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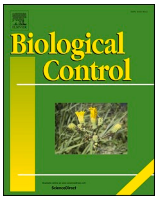

Divergent responses of the fall armyworm and a parasitoid to rising temperature

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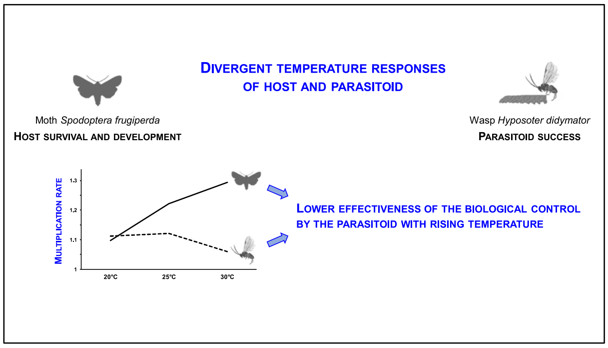
HIGHLIGHTS

- How temperature affects parasitoids-fall armyworm (FAW) outcome is poorly known.
- The parasitism success of *H. didymator* is reduced at high temperature.
- Temperature and parasitism by *H. didymator* affect FAW survival and development.
- High temperature increases the frequency of FAW escaping parasitism.
- Rising temperatures may decrease the control of FAW populations by *H. didymator*.

GRAPHICAL ABSTRACT



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ABSTRACT

Temperature is a key factor influencing insect performance and host-parasitoid interactions. Knowing how hosts and parasitoids respond to temperature variations is crucial for predicting the success of biological control strategies, especially in the context of climate change. This study aimed to assess how developmental temperature affects the interaction between the fall armyworm (FAW) *Spodoptera frugiperda*, a major invasive pest, and the larval endoparasitoid *Hyposoter didymator*. FAW caterpillars were reared under three fluctuating temperature regimes centered at 20 °C, 25 °C, and 30 °C (± 5°C of daily variation), and were either left unexposed or exposed to *H. didymator*. We analyzed host survival, developmental time, and body mass, as well as the success of the parasitoid. In unparasitized FAW, higher temperatures accelerated development and increased pupal survival but reduced larval survival and adult body mass. In parasitized FAW, the proportion of individuals that survived increased at 30 °C, suggesting that higher temperatures may undermine the biological control of this pest. For *H. didymator*, temperature accelerated development but had negative effects at 30 °C, leading to reduced survival during the endoparasitic phase and impaired cocoon formation. These contrasting responses led to opposite trends: the multiplication rate of FAW increased with temperature, while that of the parasitoid decreased at the highest temperature. This study underscores the importance of considering the thermal sensitivity of both FAW and its potential parasitoids when designing effective and sustainable pest management strategies.

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1. Introduction

Temperature is a major driver of insects. It directly affects their metabolism, development, growth, survival, and reproduction, shaping their population dynamics and distribution (Huey and Kingsolver 1989; Bale et al. 2002; Hance et al. 2007; Paaijmans et al. 2013; Colinet et al. 2015; Deutsch et al. 2018; Izadi et al. 2024). In the case of pest insects, the rising temperatures associated with climate change are expected to intensify their impact on crop production by accelerating population growth and metabolic rates (Deutsch et al. 2018), as well as expanding the range of suitable habitats (Lehmann et al. 2020). Temperature also affects pests's natural enemies, such as parasitoids (Hance et al. 2007; Jeffs and Lewis 2013), which are essential to biological control programmes and integrated pest management (IPM). When hosts and parasitoids differ in their thermal sensitivity, the regulatory effect of parasitoids can be disrupted. A number of studies have shown that the optimal temperature for the development of hymenopteran parasitoids is generally lower than that of their hosts (Furlong and Zalucki 2017), which could reduce the success of parasitoids as temperatures rise. Such an effect has been observed in a long-term study of natural populations, which reports reduced efficiency of parasitoids in controlling pest populations under warmer conditions (Ward et al. 2020). However, this pattern is not universal. Field-based studies have shown contrasting trends depending on the species involved and ecological context (Péré et al. 2013).

Despite extensive research on how temperature affects the performance of pests or parasitoids, relatively few studies have addressed both partners concurrently in the same experimental context, particularly under fluctuating thermal regimes that better reflect field conditions (Tougeron et al. 2021; Bagni et al. 2024; Hofmann et al. 2024). This gap is particularly relevant in the case of newly invasive pests such as the fall armyworm *Spodoptera frugiperda* (FAW) (J. E. Smith; Lepidoptera: Noctuidae). FAW is native to tropical and subtropical regions of the Americas. The caterpillars are polyphagous, attacking a wide range of host plants, particularly major cereals such as maize, rice and sorghum (Volp et al. 2022). They also attack other non-grassy crops like cotton (Martinelli et al. 2006). Since 2016, FAW has rapidly spread in several regions of Africa (Goergen et al. 2016; Fan et al. 2020), Asia (Jing et al. 2020; Sun et al. 2021; Tanaka et al. 2024) and Australia (Maino et al. 2021). The detection of FAW in Europe, especially in the Mediterranean region (EPPO, 2023), has raised concerns about its potential establishment on the continent, where corn, wheat and rice crops are extensively cultivated. As FAW development, reproduction and migration are highly dependent on temperature, several modelling studies have assessed its potential distribution under different climate scenarios (Montezano et al. 2019; Du Plessis et al. 2020; Huang et al. 2021; Malekera et al. 2022; Wu et al. 2022; Lee et al. 2022; Tao et al. 2023; Savadatti et al. 2023; Adan et al. 2024; Kartakis et al. 2025). In this context, understanding how temperature influences not only the pest itself but also its interactions with natural enemies becomes crucial. However, this aspect remains largely underexplored. Investigating how temperature modulates these interactions is essential for designing resilient biological control programs that will remain effective under future climatic conditions.

Among the larval endoparasitoids naturally present in Europe, *Hyposoter didymator* (Hymenoptera: Ichneumonidae) is a generalist species, known to parasitize several noctuid pests, including *Spodoptera exigua* and *Helicoverpa armigera* (Cabello 1989; Mironidis and Savopoulou-Soultani 2009; Harvey et al. 2012; Frayssinet et al. 2019). As with many other ichneumonid parasitoid species, the successful parasitism of *H. didymator* depends on a symbiotic polydnavirus (HdIV) that is injected by the female parasitoid during oviposition. This virus suppresses host immunity and promotes parasitoid development (Barat-Houari et al. 2006; Doremus et al. 2014; Visconti et al. 2019; Robin et al. 2023). In natural field populations, the parasitism rates on *H. armigera* can reach up to 10 % and more than 80 % under semi-controlled conditions (Frayssinet et al. 2019). Although *H. didymator* is not yet documented as a parasitoid of FAW, it can successfully parasitize this pest under laboratory conditions (Doremus et al. 2014). This suggests a potential for its future utilization in IPM strategies, particularly in Mediterranean or temperate regions where the parasitoid is already established. Indeed, a number of studies have reported that native parasitoids can rapidly exploit invasive FAW populations across different continents, including Asia, Africa, and the Americas (Kenis et al. 2019; Mohamed et al. 2021; Kenis 2023; Nurkomar et al. 2024; Wyckhuys et al. 2024). In light of this, it is conceivable that *H. didymator* might interact with this pest in the field where both species are present, provided that further studies are conducted to assess its potential.

