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1 *Lobesia botrana* as a preferred host of *Campoplex capitator*, the most
2 occurring larval parasitoid in European vineyards

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18

19 **Abstract**

20 Parasitoids are major biological agents in crop protection, and understanding their preference
21 towards specific host species is a key aspect of successful pest control. In the present study, we
22 have examined the host preferences of the larval parasitoid *Campoplex capitator*
23 (Hymenoptera: Ichneumonidae), one of the major natural enemies for tortricid grapevine pest
24 populations in European vineyards. Using a test choice between its two main and sympatric
25 hosts, we wanted to determine whether *C. capitator* females that emerged from *Lobesia botrana*
26 (Lepidoptera: Tortricidae) also prefer its natal host *L. botrana*, or *Eupoecilia ambiguella*
27 (Lepidoptera: Tortricidae) as host; and consequently, if it could be a good candidate as a bio-
28 agent for these species. Our results distinctly showed that naïve *C. capitator* females preferred
29 *L. botrana* over *E. ambiguella* as host, as they directly sought out new *L. botrana* hosts. Overall,
30 it reveals that *C. capitator* could be a very efficient parasitoid to control *L. botrana* populations.
31 Our results might also suggest the importance of natal host in parasitoid host preference, which
32 should be considered in the future when mass-rearing bio-agents.

33

34 **Key-words:** grapevine moth, host species preference, larval parasitoid, choice test.

35

36 **1. Introduction**

37 With more than 900,000 known species, insect herbivores represent nearly a quarter of all
38 terrestrial macroscopic biodiversity, acting as a dominant component of all terrestrial food webs
39 on Earth (Resh and Cardé 2009; Sauvion et al. 2017). While they are well regulated by both
40 host plant and natural enemies within their ecosystems (Kaplan et al. 2016), agroecosystems
41 often break this balance – through agriculture intensification, monoculture development and
42 pesticide use – and favor the emergence of pest species (Wilby and Thomas 2002). Even if only
43 2% of insect herbivores species are considered as pests (Dhaliwal et al. 2010), they are
44 responsible for an estimated crop loss of up to 50 % (Thacker 2002; Aggarwalim et al. 2006)
45 and are consequently a major human concern, with implications for public health and
46 agriculture. At a crucial time when farmers struggle to increase or at least maintain yields while
47 reducing pesticide use for environmental and health issues, biological control and integrated
48 pest management strategies appear to be the best current alternatives (Brewer and Goodell
49 2012).

50 Biological control is based on population regulation and specially on interactions
51 between a host – here, insect herbivore – and its natural enemies (e.g. parasitoids, predators,
52 pathogens) (Van Driesche et al. 2008). It includes, for example, the release of one or more
53 natural enemies into a targeted agroecosystem to control a growing pest population. Parasitoids
54 – specially hymenopterous parasitoids – are key biological agents, and have been the most
55 common type of natural enemy used in crop protection (Van Driesche et al. 2008; Giunti et al.
56 2015). Parasitoids evolve in a complex environment and therefore rely on a variety of stimuli
57 (e.g. visual, vibrational and olfactory cues) to locate a suitable habitat with host, food and/or
58 mates (see Giunti et al. 2015 for reviews). Multiple factors can influence parasitoids' host
59 foraging, including host size and density, but also importantly their learning capacity (Lin and
60 Ives 2003; Giunti et al. 2015; Morgan et al. 2016). While there is a heritable component for

61 habitat preference, it remains unclear as to exactly when this preference development occurs
62 (i.e. during early life stages, after emergence, or both), despite numerous theories informing
63 optimal parasitoid foraging (Barron 2001; Davis and Stamps 2004; Giunti et al. 2015). The
64 notion of Natal Habitat Preference Induction (NHPI) has been proposed by Davis and Stamps
65 (2004) to better understand such processes, and states that animals prefer to develop in a similar
66 habitat to the one they experience in early life stage. The learning process associated with this
67 notion is mostly related to chemical cues coming from the natal habitat which are memorized
68 during ontogeny (Corbet 1985; Ruther et al. 2002). For instance, females of the parasitoid
69 *Psytalia concolor* (Hymenoptera: Braconidae) exhibit different oviposition preferences
70 depending on their natal host – i.e. females did not always prefer to oviposit in their natal host
71 (Giunti et al. 2016). Altogether, this raises one of the most important challenges in biological
72 control: the plastic specificity between the bio-agent and targeted host.

