densities are high. Such fungi may have positive effects on fitness traits (at least demonstrated in *B. cinerea*) and this would have interfered with our objective (Savopoulou-Soultani & Tzanakakis, 1988; Mondy & Corio-Costet, 2000). The number of grouped larvae (from one to 20) for each density treatments were chosen to be congruent with densities observed in the wild (see above). Hatching eggs were collected every 3 h in order to obtain newborns (< 3 h old) which were immediately and gently deposited in the different treatments using a fine paint brush. A total of 552 newly hatched larvae (< 24 h) were individually allocated at random to the four experimental treatments (D1, D5, D10 and D20, see table 1 for detailed number of replicates). To our knowledge, cannibalism has not been recorded in this species and was not observed during these experiments.

Larval performance

Larvae from each treatment were monitored once a week until pupation. Pupae were then carefully removed from the diet and weighed to the nearest 0.1 mg. In each treatment, pupal mass was determined in a randomly chosen sub-sample of at least 40 pupae (range: 42–105). As adult moths could not be weighed with enough accuracy, we used the mass of living pupae as an index of adult body size. Pupae were then placed individually in glass tubes (70 mm, Ø 9 mm) covered with a cotton plug and stored in the test room until emergence. Adults were sexed at emergence. We recorded the following variables: (1) probability of reaching pupae (larva > pupae, equivalent to larval mortality), (2) probability of completing metamorphosis (pupae > adult, equivalent to pupae mortality), (3) pupal mass, (4) total development time (larval + pupal) and (5) adult sex ratio.

Adult performance: reproductive life history traits

All newly emerged adults resulting from the different larval densities were used to evaluate the reproductive output of females. Newly (< 1-day-old) emerged females were individually confined in 0.5 litre 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 experimental treatment were randomly assigned to virgin females 1 h before dusk, i.e., just before their sexual activity. Females could behave and oviposit freely inside the cellophane bag until death. Each mating bag was checked every morning.

Five variables were considered: (1) the percentage of mated females (female mating success) assessed by the production of fertile eggs (non-mated female lay some infertile eggs at the end of their life), (2) delay before the first egg was laid (days), (3) total achieved fecundity (number of eggs laid), (4) duration of egg laying (days) and (5) longevity of mated females (days).

Statistical analysis

Prior to all statistical analyses, replicates for each treatment were compared to ensure that they were all equivalent. No differences were ever observed and they were thus pooled by treatment. The effect of the density treatments on probability of reaching (larva > pupae) and completing (pupae > adult) metamorphosis as well as the female probability of mating was tested using binomial regression based on likelihood ratio-based χ^2-statistics for unbalanced design (Fox & Weisberg, 2011). These probabilities were assorted with their 95% confidence interval (95% CI).

For each treatment, deviation from balanced sex ratio was tested using binomial tests. Then, sex ratios were compared between treatments with χ^2 test. Total development duration, pupal mass, delay before first egg laid, egg laying duration, fecundity (controlled for female pupal mass in using this parameter as a covariate) and mated female longevity were compared between treatments using analysis of variance (ANOVA) (after checking for both normality and homoscedasticity using Shapiro–Wilk and Levene tests, respectively). The model also included a sex effect in interaction with the treatment effect in total development duration and pupal mass analyses to account for potential differences between females and males. In all cases, the statistical significance of each parameter was assessed by *F*-ratio statistics for unbalanced designs.

All statistical analyses were performed with the R software v. 3.0.1 (R Development Core Team, 2013) implemented *car* package for likelihood ratio-based χ^2-statistics analysis and *F*-ratio statistics for unbalanced designs.

Results

Larval development

The reduction in larval viability, which is the probability of reaching the pupal stage differed between treatments (binomial regression: $\chi^2_3 = 42.15$, $P < 0.0001$). Larval mortality