This study aimed to assess how developmental temperature influences the interaction between FAW and *H. didymator* in the context of the rising temperature. We hypothesized that temperature would differentially affect the performance of both the host and the parasitoid, potentially altering the outcomes of parasitism. To test this hypothesis, we measured parasitism success, escape rates from parasitism, and life history traits of both species under three realistic fluctuating temperature regimes centered around 20 °C, 25 °C, and 30 °C with daily fluctuations of ± 5 °C. This approach follows recent recommendations to more accurately simulate natural thermal conditions compared to constant-temperature protocols (Moore et al. 2021; Tougeron et al. 2021; Bagni et al. 2024; Hofmann et al. 2024). Our results will provide insight how temperature affects the performance of both FAW and *H. didymator*, and how these effects may alter the outcomes of parasitism under controlled yet ecologically relevant conditions. These insights will inform the evaluation of *H. didymator*'s potential in IPM programmes targeting FAW, particularly in the context of climate warming. More broadly, the study aims to improve our understanding of how temperature can disrupt host-parasitoid dynamics and affect the efficacy of biological control strategies.

2. Materials and methods

2.1. Insect rearing

The FAW larvae used in this study originated from a corn strain collected in Guadeloupe (Caribbean Sea) in 2005. Since that time, the colony has been maintained under quarantine and controlled laboratory conditions (25 °C ± 0.5 °C, 40 ± 10 % relative humidity (RH), 16:8h L:D photoperiod). The larvae and moths were fed *ad libitum* on the Poitout artificial diet (Poitout and Bues 1974) and a 25 % honey solution, respectively. The colony of the parasitoid *H. didymator* was maintained at a temperature of 23 °C ± 0.5 °C, with 60 % RH and 16:08 L:D photoperiod. Adult wasps were fed with honey and water. This laboratory colony was established from parasitized *H. armigera* larvae collected from alfalfa fields in the Montpellier region of southern France. The population has been maintained in the laboratory for over 17 years, using third-instar larvae of FAW for parasitization, and was periodically supplemented with new individuals collected from the field to ensure genetic diversity. *Hyposoter didymator* is a koinobiont endoparasitoid, meaning it keeps its host alive throughout its own development within the host, until pupation. The parasitoid undergoes three successive larval instars over seven days at a constant temperature of 25 °C. Upon completion of its development, the *H. didymator* larva emerges from the host, spins a cocoon, and pupates. Adult emergence occurs approximately 15 days after parasitization, and the parasitized host dies as the wasp larva begins to emerge.

2.2. Temperature regimes

The tests were conducted in environmental chambers (Pol-Eko-Aparatura Smart Pro) allowing for independent control of temperatures and relative humidity. The mean experimental temperatures were set at 20 °C, 25 °C, and 30 °C, with a daily fluctuation of 10 °C, meaning the temperatures varied ± 5°C around the average, under a photoperiod of 16:08 (L:D). This daily fluctuation was chosen to simulate the temperature variations typically observed in southern Europe (Wang and Dillon 2014). The fluctuations followed a stepwise pattern, increasing or decreasing by 1 °C every 72 min over a 24-hour period, creating a gradual and symmetrical thermal cycle. The temperature profiles for each regime are illustrated in Supplementary Fig. S1. Temperature peaks occured during the light phase. Relative humidity was maintained at 30 ± 10 % in all chambers. The accuracy of temperature and humidity conditions was checked at 30-minute intervals throughout the experiment using external data loggers (Kimo Electronic).

2.3. Experimental design and parasitism monitoring

To minimize potential parental effects (Iltis et al. 2020; Kingsolver et al. 2020) and isolate the direct response to our experimental temperatures, the laboratory colony was acclimated to fluctuating thermal regimes for a large portion of one generation. Fig. 1 illustrates the experimental design. A batch of 200 third-instar larvae was randomly assigned to each of the three different environmental chambers. The larvae were reared until adult emergence. Male and female moths, less than 24 h old, were then paired to produce a second generation. Only eggs laid within the first three days were collected for experimentation. Six to ten pairs were used per thermal regime. Once the resulting FAW larvae reached the third instar stage, they were randomly assigned to one of two experimental groups. The first group assessed the effect of temperature alone on FAW performance, defined as larval survival, development time, and adult body mass, in the absence of parasitism. The second group was exposed to parasitism to evaluate the combined effects of temperature and parasitism on the same host traits. For the parasitism assays, individual third-instar larvae were placed in a large cage containing both male and female adults of *H. didymator* kept at 23 °C. As soon as a larva was observed being parasitized, it was immediately removed from the cage to prevent superparasitism. The parasitized larvae were then transferred to individual wells of 12-well plates containing Poitout medium and promptly returned to their assigned environmental chambers. To ensure comparable physiological states across treatments, larvae were reintroduced into the chambers during the peak temperature phase of the daily cycle. Larvae in the non-parasitized group were handled in the same way, except they were removed from the parasitism cages before any contact with female wasps occurred. When conditions are suitable for parasitism, the polydnavirus injected by a female parasitoid during oviposition rapidly stops the development of the parasitized larvae. This leads to a population of FAW larvae of uniform size, smaller than those that are not parasitized, and they never progress beyond the fifth larval instar. This distinct phenotype can be observed as early as 24 h after parasitism at a constant temperature of 25 °C. In our study, we found that a small proportion of larvae (5.2 %), initially exposed to parasitoid females, showed no evidence of parasitism (no eggs or larvae detected in dissected individuals) and exhibited growth patterns similar to those of the unparasitized control group. These larvae were considered unparasitized despite exposure, possibly due to unsuccessful oviposition or egg deposition, and they were excluded from analyses. All remaining larvae were considered successfully parasitized and used in statistical analyses. These caterpillars could be categorized into two distinct groups based on the variability in their size, which indicated different responses to parasitism. The first group consisted of larvae that were uniform in size, resembling the small parasitized caterpillars usually observed in our laboratory. In this group, the developmental arrest caused by the polydnavirus was evident. The second group included larvae with a wider range of sizes, falling between those of the first group and the unparasitized control larvae. Dissection of a subset of these larvae confirmed the presence of the parasitoid, indicating that parasitism had taken place. However, no parasitoids successfully emerged from these parasitized caterpillars. Despite being parasitized, caterpillars continued their development, at least beyond that of the fully parasitized caterpillars (*i.e.*, beyond the fifth instar), albeit at a slower rate than the unparasitized ones. For the remainder of this study, we will refer to these larvae as « escaped ».

