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1 **Reproductive performance of the European grapevine moth**  
2 ***Lobesia botrana* (Tortricidae) is adversely affected by warming**  
3 **scenario**

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13

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19

20 **Abstract**

21 The European grapevine moth, *Lobesia botrana* (Denis and Schiffermüller), is an important  
22 grape pest worldwide. To forecast how this species might respond to climate change has  
23 emerged as one major challenge in recent viticultural research. Predictions about *L. botrana*  
24 population dynamics under global warming scenario are usually derived from  
25 physiologically-based demographic models (PBDMs). Despite their ecological realism,  
26 PBDMs are based on physiological equations derived from constant, unrealistic thermal  
27 regimes, and they exclude the effects of temperature on male's reproductive traits, which  
28 importantly mediates population dynamics in this species. Focused on Burgundy (a  
29 viticultural region of France), we compared the adult performance of *L. botrana* between the  
30 Current Fluctuating Regime (CFR) based on *in situ* meteorological data and the Future  
31 Fluctuating Regime (FFR) based on the outputs of climate models. Under controlled  
32 conditions complying to the scenario of local warming termed FFR, *L. botrana* individuals  
33 incurred reduced adult lifespan while their body amounts of four major energetic components  
34 (proteins, lipids, glycogen, soluble carbohydrates) remained unchanged compared to  
35 individuals exposed to the CFR. Furthermore, each sex endured reproductive costs associated  
36 with local warming scenario: females incurred reduced mating success, males bore decreased  
37 fertility (lower number of eupyrene sperms within spermatophore). Our results indicate that  
38 global warming should adversely impact the reproductive success of *L. botrana* and the local  
39 abundance of this pest. In terms of pest management, our findings might contribute to  
40 increase the ecological realism of PBDMs and improve the reliability of their predictions  
41 about the population dynamics of *L. botrana*.

42 **Keywords**

43 Fluctuating thermal regimes, global warming, grapevine pest, *Lobesia botrana*, population  
44 dynamics, sperm quality

45 **Key message**

46 . Using realistic fluctuating thermal regimes, we explored the consequences of global  
47 warming in Eastern France (Burgundian winegrowing region) for the adult performance of the  
48 grapevine pest *Lobesia botrana*.

49 . Under thermal conditions complying to a scenario of local warming, individuals of both  
50 sexes incurred reduced lifespan and decreased reproductive performance: females experienced  
51 reduced mating success, males endured decreased sperm fertility.

52 . These findings suggest that warming should negatively impact the reproductive success and  
53 local abundance of *L. botrana*.

54 **Author contribution statement**

55 All authors conceived the experiments. CI and KP run out the experiments. CI and PL  
56 analysed the data. CI, PL, JM and DT led the writing of the manuscript. All authors critically  
57 revised the intellectual content of the draft and gave their approbation for the final version to  
58 be published.

## 59 **Introduction**

60 Viticulture is facing new threats and challenges worldwide, owing chiefly to anthropogenic  
61 disturbances (Fraga et al. 2012). In the current climatic context, rising temperatures are  
62 predicted to impact grapevine cultivation by modulating the risks of pest outbreaks and  
63 emergence of insect-borne diseases (Fraga et al. 2012; Reineke and Thiéry 2016). Indeed,  
64 grapevine is targeted by numerous insect pests exerting detrimental effects on grape  
65 production through feeding on plant tissues and/or by acting as vectors of plant diseases  
66 (Reineke and Thiéry 2016; Thiéry et al. 2018). As ectothermic animals, phytophagous insects  
67 are very sensitive to environmental temperature, which regulates their physiology, individual  
68 performance and population dynamics in space (distribution range) and time (life cycle  
69 duration, phenology) (Bale et al. 2002; Reineke and Thiéry 2016). In view of the many threats  
70 global warming poses to the long-term viability of vineyards, to predict how the projected  
71 increase in global mean temperature might affect the population dynamics of major grapevine  
72 pests and anticipate the possible repercussions on grapevine cultivation has emerged as one  
73 major challenge in recent viticultural research (Reineke and Thiéry 2016; Castex et al. 2018;  
74 Thiéry et al. 2018).

75         The European grapevine moth, *Lobesia botrana* (Lepidoptera: Tortricidae), is one of  
76 the most harmful viticultural pests in the Palearctic region (Thiéry et al. 2018). Quantitative  
77 and qualitative damages are triggered by caterpillars while attacking vine fructiferous organs  
78 (floral buds, ripening and mature berries). Larval feeding on berries induces severe yield  
79 losses because of direct consumption of agricultural production. Moreover, it allows the  
80 intrusion of several fungal agents responsible for bunch rot development (*Botrytis cinerea*,  
81 *Aspergillus carbonarius*, *A. niger*) and increases the plant susceptibility to other grape berry  
82 boring pests like fruit flies (Cozzi et al. 2006; Reineke and Thiéry 2016). The economic  
83 impacts of *L. botrana* have been rated as ‘high’, provided that one caterpillar might infest

84 between 2 and 10 berries throughout its development, and that density might reach up to 20-  
85 30 larvae per bunch in heavily infested vineyards (Delbac and Thiéry 2016). High levels of  
86 economic injury due to *L. botrana* activity are also suggested by considerable yield losses like  
87 those recorded in Greece, amounting from 13.3% to 27% of the total grape production over a  
88 4-year period (Moschos 2006).

