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Does natural larval parasitism of *Lobesia botrana* (Lepidoptera: Tortricidae) vary between years, generation, density of the host and vine cultivar?

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Abstract

Populations of European grapevine moth *Lobesia botrana* Denis & Schiffermüller and its larval parasitoids were studied for two consecutive years on an experimental insecticide-free vineyard in France planted with adjacent plots of five grape cultivars (Merlot, Cabernet Franc, Sauvignon, Cabernet Sauvignon and Sémillon) using a natural *L. botrana* population during the first year, and a natural population supplemented with artificially inoculated individuals during the second year. Levels of natural populations of larval parasitoids were measured by their parasitism rate. The ichneumonid *Campoplex capitator* Aubert was the most common species collected from *L. botrana* larvae. Its incidence was higher during the spring compared to summer. The overall parasitism rate found on the experimental vineyard varied from 23% in 2000 to 53% in 2001, and was mainly due to *C. capitator*. Parasitism was not affected by the grape cultivar on which the host developed but was positively correlated with the host density, per bunch or per stock, suggesting that among the five grape cultivars tested, *C. capitator* females probably do not discriminate between hosts feeding on different grape cultivars, but rather the densities of *L. botrana* larvae.

Keywords: parasitoids, Ichneumonidae, Tortricidae, vineyard, *Campoplex capitator*, *Scambus elegans*, *Lobesia botrana*

Introduction

In vineyards, chemical control is the most common control option against grape berry moth. Four major species of tortricids, the European grapevine moth *Lobesia botrana* Denis & Schiffermüller, the grape berry moth *Eupoecilia ambiguella* (Hübner), the leaf rolling tortrix *Sparganothis pilleriana* Denis & Schiffermüller and, less frequently, the grape tortrix *Argyrotaenia ljungiana* Thunberg, cause severe damage to grapes in most European vineyards. The European grapevine moth *L. botrana* is currently one of the major pests on grapes due to its wide geographical distribution and the heavy damage it may cause to vineyards. In French vineyards, generally between two and five insecticide applications are recommended against this species. Eggs are laid almost exclusively on bunches where larvae develop, and their control remains problematic. The larva is polyphagous and can develop on almost all cultivars of grapes. Larvae rarely move from one bunch to another and the larval patch is thus mainly attributed to the females which efficiently select between different grape cultivars for oviposition (Maher *et al.*, 2000; Maher & Thiéry, 2004). Recent results show that *L. botrana* fitness components such as larval development duration, female fecundity, and egg fertility also depend on the host plant and the grape cultivar on which the larvae fed (Thiéry & Moreau, 2005), but these authors did not consider the effect of plants or grape cultivars on the parasitoids.

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Biological control is one possible future strategy against grape berry moths (Roehrich & Boller, 1991), but until now biological control against major grape pests and especially against *L. botrana* has received little attention.

In several studies releases of egg parasitoids (e.g. *Trichogramma cacaeciae* Marchal, *T. embryophagum* (Hartig), *T. dendrolimi* Matsumura or *T. evanescens* Westwood) (Hymenoptera: Trichogrammatidae) have reduced the grape berry moth populations havoc from 20 to 80% depending upon trials and sites (Remund, 1990; Castaneda-Samayoa *et al*., 1993; Barnay, 1999). However, only a few studies have evaluated the importance of larval and pupal parasitoids in controlling tortricids in grapes. Most studies report the occurrence of different species in vineyards (Schmid, 1978; Perez Moreno *et al*., 2000; Coscola, 1997; Thiéry *et al*., 2001), but only very few data are available concerning the efficiency and the biology of these parasitoids.