73 In order to conduct an efficient and sustainable pest population control, the parasitoid should
74 be able to successfully target its pest species (Van Driesche et al. 2008), even in an environment
75 susceptible to host several pest species. Agroecosystems, such as vineyards, can host a large
76 number of pests living in sympatry (Vogelweith and Thiéry 2018), and as such, investigating
77 host preference in parasitoids is crucial for biological control. The grape berry moth *Eupoecilia*
78 *ambiguella* (Hubn.) (Lepidoptera: Tortricidae) and the European grapevine moth *Lobesia*
79 *botrana* (Den. & Schiff.) (Lepidoptera: Tortricidae) are two polyphagous grapevine pests
80 (reviewed: Thiéry et al. 2018). These two species are responsible for significant damages in
81 vineyards either directly by attacking grape bunches – a larva is able to damage between 2 and
82 10 berries depending on the grape cultivar – or indirectly by favoring the development of several
83 fungi, such as *Botrytis cinerea*, *Aspergillus carbonarius*, and *Aspergillus niger* (Delbac and
84 Thiéry 2016; Thiéry et al. 2018). *Eupoecilia ambiguella* mostly occurs in central Europe while
85 *L. botrana* is widely distributed but mostly occurs at high density in Mediterranean climates

86 (Thiéry 2008). However, in several European vineyards, these two species can share common
87 distributional range where they often live in sympatry, as in Beaujolais vineyards for example
88 (North of Lyon, France) (Vogelweith et al. 2014). The density of each species within vineyards
89 can vary from 15:75 to an equal distribution 50:50 (unpublished data). Despite such differences,
90 biological control of *E. ambiguella* and *L. botrana* has always been the same, mostly performed
91 through the release of the egg parasitoid *Trichogramma* sp. (Hymenoptera:
92 Trichogrammatidae) (Vogelweith et al. 2014; Thiéry et al. 2018). For the past decade, the larval
93 parasitoid *Campoplex capitator* (Hymenoptera: Ichneumonidae) has drawn more and more
94 attention (Marchesini and Dalla Monta 1994; Xuéreb and Thiéry 2006). Cosmopolitan and
95 very plastic in its ecological requirements (Moreau et al. 2010), this parasitoid is very efficient
96 in regulating grapevine pest populations, with sometimes a level of parasitism rate up to 90%
97 in *L. botrana* (Vogelweith et al. 2013). But, attempts to massing-rear *C. capitator* for the control
98 of grapevine pests has always failed, chiefly because of the limited information about its
99 biology/ecology, including the limited understanding of its ability to switch from the rearing-
100 host (e.g. *L. botrana*) to hosts encountered in the field (e.g. *L. botrana* and *E. ambiguella*)
101 (unpublished data). For instance, the larval-pupal parasitoid *Psytalia concolor* (Hymenoptera:
102 Braconidae) reared on the fruit fly *Ceratitis capitata* (Diptera: Tephritidae) (Canale and Benelli
103 2012) did not show any difference in oviposition behaviors and host acceptance when provided
104 either with its rearing host *C. capitata* or the alternative host pest *Bactrocera oleae* (Diptera:
105 Tephritidae) (Canale and Benelli 2012).

106 Here we seek to determine, for the first time, whether *C. capitator* females emerged from
107 wild populations of *L. botrana* prefer *E. ambiguella* or *L. botrana* as host in a choice test, and
108 consequently whether it could be a good candidate as bio-agent to regulate grapevine pest
109 populations.