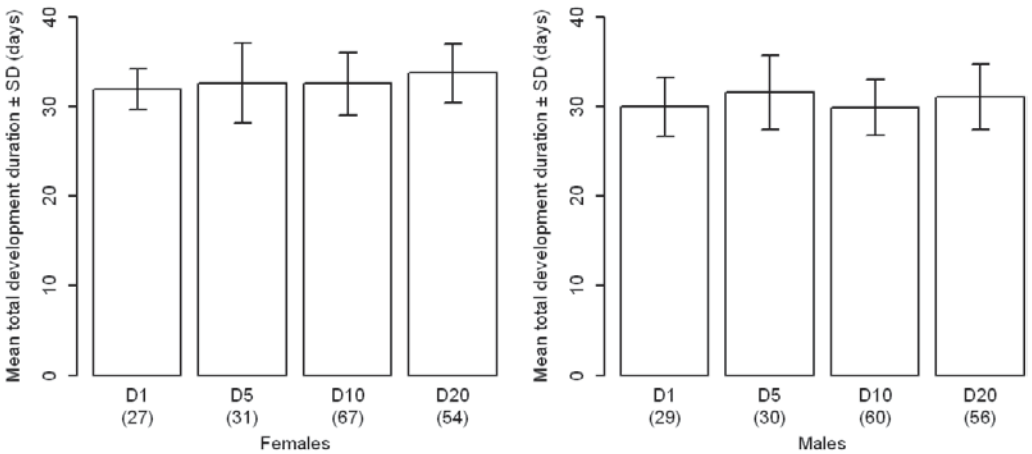

Fig. 1. Mean total development duration (larval + pupal) in male and female *L. botrana* in different treatment (larval density) assorted with standard deviation (SD). The numbers in parentheses indicate number of larvae that reached the adult stage.

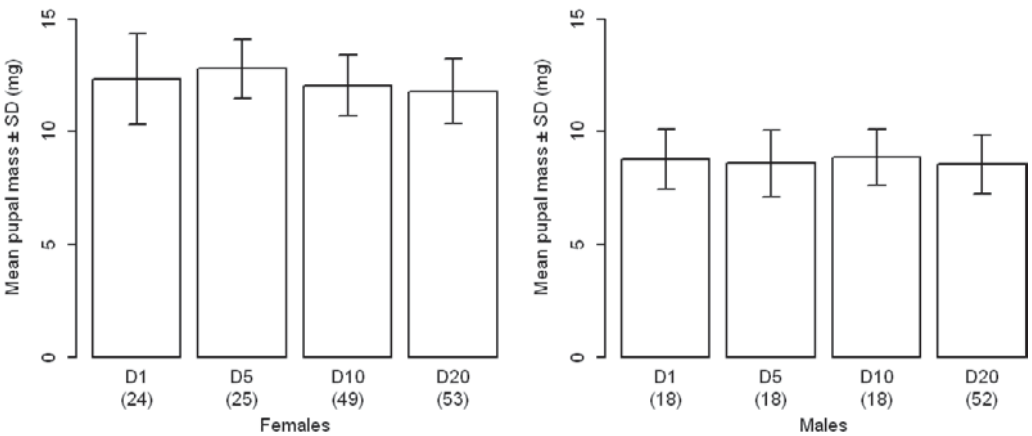

Fig. 2. Mean mass of male and female *L. botrana* pupae in different treatment (larval density) assorted with standard deviation (SD).

increased with increasing density (table 1). The probability of completing metamorphosis (pupae > adult) slightly differed between treatments according to binomial regression ($\chi^2_3 = 8.96$, $P = 0.03$). However, all 95% CIs around the probability of reaching adult stage overlapped suggesting no strong differences between treatments (table 1). Adult sex ratio was balanced (binomial tests all P-values > 0.15) and did not differ between treatments (Chi square test: $\chi^2_3 = 0.46$, $P = 0.93$).

Male development duration was always shorter than female development duration (ANOVA: $F_{1,346} = 37.76$, $P < 0.0001$) and differed between treatments ($F_{3,346} = 3.40$, $P = 0.02$, fig. 1) with a similar pattern in both sexes (i.e., no interaction sex × treatment: $F_{1,346} = 0.92$, $P = 0.43$). Overall, larval development duration was similar in all treatments except between D10 and D20 (fig. 1).

Females were heavier than males in all treatments (ANOVA: $F_{1,249} = 350.14$, $P < 0.0001$, fig. 2). There were no differences between treatments ($F_{3,249} = 2.00$, $P = 0.11$) nor interaction between sex and treatment (crowding) ($F_{3,249} = 1.30$, $P = 0.27$, fig. 2).

Reproductive life history traits

The number of matings did not differ between treatments (binomial regression: $\chi^2_3 = 4.74$, $P = 0.19$, table 2). The delay to the first egg laid and egg laying duration were not affected by crowding in development (ANOVA: $F_{3,72} = 1.18$, $P = 0.32$ and: $F_{3,72} = 1.64$, $P = 0.19$, respectively; table 2). The total number of eggs was not related to females pupal mass (ANOVA: $F_{1,59} = 2.60$, $P = 0.11$) and varied with crowding ($F_{3,59} = 2.86$, $P = 0.04$, fig. 3) without interaction with female body mass ($F_{3,59} = 2.21$, $P = 0.89$). Overall, the number of eggs laid was similar in all treatments except between D10 and D20 (fig. 3). Mated female lived around eight days and this was also not affected by crowding during larval development (ANOVA: $F_{3,71} = 1.17$, $P = 0.33$; table 2).