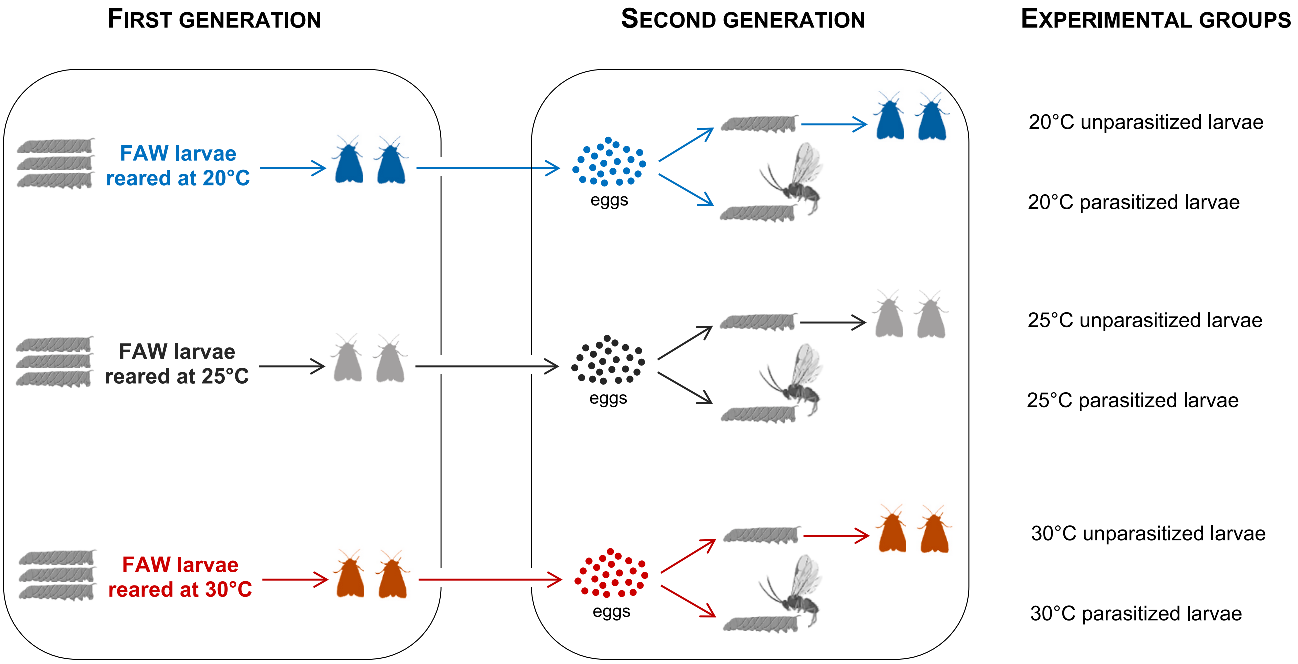

Fig. 1. Experimental design. Third instar FAW larvae were placed in environmental chambers programmed to average temperatures of 20 °C, 25 °C, and 30 °C, with a daily variation of ± 5°C. From this acclimated first generation, pairs consisting of a male and a female emerging less than 24 h apart were randomly formed to obtain egg masses. The third instar larvae of this second generation were then divided into two cohorts, one to assess the effect of temperature on FAW not exposed to parasitism and the other to study the combined effects of temperature and parasitism (created with BioRender.com).

2.4. Effect of experimental temperature on survival, body mass, sex ratio, and developmental rate of FAW

The following protocol was implemented for both parasitized and unparasitized larvae. We monitored larval survival from the third instar to pupation, as well as pupal survival, daily. Pupae that failed to produce adults after three weeks were classified as dead, except in the thermal regime of 20 °C, where the evaluation period was extended to four weeks due to a slower developmental (as detailed in the results section). The larvae were provided with fresh food every two days throughout the experiment. The body mass of male and female moths was measured within 24 h of emergence using a high-precision semi-analytical balance (Precisa LS 120A scs; ± 0.1 mg). The sex of the individuals was determined at the pupal stage. We measured the developmental rate of unparasitized individuals and those that escape parasitism from the third larval instar to pupation, and from pupation to adult emergence. This rate was calculated as the reciprocal of developmental duration (days^{-1}) (Paaijmans et al. 2013; Lyons et al. 2013), which serves as a fitness proxy for generation time (Huey and Berrigan 2001).

2.5. Effect of experimental temperature on the success and development rate of *H. didymator*

Daily observations were conducted to record the percentage of parasitoid larvae that emerged from their hosts, the percentage of cocoons formed, and the percentage of adults that emerged at each experimental temperature. The development rate was measured from oviposition to larval emergence and from cocoon formation to adult emergence. We defined the success of parasitism as the proportion of adult parasitoids that emerged relative to the initial number of parasitized FAW larvae.

2.6. Data analyses

We examined the impact of developmental temperature on FAW in terms of larval and pupal survival, developmental rates, sex ratio of pupae, and adult body mass. Additionally, we studied the effects on the parasitoid *H. didymator*, focusing on oviposition success, larval survival, cocoon formation, adult emergence, overall success, larval developmental rates before and after cocoon formation, and sex ratio. To assess oviposition success, we conducted a dissection of parasitized caterpillars in a specific experiment. The effects of temperature were analyzed using the Chi-squared test for all parameters that were binomial variables. For the continuous variables of developmental rate and body mass, we utilized the Kruskal-Wallis and Wilcoxon tests since normality and homoscedasticity were not satisfied, even after log transformation. Additionally, we examined the effects of temperature, parasitism, and their interaction (Temperature × Parasitism) on FAW using logistic models. For the analysis of developmental rates, we discretized the data into binomial variables based on the median values for each temperature. We performed post hoc tests to compare our variables between 20 °C and 25 °C, and between 25 °C and 30 °C. We did not make the comparison between 20 °C and 30 °C because of the well-known nonlinear responses to temperature in ectotherms (Paaijmans et al. 2013; Colinet et al. 2015; Stoks et al. 2017). All statistical analyses were conducted using JMP software (JMP Pro 17, SAS Institute Inc., Cary, NC). To evaluate the overall impact of temperature on FAW and *H. didymator*, we estimated the multiplication rate (asymptotic growth rate) at the population level using matrix models (Caswell 2018). This modelling was performed to synthesize the effect of temperature on our multiple traits, as advised (Bruijning et al. 2018; Mordecai et al. 2019). We constructed the life cycles of FAW and *H. didymator* using age-structured matrices, with each age class representing one day. These age-structured matrices project how the number of individuals in each age class changes across successive generations, allowing us to quantify the asymptotic population growth rate (Caswell 2018). We parameterized the models using the vital parameters estimated in the current study (all values used in the models are provided in Supplement 2), along with additional estimates from Huang et al. (2021) for FAW. As is typical in demographic models, our modeling focused solely on females, based on the assumption that male abundance is sufficiently high to ensure the reproduction of most females (Bessa-Gomes et al. 2010). This assumption aligns with our estimates, which indicate that males constitute 46 % of the FAW population and 85 % of the population of *H. didymator*. The modeling was conducted using the computer program ULM (Legendre and Clobert 1995; Ferriere et al. 1996).