110

111 2. Material and methods

112 2.1. Model insects

113 Larvae of *E. ambiguella* and *L. botrana* used in this experiment came from two independent
114 rearing facilities, maintained diapause-free at the French National Institute for Agricultural
115 Research (INRA) (Villenave d'Ornon, France) for more than 15 years (see Vogelweith et al.
116 2017). These two strains were based on multiple adults reared in flying cages to which wild
117 individuals were periodically added. Larvae of each species were provided with *ad libitum*
118 semi-artificial diet (Vogelweith et al. 2015) and maintained in similar boxes ($18 \times 11.5 \times 7$ cm)
119 under the same standard laboratory conditions ($22 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH, and a L16:D8
120 photoperiod) at a density of approximately 100 individuals per 300 ml of diet. Corrugated
121 papers were placed within each box, allowing the larvae to hide, as they did in grape berries.

122 Female parasitoids of *C. capitator* were obtained from wild parasitized *L. botrana* larvae
123 collected on Grenache cultivar in a French vineyard (N $42^\circ44'7.063''$, E $2^\circ52'56.441''$;
124 Perpignan, France) in May 2013 (see Vogelweith et al. 2013). Sampled larvae were maintained
125 in polyethylene boxes ($60 \times 40 \times 21.4$ cm) with *ad libitum* Grenache grape bunches from the
126 vineyard, at $24 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH and under the ambient photoperiod conditions. Corrugated
127 papers were placed in the boxes to facilitate pupae collection (larvae like to shelter in such
128 material before pupation) and checked daily for pupation. After pupation, pupae were
129 individually moved into glass tubes (70×9 mm diameter) closed with cotton plugs under the
130 conditions stated above and checked daily until emergence from either an adult moth or a
131 parasitoid. Different parasitoid species emerged from larvae and after identification (Thiéry
132 2008), only *C. capitator* females (easily visually identifiable with their ovipositor) were kept
133 for this experiment. Parasitoid females were transferred to clean glass tubes provided with a
134 droplet of honey and cotton plugs soaked with water, but otherwise kept at the same conditions.
135 All *C. capitator* females used in this experiment were tested two days after their emergence,

136 naïve (no prior oviposition) and were kept virgin because females of this species can also
137 reproduce parthenogenetically, producing in such case only males (Morris and Fellowes 2002;
138 Thiéry and Xuereb 2004).

139

140 2.2. Experimental design

141 A total of 22 *C. capitator* females were tested to determine their preference between *E.*
142 *ambiguella* and *L. botrana*. Tests were carried out in an experimental arena constituted of a
143 Petri dish (95 mm diameter, 62 mm high) divided into two equal zones (Fig. 1): one zone
144 dedicated to *E. ambiguella*, and the second dedicated to *L. botrana*. At the center of each zone
145 was taped a piece of corrugated paper containing a 4th instar larva of either *E. ambiguella* or *L.*
146 *botrana* (Fig. 1). Prior to the test, all larvae were checked to ensure they were at the same instar
147 (4th instar) based on the larval head capsule size (1.2 ± 0.1 mm) (Delbac et al. 2010), and without
148 physical damages. Then, larvae were moved to the small piece of corrugated paper using a
149 paintbrush washed with 90% ethanol after each larva. The female parasitoid was then released
150 in the middle of the experimental arena. Its behavior was recorded until the first attack (defined
151 as the first oviposition attempt) or for a maximum of 30 min. During this time-period, the first
152 species visited, the time spent by the parasitoid on each side of the arena (*E. ambiguella* versus
153 *L. botrana* sides), the number of visits to each larva and the chosen larva (i.e. larva which
154 suffered from an oviposition attempt) were recorded. As female *C. capitator* can perform
155 multiple oviposition attempts in few seconds, inflicting serious injuries to the larva, a test was
156 ended after the first attack. Each test was performed with a different female parasitoid and host
157 larvae. The position of each species in the experimental arena was exchanged every time and a
158 new arena was used for each repetition to avoid potential influence of cues/odor from both
159 parasitoid and larvae. The experiment was performed for two hours (four individuals during 30

160 min per day), every day during six days, at the sunset – time-period where parasitoids are the
161 most active – at $24 \pm 1^\circ\text{C}$, $60 \pm 10\%$ RH and under the ambient photoperiod conditions.