Discussion

The principal finding of this work is that density of *L. botrana* larvae has little effect on the life history traits of survivors. Thus, the timing of eclosion, the duration of

Table 2. Reproductive life history traits of adult stages according to the treatments. Mating success (i.e., the probability of mating) is assorted with its 95% CI. Mean delay before mating, mean egg laying duration and mean female longevity are assorted with their standard deviation (SD).

Treatments (larval density)	*N* female tested	*N* female mated	Mating success[1] [95% CI]	Delay before mating in days (mean ± SD)	Egg laying duration in days (mean ± SD)	Mated female longevity in days (mean ± SD)
D1	18	15	0.83 [0.66–1.00]	2.67 ± 0.98	3.93 ± 1.44	8.33 ± 1.17
D5	22	17	0.77 [0.60–0.95]	3.53 ± 1.81	4.00 ± 0.87	8.62 ± 1.54
D10	27	21	0.78 [0.63–0.93]	2.81 ± 0.98	4.67 ± 1.20	8.05 ± 1.20
D20	24	23	0.96 [0.88–1.00]	2.83 ± 1.80	4.04 ± 1.19	8.78 ± 1.51

[1] *N* female mated/*N* female tested.

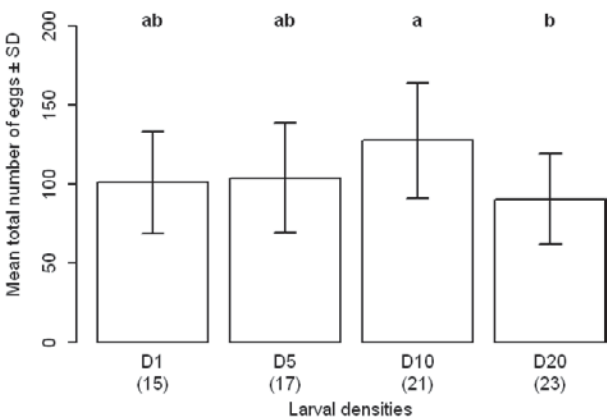

Fig. 3. Mean total number of eggs laid by female *L. botrana* reared at different treatments (larval densities) assorted with standard deviation (SD). The numbers in parentheses indicate number of mated females. Treatments (larval densities) with the same letter are not significantly different ($P > 0.05$) based on Tukey HSD tests.

subsequent oviposition and fecundity appear to be more uniform in *L. botrana* than in other species. The main effect of larval crowding in this work was the strong increase of larval mortality.

Depending on *L. botrana* population size in vineyards, large numbers of larvae per bunch can occur in the wild. For example up to 25 larvae per bunch have been observed in the wild on Merlot (Thiéry *et al.*, 2014) and 35 larvae per bunch on Cabernet sauvignon bunches (Thiéry & Chuche, unpublished data). In this study, we found that the main effect of high intraspecific competition during larval development was a strong mortality but the impact of crowding on the individual fitness was less than expected. This contrasts with effects observed in other species after crowding in the same larval stage (Chippindale *et al.*, 1997, 1998; Fantinou *et al.*, 2008). Sex ratio and pupal mass were not significantly different between treatments. In addition, larval competition had only a slight effect on reproductive life history traits. Female fecundity was slightly decreased at high density (20 larvae per container) compared to intermediate density (10 larvae), whereas the probability of mating, duration of egg laying and the delay before the first eggs were not affected by density. Finally, the longevity of mated female was not affected by density treatment. This study was conducted under laboratory conditions and obviously further field work is necessary to confirm these results.

For all densities, larval development duration was shorter for males compared to females. Such a protandry is commonly found in fruit Tortricids and several other Lepidoptera (Rodriguez-del-Bosque *et al.*, 1989; Wiklund *et al.*, 1993), and is known for *L. botrana* (Roehrich & Boller, 1991; Moreau *et al.*, 2006*a*, *b*, *c*; Thiéry *et al.*, 2014). In addition, female pupae were heavier than males, a classical trait in many lepidopteran species (Raven, 1961; Slansky & Scriber, 1985). By feeding during a longer period, *L. botrana* females may reach this larger size but in turn, this results in a slower development time (Thiéry & Moreau, 2005; Moreau *et al.*, 2006*a*, *c*).

