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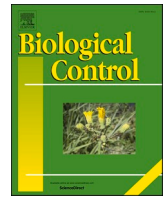
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## Influence of high temperatures on the European earwig *Forficula auricularia* s.l. and the parasitoid *Mastrus ridens*, two natural enemies of the codling moth *Cydia pomonella*

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### HIGHLIGHTS

- *Mastrus ridens* and *Forficula auricularia* are natural enemies of *Cydia pomonella*.
- *M. ridens* and *F. auricularia* stopped developing at 32 °C and 28 °C, respectively.
- *M. ridens* fecundity and *F. auricularia* predation declined at 28 °C and 30 °C, respectively.
- High temperature increased *M. ridens* susceptibility to sulfur, copper and azadirachtin.
- Rising temperatures may disrupt biological control of *C. pomonella*.

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### ABSTRACT

A key concern for agriculture is that rising temperatures may disproportionately affect pests and their natural enemies, potentially leading to disruptions in their synchronization or population dynamics, thereby compromising biological control. This study examined whether the European earwig, *Forficula auricularia sensu lato* (Dermaptera: Forficulidae), a generalist predator native to France, and *Mastrus ridens* (Hymenoptera: Ichneumonidae), a recently introduced parasitoid of the codling moth *Cydia pomonella* (Lepidoptera: Tortricidae), can tolerate high temperatures and effectively control this pest under such conditions. Our measurements indicated that the parasitoid and predator were unable to complete their development at temperatures starting from 32 °C and 28 °C, respectively, whereas previous research has shown that the codling moth can develop at 35 °C. Unexpectedly, simulations indicated that + 4 °C of global warming could reduce *M. ridens* generations during the summer in southeastern France. Furthermore, although the parasitism rate of *M. ridens* remained stable between 20 °C and 30 °C, its total fecundity declined at 28 °C, as did the predation rate of *F. auricularia* at 30 °C. Additionally, we observed that *M. ridens* susceptibility to two fungicides, sulfur and copper, and a bioinsecticide, azadirachtin, increased significantly with temperature. Our results thus highlight a significant risk of increased codling moth abundance during the hottest months, driven by the absence or reduced effectiveness of their natural enemies. This underscores the urgent need to implement measures to protect these beneficial organisms under climate change, such as creating microclimatic refuges and reducing the use of pesticides.

### 1. Introduction

To ensure an effective transition towards sustainable agriculture in

the face of global warming, it is crucial to understand the impact of climate on the various components of agroecosystems, including insects. For ectothermic species such as insects, the relationship between

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ambient temperature and the average rates or values of biological processes, covering physiological processes and behaviors, typically follows a bell-shaped curve (Abram et al., 2017). Performance increases linearly with temperature up to an optimum point, then declines rapidly as it approaches a critical thermal maximum, beyond which the biological process cannot occur (Angilletta, 2009; Huey and Stevenson, 1979). These thermal performance curves are observed, for instance, in developmental rates (Sinclair et al., 2016), locomotion speeds (Gilchrist, 1996), metabolic rates (Moiroux et al., 2012), and feeding rates (Sentis et al., 2012) of most ectothermic animals. Insects may thus benefit from global warming, as higher temperatures can reduce their development time (Furlong and Zalucki, 2017) and increase their food intake (Harrison and Fewell, 1995), thereby increasing their abundance (Skendžić et al., 2021) and the number of generations per year (Adler et al., 2022; Juszczak et al., 2013; Stoeckli et al., 2012), provided that temperature remains below their critical thermal maximum.

Due to this temperature-driven acceleration in insect pest dynamics and feeding rates, crop losses are expected to rise sharply in the future (Schneider et al., 2022), potentially increasing by 10 % to 25 % per degree Celsius of global mean surface warming for the three most consumed cereals: rice, maize, and wheat (Deutsch et al., 2018). Moreover, climate change may significantly influence the efficacy of various pest control methods, including insecticides (Perrin et al., 2022) and biological control using entomopathogens (Chen et al., 2003; Rizal et al., 2022) or entomophagous arthropods (Castex et al., 2018; Schmitz and Barton, 2014). A major concern for agriculture is that increasing temperatures may differentially affect pests and their natural enemies, since thermal performance curves vary strongly between species. Ambient temperature may indeed exceed the critical thermal maximum for the natural enemy but not for the pest, potentially leading to spatial and temporal mismatch between the two trophic levels and decreased biological control effectiveness (Damien and Tougeron, 2019; Wetherington et al., 2017). Differential temperature effects on life history traits such as fecundity or longevity between pests and their natural enemies may also disrupt population dynamics, ultimately leading to pest outbreaks (Abarca and Spahn, 2021; Gutierrez et al., 2008). Additionally, the attack rate by predators and parasitoids is commonly expected to increase with ambient temperature due to an increased metabolic rate (Brown et al., 2004), but it may drop if the critical metabolic threshold is surpassed (Moiroux et al., 2012). Some natural enemies may thus no longer be able to control pests when temperatures exceed their thermal range (Devotto et al., 2010; Duan et al., 2018; Fernandes et al., 2021). Since the risk of disruption in biological control due to climate change depends on the relative thermal ranges of the interacting species, it is impossible to establish a general pattern, and each system must be studied individually.

The codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), is the major pest affecting apples worldwide and a key pest in other pome fruits, including pears, walnuts, quinces, and the true service tree *Sorbus domestica* (Pajač et al., 2011). Without treatment, it can cause yield losses of 30 to 50 % in apple orchards, and even up to 80 % in some years (Kaplan, 2023; Lacey and Unruh, 2005). Projections suggest that this species, which is able to develop at a constant temperature of 33 °C (Aghdam et al., 2009) to 35 °C (Perrin et al., 2022), may benefit from global warming by producing an additional generation in various regions with, for example, 3 generations instead of 2 in Poland and Switzerland (Juszczak et al., 2013; Stoeckli et al., 2012). This species may also expand its range into currently too-cold latitudes, with, for example, a projected northward shift of its distribution limit from approximately 60°N to 75°N (Guo et al., 2021), while climatic conditions may become too unfavorable in other regions, such as south-eastern Italy (Svobodová et al., 2013). Moreover, in addition to the widespread emergence of resistance to chemical insecticides (Ju et al., 2021) and different isolates of *C. pomonella* granulovirus used as bio-insecticide (Siegwart et al., 2020), a recent study revealed that toxicity of two commonly used insecticides against this pest –emamectin,

employed in conventional orchards, and spinosad, used in organic orchards- decreases as temperatures rise (Perrin et al., 2022). It is therefore essential to further investigate the effects of temperature on alternative pest control methods, especially since it has been shown that efficacy of insecticides against this species may diminish in the future (Perrin et al., 2022).

Although biological control relying on entomophagous organisms is not central to the integrated management of the codling moth in Western Europe, numerous indigenous natural enemies significantly limit its abundance. These include parasitoids, such as *Ascogaster quadridentata* (Hymenoptera: Braconidae) and *Pristomerus vulnerator* (Hymenoptera: Ichneumonidae) (Maalouly et al., 2015), as well as generalist predators, such as the great tit *Parus major* (Passeriformes: Paridae) (Mols and Visser, 2002) and the European earwig *Forficula auricularia sensu lato* (Dermaptera: Forficulidae) (Unruh et al., 2016). The latter species has been reported to prey on up to 16 % of *C. pomonella* eggs under semi-natural conditions in English orchards (Glen, 1975). It is sometimes transferred by growers from stone fruit crops, where it causes damage, to apple or pear orchards to regulate the codling moth and other pests, such as aphids and psyllids (Hanel et al., 2023). Despite its potential role as an effective natural enemy in pome fruit orchards, the ability of *F. auricularia* to cope with high temperatures has been poorly studied. A notable exception is a study on Belgian populations, which reported 100 % mortality at 23 °C for eggs and at 28 °C for nymphs (Moerkens et al., 2011). Moreover, recent studies have revealed that *Forficula auricularia* is a species complex comprising three cryptic species (González-Miguéns et al., 2020), which may exhibit different thermal limits.