162

163 2.3. Statistical analyses

164 All data analyses were conducted using the software R v3.5.1 loaded with *car* and *lme4*
165 packages. The proportion of time spend by the female parasitoid on each side was tested using
166 a Chi-squared test for given probabilities where the proposition of time spent on the *L. botrana*
167 side was compared to a probability of 0.5. The number of visits per host species was tested
168 using a generalized linear model (GLM) with poisson distribution, and the species (*L. botrana*
169 or *E. ambiguella*) entered as explanatory categorical factors. Finally, the first species visited as
170 well as the choice made by the female parasitoid were tested using a generalized linear model
171 (GLM) with binomial error distribution, and the species (*L. botrana* or *E. ambiguella*) entered
172 as explanatory categorical factors.

173

174 3. Results

175 The first choice (i.e. the first larva visited) by *C. capitator* females was almost always *L.*
176 *botrana* (95.45 % of the cases; $F_1 = 44.72$; $p < 0.0001$). Moreover, females spent significantly
177 more time on *L. botrana* side of the experimental arena ($\chi^2_1 = 7.68$; $p = 0.006$; IC 95% = [0.59;
178 0.94]; Fig. 2a) and visited more often *L. botrana* larvae compared to *E. ambiguella* larvae (F_1
179 = 10.11; $p = 0.001$; Fig. 2b). Finally, *C. capitator* females almost exclusively attacked *L.*
180 *botrana* larvae ($F_1 = 31.18$; $p < 0.0001$; Fig. 2c).

181

182 4. Discussion

183 Although host preference in parasitoids has been well studied, whether a parasitoid prefers its
184 natal host or an alternative host in an agroecosystem hosting sympatric pest species remains

185 unexplored. Based on a choice test experiment, our results clearly showed that *C. capitator*
186 females emerged from wild population of *L. botrana* preferred the latter as host over *E.*
187 *ambiguella*. Indeed, they went mostly directly to the *L. botrana* side, spent more time on this
188 side and visited it more often compared to *E. ambiguella* larvae. Finally, *L. botrana* larvae were
189 almost exclusively choose/attacked by *C. capitator* females.

190 At least three non-mutually exclusive hypotheses could explain such preference. The first
191 hypothesis relies on the notion of NHPI (Davis and Stamps 2004), meaning that *C. capitator*
192 females emerged from *L. botrana* prefer to lay their eggs in *L. botrana* larvae due to special
193 stimuli received in early-life in their native habitat. Mounting evidence suggests the importance
194 of the cues learned during ontogeny on parasitoid choice (Morris and Fellowes 2002; Bodino
195 et al. 2016; Giunti et al. 2016). Such learning can take place after emergence or during pre-adult
196 stages (when the parasitoid is still on/inside its host) and/or during adult emergence (Giunti et
197 al. 2015), as illustrated by the endoparasitoid *P. concolor*. Females from the latter excised from
198 their host just before emergence – and consequently did not have contact with a natal host in
199 early adult life – were unable to show a preference for the natal host (Giunti et al. 2016). Our
200 results are consistent with the NHPI hypothesis even though we cannot determine whether *C.*
201 *capitator* females are using pre- or post-emergence learning. The same experiment should be
202 performed with *E. ambiguella* as natal host to confirm that statement. Parasitoid learning could
203 also occur through an associative learning where they learn to associate cues from their
204 environment to increase their foraging efficiency (Hoedjes et al. 2011). In our study, parasitoid
205 cocoons were removed from their environmental complex and placed under control conditions,
206 meaning that associative learning was not tested here. As such, we do not know the
207 consequences of host species choice upon *C. capitator* fitness. This point should be investigated
208 in a further field survey where *C. capitator* live in an environment where *L. botrana* and *E.*
209 *ambiguella* are in sympatry.