89 Predictions about *L. botrana* population dynamics under global warming scenario are  
90 usually derived from physiologically-based demographic models (PBDMs) (Gutierrez et al.  
91 2012, 2017). These mechanistic models rely on equations describing the effects of  
92 temperature on physiological processes enabling to infer population growth, above all  
93 developmental rates, survival and *per capita* fecundity (total number of eggs laid by one  
94 female) (Gutierrez et al. 2012, 2017; Gilioli et al. 2016). PBDMs can be coupled with *in situ*  
95 weather data and climate change scenarios to project the current and future geographical  
96 distribution of *L. botrana* across a lattice of spatial cells. This way, PBDMs allow to  
97 anticipate the local dynamics of *L. botrana* populations in terms of abundance and phenology  
98 (Gutierrez et al. 2012, 2017). These models predict that, concurrently with grape yield, the  
99 abundance of *L. botrana* populations should increase northward and in higher elevations of  
100 the Euro-Mediterranean region, while the opposite trend should be observed for southern  
101 areas where summer conditions will adversely impact the moth vital functions and reduce  
102 grape yields (Gutierrez et al. 2017).

103 Notwithstanding their ecological realism (i.e. the possibility to include the bottom-up  
104 effects of grapevine phenological stage on *L. botrana* physiology), PBDMs suffer from  
105 shortcomings that could limit their ability to accurately forecast the future of *L. botrana*  
106 populations in a rapidly changing climatic context. First, their equations are based on data  
107 obtained under constant temperatures (Gutierrez et al. 2012). For that reason, their predictions  
108 might differ from biological conclusions drawn by comparing the performance of *L. botrana*

109 under daily fluctuating thermal regimes, which reflect more realistically the day/night  
110 variations of temperatures experienced by insects in their natural environment (Colinet et al.  
111 2015). Second, by expressing fecundity as a function of temperature and female's age,  
112 PBDMs implicitly rule out the importance of male's reproductive performance on female's  
113 egg production. Nonetheless, in *L. botrana* as in many other lepidopteran species, the  
114 spermatophore delivered during copulation does not only include sperm but also accessory  
115 gland secretions containing nutrients absorbed by female to boost her egg production (South  
116 and Lewis 2011). Since *L. botrana* is a capital breeding species (i.e. with a non-feeding adult  
117 stage), the quality of the nutritive ejaculate delivered by male during copulation importantly  
118 mediates the resources allocated to egg production and the reproductive output of the pair  
119 (number of eggs laid, hatching success) (Muller et al. 2015, 2016a). Provided that ejaculate  
120 quality is usually temperature-dependent in arthropod species (Zeh et al. 2012; Vasudeva et  
121 al. 2014), addressing the effects of warming on male's ejaculatory traits is required for a  
122 better understanding of the consequences of climate change for *L. botrana* reproduction and  
123 population dynamics.

124 In view of the concerns raised above, we performed laboratory experiments to  
125 investigate the consequences of local warming scenario for the performance of *L. botrana*  
126 adult females and males. More specifically, our study aimed at investigating the consequences  
127 of temperatures experienced by *L. botrana* individuals during their whole life on the  
128 expression of reproductive traits. For this purpose, we compared the performance of each sex  
129 separately between two daily fluctuating thermal regimes designed to reflect current or  
130 simulate future thermal conditions in our study area (Burgundy, Eastern France). We recorded  
131 several surrogates for overall performance in both sexes, including body amounts of four  
132 major energetic components available upon moth emergence (proteins, lipids, glycogen,  
133 soluble carbohydrates), and adult lifespan. Additionally, we assessed the effects of

134 temperature on the reproductive traits of females (mating success, number of eggs laid,  
135 hatching success, oviposition dynamics) and males (mating success, spermatophore volume,  
136 sperm quality).

137 Previous works focused on the consequences of rising temperatures for *L. botrana*  
138 larval performance reported that caterpillars of this species respond to warmer conditions by  
139 speeding up their larval development, which implies a reduced time allowed for feeding (Iltis  
140 et al. 2018, 2019). Importantly, such findings have been observed when comparing the two  
141 fluctuating regimes used in this study (Iltis et al. 2019). We therefore expect that this plastic  
142 reduction in the duration of the feeding stage should negatively adult performance, resulting  
143 in lower stocks of energetic components available upon moth emergence, shortened adult  
144 lifespan and decreased reproductive performance of both sexual partners, which crucially  
145 hinges on resources acquired through the alimentation of larval stages (Moreau et al. 2006;  
146 Muller et al. 2015).

## 147 **Materials and methods**

### 148 *Thermal regimes*

149 This study involved two daily fluctuating thermal regimes designed to reflect current and  
150 expected future thermal conditions in Burgundy, Eastern France (Longvic-Dijon weather  
151 station, 47,27°N; 5,09°E; altitude = 219 m) ([www.meteofrance.com](http://www.meteofrance.com)). Both these two regimes  
152 aimed at emulating an average day during summer period (15<sup>th</sup> July – 15<sup>th</sup> August), because *L.*  
153 *botrana* exhibits high levels of activity (i.e. one peak of adult emergence) over this date range  
154 (Barnay et al. 2001; Martín-Vertedor et al. 2010). The regime used to simulate summer  
155 conditions currently found in Burgundy, called the Current Fluctuating Regime (CFR), was  
156 built based on a 20-year recording of *in situ* hourly temperatures over a recent period (1995-  
157 2014). The CFR was composed of six segments of temperatures, each lasting 4h and



158 calculated as the mean segment over the 30 days (15<sup>th</sup> July – 15<sup>th</sup> August) and the 20 years  
159 studied.