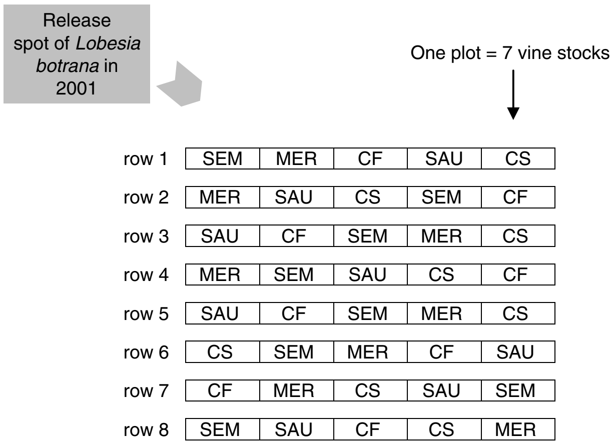
Physiology and behaviour of parasitoids are influenced by elements from their host and their host food (Price *et al*., 1980; Campbell *et al*., 1990; Vet & Dicke, 1992; Kalule & Wright, 2002). Wäckers (1994) and Takasu & Lewis (1995) demonstrated that sugar deprivation reduces host searching efficiency, partly due to a general reduction in activity and to a shift from host searching to food searching. In tritrophic systems, parasitoids are known to often use chemical cues for the location of their host (Vet & Dick, 1992; Steidle & van Loon, 2003). These cues may originate directly from the host or from their products, such as faeces or silk, or they may be emitted from the food plant of the host or from other feeding substrates. Parasitoids may also find their host due to volatile emissions from the damaged plant (Turlings & Fritzsche, 1999). All these factors may play an important role in natural parasitism. Thus, in order to efficiently use natural enemies, it is necessary to study interactions between parasitoid communities, their hosts and the host plant.

The work presented here reports field investigations on the effect of several factors on the larval parasitism by several species with special reference to *Campoplex capitator* Aubert (Hymenoptera: Ichneumonidae). The way parasitoids distribute themselves among a host patch was analysed in order to answer three questions: (i) Which larval parasitoid species are naturally occurring in vineyards? (ii) Are the same parasitoid species occuring among the generations of the *L. botrana*? and (iii) Is their distribution related to cultivars and/or host density?

Materials and methods

Experimental vineyard

The experimental vineyard is located at the INRA La Grande Ferrade, Bordeaux, France and was planted in 1973 with eight rows of 35 stocks and composed of five cultivars arranged in a patch of 40 plots of seven adjacent stocks, each cultivar being present in each row (fig. 1). Three red grape cultivars (Cabernet Franc, Cabernet Sauvignon and Merlot) and two white (Sauvignon and Sémillon) were used. Within a row, stocks are 1.1 m apart and 1.2 m separates the rows. Some stocks died during the two-year experiment and the number was then updated each year for calculations. A thicket, fruit trees, olive trees, tansy flowers, small buildings and a road surround the vineyard. This vineyard was surveyed for pests since it was planted and the only grape moths which occurred on it were *L. botrana* (from April to October) and *Ephestia parasitella* Staudinger (Lepidoptera: Pyralidae) collected from dry grapes (in October and November) (Xuéreb *et al*., 2003).



row 1	SEM	MER	CF	SAU	CS
row 2	MER	SAU	CS	SEM	CF
row 3	SAU	CF	SEM	MER	CS
row 4	MER	SEM	SAU	CS	CF
row 5	SAU	CF	SEM	MER	CS
row 6	CS	SEM	MER	CF	SAU
row 7	CF	MER	CS	SAU	SEM
row 8	SEM	SAU	CF	CS	MER

Fig. 1. Patch arrangement of the experimental vineyard, and experimental procedure. Each cultivar is represented by one plot of seven stocks in each row. SEM, Sémillon; SAU, Sauvignon; CF, Cabernet Franc; MER, Merlot; CS, Cabernet Sauvignon. Larvae were extensively collected from rows 1 to 8 except in August 2001 (rows 1 to 5).

Insect populations and collections

The study was conducted on natural populations of parasitoids. Insects were collected in 2000 and 2001 from the first and second generation *L. botrana* (i.e. in mid-June and the beginning of August). When most of the *L. botrana* larvae reached at least the fourth instar, all the larvae found were collected. They were then reared in the laboratory under controlled conditions (temperature: 22°C, relative humidity 65%, 16 : 8 L : D photoperiod) on an artificial diet as described in Maher (2002). Parasitoid cocoons were separated from *L. botrana* chrysalids and placed individually in glass tubes until the adult emerged. Sex and species of parasitoids were then determined. The emergence of both male and female moths began in the laboratory a week after collection.

In 2000 and in June 2001, the larvae were all collected from the natural population in the whole vineyard and were separated per cultivar. In 2001, the second generation of *L. botrana* was due to both natural and artificial populations: on the 6 July, about 400 *L. botrana* adults were released in one spot in order to increase the population and create a natural gradient of host density (fig. 1) The larvae were collected in August from rows 1 to 5 and separated by plots. The number of bunches per plot was also noted in order to check the effect of differences between cultivars in bunch production and the effect of the release point on the egg (and thus larval) distribution. In some parasitoid species, hyperparasitism produces males, so the sex of the emerging parasitoids was always checked in this study.