210 Secondly, parasitoids can also inherit natal environmental preferences related to a local
211 adaptation that may result in a parasitoid population specializing on one host (Gutiérrez-Ibáñez
212 et al. 2007; Zepeda-Paulo et al. 2013; Bodino et al. 2016). A previous study suggested a local
213 adaptation of *L. botrana* larvae to existing parasitoid pressure (Vogelweith et al. 2013). Since
214 *L. botrana* and *C. capitator* co-evolved in vineyards for many years, it is also likely that *C.*
215 *capitator* have adapted to local host species. Indeed, *C. capitator* used in this experiment came
216 from an area where *L. botrana* are predominant compared to *E. ambiguella* (Ricaud 2013).

217 Finally, the third hypothesis involves the defense strategies used by *E. ambiguella* and *L.*
218 *botrana* larvae (Vogelweith et al. 2014). Despite many similarities in their ecological
219 requirements and their natural enemies, these two species have been shown to invest differently
220 in the defense mechanisms which might influence parasitoid choice (Brodeur et al. 1996;
221 Vogelweith et al. 2014). Indeed, even though *L. botrana* larvae have been shown to express
222 strong behavioral defenses, their cuticle and immune system are less resistant to parasitoids
223 compared to *E. ambiguella*'s (Vogelweith et al. 2014). Therefore, the choice performed by *C.*
224 *capitator* is very consistent, and could be the result of a local adaptation of *C. capitator* to *L.*
225 *botrana* larvae in the field, as mentioned in the second hypothesis.

226 In conclusion, these results show that biological control by augmentation – relying on the
227 release the of natural enemies (i.e. *C. capitator*) that occur in the agroecosystem – could be very
228 efficient against *L. botrana* populations due to the high specificity of its parasitoid. However,
229 it might be less efficient against *E. ambiguella* populations, at least if *C. capitator* has *L.*
230 *botrana* as natal host. More investigations about the relationship between *C. capitator* and *E.*
231 *ambiguella* should be performed in order to consider this parasitoid as a potential bio-agent.
232 But, it is important to recall that studies and field reports indicated that *C. capitator* is
233 parasitizing *E. ambiguella* in European vineyards (Colombera et al. 2001; Thiéry et al. 2011,
234 2018; Rusch et al. 2015), even if parasitism success is higher in *L. botrana* than in *E. ambiguella*

235 when the ratio of both species in the population is close to 50:50 (Vogelweith et al. 2014).
236 Further investigations should be done in order to determine whether it would also be a good
237 candidate to control *E. ambiguella* populations. Altogether, this study is one of the first to reveal
238 *C. capitator*'s potential as a valuable and efficient bio-agent for the control of grapevine moths
239 in European vineyards.

240

241 **Conflict of interest**

242 The authors declare no competing financial interests.

243

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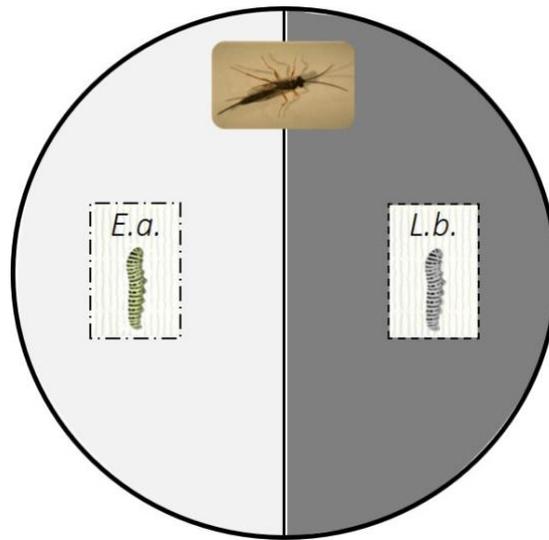
349 **Figure legends**

350 **Figure 1.** Diagram of the experimental arena used to test the preference of the female *C.*
351 *capitator* between the two grapevine moth species: *E. ambiguella* and *L. botrana*. The big circle
352 represents the Petri dish. The middle line represents the border between the *E. ambiguella* zone
353 (white) and the *L. botrana* zone (grey). The two ribbed squares represent the corrugated papers
354 with either *E. ambiguella* (*E.a.*; dashed/dotted line) or *L. botrana* (*L.b.*; dashed line) inside.