In addition to the biological control provided by indigenous species, an exotic, specialist ectoparasitoid, *Mastrus ridens* (Hymenoptera: Ichneumonidae), was introduced to France starting in 2018 as part of an importation-based biological control program aimed at the permanent establishment of this species for sustainable control of the codling moth (Borowiec et al., 2020). Originating from Central Asia, *M. ridens* was first successfully introduced in the USA in 2002, where it was reported to parasitize up to 56 % of overwintering *C. pomonella* cocoons in unsprayed orchards (Mills, 2005). It was subsequently introduced in Argentina in 2003, Chile in 2006, New Zealand in 2012, and Australia in 2015. In addition to its high parasitism rate, this gregarious, idiobiont, and synovigenic parasitoid has a short generation time. It produces a large number of offspring compared to other codling moth parasitoids and exhibits remarkable dispersal capacity (Devotto et al., 2010). It is thus a promising candidate for the biological control of the codling moth in France and Europe. However, as with *F. auricularia*, its thermal biology has been poorly investigated, with the exception of the study by Devotto et al. (2010), which reported development at 25 °C but no development at 35 °C. Moreover, classical biological control programs are typically associated with a loss of genetic diversity compared to natural populations, as strains are often developed from a limited number of individuals. This reduced genetic diversity may compromise the adaptive capacity of released strains in the face of climate change (Aguilar-Fenollosa and Jacas, 2014). Determining the thermal requirements of such strains is therefore a key question when projecting the potential impact of global warming on the effectiveness of biological control. Beyond climate, the use of pesticides and their interactions with temperature may represent a significant barrier to the establishment of *Mastrus ridens* in orchards. A previous study reported that the toxicity of emamectin, chlorantraniliprole and spinosad against the parasitoid increased with temperature (Perrin et al., 2024). Understanding the combined effects of temperature and other phytosanitary products on *M. ridens* could help promote the long-term establishment of this parasitoid.

The aim of this study was to assess, through controlled experiments, the ability of the parasitoid *Mastrus ridens* and the predator *Forficula auricularia* to develop under high temperatures comparable to those endured by *Cydia pomonella*. To date, there remains some uncertainty

regarding the exact species present, as two cryptic species—*Forficula auricularia* and *Forficula dentata*—are known to occur in the region (González-Miguéns et al., 2020); however, we refer to *F. auricularia* in the broad sense throughout this study. The study also sought to evaluate the biocontrol potential of these two natural enemies in managing this pest in the context of global warming in southeastern France, a region characterized by a Mediterranean climate. Additionally, we simulated how global warming might affect the voltinism of the parasitoid and investigated how temperature influences its susceptibility to three widely used products in organic farming: sulfur, copper, and azadirachtin. Considering that geographic variations and local adaptations are common in the thermal performance curves of insects (Moiroux et al., 2010), we based our study on the strain used for the releases of *Mastrus ridens* in France and individuals from local populations for the earwig. This approach allowed us to test whether local populations of earwigs and the *Mastrus ridens* strain released in France are capable of adapting to climate warming, providing insights into how climate change may impact biological control strategies targeting a major orchard pest.

## 2. Materials and methods

### 2.1. Insect sampling and rearing

#### 2.1.1. *Cydia pomonella*

The *C. pomonella* laboratory strain used to rear the *M. ridens* individuals that were used in our experiments originates from orchards located in Graveson, Southern France. This strain is also used for mass rearing of *M. ridens* individuals released within the framework of the national biological control program in France. It has been continuously mass-reared since 1995 (Sauphanor and Bouvier, 1995) in the laboratory of the PSH Research Unit (Plants and Cropping Systems in Horticulture) at INRAE (France's National Research Institute for Agriculture, Food, and Environment), Avignon Research Center. Moths were maintained on an artificial corn-based diet without formaldehyde (Guennelon et al., 1981) under controlled conditions:  $23 \pm 0.5$  °C, 60 % ( $\pm 10$  %) relative humidity (RH), and a photoperiod of L16:D8.

#### 2.1.2. *Mastrus ridens*

*Mastrus ridens* was reared in insect-proof cages ( $32.5 \times 32.5 \times 32.5$  cm; mesh size: 650  $\mu$ m) under the same controlled conditions as those used for *C. pomonella*. The strain used in our experiments corresponds to the population released in France starting from 2018, which originated from a mix of strains collected in New Zealand (2015), Chile (2016), and Kazakhstan (2018). Each cage contained approximately 50 females and 35 males, which were fed ad libitum with fresh honey and water. Overwintering *C. pomonella* cocoons (50–60) were provided every 3–4 days as a host resource. To obtain overwintering cocoons, codling moth larvae were kept under the same rearing conditions as described above, except for a modified photoperiod of 12 h of daylight and 12 h of darkness throughout their larval development. When they left the artificial diet to weave their hibernacula, they were manually placed in small pieces of corrugated cardboard (approximately 1.5 cm  $\times$  1.5 cm) and stored at 4 °C until used for *M. ridens* rearing.

#### 2.1.3. *Forficula auricularia*

Adults of *F. auricularia* were collected from peach orchard located at INRAE Avignon using corrugated cardboard traps during the autumns of 2019 and 2020. These experimental orchards were managed under a minimal pesticide program. Couples of earwigs were then isolated in ventilated circular cages (5 cm diameter  $\times$  2 cm height) maintained at  $10 \pm 1$  °C, 60 % ( $\pm 10$  %) RH, and L16:D8. They were fed a diet similar to that of codling moths. Wet sand was provided as a substrate for egg-laying and was re-humidified once a week.

## 2.2. Experiments

### 2.2.1. Effects of temperature on *Mastrus ridens*

**2.2.1.1. Life history traits and behavior.** Thirty freshly emerged females per temperature group were placed with fifteen males in insect-proof cages ( $32.5 \times 32.5 \times 32.5$  cm; mesh size: 650  $\mu$ m) for 24 h at 20, 25, 28, 30, or  $32 \pm 0.5$  °C. A mixture of 75 % honey and 25 % water was provided as food. Afterward, females were placed individually in ventilated cages (19  $\times$  13.5  $\times$  9 cm) under the same thermal treatment, with one *C. pomonella* cocoon added and replaced daily throughout their lifespan. Each cocoon was transferred to a 4 cm diameter Petri dish, maintained in the same climatic conditions, and monitored daily until the emergence of a parasitoid or a moth.

Parasitism rate was determined as the proportion of cocoons from which *M. ridens* emerged, relative to the total number of cocoons initially offered to the mother during her lifetime. Total fecundity was measured as the cumulative number of *M. ridens* emerging from all cocoons provided to each female, while daily fecundity was calculated as the average number of *M. ridens* emerging per cocoon. Development time for each sex was calculated as the number of days from oviposition to the emergence of males or females. These data allowed us to calculate critical thermal maximum, upper developmental threshold and optimal developmental temperature of this species, and to project its voltinism under two global warming scenarios ( $+2$  °C and  $+4$  °C) using different phenological models. To assess *M. ridens* longevity, the progeny were maintained under the same conditions as for their development, provided with fresh honey and water, and monitored daily until death.