The most important effect of intraspecific competition was the decrease of the probability of larval survival with the increasing crowding. Many studies have found that larval densities increase larval mortality and our results are in agreement with this general trend (Hooper *et al.*, 2003; Ireland & Turner, 2006; Frouz *et al.*, 2009). The proximal factors behind this increased mortality were not identified in this study. Cannibalism is not recorded in this species and can be excluded as a main factor. However, aggressive contacts among individuals may increase with higher density and induce more stress. Such stressed larvae may stop feeding, grow more slowly and thus would be increasingly exposed to aggressive encounters. In turn, this could increase the probability of death (see Renshaw *et al.*, 1993 for an example). It is also possible that higher larval density increased larval movement to find food or that the ingestion of frass could slow their growth or increase their mortality (Bédhomme *et al.*, 2005).

Although there was a strong effect on larval survival, the duration of development, pupal mass and reproductive life history traits were not strongly affected by density. We observed slightly prolonged larval development duration and a marginally decreased fecundity at high density (20 larvae per container) compared to intermediate density (10 larvae). Previous studies on insects investigating the role of intraspecific competition do not all reach the same conclusions. In general, strong intraspecific competition during the larval stage has important consequences for larval development and on reproductive life history traits and thus on adult reproductive success (Mercer, 1999; Tammaru *et al.*, 2000; Gibbs *et al.*, 2004; Fantinou *et al.*, 2008; Frouz *et al.*, 2009; Reiskind & Lounibos, 2009; Tsurim *et al.*, 2013). In *L. botrana* despite high larval crowding that may have caused a high level of stress as indicated by the mortality at the highest density, the effect of larval competition on developmental and reproductive life history traits is insignificant. The duration of larval development (around 30 days of development) and number of eggs laid (around 100 eggs per female) are similar

between the different treatment densities. In addition, the pupal mass of the two sexes considered together was not different between treatments. The absence of a strong difference between larval densities could be explained by larval mortality which was highest at high density and in turn the *per capita* food available for the survivors could be the same in each treatment especially if larval mortality occurs during the initial phase of development just after larval hatch as observed in *Glyptotendipes paripes* (Frouz *et al.*, 2009). Therefore, one may hypothesize a compensatory mortality at high density with the result that more food *per capita* is available for survivors. Thereby, survivors could reach the same mass as larvae at low densities in contrast to the numerous studies reporting a decrease in adult body size at high density (Renshaw *et al.*, 1993; Ireland & Turner, 2006). In our experimental design, females did not have access to additional food, so resources mobilized for the production of eggs derived from reserves accumulated during the larval stage (Awmack & Leather, 2002). Previous studies showed that pupal mass is often a good predictor of fecundity in this species (Moreau *et al.*, 2007). Therefore, the lack of pupal mass reduction is consistent with the minor penalty on reproductive success that we found as a consequence of larval crowding. An alternative explanation is that several dead larvae may be eaten by survivors as extra food. As larval mortality increases with density, the number of available dead bodies would also increase. The occurrence of cannibalism in our model species is probably marginal but necrophagy may have occurred as in other Lepidoptera (see Chapman *et al.*, 1999, 2000 for example). Therefore, we cannot completely exclude this additional food source in our competition treatments. This latter argument explains faster growth of survival in Chrironomidae (McLachlan, 1983). In addition, a study on mosquitoes demonstrates that, with larvae under low-food supply, individuals who have the opportunity to cannibalize may survive longer than those which do not, indicating a strong benefit of this behaviour (Church & Sherratt, 1996). Further experiments should thus consider dead body removal or incorporating larval powder in the basic food to assess the relevance of such hypothesis. Finally, we cannot completely exclude that individual trait variation could have been masked by the high mortality at the higher density and in such context only the best competitors would have reached the adult stage, explaining the absence of difference between treatments.

One of this study's goals was to assess the effect of larval density on the life history traits of *L. botrana* in order to know if incorporating such factors into mathematical models would improve predictive capability. In the light of our results, it is clear that larval crowding does not fundamentally alter the development time or the reproductive capacity of this pest. Therefore, we believe that this feature does not need to be incorporated into the *L. botrana* mathematical models, and the effect of larval competition in *L. botrana* appears lower than the effects of grape cultivars for example (Moreau *et al.*, 2006*a*, *b*, 2007; Thiéry *et al.*, 2014). Further experiments in natural conditions should confirm such results by considering the number of berries in bunches, the cultivar and also the bunch growth stage which all have been shown to affect the individual fitness.

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