355

356 **Figure 2.** (a) Percentage of time spend by the female *C. capitator* on *E. ambiguella* (*E. a.*) or
357 *L. botrana* (*L.b.*) sides (\pm C.I. 95%); (b) Number of visits to each host species by *C. capitator*
358 female (\pm C.I. 95%); (c) Percentage of *C. capitator* females performing a choice for either *E.*
359 *ambiguella* or *L. botrana*. Note that 3 of the 22 female parasitoids did not perform any attack
360 on either host. Asterisks indicate statistically significant differences ($p < 0.05$).

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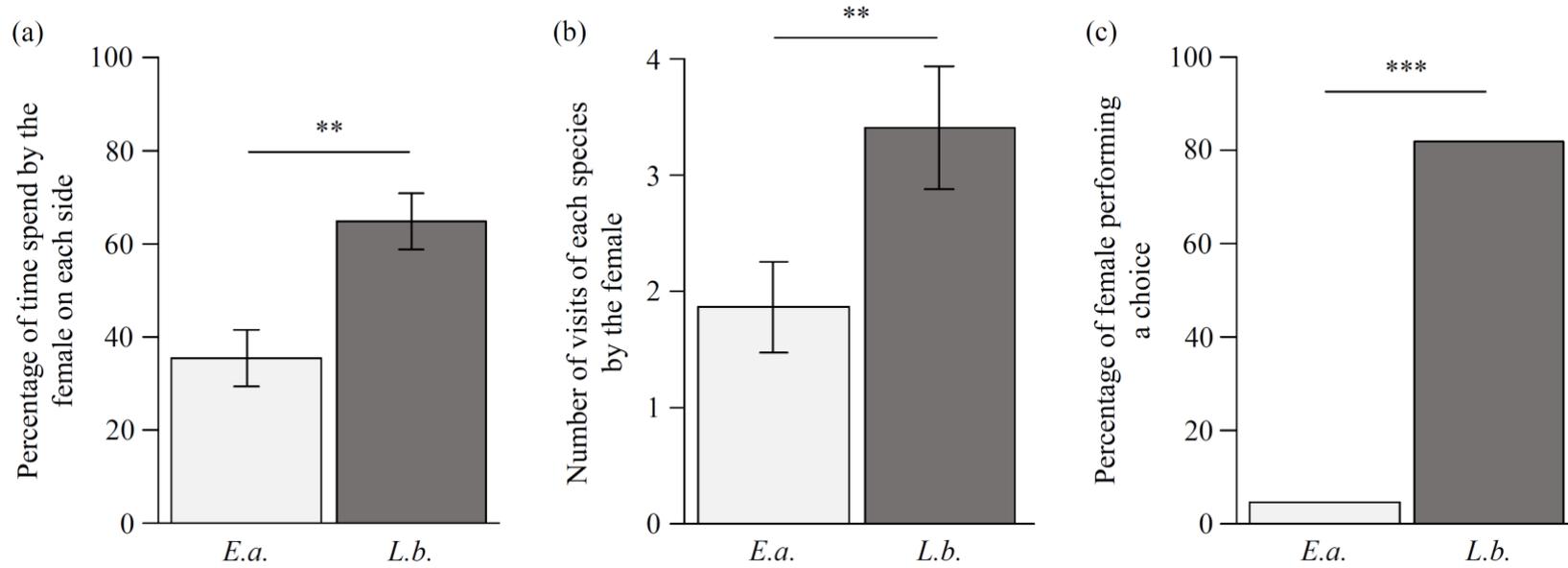
Figure 1

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Figure 2

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