**2.2.1.2. Susceptibility to pesticides.** In a first experiment, we evaluated the influence of temperature on the mortality of *M. ridens* after ingestion of pesticides at different temperature. Only adult males were used in this experiment, as females were preserved for our rearing and biological control program. Three widely used pesticides permitted in France for organic farming were tested: sulfur and copper, both fungicides, and azadirachtin, a plant-derived bioinsecticide primarily used against aphids. The commercial formulation of copper (Bouillie Bordelaise RSR® Disperss® 20 %), sulphur (Microthiol® Spécial Disperss® 80 %) were purchased from UPL Holdings Coöperatief (Puteaux, France) and the commercial formulation of azadirachtin (NeemAzal®-T/S 9.8 g/L) was purchased from Andermatt (Bassussarry, France). To conduct the experiment, small pieces of paper (1 cm<sup>2</sup>) were soaked with 15  $\mu$ L of a honey/water solution (3:1), either untreated (control) or contaminated with five concentrations of each pesticide, defined relative to the recommended field concentration (X dose, Table 1), according to the Ephy database (<https://ephy.anses.fr/>). The five concentrations tested were X/5, X/2, X, 2X and 5X for the fungicides, and X/2, X, 2X, 5X and 10X for azadirachtin. The soaked papers were placed in the caps of 10-mL glass vials. Then, five freshly emerged males (<48 h old) were introduced into each vial, and the caps were partially screwed on to allow airflow. The vials were then placed in climatic chambers set at 23, 28, or 33 °C. Each test, consisting of five individuals, was repeated four times for each combination of pesticide concentration and temperature, including the control treatment. Mortality rates were assessed daily for 72 h. Missing

**Table 1**

Concentrations of pesticide active substances used in ingestion bioassays on males of the parasitoid *Mastrus ridens*. Concentrations are expressed in mg/L and converted into multiples of the field doses authorized in French orchards (X doses, available in the Ephy database, <https://ephy.anses.fr/>).

Pesticides	Concentrations (mg/L)					
	X/5	X/2	X	2X	5X	10X
Sulfur	0.0018	0.0045	0.009	0.018	0.045	NA
Copper	0.0026	0.0065	0.013	0.026	0.065	NA
Azadirachtin	NA	0.0015	0.003	0.006	0.015	0.03

individuals were excluded from the dataset. Corrected mortality was calculated using Abbott's formula (Abbott, 1925). These data were subsequently used to determine the dose required to kill half of the parasitoids for each treatment (LD50).

In a second experiment, we evaluated the effect of temperature and pesticide exposure through tarsal contact on the mortality of *M. ridens* males. Glass vials were pre-treated with 500 µL of either acetone (control) or a pesticide solution diluted in acetone to match crop application concentrations (Table 1). The vials were gently laid on their sides and rolled to ensure uniform distribution of the solution across the inner surface, then left to dry completely. Additionally, small paper squares (1 cm<sup>2</sup>) were soaked with 15 µL of an untreated honey/water solution (3:1) and placed in the caps of the vials. After two hours of drying, five males were introduced into each vial, and the caps were partially screwed on to allow airflow. The bioassay vials were then placed in climatic chambers set to 23, 28, or 33 °C. Mortality was assessed and corrected, as in the previous experiment, to calculate the mortality rate for each temperature. Each test, involving five individuals, was repeated four times per temperature.

## 2.2.2. Effects of temperature on *Forficula auricularia*

**2.2.2.1. Life history traits.** Earwig couples were checked daily in the rearing cages until egg laying occurred. Males were then removed to prevent cannibalism (Dib et al., 2017). Ten mothers per temperature treatment were immediately transferred with their progeny to conditions of 20, 25, 28, or 30 ± 0.5 °C, 60 % (±10 %) RH, and a photoperiod of L16:D8. Insects were fed ad libitum with ground sunflower pollen, and the sand was re-humidified as needed. *F. auricularia* has four nymphal stages, with nymph dispersion into trees typically starting at the 3rd instar, following the familial phase that normally occurs in the soil (Dib et al., 2017). Based on this behavior, after the second molting, 3rd instar nymphs were transferred without their mother to larger ventilated cages (19 × 13.5 × 9 cm) containing wet sand. Since *F. auricularia* is nocturnal and seeks shelter during the day (Dib et al., 2017), a cardboard strip was added to the cages to provide hiding places. Individuals were fed ad libitum with an artificial corn-based diet until they reached adulthood. Development time was calculated as the number of days from egg laying to the adult instar, while survival rate was measured as the ratio of earwigs reaching adulthood to the total number of eggs laid by each female.

**2.2.2.2. Predation rate.** After a 12-hour fasting period, 150 adult male and female *F. auricularia* individuals were randomly sampled from rearing cages. Each earwig was placed individually in a ventilated cage (19 × 13.5 × 9 cm) equipped with a small corrugated cardboard strip for shelter and 200C. *pomonella* eggs placed on a leaf cutting. Between 20 and 25 cages per temperature, with an approximately equal number of males and females, were assigned to one of the following temperatures: 20, 25, 28, 30, 32, or 35 °C. After 24 h, the number of remaining eggs was counted to estimate the predation rate of *F. auricularia*. Mortality of the earwigs was also recorded.

## 2.3. Statistical analysis

All data analyses were carried out using R software, version 4.0.2 (R Core Team, 2020).

### 2.3.0.1. Life history traits and behaviors of *Mastrus ridens* and *Forficula auricularia*

We investigated the effect of temperature on the total and daily fecundity of *M. ridens* using a generalized linear model (GLM) with a quasipoisson family to account for variability in count data. The survreg function in R was used to assess the effects of temperature, sex, and their interaction on the longevity of this species. The effect of temperature on

the parasitism rate of the parasitoid was analyzed using a GLM with a quasibinomial family. Similarly, we examined the effects of temperature, sex, and their interaction on the predation rate of *F. auricularia* using a GLM with a quasibinomial family. Since data on the survival rate and development time of *F. auricularia* were available for only two temperature treatments, differences between these treatments were analyzed using non-parametric chi-square and Wilcoxon tests, respectively.

### 2.3.0.2. Phenological models for *Mastrus ridens*

To determine the relationship between temperature and the developmental rate of *M. ridens*, we used the devRate R package (Rebaudo et al., 2018). A total of 37 models included in the devRate package were tested, ranging from simple linear to complex quadratic models with thermal limits. Model selection was based on two criteria: (1) goodness-of-fit metrics for our data (R<sup>2</sup>, RMSE, and AIC), and (2) the ability to accurately predict the critical thermal maximum (CTmax) and upper developmental threshold (XTmax) observed in our experiments. This procedure allowed us to select the best model for simulating the life cycle and voltinism of *M. ridens* using daily temperature data recorded by a weather station in an orchard at the INRAE Saint-Paul center in Avignon (South-Eastern France) in 2023, via the devrate.IBM function from the devRate package. Predictions were also performed for two simplified warming scenarios: current temperatures + 2°C and + 4°C. Based on the observed life cycle in the orchard, simulations began on April 1st, with two possible end dates for the season: September 30th and October 31st, due to the lack of information on the end of the active period for *M. ridens*.

This entire procedure could not be applied to *F. auricularia*, as developmental data were available for only two temperatures.

### 2.3.0.3. *Mastrus ridens* susceptibility to pesticides

The drm function from the drc package available in R software (Ritz et al., 2015) was used to calculate the different LD50 values and provide standard errors by fitting dose-response models to our data. The EDcomp function was subsequently used to test the influence of pesticide concentration and temperature on the LD50 of parasitoid males exposed to the pesticide by ingestion. For tarsal contact bioassays, differences in mortality between temperatures for a given pesticide were analyzed using a Chi-square test.