Statistical analysis

Rates of parasitism were calculated per cultivar as the ratio between the number of larvae successfully parasitized and the total number of lavae. The relative contribution

Table 1. Parasitoid species collected in 2000 and 2001 on different grape cultivars in an experimental vineyard in Bordeaux, France, and their proportion of the total number of individuals collected during the two years ($n = 307$).

Date	Cultivar	*Campoplex capitator*	*Scambus elegans*	*Dicaelotus inflexus*	*Itoplectis maculator*	Cryptinae	Braconidae	Total
June 2000	Cabernet Franc	6						6
	Cabernet Sauvignon	2						2
	Merlot	3						3
	Sauvignon	8						8
	Sémillon	2						2
August 2000	Cabernet Franc	1	2	1		0	0	4
	Cabernet Sauvignon	3	6	0		0	0	9
	Merlot	20	1	1		1	0	23
	Sauvignon	8	2	1		1	0	12
	Sémillon	24	1	1			1	27
June 2001	Cabernet Franc	1						1
	Cabernet Sauvignon	3						3
	Merlot	1						1
	Sauvignon	1						1
	Sémillon	7						7
August 2001	Cabernet Franc	23	2					25
	Cabernet Sauvignon	13	1					14
	Merlot	60	2					62
	Sauvignon	35	6		3	1		45
	Sémillon	48	2		2			52
Proportions of each species/total parasitoids for the two years		87.6%	8.14%	1.30%	1.63%	0.98%	0.32%	307

Table 2. Parasitism rates in % of the total per cultivar for two generations of *Lobesia botrana* in 2000 and 2001.

Parasitoid/cultivar	2000		2001		Mean Pr per cultivar
	G1	G2	G1	G2	
All parasitoids					
Cabernet Franc	50.00	19.05	100.00	21.01	47.51
Cabernet Sauvignon	66.67	34.62	30.00	24.56	38.96
Merlot	20.00	30.67	25.00	31.16	26.71
Sauvignon	36.36	26.67	33.33	20.28	29.16
Sémillon	33.33	33.33	77.78	17.20	40.41
Mean Pr per collection	41.27	28.87	53.22	22.84	
Campoplex capitator					
Cabernet Franc	50.00	4.76	100.00	19.33	43.52
Cabernet Sauvignon	66.67	11.54	30.00	22.81	32.75
Merlot	20.00	26.67	25.00	30.15	25.48
Sauvignon	36.36	17.78	33.33	15.57	25.76
Sémillon	33.33	29.63	77.78	16.96	39.43
Mean PrC per collection	41.27	18.07	53.22	20.96	

G1, first generation; G2, second generation; Pr, parasitism rate; PrC, relative contribution of the most abundant larval parasitoid.

of the most abundant larval parasitoid was calculated as the ratio between larvae successfully parasitized by *C. capitator* and the total number of larvae in each sample. Larval parasitism was derived from each of the two generations of *L. botrana* in 2000 and 2001. The parasitism rates of the four collections were compared using a Friedman ANOVA (referred as F values). Kruskal-Wallis ANOVA (referred as H values) was performed in order to test differences between generations and between years. Differences between cultivars were analysed for each of the four collections (Kruskal-Wallis ANOVA).

Because of the artificial infestation during the second generation of *L. botrana* in 2001, and the gradient of density of *L. botrana*, additional analyses were performed. Thus, data were arranged not only per cultivar but also per plot and sex of emerged individuals was checked. Parasitism rates were calculated for each plot, which yields five parasitism rates per cultivar. Differences in parasitism rate were compared between cultivars using a Kruskal-Wallis ANOVA, and the parasitism rate obtained for each plot was correlated to the number of bunches of the plot using a Spearman correlation. Host density dependence was analysed correlating the number of parasitoids and the parasitism rate to the number of larvae collected (Spearman correlation). Sex ratios of unparasitized and emerging *L. botrana* and parasitoids were compared to a 1 : 1 ratio using a χ^2 test. Differences of sex-ratio between cultivars were also tested (Pearson χ^2).