160         Alongside the CFR, we designed a scenario termed Future Fluctuating Regime (FFR),  
161 aimed at simulating one possible trajectory for local climate in Burgundy, and based on  
162 summer thermal conditions likely to occur in this region for a period covering the years 2081  
163 to 2100. The FFR was generated according to the projections provided by six different climate  
164 simulations (spatial resolution: 12.5 km), each involving a combination of one General  
165 Circulation Model and one Regional Climate Model nested within (Taylor et al. 2012; Jacob  
166 et al. 2014). All these simulations were run with the most pessimistic of the Representative  
167 Concentration Pathway (RCP) scenarios, termed RCP 8.5, which predicts the highest positive  
168 radiative forcing (i.e. high absorbance of solar and infrared radiation) as a consequence of  
169 massive and growing future emissions of greenhouse gas (Moss et al. 2010). The FFR  
170 included six segments of temperatures, each lasting 4h and corresponding to the mean  
171 segment over the six simulations performed. All meteorological data used to design the  
172 thermal regimes are freely available on the Drias portal ([www.drias-climat.fr](http://www.drias-climat.fr)). The  
173 comparison of CFR and FFR indicates that global warming is likely to increase both the mean  
174 temperature (+ 5.3°C) and the daily thermal range (+ 0.6°C) in our focal area (Table 1).

#### 175 *Moth rearing and larvae collection*

176 An inbred strain of *L. botrana* provided the individuals used in this study (French National  
177 Institute for Agricultural Research, Villenave-d'Ornon, France). Insect stock arose from large  
178 numbers of caged adults (several thousand each week), kept without diapause under standard  
179 laboratory conditions ( $20 \pm 0.5^\circ\text{C}$ ,  $60 \pm 5\%$  relative humidity, photoperiod of L17: D6 with 1h  
180 of dusk). During photophase, luminosity varied between 600 lx (daytime) and 100 lx (dusk).  
181 Bands of waxed paper (5 x 10 cm) were hung inside rearing cages for eggs laying. Once these  
182 oviposition supports received a sufficient number of eggs (after 2-3 days), they were renewed

183 and placed in plastic boxes covered with a daily humidified piece of paper towel to protect  
184 eggs from desiccation until hatching.

185 Adults were obtained by initially collecting 2043 newly hatched larvae (age < 24h)  
186 from the rearing stock with a fine paintbrush. To avoid any experimental bias attributable to  
187 larval competition and subsequent food deprivation (Thiéry et al. 2014), larvae were  
188 individually reared in Eppendorf tubes filled with 1.5 ml of artificial culture medium  
189 (composition for 1000 ml: 1000 ml water, 15 g agar, 86.6 g maize flour, 41.3 g wheat germ,  
190 45.5 g beer yeast, 6 g ascorbic acid, 3.4 g mineral salt, 128 mg pyrimethanil, 2.7 g benzoic  
191 acid, 2.8 g methyl 4-hydroxybenzoate and 5 ml 95% ethanol). Tube lids were pierced for air  
192 circulation and covered with a piece of fine mesh fabric to prevent larvae from escaping.  
193 Freshly hatched larvae were then randomly allocated to one thermal regime (CFR or FFR)  
194 programmed with climate chambers (ST 2/2 BASIC, Pol-Eko Aparatura, Wodzisław Śląski,  
195 Poland). Abiotic conditions inside these incubators were controlled (temperature  $\pm 0.1^\circ\text{C}$ , 50  
196  $\pm 10\%$  relative humidity, L18: D6, 650 lx). According to a previous study, daily monitoring of  
197 pupation started only 2 weeks (if caterpillars were reared in the FFR) or 4 weeks (if they were  
198 reared in the CFR) after initial collection to minimise disturbance (Iltis et al. 2019).

199 Immediately following pupation, chrysalises were delicately extracted from their  
200 cocoon and weighted to the nearest 0.1 mg with a balance (Pioneer PA214C, OHAUS,  
201 Greifensee, Switzerland). They were then individually transferred into glass tubes (70 x 9 mm  
202 diameter) closed with cotton and were returned to their rearing thermal regime to end their  
203 development. Tubes were inspected once a day to monitor adult emergence. Freshly emerged  
204 moths were sexed and supplied with water *ad libitum* through daily soaked cotton plugs. They  
205 were then randomly distributed among three groups all along the experiments, because the  
206 array of measurements included in the study could not have been performed on the same  
207 individuals. In Group 1, adults were frozen to subsequently quantify their body amounts of

208 four major energetic components upon adult emergence. In Group 2, adults were held in their  
209 rearing thermal regime until death to record adult lifespan. In Group 3, adults were mated  
210 with standard individuals (originating from the laboratory insect stock) to assess the  
211 reproductive performance of each sex separately.