## 3. Results

### 3.1. Effects of temperature on *Mastrus ridens*

#### 3.1.1. Life history traits and behavior

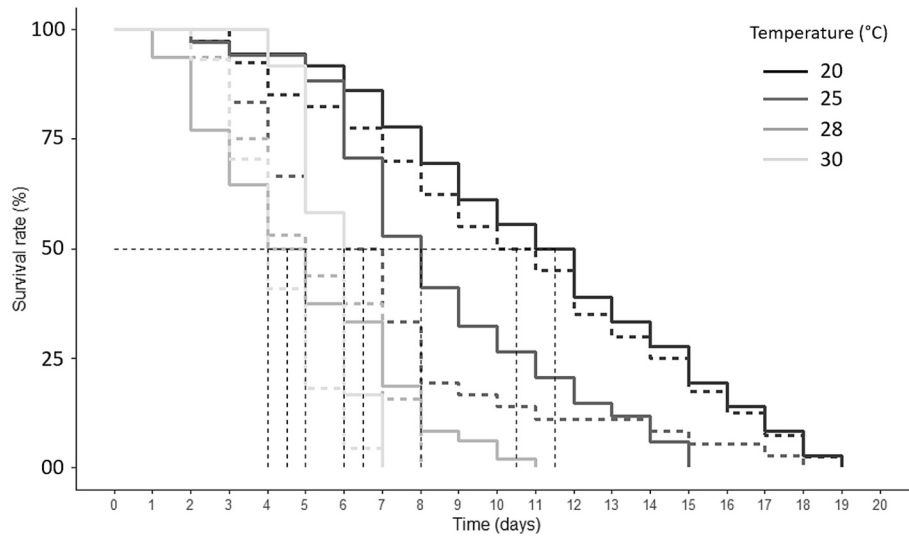
Temperature did not significantly influence daily fecundity (Estimate = 0.004, t = 0.153, p = 0.879) or the parasitism rate (Estimate = 0.081, z = 1.039, p = 0.299) of *M. ridens*. However, total fecundity was significantly lower at 28 °C and 30 °C compared to 20 and 25 °C (Estimate = -0.102, t = -2.891, p = 0.005, Table 2).

The longevity of *Mastrus ridens* decreased significantly with increasing temperature (z = -9.18, df = 3, p < 0.001), although no significant difference was observed between 28 °C and 30 °C (Table 2;

**Table 2**

Parasitism rate, total and daily fecundity, and longevity (mean ± SE) of *Mastrus ridens* females measured at four different temperatures. Different letters indicate significant differences between treatments (p < 0.05).

T°C	Total fecundity	Daily fecundity	Parasitism rate	Longevity♀ (days)
20	4.23 ± 1.08 a	0.43 ± 0.12 a	0.17 ± 0.03 a	11.72 ± 4.44 a
25	3.73 ± 1.09 a	0.55 ± 0.17 a	0.18 ± 0.04 a	9.00 ± 3.30b
28	1.93 ± 0.71b	0.46 ± 0.23 a	0.18 ± 0.05 a	5.42 ± 2.62c
30	1.41 ± 0.27b	0.29 ± 0.11 a	0.22 ± 0.06 a	6.17 ± 0.72c



**Fig. 1.** Kaplan–Meier curves showing the survival probability over time of *Mastrus ridens* females (solid lines) and males (dashed lines) developed and maintained at four different temperatures (20, 25, 30, and 35 °C).

**Fig. 1.** Longevity was not significantly influenced by sex ( $z = 0.64$ ,  $df = 3$ ,  $p = 0.52$ ) or by the interaction between temperature and sex ( $z = -0.93$ ,  $df = 3$ ,  $p = 0.35$ ).

3.1.2. Phenological models

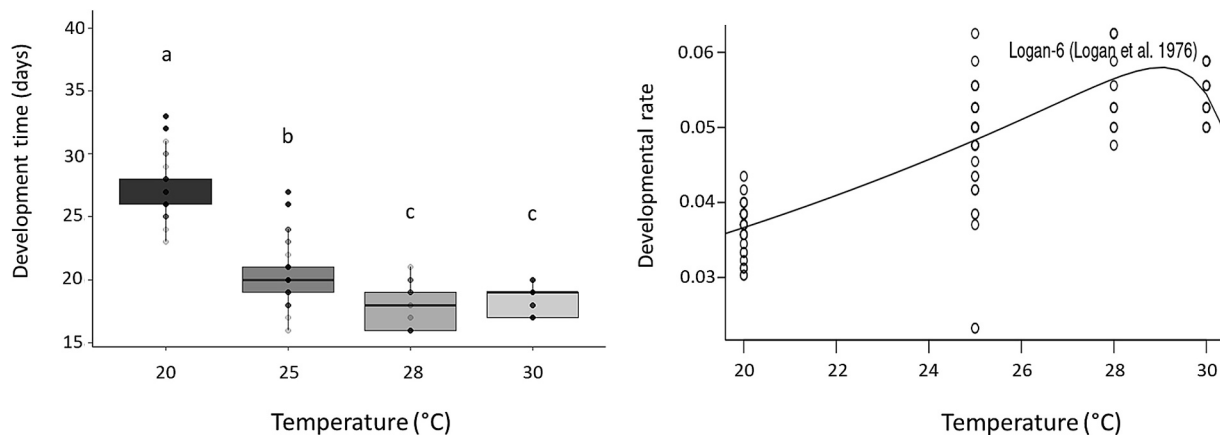
*Mastrus ridens* was able to complete its development within the temperature range of 20–30 °C but could not develop at 32 °C. Development time from oviposition to adult emergence significantly decreased from 20 to 28 °C while there was no significant difference between 28 °C and 30 °C (Fig. 2A).

Among the 37 models available in the devRate package, 12 fitted our data. All 12 models showed very similar AIC ( $-1470 \pm 4$ ) and RMSE ( $0.0053 \pm 0.0002$ ) values. The optimal development temperature was consistent across the ten models that provided this value, with an average of 29.7 °C and a range of  $\pm 0.8$  °C, depending on the model. Of these ten models, only two accurately predicted the upper developmental threshold (XTmax) and critical thermal maximum (CTmax), experimentally estimated to lie between 30 and 32 °C: Logan6\_76 (Logan et al., 1976) (Fig. 2B, Table 3) and Bayoh\_03 (Bayoh and Lindsay, 2003) (Table 3). In contrast, five models were unable to predict this value, while the remaining five significantly overestimated it (ranging from 34.8 to 44.3 °C). The Logan 6 model was selected to simulate the life cycle and voltinism of *M. ridens*.

**Table 3**

Logan6 and Bayoh development models for *Mastrus ridens*: adjusted parameters based on experimental data, goodness-of-fit statistics, and developmental metrics. T = Temperature; CTmax = Critical Thermal Maximum; Topt = Optimal Developmental Temperature; XTmax = Upper Developmental Threshold.

Logan6 model: $rT = phi * \left( e^{bb*T} - e^{bb*T_{max} - \frac{T_{max}-T}{\Delta T}} \right)$				
Parameters	$\phi$	bb	Tmax	deltaT
Goodness-of-fit	0.01214	0.0527	31.433	0.714
	R <sup>2</sup>	RSS	RMSE	AIC
	0.82	0.003792	0.005186	-1473.825
Metrics of development	CTmax	Topt	XTmax	
	31.5	29.03	31.5	
Bayoh model: $rT = aa + bb*T + cc*e^T + dd*e^{-T}$				
Parameters	aa	bb	cc	Dd
	-3.017e-02	3.141e-03	-9.010e-16	1.945e + 06
Goodness-of-fit	R <sup>2</sup>	RSS	RMSE	AIC
	0.82	0.003792	0.005186	-1473.825
Metrics of development	CTmax	Topt	XTmax	
	32.0	28.88	32.0	



**Fig. 2.** (A) Boxplots showing the development time from oviposition to adult emergence of *Mastrus ridens* at four different temperatures. (B) Logan-6 model (line) fitted to the developmental rates measured at the same temperatures. Different letters indicate significant differences between treatments ( $p < 0.05$ ).

Simulations of the *M. ridens* life cycle and voltinism, based on the Logan6 model (selected among other models for its goodness-of-fit) and daily temperature data recorded in Southeastern France in 2023, predicted six generations from April to the end of September (Fig. 3A), and seven generations by the end of October (Fig. 3B). The same predictions were obtained under a +2°C warming scenario. In the +4°C scenario, one generation was lost when the simulation ended in September, while no difference was observed when the simulation extended to the end of October (Fig. 3).