Results

Parasitoid species

During the two-year experiment, 1203 caterpillars were collected from which a total of 307 parasitoids emerged. The only species of Lepidoptera occurring in the experimental vineyard during these 2 years was *L. botrana*. Two parasitoids, *C. capitator* and *Scambus elegans* Woldstedt, represented 95.8% of the parasitoids collected in both years but for the first generation population only *C. capitator* was found parasitizing *L. botrana* (table 1). Both species are solitary ichneumonids. Because we collected only late host larval instars (L4 and L5), egg parasitoids such as Trichogrammatidae were not considered in this study.

Our laboratory observations showed that *C. capitator* is able to parasitize at least from the second to the fourth instars of *L. botrana*. The biology of *S. elegans* is less well known, but it has been described on many different Lepidoptera, e.g. *Cydia funebrana* (Treitschke) and *Rhyacionia buoliana* (Denis & Schiffermüller) (Fitton *et al*., 1988).

Parasitism rates

The parasitism rates found for the four collections were not significantly different (table 2, Friedman ANOVA = 2.87, $P = 0.410$). However, parasitism rates due to *C. capitator* (table 2) were significantly different (Friedman ANOVA, F = 10.68, $P = 0.014$) between the four collections. They did not vary between years (Mann-Whitney U test, z = 0.246, $P = 0.791$) but between generations (MW U test, z = 3.175, $P = 0.0015$), with a parasitism rate greater for the first generation.

Cultivar effects

Statistics performed on the four collections (two generation populations, two years), harvested no differences in parasitism rates between cultivars (ANOVA, H = 1.27, $P = 0.865$), or between the total numbers of larvae collected per cultivar (ANOVA, H = 0.94, $P = 0.918$).

Statistics performed on the data of the second generation of 2001 (data per plot) indicated no significant difference in bunch production between cultivars (ANOVA, H = 2.88, $P = 0.577$). The total number of larvae was not different between cultivars (Kruskal-Wallis ANOVA, H = 8.93, $P = 0.062$) and was not correlated to the number of bunches (rs = 0.27, $P = 0.181$). The number of parasitoids was not different between cultivars (ANOVA, H = 4.81, $P = 0.306$), neither was the number of *C. capitator* (ANOVA, H = 3.56, $P = 0.469$).

There was no correlation between parasitism rates and number of bunches (rs = 0.156, $P = 0.456$).

Host density dependence

For the second generation of 2001, the release of *L. botrana* created host densities significantly different between plots ($\chi^2 = 968.28$; $P = 0.001$): the closer to the release point, the more eggs laid by *L. botrana* females (fig. 2).

The number of parasitoids (all species together) was correlated to the total number of larvae (fig. 2, Spearman correlation: rs = 0.89, $P = 0.000$) and so was the number of *C. capitator* (fig. 3, Spearman correlation: rs = 0.86, $P < 0.0001$) but parasitism rates were not (rs = −0.18, $P = 0.379$ all parasitoids considered; and rs = 0.174, $P = 0.404$ for *C. capitator* alone).