212 *Group 1: Body amounts of four major energetic components upon emergence*

213 Energetic assessments were run on 75 females ( $n = 37$  for CFR,  $n = 38$  for FFR) and 80 males  
214 ( $n = 36$  for CFR,  $n = 44$  for FFR). Within the 12h following their emergence, moths were  
215 individually placed in Eppendorf tubes and immediately frozen in liquid nitrogen. They were  
216 kept at  $-80^{\circ}\text{C}$  for later quantification of their energetic states. Wings were cut before moths  
217 were crushed in lysis buffer, as they are covered with scales which might disturb the  
218 biochemical assays based on absorbance measurements. Four major energetic components  
219 involved in energy production in insects were quantified through spectrophotometry methods:  
220 proteins, lipids, glycogen and soluble carbohydrates. The total amounts of soluble proteins  
221 available was quantified using a DC Protein Assay kit involving Bradford reagent (Bio-Rad,  
222 Hercules, USA). The assessments of other energetic components (lipids, glycogen, soluble  
223 carbohydrates) were performed with the method described by Foray et al. (2012). The  
224 repeatability of the measurements was assessed by calculating the coefficient of variation over  
225 two replicates for protein and lipid body amounts, and excluding the individuals for which  
226 this coefficient exceeded 30% (see Iltis et al. 2019). Repeatability was relatively high, as  
227 indicated by the low percentages of individuals removed from the protein dataset (3.2%) and  
228 the lipid dataset (0.6%). More specifically, this selection procedure led to the exclusion of 3  
229 females ( $n = 2$  for CFR,  $n = 1$  for FFR) and 2 males ( $n = 2$  for FFR) from the protein dataset,  
230 and 1 female ( $n = 1$  for FFR) from the lipid dataset.

231 *Group 2: Adult lifespan*

232 This group involved 76 females ( $n = 28$  for CFR,  $n = 48$  for FFR) and 73 males ( $n = 24$  for  
233 CFR,  $n = 49$  for FFR). Immediately following their emergence, freshly emerged moths were  
234 individually kept in clean glass tubes (100 x 15 mm diameter) within their rearing thermal  
235 regime. They were supplied daily with water *ad libitum* through soaked cotton plug, and  
236 monitored once a day (during water provisioning) until death. We then recorded the adult  
237 lifespan (in days), expressed as the time elapsed between imaginal emergence and death.

238 *Group 3: Reproductive performance of females and males*

239 A total of 99 females ( $n = 42$  for CFR,  $n = 57$  for FFR) and 105 males ( $n = 53$  for CFR,  $n = 52$   
240 for FFR) were allowed to mate in order to assess their reproductive performance. All these  
241 individuals were virgin and 24h-old. At dusk, one randomly selected 24h-old virgin individual  
242 (female or male) reared in either the CFR or the FFR was confined in a glass mating tube (100  
243 x 15 mm diameter) with one 24h-old virgin standard individual of the opposite sex. These  
244 standardised individuals were obtained from the inbred stock population and were weighted  
245 as pupae (precision:  $\pm 0.1$  mg) with a balance (Pioneer PA214C, OHAUS, Greifensee,  
246 Switzerland). They were considered equivalent in terms of quality as sexual partners given the  
247 relatively low genetic variation between them and the same standard environmental  
248 conditions (see above) they met during development (Moreau et al. 2006). Using standardised  
249 individuals as sexual partners for individuals assigned to the two thermal treatments enabled  
250 to specifically assess the effects of rearing temperature on the reproductive performance of  
251 each sex separately (see Moreau et al. 2006; Muller et al. 2015). Mating trials lasted 3h under  
252 controlled conditions ( $23.1 \pm 0.5^\circ\text{C}$ ,  $60 \pm 5\%$  relative humidity, 100 lx). This duration was  
253 selected because the latency to mate in this species does not exceed 3h in cases of no-choice  
254 mating trials (Muller et al. 2016b). Temperature was set at  $23.1^\circ\text{C}$  (intermediate temperature  
255 between the mean temperature of the CFR and the FFR) during mating experiments,

256 irrespectively of the thermal regime from which tested individuals originated. Luminosity  
257 during mating trials was set at 100 lx to reflect dusk conditions, as the reproduction of this  
258 species occurs at dusk in natural settings. Mating tubes were examined every 15 min to check  
259 if genital coupling was initiated. In this species, the complete transfer of the spermatophore  
260 during copulation requires approximatively 1h (Muller et al. 2015, 2016a, b). Hence, a time  
261 lapse of 15 min between two successive inspections is short enough to ensure that every  
262 effective mating could have been detected. Individuals for which no copulation was observed  
263 within 3h were considered unmated and were discarded from the rest of the experiments.

264         In cases where a female reared in either the CFR or FFR was mated with a standard  
265 male, the male was immediately removed after the pair separation and no longer used in the  
266 experiments. The female was left in her mating tube and her rearing thermal regime for  
267 oviposition. Water was daily provided *ad libitum* through soaked cotton plug. Each tube was  
268 checked every morning (during water supply) through visual inspection to count the number  
269 of eggs deposited by female until death. Ten days after the end of laying period (which  
270 extended over approximately 6 days within the CFR and 4 days within the FFR), egg tubes  
271 were examined with a stereomicroscope at 8x magnification to calculate the proportion of the  
272 eggs that successfully hatched (fertile eggs). An incubation period of at least 10 days ensured  
273 that all viable larvae had hatched from the fertile eggs (Torres-Vila et al. 1999; Moreau et al.  
274 2006; Muller et al. 2015). Mating was considered successful when the tested female laid at  
275 least one fertile egg, thus indicating an effective delivering of the spermatophore during  
276 copulation. Based on these observations, we recorded four metrics indicative of female's  
277 reproductive performance: (i) mating success (proportion of the females that laid at least one  
278 fertile egg), (ii) fecundity (total number of eggs deposited by each mated female), (iii) fertility  
279 (proportion of the eggs that successfully hatched) and (iv) laying rate (in  $\text{eggs}\cdot\text{day}^{-1}$ , expressed  
280 as the ratio between the total number of eggs deposited by each mated female and the number

281 of days elapsed between the appearance of the first and the last eggs laid) (Moreau et al.  
282 2006).