### 3.1.3. Susceptibility to pesticides

When *M. ridens* males ingested pesticides, the LD50 values for sulfur and copper were significantly lower at 28 °C (sulfur:  $t = 3.25$ ,  $p = 0.001$ ; copper:  $t = 3.79$ ,  $p < 0.001$ ) and 33 °C (sulfur:  $t = 3.06$ ,  $p = 0.002$ ; copper:  $t = 2.33$ ,  $p = 0.019$ ) compared to 23 °C. However, there was no significant difference in LD50 values between 28 °C and 33 °C (sulfur:  $t = -0.70$ ,  $p = 0.482$ ; copper:  $t = -0.62$ ,  $p = 0.535$ ) (Fig. 4). These results indicate a substantial increase in the susceptibility of parasitoid males to these fungicides under high temperature conditions. In contrast, no statistically significant effect of temperature was observed on the LD50 for azadirachtin, although a notable decrease was apparent between 23 °C and 33 °C ( $t = 1.68$ ,  $p = 0.09$ ) (Fig. 4).

When *M. ridens* males were exposed to field concentrations through tarsal contact, we observed significantly higher mortality at 33 °C compared to 23 °C and 28 °C for sulfur, at 28 °C and 33 °C compared to 23 °C for azadirachtin, and no significant influence of temperature on mortality for copper (Table 4).

## 3.2. Effects of temperature on *Forficula auricularia*

### 3.2.1. Life history traits

Temperature had a strong influence on the nymphal survival rate of *F. auricularia*, as no individuals were able to hatch at 28 °C or 30 °C. Nymphs could develop at 20 °C and 25 °C, but the survival rate was

significantly lower at 25 °C than at 20 °C ( $\chi^2 = 13.541$ ,  $df = 1$ ,  $p < 0.01$ ) (Fig. 5). No significant difference was observed in development time from egg-laying to adulthood between 20 °C and 25 °C ( $83.00 \pm 4.57$  days at 20 °C vs.  $75.44 \pm 5.52$  days at 25 °C;  $W = 107$ ,  $p = 0.1$ ).

### 3.2.2. Predation rate

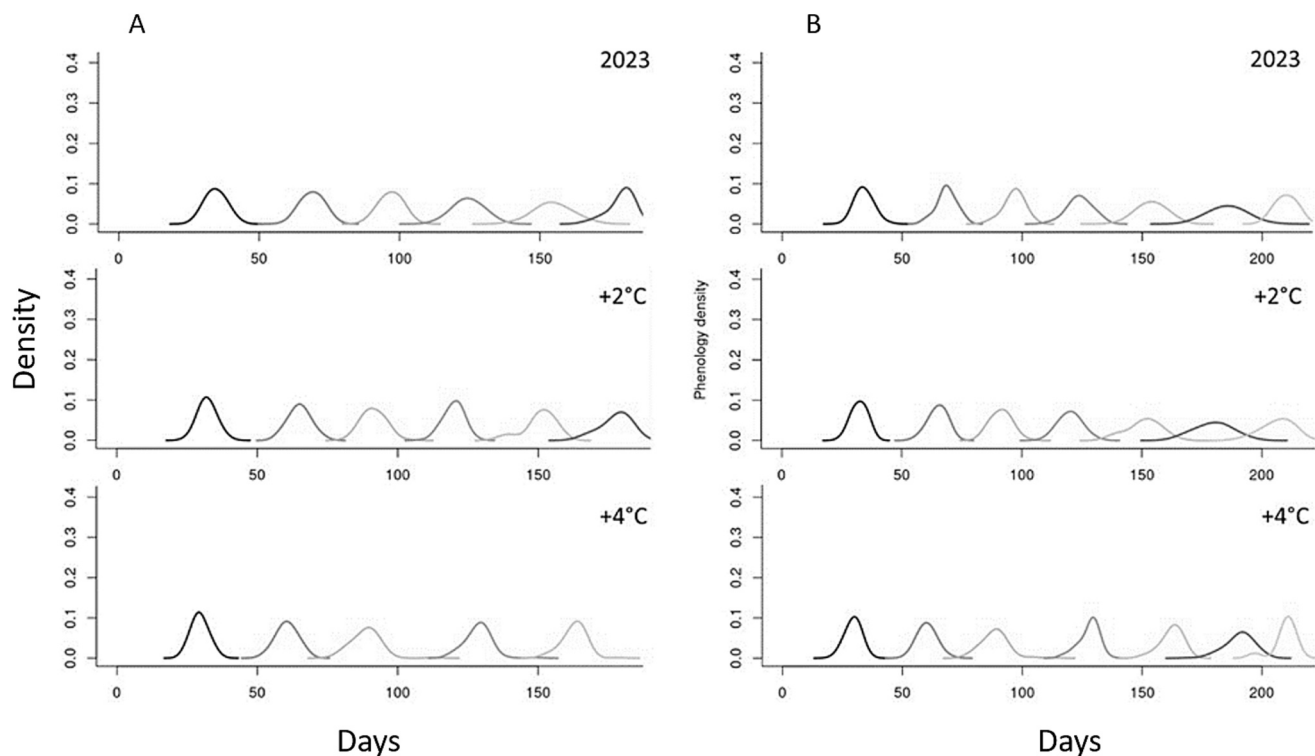
Temperature significantly influenced the predation rate of *C. pomonella* eggs by *F. auricularia* (Estimate = -0.258,  $t = -9.461$ ,  $p < 0.001$ ), whereas sex (Estimate = -0.841,  $t = -0.532$ ,  $p = 0.596$ ) and the interaction between the two factors (Estimate = 0.039,  $t = 0.695$ ,  $p = 0.498$ ) did not. This rate strongly and significantly declined starting from 30 °C, with no significant differences observed between 20 °C, 25 °C and 28 °C or between 30 °C, 32 °C and 35 °C (Fig. 6). Notably, 7 out of 20 individuals died at 35 °C during the 24-hour experiment, whereas no mortality occurred at other temperatures.