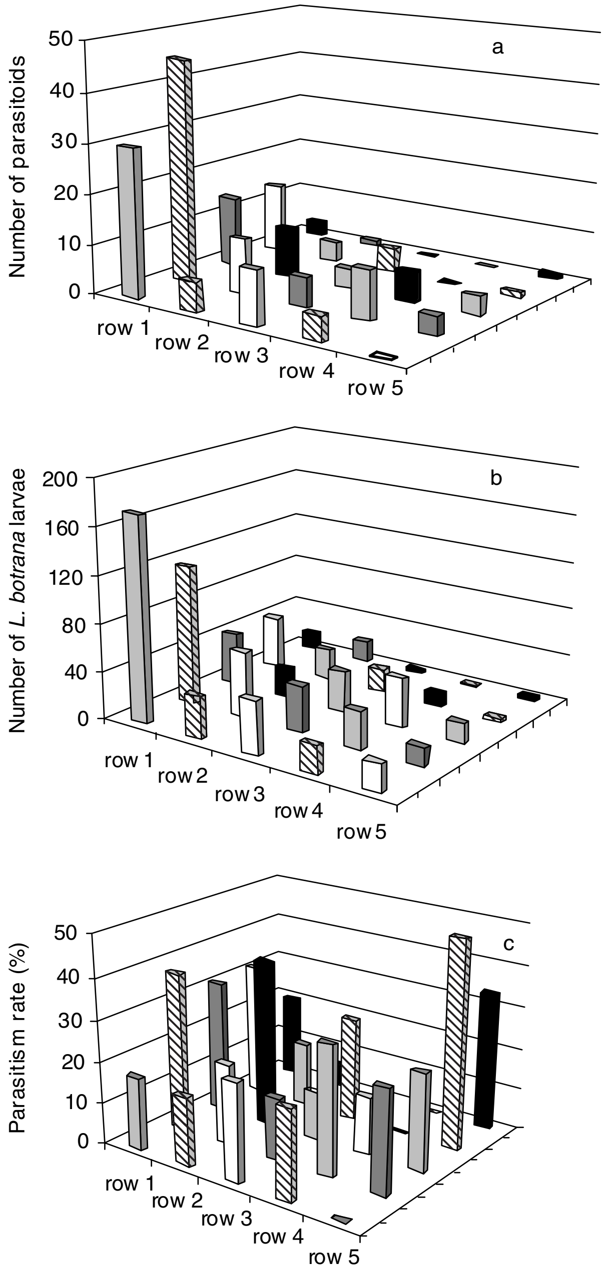


Fig. 2. Spatial representation of the data of August 2001: (a) number of parasitoids; (b) number of *Lobesia botrana* larvae; and (c) parasitism rate. Bars represent values of one plot (seven stocks of the same cultivar). ▒, Sémillon; □, Sauvignon; ▓, Cabernet Franc; ■, Cabernet Sauvignon; ▨, Merlot.

Sex ratio

Statistics were performed on data from the second generation of *L. botrana*. The unparasitized *L. botrana* pupae produced significantly more females than males (366 vs. 308; $\chi^2 = 4.99$; $P = 0.025$). This sex ratio did not depend upon the grape cultivars (Pearson $\chi^2 = 1.36$, $P = 0.823$). The sex-ratio of *C. capitator* was significantly female biased (104 females and 69 males; $\chi^2 = 7.08$; $P = 0.008$). It was not different between cultivars (Pearson $\chi^2 = 1.82$, $P = 0.769$).

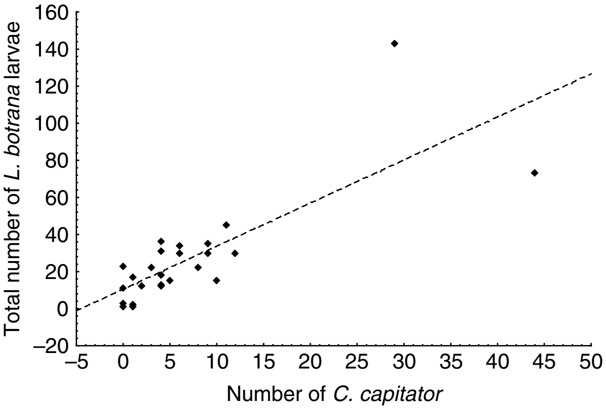


Fig. 3. Correlation between the total number of *Lobesia botrana* larvae and the number of *Campoplex capitator* (data from August 2001, Spearman correlation: R = 0.85; *P* = 0.000): each point represents one plot.

Concerning *S. elegans*, 18 individuals emerged from the collections, with significantly more males ($n = 15$) than females ($n = 3$), ($\chi^2 = 8.00$; $P = 0.0047$). Differences between cultivars were not tested because the number of individuals was too low.

Discussion

During the two-year experiment, variations of parasitism of *L. botrana* are similar: diversity is greater for second generations than for first generations and the dominant species is *C. capitator* (table 1). These results perfectly match previous observations in Italian and Spanish vineyards (Marchesini & Della Monta, 1994; Coscolla, 1997). *Campoplex capitator* is generally the only species collected from pupae of first generation *L. botrana* larvae. As consequence, parasitism rates due to this species are greater for the first generations of *L. botrana* in June than for the following generations. These parasitism rates were relatively close between years: 41.27% and 53.22% for the first generations, 18.07% and 20.96% for the second generations of *L. botrana*, but despite this reduced rate of parasitism, the number of individuals emerging from the chrysalids was higher in the second generation. Further observations would thus be needed to compare the parasitism rates between successive generations of *L. botrana*.