3. Results

Three categories of FAW caterpillars were distinguished according to whether or not they were exposed to parasitism by *H. didymator*:

1. Unparasitized larvae that were introduced into parasitoid cages but removed before any oviposition attempt could occur. These individuals served as baseline controls to assess the effects of temperature on host development and survival in the absence of parasitism (results in 3.1.).
2. Escaped larvae that were exposed to parasitoid females and experienced oviposition, with a slowdown in growth typical of parasitized larvae, but with no parasitoid emergence. These individuals were considered to have been parasitized, but parasitoid development failed (results in 3.2.).
3. Successfully parasitized larvae in which parasitism led to the development and emergence of a parasitoid, evidenced either by host developmental arrest or parasitoid cocoon formation. These individuals formed the core of the parasitism analysis (results in 3.3.).

3.1. Effects of temperature on unparasitized FAW

The influence of developmental temperature on unparasitized FAW was evaluated by examining larval and pupal survival rates, developmental rates for both stages, the sex ratio of pupae, and the body mass of adults. The survival rates of caterpillars reared at 20 °C and 25 °C did not significantly differ ($\chi^2_1 = 1.1$, $P = 0.301$). However, survival decreased significantly when comparing 25 °C to 30 °C ($\chi^2_1 = 12.7$, $P < 0.001$) (see Fig. 2A). Survival rates of female and male pupae at 20 °C were significantly lower than those at 25 °C (Fig. 2B; $\chi^2_1 = 58.2$, $P < 0.001$ for females; $\chi^2_1 = 52.2$, $P < 0.001$ for males). There was no significant difference in survival between female pupae reared at 25 °C and 30 °C ($\chi^2_1 = 1.5$, $P = 0.222$). However, survival increased significantly for male pupae when comparing 25 °C to 30 °C ($\chi^2_1 = 7.0$, $P = 0.008$) (Fig. 2B). These results indicate that larval survival was more negatively affected by high temperatures, while pupal survival appeared more sensitive to lower temperatures. Regardless of the developmental stage or sex, an increase in temperature accelerated the developmental rate of FAW (Fig. 3). The increase was observed in larvae ($\chi^2_2 = 596.4$, $P < 0.001$), female pupae ($\chi^2_2 = 228.3$, $P < 0.001$), and male pupae ($\chi^2_2 = 201.9$, $P < 0.001$). These increases were significant between 20 and 25 °C ($P < 0.001$ in larvae, females, and males) and between 25 and 30 °C ($P < 0.001$ in larvae, females, and males). The developmental temperature did not affect the sex ratio of the pupae ($\chi^2_2 = 1.3$, $P = 0.535$; the values for the sex ratio are presented in Table S2a of Supplement 2). Adult body decreased significantly with increasing developmental temperature in both females ($\chi^2_2 = 28.1$, $P < 0.001$) and males ($\chi^2_2 = 24.8$, $P < 0.001$), with significant reductions observed between 25 °C and 20 °C ($P < 0.001$) and between 30 °C and 25 °C ($P = 0.002$) (Fig. 4).

3.2. Effects of temperature on FAW that escaped from parasitism

We examined how developmental temperature influences the

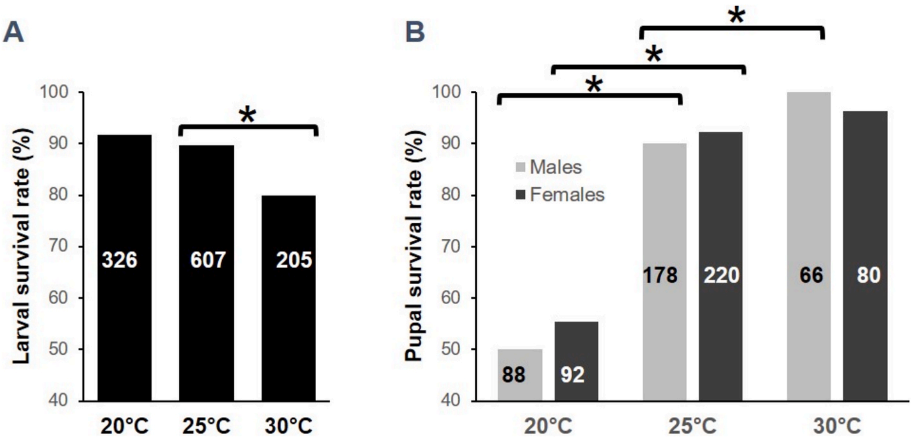

Fig. 2. Survival rates of larvae and pupae of unparasitized FAW as a function of developmental temperature. (A) Survival rate of larvae from the third instar to the pupa. (B) Survival rate of male and female pupae. Numbers in the bars indicate the number of individuals analysed in each treatment. An asterisk indicates a significant difference between pairwise comparisons ($p < 0.01$).

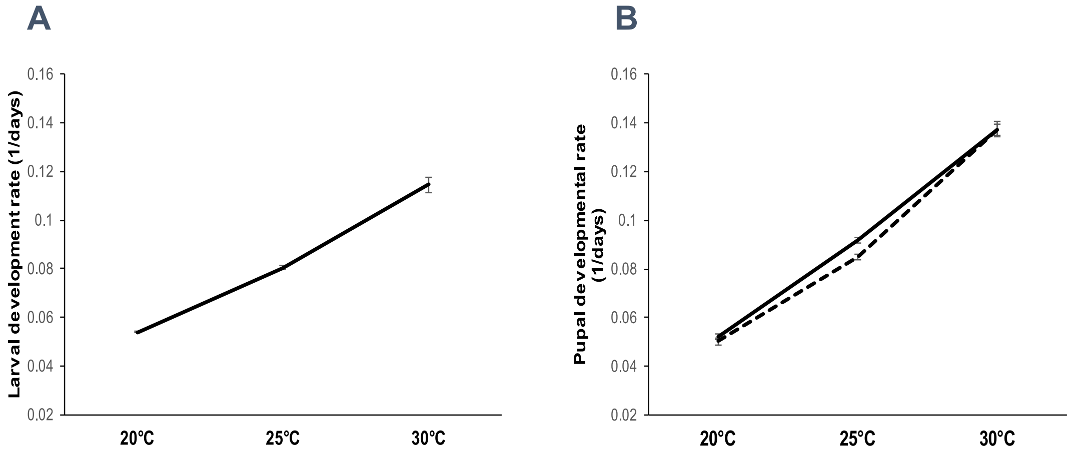

Fig. 3. Developmental rate of unparasitized FAW as a function of developmental temperature. (A) Developmental rate from the third instar to pupa. (B) Developmental rate during the pupal stage for females (solid line) and males (dashed line). Error bars indicate SE. Respectively for 20, 25 and 30 °C, sample sizes are 233, 447 and 154 for larval developmental rate, 51, 207 and 78 in females, and 45, 161 and 66 in males.