## 4. Discussion

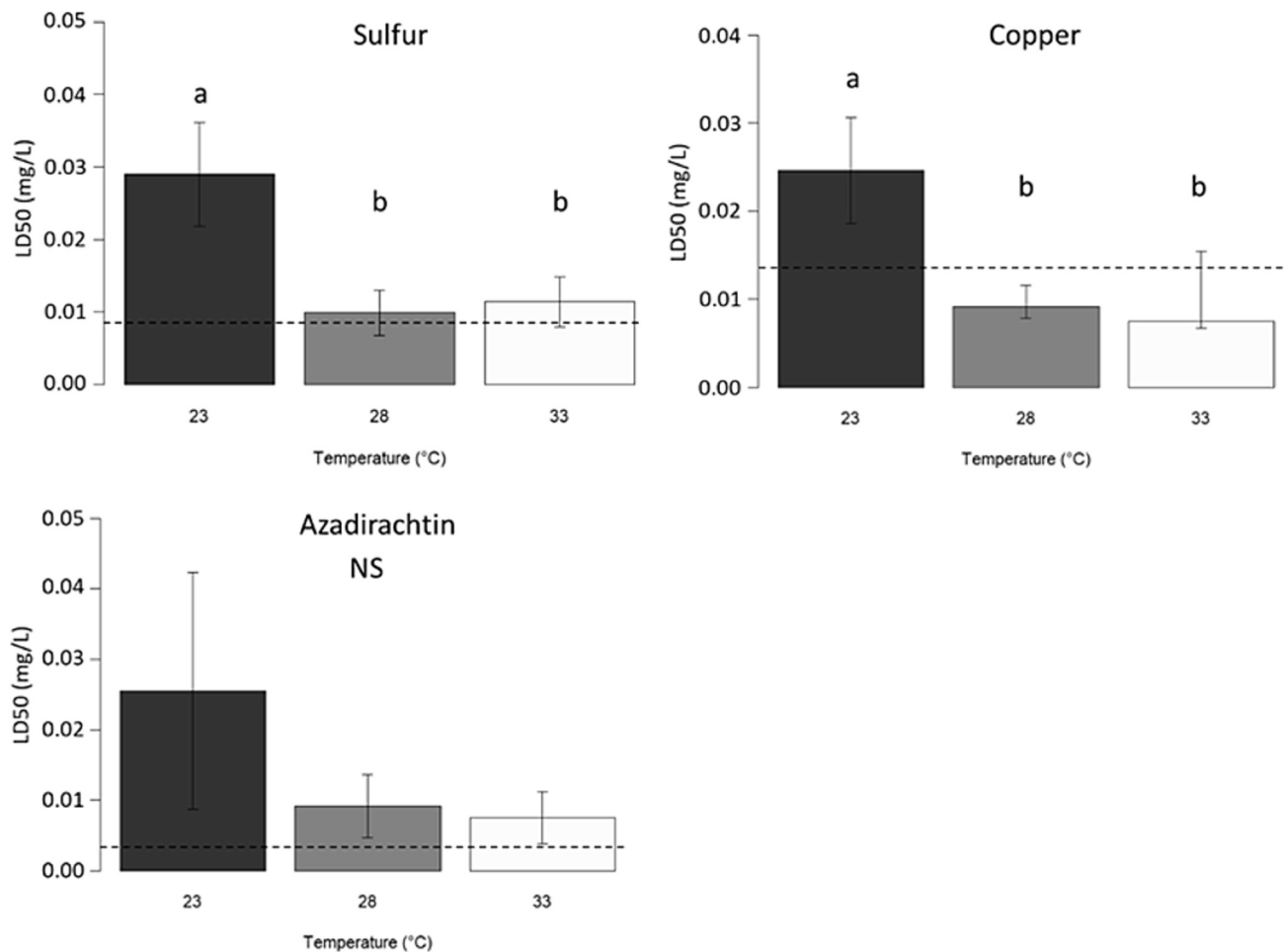
The present study examined the effects of high temperatures on two natural enemies of the codling moth, *Cydia pomonella*: the specialist parasitoid *Mastrus ridens* and the generalist predator *Forficula auricularia*. Our findings revealed that: (i) the parasitoid and predator could not complete their development at temperatures of 32 °C and 28 °C, respectively; (ii) the number of *M. ridens* generations may decrease during summer under a +4°C global warming scenario in southeastern France; (iii) the total fecundity of *M. ridens* and the predation rate of *F. auricularia* declined when ambient temperatures reached 28 and 30 °C, respectively; and (iv) the susceptibility of *M. ridens* to sulfur, copper, and azadirachtin increased with rising temperatures.

### 4.1. Development and phenology

The codling moth *C. pomonella*, a major pest of apple and pear orchards, exhibits an extremely wide distribution range (Kaplan,



**Fig. 3.** Predictions of the *Mastrus ridens* life cycle and voltinism in southeastern France under three climate scenarios: (i) no global warming (2023 temperatures), (ii) +2°C, and (iii) +4°C of global warming. Each peak represents a generation. Simulations begin on April 1st and end at the end of September (A) or the end of October (B).



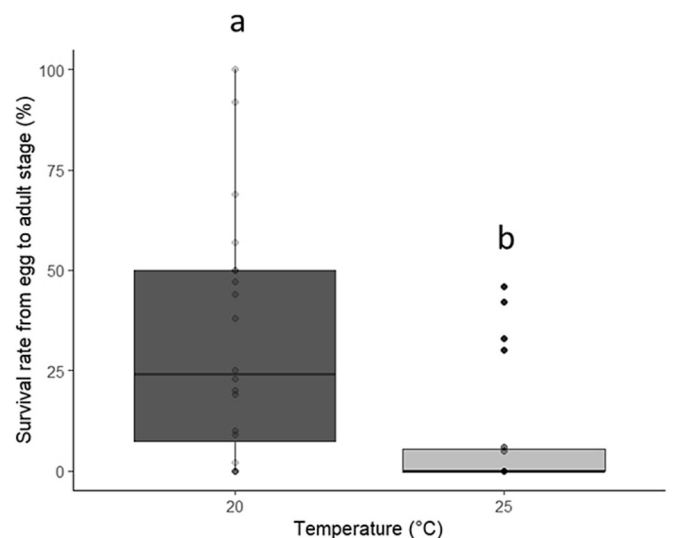
**Fig. 4.** Effects of temperature on doses (mean ± standard error, SE) of two fungicides (copper and sulfur) and a plant-derived insecticide (azadirachtin) required to kill 50 % of *Mastrus ridens* males (LD50). Dashed lines represent the concentrations allowed in orchards. Different letters indicate significant differences between treatments ( $p < 0.05$ ), while 'NS' indicates a non-significant difference. LD50 values were calculated using the `drm` function from the `drc` package in R, with standard errors provided to indicate the precision of the estimates. Each combination of pesticide concentration and temperature, used to calculate the LD50, was replicated four times ( $n = 4$ ), with each replicate consisting of a batch of five males.

**Table 4**

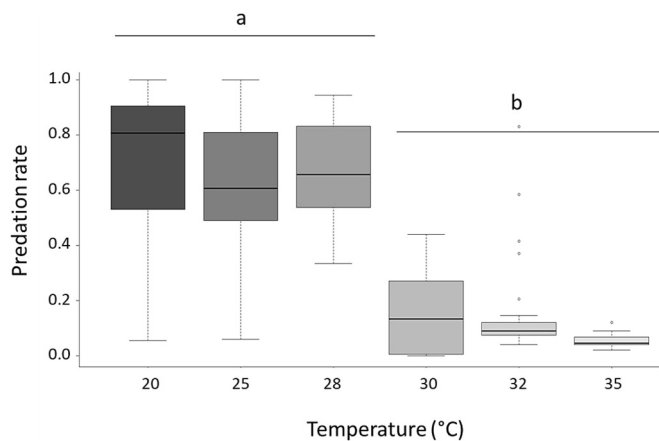
Corrected mortality, using Abbott's formula (Abbott, 1925), of *Mastrus ridens* males exposed to field concentrations of two fungicides (copper and sulfur) and a plant-derived insecticide (azadirachtin) via tarsal contact at three different temperatures. Different letters indicate significant differences in mortality between 23 °C and either 28 °C or 33 °C ( $p < 0.05$ ).

Pesticide	Corrected mortality (%)		
	23 °C	28 °C	33 °C
Sulfur	36.84 a	25.00 a ( $\chi^2 = 1.05$ )	88.89b ( $\chi^2 = 24.28$ )
Copper	31.58 a	20.00 a ( $\chi^2 = 1.13$ )	55.56 a ( $\chi^2 = 5.64$ )
Azadirachtin	0.00 a	15.00b ( $\chi^2 = 39.60$ )	33.33b ( $\chi^2 = 211.20$ )

2023). Its ability to tolerate high developmental temperatures likely explains its successful establishment in warm regions, including the Mediterranean Basin. Experimental studies measuring its thermal development curves across a broad range of temperatures reported effective development at constant temperatures of 33 °C or 35 °C (Aghdam et al., 2009; Perrin, 2022). Models used in the same studies predicted an optimal developmental temperature ranging between 30.35 °C and 32.37 °C. These high thermal optima and upper developmental thresholds may enable the codling moth to cope with climate change and complete additional generations in many regions worldwide (Juszczak et al., 2013; Stoeckli et al., 2012), particularly in warmer areas, as long as food plants are readily available.