Because of its natural efficiency and because it is the only parasitoid occurring early in the season and also occurring in the summer, *C. capitator* can be a good candidate for controlling successive generations of *L. botrana*. It also occurred in the autumn in Bordeaux as diapausing pupae, which indicates that it can also parasitize the late autumn third generation of *L. botrana* larvae (A. Xuéreb & D. Thiéry, unpublished data). The present results show that in the specific arrangement of our experimental plot, the parasitism rate of *C. capitator* does not depend on the grape cultivar offered to the host larvae but on the host density. This effect should, however, be confirmed with other grape cultivars or by studies on different crop architectures or different patch arrangements. The fact that *C. capitator* is mainly influenced by its host density is, however, rather classical, and confirms previous observations on a single cultivar vineyard planted with Cabernet Franc (A. Xuéreb & D. Thiéry, unpublished data). This result seems in favour of biological control applications, suggesting that parasitism is probably not influenced by the grape cultivars surveyed in this study.

The sex-ratio of emerged *L. botrana* was slightly female-biased: *c.* 54% of *L. botrana* ($n = 896$) were females. This corresponds to other results obtained from larvae collected in autumn 2004 in a vineyard planted with different cultivars: 752 larvae yielded more than 52% of females (D. Thiéry & A. Xuéreb, unpublished data). Rather classically, most of the larval parasitoids prefer to lay female eggs on the biggest hosts when they have a choice (Van den Assem, 1971; Charnov, 1982) and female *L. botrana* larvae with no food limitation are always bigger than males and especially on any grape cultivars tested (J. Moreau & D. Thiéry, unpublished data). Thus, one could have expected a male-biased sex ratio. The fact that the sex ratio of emerging *L. botrana* corresponds with what is usually observed in the field, suggests that big larvae have probably not been preferred to smaller ones by *C. capitator* females.

According to the slow-growth-high-mortality hypothesis, the prolonged larval development of herbivores results in a greater vulnerability and thus a greater mortality due to natural enemies (Clancy & Price, 1987). Although the food quality and the cultivar on which larvae develop affect the duration of the third and fourth larval instars (Savoupoulou Soultani & Tzanakakis, 1988; Thiéry & Moreau, 2005), we found no difference in parasitism between cultivars. *Scambus elegans* produces males (unfertilized eggs), when it behaves as a hyperparasitoid and females (fertilized eggs) when parasitizing moths. The sex ratio is therefore a good indicator of the parasitic behaviour of this species. In 2000, it was balanced indicating that *S. elegans* parasitized both *L. botrana* and other parasitoids, while in 2001 it parasitized almost exclusively (83% of males) other parasitoids. Thus, this species could limit the population of *C. capitator*. In 2001, *S. elegans* probably exploited other hosts around the vineyard to produce females. This species is known to parasitize a wide number of Lepidoptera such as *Cydia funebrana*, the plum fruit moth and *Rhyacionia buoliana*, the pine tip moth (Fitton *et al*; 1988), two hosts that could be present around the vineyard, on the plum trees and the pines. It is also likely that *S. elegans* exploited *L. botrana* when these hosts were no longer available, which can explain why they are collected in the vineyard during the second generation of *L. botrana*.

Campoplex capitator shows a female biased sex-ratio (about 60% of females) which is common in parasitoids, males being able to fecundate several females. The wasp *C. capitator* is considered as a specialist of *L. botrana*, which is a polyphagous lepidopteran, but its specialist status could be reconsidered since it has been described parasitizing the microlepidopteran *Ancylis mitterbacheriana* (Denis & Schiffermüller) on the oak *Quercus pubescens* (Aubert, 1983), and has been found in several vineyards on another tortricid of grape, *Eupoecilia ambiguella* (Thiéry *et al*., 2001). Although the length of the ovipositor seems to differ between the *C. capitator* found on *L. botrana* and *E. ambiguella* (C. Villemant, unpublished data), which suggests the occurrence of subspecies presenting morphological adaptations to the larval host feeding habits (C. Villemant, personal communication), the existence of such sub-species has still to be confirmed. Additional observations are also needed to conclude on its specialist status and to under-stand its host selection behaviour. The significant efficiency of *C. capitator* in the spring generation, either with low or important population levels of *L. botrana* (D. Thiéry *et al*., unpublished data) is interesting because it might control efficiently the pioneering generation of *L. botrana* in vineyards. A logical biological strategy based on this parasitoid would be to produce and release it early in the season in order to reduce the demography of further generations of the moth.

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