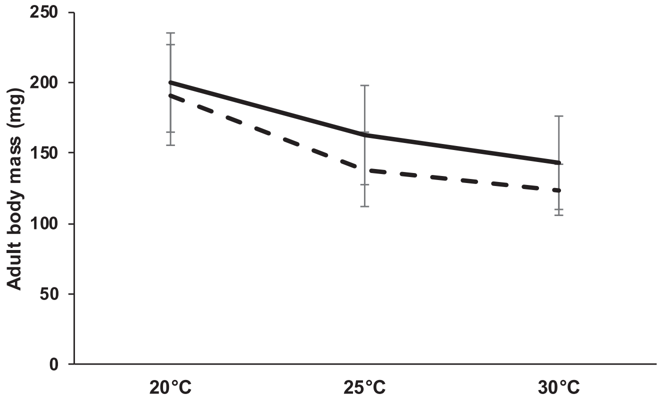

Fig. 4. Adult body mass of unparasitized FAW as a function of developmental temperature. Moths were weighed 24 h after emergence for females (solid line) and males (dashed line). Error bars indicate SE. Respectively for 20, 25 and 30 °C, sample sizes are 20, 111 and 37 in females, and 9, 83 and 38 in males.

frequency, survival, and sex ratio of FAW caterpillars that were exposed to *H. didymator* and initially parasitized, but escaped parasitism. Temperature had a significant effect on the frequency of these individuals (Fig. 5A). More escaped caterpillars were observed at 30 °C compared to 25 °C ($\chi^2_1 = 5.7$, $P = 0.017$). However, the difference between 20 °C and 25 °C was not significant ($\chi^2_1 = 2.2$, $P = 0.138$). The survival rate of escaped caterpillars significantly increased from 20 °C to 25 °C ($\chi^2_1 = 9.2$, $P = 0.002$), but it declined at 30 °C compared to 25 °C ($\chi^2_1 = 3.9$, $P = 0.048$) (Fig. 5B). Due to the small sample sizes of sexed pupae ($n = 55$, distributed across sexes and the three temperature treatments), we combined data from all pupae for pupal survival analysis after we checked for a lack of difference between sexes ($\chi^2_1 = 0.2$, $P = 0.661$). When examining the temperature effect, pupal survival rates did not differ significantly between 20 °C and 25 °C ($\chi^2_1 = 0.1$, $P = 0.747$). However, pupal survival increased significantly at 30 °C compared to 25 °C ($\chi^2_1 = 10.8$, $P = 0.001$; Fig. 5C). Finally, the sex ratio of escaped pupae was unaffected by temperature ($\chi^2_2 = 0.6$, $P = 0.745$).

To investigate the cost of host defense or ineffective parasitism in escaped caterpillars, we compared their survival rate to that of unparasitized caterpillars. Our findings revealed a significant difference in survival between the two groups ($\chi^2_1 = 252.6$, $P < 0.001$). Additionally, the effect of developmental temperature on survival also varied between them ($\chi^2_1 = 11.1$, $P = 0.004$ for the interaction between group and temperature factors). The survival rate of escaped caterpillars was lower than that of the unparasitized caterpillars (see Fig. 5B vs. Fig. 2A), indicating a cost associated with host defense or ineffective parasitism. Furthermore, while a decrease in survival was observed in both escaped

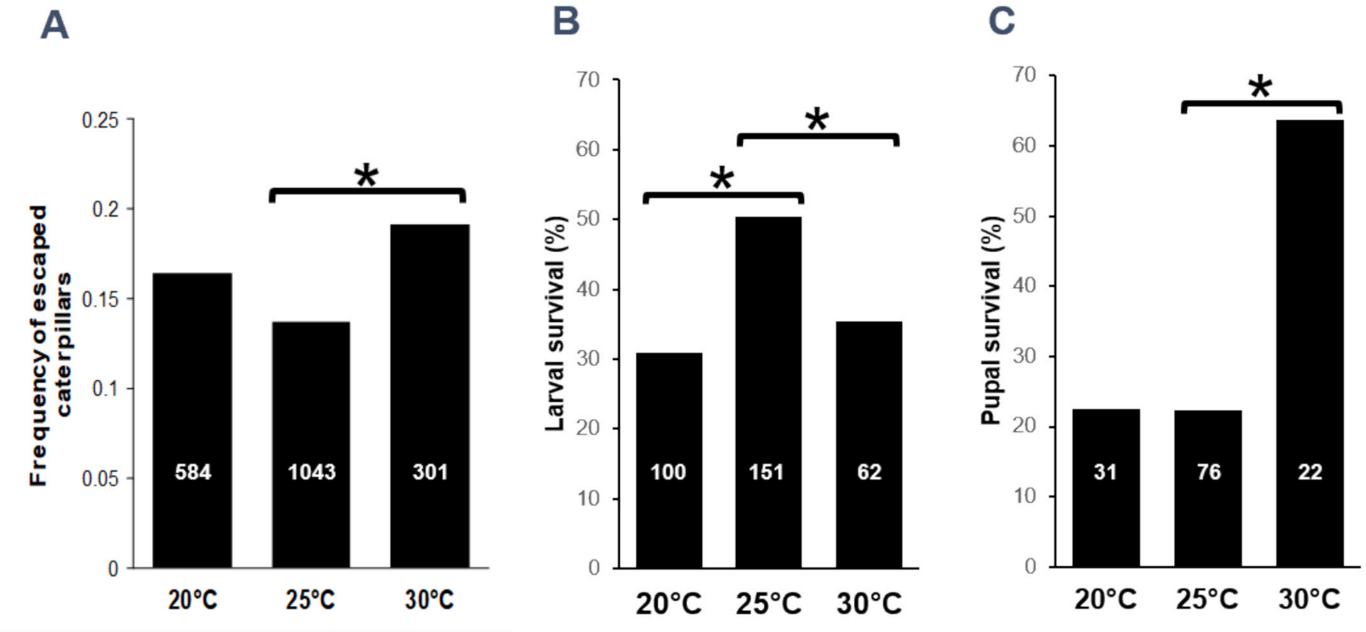

Fig. 5. Frequency and survival of FAW escaping parasitism. Frequency (A), larval (B) and pupal (C) survival rates of escaped FAW were evaluated as a function of developmental temperature. The numbers in the bars indicate the number of individuals analysed at each temperature. An asterisk indicates a significant difference between pairwise comparisons ($p < 0.01$).

and unparasitized caterpillars when the temperature rose from 25 °C to 30 °C, a significant increase in survival between 20 °C and 25 °C was noted only in the escaped caterpillars (Fig. 5B), not in the unparasitized group (Fig. 2A).