**Fig. 5.** Boxplots of the survival rate (%) of *Forficula auricularia*, from egg-laying to adulthood, measured at 20 °C and 25 °C. Different letters indicate significant differences between treatments ( $p < 0.05$ ).



**Fig. 6.** Boxplots of predation rate of 200 *Cydia pomonella* eggs by *Forficula auricularia* adults ( $n = 22, 25, 21, 25, 25$  and  $20$  adults at  $20\text{ }^{\circ}\text{C}, 25\text{ }^{\circ}\text{C}, 28\text{ }^{\circ}\text{C}, 30\text{ }^{\circ}\text{C}, 32\text{ }^{\circ}\text{C},$  and  $35\text{ }^{\circ}\text{C}$ , respectively) over 24 h. Different letters indicate significant differences between treatments ( $p < 0.05$ ).

In comparison, our observations showed that the strain of *Mastrus ridens* released in France since 2018 for the biological control of this pest was unable to complete its development at  $32\text{ }^{\circ}\text{C}$ . Moreover, ten out of the twelve models fitted to our experimental data indicated an optimal developmental temperature between  $28.9\text{ }^{\circ}\text{C}$  and  $29.9\text{ }^{\circ}\text{C}$ , with an upper developmental threshold and critical thermal maximum ranging from  $31.5\text{ }^{\circ}\text{C}$  to  $32\text{ }^{\circ}\text{C}$ . These findings align with those of Devotto et al. (2010), who suggested that the optimal and critical maximum temperatures for this species fall within a broad range of  $25\text{ }^{\circ}\text{C}$  to  $35\text{ }^{\circ}\text{C}$ . The differences in thermal development curves between *C. pomonella* and *M. ridens* suggest that the parasitoid might struggle to maintain stable populations in hot regions where the pest thrives.

Moreover, our climate warming simulations revealed that a  $+4\text{ }^{\circ}\text{C}$  increase in southern France, based on 2023 climatic data, could suppress one parasitoid generation during the summer. This suppression is likely due to more frequent temperatures exceeding the parasitoid's optimal range, which slows its development during the hottest months. However, this delayed development might be offset by faster development later in the season if the species' lifecycle extends into late autumn in France, as has been observed in some regions of New Zealand (Charles et al., 2019). Further research is therefore needed to better understand the activity period of *M. ridens* in France in order to refine our predictions accordingly.

While *Mastrus ridens* may face challenges with rising temperatures, these effects are likely to be even more severe for the European earwig, *Forficula auricularia* s.l. In our experiments, this predator was unable to develop at  $28\text{ }^{\circ}\text{C}$ , and its critical thermal maximum appears to be only slightly above  $25\text{ }^{\circ}\text{C}$ , as indicated by the very low survival rate (6 %) observed at this temperature, particularly among eggs. This result is consistent with a previous study on Belgian populations, which reported 100 % mortality at  $23\text{ }^{\circ}\text{C}$  for eggs and  $28\text{ }^{\circ}\text{C}$  for nymphs (Moerkens et al., 2011). Although some eggs successfully developed at  $25\text{ }^{\circ}\text{C}$  in our experiment, we might have expected a higher critical thermal maximum in our population compared to the Belgian populations, as local adaptation to climate commonly occurs in insects (Traoré et al., 2006). The individuals we studied were indeed sampled from an area where temperatures frequently exceed  $25\text{ }^{\circ}\text{C}$ , especially during the development of the second brood (late April to early July) and the potential third brood, which some females produce during the summer (Dib et al., 2017). Previous studies reported that another sympatric earwig species, the ring-legged earwig *Euborellia annulipes* (Dermaptera: Anisolabididae), exhibited high egg survival rates to adulthood at  $28\text{ }^{\circ}\text{C}$  and  $30\text{ }^{\circ}\text{C}$  (Lemos et al., 2003; Rankin et al., 1995). Similarly, *Forficula auricularia* eggs have been reported to tolerate brief exposures to temperatures up to

$36\text{ }^{\circ}\text{C}$  without damage (Chauvin et al., 1991). However, a recent study demonstrated that eggs from *F. auricularia* populations exposed to a warm autumn experienced higher mortality during development. This increased mortality rate may be attributed to reduced egg quality, less effective maternal care, or egg predation by females to minimize excessive energy loss (Tourneur and Meunier, 2020). This last study and our findings thus suggest that warm temperatures can be detrimental to *F. auricularia*, even for Mediterranean populations; however, since the egg stage of the first brood typically occurs in winter or early spring, it is unlikely to be exposed to such extreme conditions. The risk posed by high temperatures may therefore primarily affect the second brood, and potentially a third one, occasionally observed in Southeastern France. Moreover, our results may have been significantly influenced by the experimental setup.

Acclimatization is a physiological process by which organisms gradually adjust their biological functions in response to changes in environmental factors, such as temperature. This adjustment allows them to maintain optimal biological functions and improve their chances of survival under new conditions (González-Tokman et al., 2020). In our study, females and their eggs were abruptly transferred from a winter egg-laying temperature ( $10\text{ }^{\circ}\text{C}$ ) to  $20\text{ }^{\circ}\text{C}$  or higher, without being given the opportunity to gradually acclimatize. While adult females may physiologically withstand such rapid changes, as evidenced by the absence of mortality in our predation rate experiments (except at  $35\text{ }^{\circ}\text{C}$ ), eggs and young nymphs are known to be far more sensitive to environmental changes (Dib et al., 2017). This abrupt shift likely accounted for the very low survival rates observed at  $25\text{ }^{\circ}\text{C}$ , and possibly the absence of development at  $28\text{ }^{\circ}\text{C}$  or  $30\text{ }^{\circ}\text{C}$ . Further investigation is therefore needed to accurately characterize the developmental curve of southern *F. auricularia* populations, as we did for *M. ridens*. Additionally, fluctuating thermal regimes should be tested for both species, as they better reflect field conditions compared to the constant regime used in this experiment. Such research is essential to predict potential changes in the lifecycle and voltinism of natural enemies under global warming scenarios.

#### 4.2. Biological control of *Cydia pomonella*

Total fecundity of *M. ridens* decreased at high temperatures, while no effect of temperature on daily fecundity or parasitism rate was observed in our experiment. Parasitism rates ranged from 17 % to 22 %, which is consistent with other laboratory studies reporting rates between 13.4 % (Bezemer and Mills, 2003) and approximately 28 % (Bueno et al., 2017). In their study, Bezemer and Mills (2003) provided eight cocoons daily to each female, while we offered only one cocoon per day. This suggests that *M. ridens* females do not adjust their parasitism rate based on oviposition opportunities, although this hypothesis requires further investigation.

A decreased life expectancy associated with higher or sudden temperature changes is generally expected to increase oviposition rates in parasitic wasps (Amat et al., 2006; Moiroux et al., 2015). However, we did not observe this pattern in *M. ridens* females, which did not adjust their parasitism rate or daily fecundity to temperature, despite having a shorter lifespan at  $28\text{ }^{\circ}\text{C}$  and  $30\text{ }^{\circ}\text{C}$  compared to  $20\text{ }^{\circ}\text{C}$  and  $25\text{ }^{\circ}\text{C}$ . The absence of an effect of temperature on the parasitism rate of *M. ridens* is consistent with studies on many parasitoid species, such as *Telenomus cyamophylax* (Hymenoptera: Scelionidae) (Foerster and Butnariu, 2004) and *Hyssopus pallidus* (Hymenoptera: Eulophidae) (Häckermann et al., 2008), but contrasts with results for other species, such as *Microplitis similis* (Yi et al., 2020) and *Aphidius ervi* (Hymenoptera: Braconidae) (Malina and Praslicka, 2008). The relationship between temperature and parasitism rate is thus highly species-dependent, and *M. ridens* appears to be insensitive to temperature for parasitism.