283 In cases where a male reared in either the CFR or FFR was mated with a standard  
284 female, the female was removed at the end of copulation and frozen at  $-80^{\circ}\text{C}$ , while the male  
285 was no longer used in the experiments. The standard female was further dissected on a glass  
286 side to extract the bursa copulatrix containing male's spermatophore. The dissection first  
287 enabled to check for the presence of male's spermatophore inside female's reproductive tract  
288 (thus indicating successful mating), provided that spermatophore transfer might sometimes  
289 fail despite genital coupling. Once the spermatophore was collected, we extrapolated its size  
290 (volume), which provides information about the quantity of sperm and energetic substances  
291 transferred to female during copulation (Torres-Vila et al. 1999; Muller et al. 2015). For this  
292 purpose, we measured spermatophore dimensions – including length  $l$ , width  $w$  and thickness  
293  $t$  – using a stereomicroscope (Stemi 508, Zeiss, Göttingen, Germany) at 50x magnification  
294 (precision  $\pm 1\ \mu\text{m}$ ). Considering the spermatophore as an ellipsoid balloon, we then assessed  
295 its volume  $V$  using the mathematical expression  $V = \pi / 6 (l \times w \times t)$ . Analyses of these  
296 photographic data were performed with the ZEN imaging software (version 2.3, Zeiss,  
297 Göttingen, Germany). Alongside spermatophore volume, we also evaluated sperm quality  
298 following the standard procedure developed by Muller et al. (2015). This involved rupturing  
299 the spermatophore in a drop of distilled water, delicately stirring the sperm mass to distribute  
300 the sperm evenly throughout the water and to isolate encysted eupyrene bundles. Each bundle  
301 contains 256 nucleated sperms involved in egg fertilisation. For this reason, the number of  
302 eupyrene bundles in the spermatophore can be interpreted as a surrogate for sperm quality,  
303 with demonstrated consequences for female's reproductive output (Muller et al. 2015, 2016a).  
304 In summary, we included three metrics related to male's reproductive performance: (i) mating  
305 success (expressed as the proportion of males that successfully delivered a spermatophore

306 during copulation), (ii) spermatophore volume and (iii) number of eupyrene bundles (sperm  
307 quality).

### 308 *Statistical analyses*

309 For the body amounts of four energetic components, statistical models incorporated thermal  
310 regime, sex, their interaction and pupal mass as a single covariate to control for allometric  
311 effect on these energetic stocks. The data for body amounts of proteins, lipids and glycogen  
312 satisfied both normality and homoscedasticity assumptions. Hence, the variation in the  
313 amounts of these energetic components was decomposed by means of Analyses of Covariance  
314 (ANCOVAs). The distribution of soluble carbohydrates data was skewed towards zero and  
315 thus required a Generalised Linear Model (GLM)-negative binomial error to be analysed.  
316 Adult lifespan was treated as a function of thermal regime, sex and their interaction within a  
317 Cox proportional hazards regression model. For all reproductive traits measured in females  
318 (mating success, fecundity, fertility, laying rate) and males (mating success, spermatophore  
319 volume, number of eupyrene bundles), statistical models included thermal regime as an  
320 explanatory variable and the pupal mass of tested individuals along with the one of their  
321 standard partners as two covariates. Mating success of both females and males were compared  
322 among thermal regimes with GLM-binomial error. Data for fecundity and spermatophore  
323 volume met the criteria of normality and homoscedasticity, while for laying rate a square root  
324 transformation was needed to reach normality. Consequently, all these data were studied with  
325 ANCOVAs. Fertility was expressed in proportions and therefore tested using a GLM-quasi  
326 binomial error with a logit link function. As discrete count data, the number of eupyrene  
327 bundles was analysed with a GLM-negative binomial error. Normality and homoscedasticity  
328 were evaluated with a Shapiro-Wilk and a Levene test, respectively. All statistical analyses  
329 were carried out using R 3.6.2 software.

330 **Results**

331 *Group 1: Body amounts of four major energetic components upon emergence*

332 The four energetic components were impacted by sex in the same way, but did not respond to  
333 thermal regime or to the interaction between thermal regime and sex (Table 2). Females  
334 stocked higher amounts of proteins, lipids, glycogen and soluble carbohydrates than males  
335 (Table 2). Furthermore, the amounts of the four energetic components were positively  
336 influenced by pupal mass: heaviest individuals possessed higher amounts than lightest ones  
337 (proteins:  $F_{1,145} = 81.2$ ,  $P < 0.001$ , slope = 80.1; lipids:  $F_{1,149} = 11.1$ ,  $P < 0.001$ , slope = 45.1;  
338 glycogen:  $F_{1,150} = 60.7$ ,  $P < 0.001$ , slope = 13.0; soluble carbohydrates:  $\chi_1^2 = 12.7$ ,  $P < 0.001$ ,  
339 slope = 0.21).