3.3. *Effect of temperature on H. didymator*

The influence of developmental temperature on *H. didymator* was investigated by assessing various parameters, including the rates of oviposition success, the emergence of parasitoid larvae from the host, cocoon formation after larval emergence, adult emergence from the cocoon, and overall parasitism success (measured as the adult emergence rate relative to the initial number of larvae of FAW that were parasitized). Additionally, the study evaluated developmental rates during the endoparasitoid phase, after cocoon formation, and the resulting sex ratio of adults. The developmental temperature did not influence the success of oviposition ($\chi^2_2 = 2.6$, $P = 0.273$). The oviposition rates were 66.7 % at 20 °C ($n = 36$), 77.5 % at 25 °C ($n = 30$), and 79.9 % at 30 °C ($n = 40$). However, during the endoparasitoid phase, the rate of larval emergence decreased significantly with increasing temperatures: between 20 °C and 25 °C ($\chi^2_1 = 10.9$, $P < 0.001$) and between 25 °C and 30 °C ($\chi^2_1 = 98.2$, $P < 0.001$) (see Fig. 6A). Similarly, the formation of parasitoid cocoons after larval emergence also declined at higher temperatures: between 20 °C and 25 °C ($\chi^2_1 = 26.2$, $P < 0.001$) and between 25 °C and 30 °C ($\chi^2_1 = 42.5$, $P < 0.001$) (Fig. 6B). Temperature did not significantly affect adult emergence from cocoons ($\chi^2_2 = 2.6$, $P = 0.270$), with rates of 53.2 % at 20 °C ($n = 355$), 54.4 % at 25 °C ($n = 542$), and 43.8 % at 30 °C ($n = 64$). The overall success of the parasitoid did not significantly differ between 20 °C and 25 °C ($\chi^2_1 = 2.1$, $P = 0.152$), but decreased significantly from 25 °C to 30 °C ($\chi^2_1 = 44.9$, $P < 0.001$) (Fig. 6C).

The developmental rate of the parasitoid *H. didymator* was measured during two phases: the endoparasitoid phase (Fig. 7A) and the external phase (Fig. 7B), which includes the period from cocoon formation to adult emergence. During the endoparasitoid phase, larval development was slightly accelerated between 20 and 25 °C ($Z = 3.4$, $P < 0.001$) and was two times faster at temperatures between 25 and 30 °C ($Z = 8.1$, $P < 0.001$) (Fig. 7A). For the external phase, development was accelerated

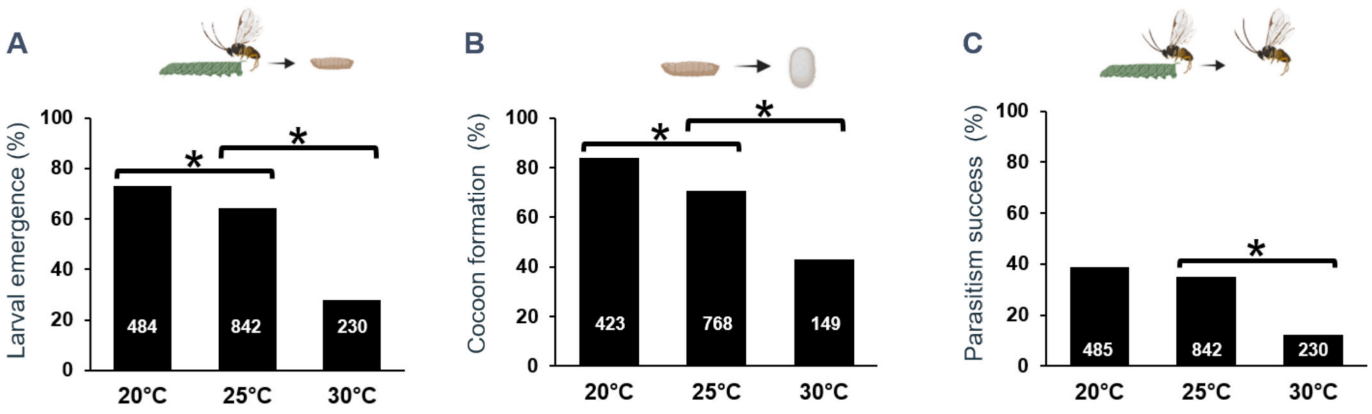

Fig. 6. Success of *H. didymator* with developmental temperature. The rate of emergence of immature stages (A), the rate of cocoon formation (B), and the overall success of parasitism (C) at the three experimental temperatures. The overall success of parasitism was calculated from oviposition to adult emergence. The numbers in each bar indicate the sample size. An asterisk indicates a significant difference between pairwise comparisons ($p < 0.01$).

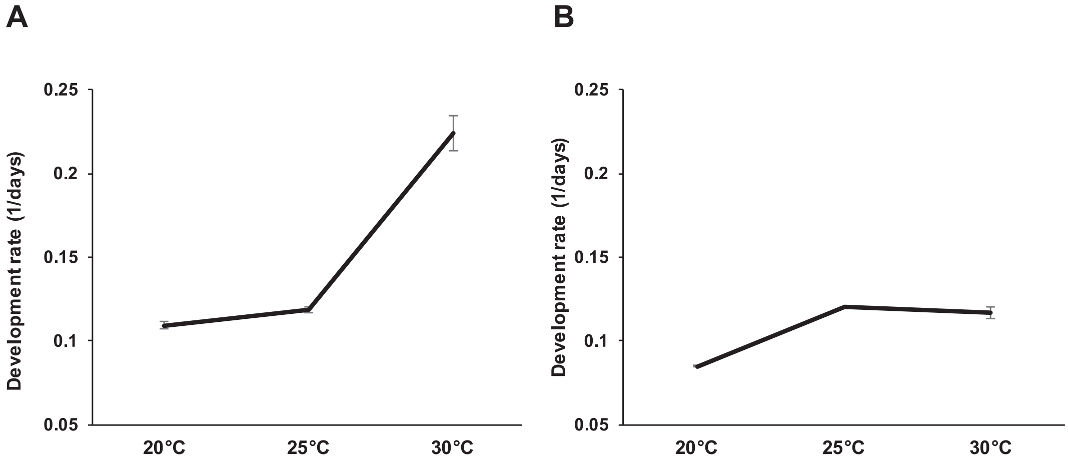

Fig. 7. Developmental rate of *H. didymator* as a function of developmental temperature. (A) Developmental rate from egg oviposition to larval emergence. Sample sizes are 189, 295 and 28, respectively for 20, 25 and 30 °C. (B) Developmental rate from cocoon formation to adult emergence. Sample sizes are 355, 542 and 64, respectively for 20, 25 and 30 °C. Error bars indicate SE. (Drawings created with BioRender.com).

between 20 to 25 °C ($Z = 23.1$, $P < 0.001$), but slightly slower at 30 °C than 25 °C ($Z = -3.9$, $P < 0.001$) (Fig. 7B). The sex ratio of *H. didymator* was not significantly influenced by temperature ($\chi^2_2 = 4.1$, $P = 0.130$; the values for the sex ratio can be found in Table S2b of Supplement 2).

3.4. Multiplication rates of FAW and H. didymator

We used demographic models to determine the multiplication rates of FAW and *H. didymator* at the three experimental temperatures. These models were parameterized using estimates derived from the study (Supplement 2). All models indicated multiplication rates exceeding 1, showing that the rearing conditions were favorable for FAW and the parasitoid. However, the response to temperature varied between the two species (Fig. 8). The impact of rising temperature within the range of 20 to 30 °C was beneficial for FAW but detrimental for *H. didymator*. The multiplication rate of FAW increased from 20 to 25 °C due to enhanced pupal survival (Fig. 2) and faster development of both larvae and pupae (Fig. 3). There was also an increase in the multiplication rate of FAW between 25 and 30 °C, which is attributed to the faster development of larvae and pupae, despite a decline in larval survival. In contrast, the multiplication rate of *H. didymator* remains relatively consistent between 20 and 25 °C but decreases from 25 to 30 °C due to lower parasitoid success (Fig. 6). Overall, the divergence in multiplication rates between FAW and the parasitoid increased with increasing temperature.