The decreased longevity at high temperatures that we observed in *M. ridens* likely accounted for the reduced total fecundity observed under these thermal conditions. Since females did not adjust their

parasitism rate or daily fecundity in response to temperature but lived shorter lives, fewer progeny were produced over their lifetime. Global warming may therefore reduce *M. ridens* abundance through decreased longevity and total fecundity, although females may adapt their behavior to this constraint in the future. It is worth noting that the total fecundity we measured at 20 °C ( $4.23 \pm 1.08$ ) and 25 °C ( $3.73 \pm 1.09$ ) was very low compared to the observations by Devotto et al. (2010), who reported a mean total fecundity of around 18 descendants per female at 25 °C. Such a difference may be due to the use of non-overwintering codling moth cocoons in our experiment. *Mastrus ridens* females indeed prefer overwintering cocoons for oviposition, which result in higher developmental success of their progeny, as observed in our rearing.

For *F. auricularia*, temperature had a pronounced effect on the predation rate, which dropped sharply above 30 °C, decreasing from an average of 65 % (at 20–28 °C) to just 12 % (at 30–35 °C) of eggs consumed. No significant difference in predation rates was observed among the three temperatures tested below 30 °C (20, 25, and 28 °C) or among those above 30 °C (30, 32, and 35 °C). Numerous studies on entomophagous insects have reported a positive relationship between predation rate and temperature, attributed to increased metabolic and locomotor activity, provided the temperature does not exceed the species' physiological limits (Abram et al., 2017; Sentis et al., 2012). For instance, in the striped earwig *Labidura riparia* (Dermaptera: Labiduridae), predation rates increased from 25 °C to 30 °C but declined at 35 °C (Kharboutli and Mack, 1993). In the case of *F. auricularia*, the drop in predation rate at 30 °C is likely due to this temperature exceeding its upper metabolic limits (Moiroux et al., 2012), as evidenced by the high mortality observed at 35 °C during the 24-hour experiment. However, it remains unclear why temperature did not influence the predation rate within the 20–28 °C range. Dib et al. (2011) reported an increased predation rate of the rosy apple aphid *Dysaphis plantaginea* (Hemiptera: Aphididae) by third- and fourth-instar nymphs of European earwigs between 15 °C and 20 °C. Between 20 °C and 25 °C, however, the predation rate declined for third-instar nymphs but remained stable for fourth-instar nymphs. Thus, it is likely that in our study, *F. auricularia* reached its maximum predation rate at 20 °C, which remained stable until temperatures became stressful, i.e., at 30 °C. This finding is consistent with the circadian rhythm of *F. auricularia*, a nocturnal predator that hunts primarily at dusk when temperatures are milder (Vancassel, 1973). As a result, it is rarely exposed to temperatures exceeding 25 °C during its hunting activity, even in summer in the Mediterranean Basin.

It should be noted that there is still uncertainty regarding the species occurring in orchards in southeastern France, which may be either *F. auricularia* or *F. dentata*. Regardless of the exact species identity, the individuals we studied are those currently established in the area and are confirmed predators of codling moth eggs. Therefore, our findings provide valuable insights from both an agronomic and biological control perspective. However, molecular analyses should be conducted to clearly identify which species of the *Forficula auricularia* complex is (or are) present.

#### 4.3. *Mastrus ridens* susceptibility to pesticides

Studies on various insect species have shown that the toxicity of a wide range of insecticides is strongly influenced by temperature, with results varying depending on the compound (Boina et al., 2009), insect order (Li et al., 2024), species (Sparks et al., 1982, 1983), or life stage (Medrzycki et al., 2010). Perrin et al. (2022) reported that the efficacy of emamectin and spinosad, two insecticides used against the codling moth in conventional and organic orchards, respectively, decreased as temperatures rose, while the efficacy of chlorantraniliprole against this pest remained unaffected by temperature. In contrast, higher temperatures increased the toxicity of these three insecticides to *M. ridens* and of emamectin to *F. auricularia* (Perrin et al., 2024). In this study, we

observed similar results for sulfur and copper, two widely used fungicides, as well as for azadirachtin, a plant-derived bioinsecticide commonly used against aphids. The dose required to kill half of the parasitoids (LD50) indeed decreased with rising temperatures. Furthermore, while the LD50 exceeded the doses typically applied in orchards in France at 23 °C, it was similar to or lower than these doses for all compounds at 28 °C and 33 °C. These products are primarily used from late winter to mid-spring in southern France, when fungi and aphids are most abundant. However, to control apple scab, growers may apply copper later in the season, in July and September, if rain occurs. Therefore, *M. ridens* populations may struggle to persist in orchards where these pesticides are used during warm periods. To mitigate *M. ridens* mortality, applications of these products should thus be limited to periods when temperatures do not exceed 25 °C.

## 5. Conclusion

The Mediterranean Basin is projected to be particularly affected by rising temperatures and decreasing precipitation in the coming decades (IPCC, 2022). In this context, the codling moth, *Cydia pomonella*, is expected to adapt well to global warming due to its high thermal optimum (30.35 °C to 32.37 °C) and critical thermal maximum (35 °C). It may even benefit from an additional generation. Moreover, the negative relationship between temperature and the toxicity of insecticides (Perrin et al., 2022) could further reduce biological pest control efficiency in orchards.

In southern France, the codling moth produces three generations per year, with the first generation occurring in April. During this period, a spatial or temporal mismatch between the pest and its natural enemies seems unlikely, as temperatures are most suitable for the development and activity of the indigenous predator *Forficula auricularia* (Dib et al., 2017) and the introduced parasitoid *Mastrus ridens*. Furthermore, their predation rate and total fecundity are maximized at mild temperatures compared to higher ones. These two species should, therefore, be capable of providing effective biological control of the first generation of codling moth. However, for the second and third generations of *Cydia pomonella* occurring in summer, the likelihood of a disruption between the pest and its natural enemies is expected to increase with global warming. The natural enemies have lower critical thermal maxima than the pest and may face challenges in developing (*F. auricularia*) or producing additional generations (*M. ridens*) if temperatures exceed their thermal optima. Furthermore, the predation rate of *F. auricularia* drops sharply above 30 °C. Although this predator is primarily active at dusk, it could still experience these high temperatures in the future, as nighttime minimum temperatures are rising faster than daytime maximum temperatures (Davy et al., 2017), further reducing its efficiency in controlling codling moth. Similarly, the reduced fecundity and shortened longevity of *M. ridens* at high temperatures may contribute to larger *C. pomonella* populations during summer, a problem exacerbated by the increased toxicity of commonly used pesticides to the parasitoid. It is important to note that all of our results were obtained under controlled laboratory conditions, where the systems are highly simplified. Including *Cydia pomonella* host and non-host plants, as well as the semiochemicals involved in intra- and inter-specific relationships in orchards, would help refine our predictions of the impact of climate warming on biological control of this pest.

This study underscores nevertheless the urgent need to implement measures aimed at protecting beneficial organisms under climate change to ensure the continued effectiveness of biological pest control. Strategies such as planting flower strips (Harvey et al., 2023) and promoting spontaneous flowering vegetation (Laffon et al., 2024) can provide essential food sources for natural enemies while also serving as potential microclimatic refuges, and should be actively encouraged to mitigate the impacts of global warming on agroecosystems.

## CRediT authorship contribution statement

**Marie Perrin:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas Delattre:** Writing – review & editing, Validation, Software, Formal analysis, Data curation, Conceptualization. **Nicolas Borowiec:** Writing – review & editing, Supervision, Funding acquisition. **Hazem Dib:** Writing – review & editing, Validation, Methodology, Conceptualization. **Elodie Lecerf:** Writing – review & editing, Methodology, Investigation. **Emile Melloul:** Writing – review & editing, Project administration, Methodology. **Myriam Siegwart:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Joffrey Moiroux:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

## 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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