340 *Group 2: Adult lifespan*

341 Adult lifespan was impacted by thermal regime (Cox proportional hazards regression model,  
342  $\chi_1^2 = 55.3$ ,  $P < 0.001$ ), but not by sex ( $\chi_1^2 = 3.06$ ,  $P = 0.08$ ) or by the interaction between these  
343 two factors ( $\chi_1^2 = 1.19$ ,  $P = 0.28$ ). Individuals of both sexes reared and kept in warm  
344 conditions died faster than those reared and held in cool conditions (Fig. 1).

345 *Group 3: Reproductive performance of females and males*

346 Females reared in warm conditions had a lower mating success compared with females reared  
347 in cool conditions (GLM-binomial error:  $\chi_1^2 = 7.28$ ,  $P = 0.01$ ) (Fig. 2A). By contrast with  
348 mating success, fecundity (ANCOVA:  $F_{1,59} = 0.22$ ,  $P = 0.64$ ), fertility (GLM-quasi binomial  
349 error:  $\chi_1^2 = 0.88$ ,  $P = 0.06$ ) and laying rate (ANCOVA:  $F_{1,59} = 2.70$ ,  $P = 0.10$ ) did not respond  
350 to temperature (Fig. 2B,C,D). Among female's reproductive traits, only fecundity was  
351 affected (positively) by female's pupal mass ( $F_{1,59} = 4.71$ ,  $P = 0.03$ , slope = 10.5) and the



352 pupal mass of the standard male ( $F_{1,59} = 4.06$ ,  $P = 0.04$ , slope = 11.1): the heavier the female  
353 and the standard male mated with, the higher the number of eggs produced.

354         Among male's reproductive traits, mating success (GLM-binomial error:  $\chi_1^2 = 0.77$ ,  $P$   
355 = 0.38) and spermatophore volume (ANCOVA:  $F_{1,77} = 0.14$ ,  $P = 0.71$ ) remained unaffected  
356 by thermal regime (Fig. 3A,B). However, spermatophores from males reared in warm  
357 conditions contained fewer eupyrene bundles than those produced by males reared in cold  
358 conditions (GLM-negative binomial error:  $\chi_1^2 = 18.3$ ,  $P < 0.001$ ) (Fig. 3C). None of the  
359 male's reproductive traits was impacted by either male's pupal mass or the pupal mass of the  
360 standard female mated with.

## 361 **Discussion**

362 Using realistic fluctuating regimes, this study sought to investigate the impacts of global  
363 warming on the reproduction of a major grapevine pest, the European grapevine moth (*L.*  
364 *botrana*). We found clear evidence revealing that moth physiology and reproduction are  
365 influenced by temperatures experienced throughout ontogeny. When reared in warmer  
366 conditions complying to a scenario of local warming (FFR), individuals of both sexes  
367 incurred a reduced adult lifespan but their body amounts of four major energetic components  
368 remained unchanged compared with individuals reared in thermal conditions similar to those  
369 currently found in Burgundy (CFR). Focusing on reproductive traits, females that developed  
370 in warm conditions underwent reduced mating success (-26%), while males reared in warm  
371 conditions suffered decreased sperm quality, that is, a lower number of eupyrene bundles  
372 contained in their spermatophore (-50%).

373         The absence of temperature-related differences in the body amounts of four energetic  
374 components suggests that caterpillars are able to compensate for a shortened time allowed for  
375 feeding (accelerated larval development) in warm conditions. These findings match the results

376 of a previous study conducted on *L. botrana*, which outlined an increase in daily gain of body  
377 mass (i.e. growth rate) with mean temperature (Iltis et al. 2018). In agreement with these  
378 conclusions, several phytophagous species – with examples found in the Lepidoptera order –  
379 are known to elevate their food intake rate as temperature increases, probably to fuel higher  
380 basal metabolic rates induced by warming (Lee and Roh 2010; Bauerfeind and Fischer 2013;  
381 Pandey et al. 2015). We also reported here a reduced adult lifespan for individuals reared and  
382 held in warm conditions, presumably because, as capital breeders, *L. botrana* adults cannot  
383 feed to compensate for the higher energetic losses and reserves consumption occurring with  
384 warming (for similar results on capital breeding species, see Laughton et al. 2017). Such a  
385 reduction in adult lifespan should have important repercussions for the reproduction of *L.*  
386 *botrana*. In males, it should imply a shorter time allowed for mate sampling in natural and  
387 complex habitats, thereby possibly impairing the encounter between sexual partners. In  
388 females, it can entail a reduced time available for oviposition and egg dispersion in space,  
389 potentially leading to complex consequences for larval density, levels of intraspecific  
390 competition and offspring survival on infested bunches (Thiéry et al. 2014).

391 In females, the 26% reduction in mating success observed when comparing the two  
392 thermal regimes can be explained by the effects of temperature on the precopulatory phase of  
393 reproduction, that is, the pheromonal communication between females willing to mate and  
394 males. In *L. botrana*, females signal their sexual receptivity by emitting sex pheromones  
395 through calling behaviour (Muller et al. 2015, 2016a). In our study, rearing temperatures  
396 experienced by females before mating tests are likely to have influenced calling behaviour by  
397 altering pheromone production in quantitative (titres, duration of calling behaviour) and/or  
398 qualitative ways (blends of chemical compounds constituting the olfactory signal for mating)  
399 (Ono 1994; Konopka and McNeil 2017). This thermal modulation of pheromone emission  
400 should further affect the outcomes of the behavioural interaction between sexual partners (e.g.