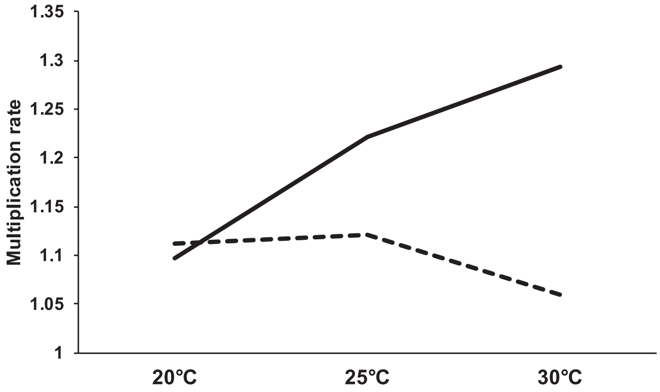

Fig. 8. Multiplication rate with developmental temperature for FAW (black line) and *H. didymator* (dashed line).

4. Discussion

This study aimed to evaluate the influence of fluctuating developmental temperatures on the performance of the larval endoparasitoid *H. didymator* when interacting with FAW, a major invasive crop pest. We assessed host survival and development in both parasitized and non-parasitized conditions, along with the developmental success of the parasitoid. The fluctuating thermal regimes employed in this study reflect realistic field conditions during maize growing seasons in southern Europe, where FAW is likely to become established (Gilioli et al. 2023; Wang et al. 2023; Kartakis et al. 2025).

4.1. Thermal responses of unparasitized FAW under fluctuating temperatures

In the absence of parasitism, the developmental temperature significantly influenced FAW in terms of survival, developmental rate, and adult body mass. Thermal conditions of 20 °C and 25 °C enabled caterpillars to maintain a viability rate of over 90 %, indicating that these temperatures are within the optimal range for this developmental stage. Conversely, FAW pupal survival was higher at 30 °C. The significant decline observed at 20 °C suggests that this temperature, particularly with daily fluctuations between 15 °C and 25 °C, is suboptimal for successful metamorphosis, potentially due to a metabolic slowdown or impaired ability to mobilize the energy reserves required for pupation (Merkey et al. 2011). These stage-specific responses to temperature are consistent with previous studies on FAW thermal biology (Montezano et al. 2019; Tao et al. 2023), and may influence the timing and efficiency of biological control interventions.

The developmental rate of FAW larvae and pupae increased twofold when the temperature rose from 20 °C to 30 °C. This effect is commonly observed in ectothermic organisms, where increasing temperatures accelerate metabolic processes and development up to a certain threshold. Beyond this point, excessively high temperatures can become harmful (Colinet et al. 2015). As temperatures rise and remain below critical levels, the life cycle of FAW should shorten, potentially resulting in more generations per year and increasing crop damage. The accelerated development was associated with a reduction in the body mass of moths. This finding aligns with the temperature-size rule commonly observed in ectotherms, which states that body size decreases as developmental temperature increases (Atkinson and Sibly 1997). At higher temperatures, the accelerated development limits the time available for accumulating energy reserves to sustain growth (Atkinson and Sibly 1997). While this rapid growth can reduce generation time, it may come at the cost of smaller moths and possibly lower fecundity.

It is to note that the laboratory strain of FAW was maintained under stable laboratory conditions for many generations prior to the experiments. Long-term rearing in controlled environments may affect their response to temperature variations (Partridge et al. 1995). To reduce potential biases linked to long-term rearing at 25 °C, FAW individuals were pre-acclimated for one generation to the three experimental temperature regimes before the main experiment. While experimental studies on a laboratory strain is a common practice, it will be interesting to replicate our study on FAW newly collected in the field.

4.2. Effect of temperature on the success of *H. didymator*

The observed thermal sensitivity of FAW development and survival raises critical questions about how temperature affects not only the pest itself but also its natural enemies, such as parasitoids. Identifying these effects is essential to fully understand the dynamics of the FAW-parasitoid interaction, particularly in the context of biological control and climate warming. Previous studies using constant temperatures and *H. armigera* as a host have shown that *H. didymator* develops normally between 15 °C and 30 °C but fails to survive at 33 °C (Mironidis and Savopoulou-Soultani 2009). Our results build on this by showing that parasitoid development is impaired under high temperatures, particularly when daily fluctuations reach 35 °C (30 ± 5°C). This effect occurs during its development within the host (from oviposition to larval emergence), and may be due to heat-induced cellular damage or metabolic disruption (Neven 2000). In contrast, once the cocoon is formed, the effects of high temperatures seem negligible, possibly due to the protective properties of the cocoon or physiological adaptations that provide tolerance at this stage. Although *H. didymator* developed faster at 30 °C, its overall success from oviposition to adult emergence was significantly reduced compared to 20 °C and 25 °C. These results suggest that 30 °C may approach or even exceed the thermal tolerance threshold of the parasitoid. The accelerated intra-host development at this temperature could reflect a strategy to keep pace with the faster development of the host. However, this response does not compensate for the reduced survival, as shown by a lower multiplication rate. These findings align with the observation that in some species, parasitoids tend to have lower thermal optima than their hosts (Hance et al. 2007; Furlong and Zalucki 2017).

4.3. Thermal divergence between FAW and *H. didymator* and implications for biological control

Hyposoter didymator can parasitize up to 10 % of *H. armigera* individuals in the field, and up to 80 % under semi-controlled conditions (Frayssinet et al. 2019), demonstrating its capacity to reach high parasitism levels under favourable conditions. Experimental studies have confirmed successful rearing of *H. didymator* on *S. littoralis* and *H. armigera* with high parasitism rates, as well as improved mass-rearing protocols based on host stage selection and sex allocation (Schneider and Viñuela 2007; Hatem et al. 2016). In our study, the percentage of adult wasp emerging from cocoons under controlled conditions ranged from 43.8 % to 54.4 %. These values are roughly comparable to those reported for *H. armigera*, suggesting that FAW is a suitable host. While interactions between both species are undocumented in the field, our findings point to the interest of further assessing the potential of *H. didymator* as a biocontrol agent, especially in agroecological settings or through semi-field trials.