401 specific recognition, mating success). With respect to this hypothesis, we expect the negative  
402 effects of warming on female's mating success to be exacerbated in natural, highly  
403 heterogeneous environments, where pheromonal signal plays a key role in facilitating the  
404 encounter between sexual partners. Despite its negative effects on mating success, warming  
405 did not influence fecundity and fertility, in accordance with the absence of differences  
406 regarding female's body amounts of energetic components observed between thermal  
407 treatments.

408         In males, thermal conditions did not influence mating success, suggesting no  
409 differences between males reared in the CFR and the FFR in terms of access to reproduction  
410 and ability to transfer the sperm material during copulation. Temperature did not either  
411 modify spermatophore volume as a surrogate for the quantity of sperm and accessory gland  
412 secretions delivered to female during mating. As spermatophore was included in our energetic  
413 assays, these results are congruent with the absence of differences in body amounts of  
414 energetic components found when comparing males reared in the two thermal regimes.  
415 However, our study showed that male's sperm quality – approximated by the number of  
416 eupyrene bundles contained in the ejaculate – was severely reduced (-50%) in warm  
417 conditions. The negative impacts of warming on male's fertility traits are becoming more and  
418 more evident in arthropod species, including sperm number (Zeh et al. 2012; Sales et al.  
419 2018), viability (Stürup et al. 2013; Sales et al. 2018), size (Vasudeva et al. 2014; Iossa et al.  
420 2019), and ability to migrate through the female's genital apparatus (Sales et al. 2018). Our  
421 study brings new evidence showing that eupyrene spermatogenesis in butterfly species is very  
422 sensitive to prevailing environmental conditions, particularly temperature (Hiroyoshi and  
423 Mitsuhashi 1998; Iossa et al. 2019). Considering that the number of eupyrene bundles  
424 included in male's spermatophore primarily mediates female's egg production in *L. botrana*  
425 (Muller et al. 2015, 2016a), further experimental investigations are needed to determine to

426 what extent the decline in male's fertility observed for individuals reared in warm conditions  
427 will lower the reproductive success of the pair. In this regard, it is reasonable to think that the  
428 50% reduction in sperm quality we highlighted will perceptibly reduce female's egg  
429 production after mating. For example, a less important decline in the amount of eupyrene  
430 sperm (approximately -33%) due to larval alimentation had been shown to negatively impact  
431 both female's fecundity (-30%) and fertility (-10%) in a previous study (Muller et al. 2015).

432 In terms of pest management, our study has two main implications for PBDMs design,  
433 which could contribute to improve the ecological realism of these models and the accuracy of  
434 their local and global predictions about the future of *L. botrana* populations. First, our results  
435 show that, using realistic fluctuating thermal regimes, climate change would not impact  
436 female's fecundity. By contrast with this absence of difference in female's fecundity observed  
437 when comparing fluctuating regimes, equations constituting PBDMs – based on constant  
438 temperatures – predict that *per capita* egg production will likely increase over the range of  
439 temperatures here examined (considering an increase in mean temperature from 20.5°C to  
440 25.8°C) (Gutierrez et al. 2012, 2017). We argue that differences between constant and  
441 fluctuating regimes probably arise from the negative effects of thermal fluctuations on egg  
442 production, which would likely expose the organism to stressful thermal conditions during the  
443 hottest hours of the cycle. Such a phenomenon is likely to become more and more frequent if  
444 mean temperature and the range of daily fluctuations increase concomitantly as two facets of  
445 global warming, as predicted in Colinet et al. (2015). Second, by demonstrating that male's  
446 fertility was halved with respect to warming scenario, our study highlights the need for  
447 PBDMs to consider (i) how male's reproductive performance is expected to vary according to  
448 temperature and (ii) how this variation in male's traits modulates the offspring production of  
449 the pair. In light of our findings, we are firmly convinced that the implementation of realistic  
450 patterns of fluctuations together with male's reproductive traits as an integral component of *L.*

451 *botrana* reproductive success within PBDMs should substantially improve their reliability as  
452 tools to develop adequate pest management practices and policies.

453 In conclusion, we expect climate change to reduce the reproductive success of *L.*  
454 *botrana* and the abundance of this pest over generations in Eastern France due to the negative  
455 effects of the local warming scenario observed for adult lifespan and the reproductive  
456 performance of both sexual partners. At this point, two considerations should be examined  
457 before inferring future pest population dynamics based on the results of this study. First, this  
458 work explored the plastic response of one single *L. botrana* generation that experienced an  
459 abrupt shift in mean temperature between rearing conditions – whose mean temperature  
460 basically corresponded to the one of the CFR – and FFR. Hence, our findings do not account  
461 for the insect ability to adapt to a gradual warming experienced over several successive  
462 generations, as expected in natural conditions (Bale et al. 2002; Hoffmann 2017). It could  
463 therefore be hypothesised that *L. botrana* populations will be able to cope with an incremental  
464 increase in mean temperature through evolutionary response, such that the negative effects of  
465 warming on the reproduction of this pest species should be less important within natural  
466 populations than suggested in this study. Second, the abundance of *L. botrana* populations is  
467 not solely be determined by the reproductive success of this pest, but also by the mortality of  
468 immature stages (mostly eggs and larvae) induced by parasitoids in agroecosystems, which  
469 will likely be affected by changing thermal conditions (for reviews, see Jeffs and Lewis 2013;  
470 Thierry et al. 2019). The physiological response of these natural enemies to rising  
471 temperatures in terms of development, fecundity and adult longevity (which all influence  
472 effective parasitism rates among pest populations) is thus pivotal to develop a more thorough  
473 understanding of the consequences of climate change for *L. botrana* populations (Reineke and  
474 Thiéry 2016; Castex et al. 2018). Sound knowledge about the influence of temperature on  
475 parasitoid vital rates could be incorporated to PBDMs in order to provide predictions about

476 future *L. botrana* abundances relevant in the context of tritrophic interactions (for an exemple  
477 with another pest species, see Gutierrez et al. 2011).