However, from a biological control perspective, the pronounced temperature sensitivity of *H. didymator* raises concerns about its effectiveness in the field. One important limitation is that, the rapid development of FAW larvae at high temperatures results in a shorter larval stage. This could potentially limit the time available for the parasitoid to locate and parasitize FAW larvae in the field. However, *H. didymator* is a generalist parasitoid and may overcome this challenge by targeting alternative hosts suitable stages. In addition, the estimated multiplication rates of the two species diverged with temperature. At 30 °C, the FAW multiplication rate increased, while that of *H. didymator* decreased compared to 20 °C and 25 °C. This contrast suggests that warming could benefit the pest while reducing the performance of the parasitoid. This underlines the challenges for biological control programmes, particularly in Mediterranean regions, where the parasitoid is already established, and where FAW is expected to expand under projected climate warming (Gilioli et al. 2023; Kartakis et al. 2025). *H. didymator* would likely be most effective in temperate or mid-altitude zones for early-season releases, when temperatures remain below its thermal limits. To maintain effective pest control throughout the cropping season, combining *H. didymator* with more thermotolerant parasitoid species may be beneficial.

Beyond short-term implications for biocontrol strategies, *H. didymator* might face selective pressures to adapt to warmer conditions or to shift host preferences over evolutionary timescales. This opens questions about the evolutionary trajectory of generalist parasitoids in response to climate change. Further research conducted under natural conditions will be essential to evaluate this hypothesis.

4.4. Higher temperature may benefit FAW by escaping parasitim

An intriguing result of our study was the observation of caterpillars escaping parasitism across all our thermal regimes. These caterpillars continued to develop beyond the stage reached by those from which the parasitoid emerged, although their development was delayed compared to unparasitized controls. While their survival rate was lower than that of control group, some completed their development to adulthood. This suggests that they successfully overcome parasitism, possibly by creating unfavorable internal conditions for the parasitoid or by directly neutralizing it through immune activation.

Although caterpillar escape was significantly more frequent at 30 °C. Similar temperature-dependent escapes from parasitism have been reported in other parasitoid systems (Seehausen et al. 2017b, 2018; Moore et al. 2021). For instance, *Manduca sexta* caterpillars escaped parasitism by *Cotesia congregata*, which is associated with the polydnavirus CcBV, when exposed to a fluctuating temperature regime of 30 ± 10 °C, but not under a temperature of 25 ± 10 °C or a constant 30 °C. These caterpillars were heavier and lived longer than parasitized individuals. However, none of them survived to pupation (Moore et al. 2021). While the molecular basis behind this escape remains unclear, studies in another polydnavirus-associated system (Seehausen et al. 2017b, a, 2018) suggest that elevated temperatures may impair parasitism by upregulating host immune gene expression and downregulating viral gene expression. In our study, escaped caterpillars showed developmental delays compared to non-parasitized controls. Dissections of a subset of them revealed viable, non-encapsulated *H. didymator* larvae, indicating that immune evasion occurred. However, most hosts died before pupation, and only a few reached the moth stage. Given the extensive tissue remodelling that occurs during metamorphosis, it is highly unlikely that the parasitoid survives in these cases. Thus, although *H. didymator* larvae may initially develop within the host, they fail to persist. If, as suggested by Seehausen et al. (2017b, 2018), temperature disrupts the polydnavirus activity, our results indicate that the polydnavirus HdIV retains sufficient activity to prevent encapsulation and partially inhibit host development. Future work will investigate the timing and molecular basis of parasitism failure in the FAW-*H. didymator* system.

Alternatively, the occurence of caterpillars escaping parasitism by *H. didymator* may be attributed to nutritional competition between the host and the parasitoid. During parasitism, caterpillars must fulfill their own nutritional needs while also supplying resources to the developing endoparasitoid, which consumes host tissues (Vinson et al. 2001; Strand and Casas 2008; Rossi et al. 2014). When nutrient availability is limited or the resource balance between the two organisms is disrupted, competition may result in negative effects for one or both partners. Caterpillars with limited nutritional reserves may not cover the needs of the parasitoid, which hinders its development and survival. As a result, the host may continue developing, albeit more slowly than non-parasitized individuals. In severe cases, this could even lead to the caterpillar's death before reaching adulthood, which is consistent with the reduced survival observed in escaped caterpillars. Elevated temperature may influence this nutritional competition, as more escaped caterpillars were found at 30 °C. Reshma et al. demonstrated that thermal stress during the larval stage alters the accumulation of metabolic reserves (such as total sugars, glycogen, lipids, and proteins) in adult FAW, with some effects persisting across generations (Reshma et al. 2023). Similarly, reduction in lipid reserves and storage efficiency have been observed at elevated temperatures in other Lepidoptera, including *Lobesia botrana* (Iltis et al. 2019), and *S. exigua* (Lee and Roh 2010). These changes, whether due to depletion or altered energy reserves, may exacerbate host-parasitoid nutritional mismatches between host and parasitoid, compromising larval developement and survival. Furthermore, if escaped caterpillars have limited energy resources, their capacity to mount an effective immune response may also be compromised. This could explain why parasitoid larvae are not encapsulated by FAW hemocytes. To clarify the mechanisms behind these observations, further metabolic and immune analyses under various thermal conditions will be essential.

4.5. *Long-term implications of temperature-driven parasitism escape*

We observed that the frequency of escaped caterpillars increased at warmer temperature. While the differences between temperature treatments were statistically significant, they were relatively moderate. This small difference may be considered biologically insignificant given current climatic conditions. However, our experimental temperatures are representative of those typically encountered in the field. As average temperatures rise, even gradual increases could have cascading effects on population dynamics, particularly by increasing escape rates, which may significantly impact pest population regulation. Furthermore, the long-term fate of escaped caterpillars in natural populations remains uncertain. Future research should investigate whether they are fertile and, if so, whether their offspring inherit enhanced resistance to parasitoids or other bioaggressors through transgenerational priming. While speculative, such effects have been documented in other systems (Eggert et al. 2015). Additionally, findings by Reshma *et al.* suggests that thermal conditions can have persistent transgenerational effects on FAW, potentially influencing their adaptation to biological control efforts under warming conditions (Reshma et al. 2023). From an evolutionary perspective, these temperature-mediated interactions could drive adaptive responses in both hosts and parasitoids, ultimately influencing the population dynamics over time.

5. Conclusion

In conclusion, our study shows that rising temperatures affect FAW and the parasitoid *H. didymator* differently. While higher temperatures increase the multiplication rate of FAW, they impair the performance of the parasitoid. This divergent response may reduce the effectiveness of *H. didymator* as a biological control agent in warmer regions, or regions that will become warmer due to climate change. The phenomenon of host escape also highlights the importance of understanding the physiological mechanisms behind parasitism failure. Although *H. didymator* has not been reported to attack FAW for now, our results provide valuable insights into its thermal compatibility with this major pest under controlled conditions. Further research under semi-field or field conditions is essential to validate these findings in more complex and variable environments, and to evaluate the potential contribution of *H. didymator* to integrated pest management strategies in temperate regions where both species are expected to co-occur in the future.

Authors contribution

I.D. and M.M. conceived and designed the study and obtained financial support for the research. S.A., V.J., M.M. and I.D. conducted the experiments and analyzed the data. I.D. drafted the original manuscript with contributions from M.M. and S.A. All authors reviewed and approved the final version of the submitted manuscript.

CRediT authorship contribution statement

Shannon Alary: Formal analysis. **Manuel Massot:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Véronique Jouan:** Methodology. **Isabelle Darboux:** Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2025.105843.

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