#### 478 **Compliance with ethical standards**

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484 Ethical approval: All applicable institutional and/or national guidelines for the care and use of  
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608 **Table 1**

609 Thermal conditions (°C) for the two daily fluctuating thermal regimes involved in this study  
610 (CFR and FFR), that were divided into 6 periods of 4h. Daily thermal range corresponds to  
611 the difference between daily maximum and minimum temperatures.

<b>Hour</b>	<b>Current Fluctuating Regime (CFR)</b>	<b>Future Fluctuating Regime (FFR)</b>
<b>0h – 4h</b>	16.4	21.4
<b>4h – 8h</b>	17.8	22.9
<b>8h – 12h</b>	22.3	27.8
<b>12h – 16h</b>	24.9	30.5
<b>16h – 20h</b>	22.9	28.3
<b>20h – 0h</b>	19.0	24.2
<b>Mean temperature (°C)</b>	20.5	25.8
<b>Daily thermal range (°C)</b>	8.5	9.1

612

613 **Table 2** Mean values and their 95% confidence intervals of the body amounts of four energetic components for the two thermal regimes and  
614 sexes. For each energetic component, significant differences ( $P < 0.05$ ) between regimes or sexes are shown by superscript letters. Data for  
615 proteins, lipids and glycogen were compared among thermal regimes and sexes with Analyses of Covariance while for soluble carbohydrates, a  
616 Generalised Linear Model-negative binomial error was performed. All these statistical models accounted for pupal mass as a single covariate.  
617 There was no significant interaction between thermal regime and sex for any of the four energetic components (proteins:  $F_{1,145} = 0.88$ ,  $P = 0.35$ ;  
618 lipids:  $F_{1,149} = 0.16$ ,  $P = 0.68$ ; glycogen:  $F_{1,150} = 0.93$ ,  $P = 0.34$ ; soluble carbohydrates:  $\chi^2_1 = 0.24$ ,  $P = 0.63$ ).

	Proteins ( $\mu\text{g}$ )	Lipids ( $\mu\text{g}$ )	Glycogen ( $\mu\text{g}$ )	Soluble carbohydrates ( $\mu\text{g}$ )
Thermal regime				
CFR	664 [586; 742] <sup>a</sup>	474 [417; 530] <sup>a</sup>	57.5 [47.6; 67.5] <sup>a</sup>	36.1 [28.5; 43.5] <sup>a</sup>
FFR	649 [575; 724] <sup>a</sup>	454 [404; 504] <sup>a</sup>	53.4 [44.3; 62.6] <sup>a</sup>	37.4 [30.9; 43.9] <sup>a</sup>
Test value	$F_{1,145} = 0.66$	$F_{1,149} = 0.49$	$F_{1,150} = 1.41$	$\chi^2_1 = 0.09$
Sex				
Females	967 [924; 1011] <sup>a</sup>	617 [568; 666] <sup>a</sup>	90.1 [82.5; 97.7] <sup>a</sup>	55.8 [48.6; 62.9] <sup>a</sup>
Males	369 [354; 384] <sup>b</sup>	321 [288; 354] <sup>b</sup>	22.8 [19.7; 25.8] <sup>b</sup>	19.0 [15.3; 22.6] <sup>b</sup>
Test value	$F_{1,145} = 1093$	$F_{1,149} = 108$	$F_{1,150} = 387$	$\chi^2_1 = 71.3$

619

620 **Figure captions**

621 **Fig. 1** Effect of thermal regime (grey: Current Fluctuating Regime, black: Future Fluctuating  
622 Regime) on adult lifespan ( $\pm$  95% confidence interval), expressed as a survival probability  
623 function of individual age. Data for males and females were pooled together as non-  
624 statistically different.

625 **Fig. 2** Effect of thermal regime (CFR = Current Fluctuating Regime, FFR = Future  
626 Fluctuating Regime) on the mean ( $\pm$  95% confidence interval) of four reproductive traits  
627 measured in females: **A** mating success, **B** fecundity (total number of eggs laid by one  
628 female), **C** fertility (proportion of the eggs that successfully hatched), and **D** laying rate  
629 (fecundity/oviposition duration). Asterisks indicate significant differences (\*\*\*  $P < 0.001$ , \*\*  
630  $P < 0.01$ , \*  $P < 0.05$ ), n.s means non-significant and numbers refer to sample sizes.

631 **Fig. 3** Effect of thermal regime (CFR = Current Fluctuating Regime, FFR = Future  
632 Fluctuating Regime) on the mean ( $\pm$  95% confidence interval) of three reproductive traits  
633 measured in males: **A** mating success, **B** spermatophore volume, and **C** number of eupyrene  
634 bundles contained in sperm. Asterisks indicate significant differences (\*\*\*  $P < 0.001$ , \*\*  $P <$   
635  $0.01$ , \*  $P < 0.05$ ), n.s means non-significant and numbers refer to sample sizes.