

## High temperatures adversely affect the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) fitness and aphid prey consumption

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**Abstract:** Numerous studies have shown that an increase of environmental temperature could directly disturb insect larval development. Natural enemies of insect pests, particularly predators of aphid populations, are not spared. Following temperature predictions of Belgian climate change scenario, the goal of this study is to measure life-history traits, such as the mass, body length and aphid consumption (*Acyrtosiphon pisum* (Harris, 1776)) (Hemiptera: Aphididae) of *Episyrphus balteatus* (De Geer, 1776) (Diptera: Syrphidae) larvae under three constant temperature treatments (i.e. 20, 23, and 26 °C). We detected no significant differences between 20 °C and 23 °C on the hoverflies larval development, their aphidophagous potential, as well as their mortality, pupation and emergence rates, while 26 °C had a deleterious effect on these parameters and the fitness of *E. balteatus* except for the total of consumed aphid per larva. Therefore, the high temperature could be disadvantageous for larval predation efficiency of *E. balteatus*. The outcomes of this study provide a new overview about ecological features of *E. balteatus* in the context of biological control under Belgian climate change.

**Keywords:** Climate change, larval development, *Episyrphus balteatus*, Aphid consumption, *Acyrtosiphon pisum*

### 1. Introduction

Since the beginning of the industrial era, the atmospheric climate is drastically changing and tends to increase the likelihood of extreme events such as heat waves or cold snaps (Diffenbaugh et al. 2005, Ganguly et al. 2009). Climatic models forecast an increase of the average Earth surface temperature up to 4.8 °C for the end of the 21<sup>st</sup> century (IPCC 2013). As poikilotherm organisms, insects are tightly dependent on the environmental temperature, which is one of the main drivers for their growth (Roitberg and Mangel 2016). Indeed, an increase in temperature can affect directly their physiology and ecology, or indirectly through modifications of their interactions with other organisms (Callier and Nijhout 2013, González-Tokman et al. 2020). Particularly, the increase in temperature can influence functional traits of aphidophagous insects, such as aphid consumption (Miller et al. 2017, Wang et al. 2017, Schwarz and Frank 2019, Speights and Barton 2019, Ferreira et al. 2020), pupal duration (Faheem et al. 2019), body thermoregulation by abdominal color patterns (Holloway et al. 1997, Marriott and J. Holloway 1998), biological fitness and survivability (Papanikolaou et al. 2013, Zhang et al. 2014). In particular, hoverflies (Diptera: Syrphidae) are beneficial insects offering several

ecosystem services. In addition, to act as pollinators, some species provide strong control of aphid populations in agro-ecosystems (Sommaggio 1999, Dunn et al. 2020).

*Episyrphus balteatus* (De Geer, 1776) (Diptera: Syrphidae) is a generalist aphidophagous hoverfly and common in European natural and agro-ecosystems (Sarhou et al. 2005). Its predatory larvae are particularly voracious and can consume large amounts of aphids during their development (Freier et al. 2007, Borah and Dutta 2010, Amiri-Jami and Sadeghi-Namaghi 2014, Faheem et al. 2019). Depending on the aphid species, *E. balteatus* larvae have differential feeding behavior under high temperatures (Ankersmit et al. 1986, Tenhumberg and Poehling 1995, Hong and Hung 2010) meaning that natural populations of *E. balteatus* may be altered to control aphid colonies in crops. Temperature also strongly affects voltinism (Hart et al. 1997), cold tolerance (Hart and Bale 1997), larval survival and fitness of the emerging individuals (Ankersmit et al., 1986), despite the proven correlation of the diet quality on the physiological traits which is a constitutional driver to define development rate and body length variation in insects (Dell et al. 2011, Roitberg and Mangel 2016). Therefore, as proficient species in Integrated Pest Management (IPM), it is important to

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assess how the larvae of *E. balteatus* perform as biological control vector under the temperature rise in Belgium (UNFCCC 2017, Ramon et al. 2020).

However, the effect of a rise in environmental temperature on their life-history traits at the larval stage and predation rate or voracity of larvae remain understudied in the context of climate warming for temperate regions and particularly in Belgium. Because elevated temperatures could affect *E. balteatus* fitness and aphid prey consumption, we hypothesize that (i) *E. balteatus* larval development, (ii) its aphid consumption and (iii) its survival rate will be impacted under constant temperatures driven by Belgian climate change forecast.

## 2. Materials and methods

### 2.1. Insects and plants

A field-originated population of *E. balteatus* from Gembloux (Belgium) was maintained for several generations in breeding cages (47.5 × 47.5 × 95 cm) under controlled conditions (20 ± 1 °C; 60 ± 10% RH; 16h light photoperiod). This pool was renewed each year by adding hoverflies from various origins in Walloon region. Adults were fed with fresh pollen and honey. To induce oviposition, a batch of broad bean plant *Vicia faba* (L.) (var. “major”) infested with pea aphid *Acyrtosiphon pisum* (Harris, 1776) (Hemiptera: Aphididae) was set into the cage for 24h. The hatching larvae were fed *ad libitum* on *A. pisum* diet until they reached the pupal stage. Once emerged, adults were transferred into the adult rearing cage. We used a laboratory strain of *A. pisum*, which has been maintained for several years in our laboratory (Boullis et al. 2018).

### 2.2. Experimental design

The experiment was carried out in 2018 at the Functional and Evolutionary Entomology laboratory (Gembloux, Belgium). We performed the experiment in three climate chambers with different temperatures. To evaluate the impact of constant temperature on *E. balteatus* larval development, we selected three temperature regimes based on climatic data available from the Royal Meteorological Institute of Belgium. In Brussels, 20 °C ± 1°C is considered as the mean temperature recorded from May to August under daytime conditions (10 am to 6 pm) between 2012 and 2017; 23 °C ± 1°C is the expected mean temperature for the same period for the end of the 21<sup>st</sup> century, as forecasted by climatic prediction (IPCC, 2013); and 26 °C

± 1°C is the daily mean extreme value recorded in Brussels. Thirty newly-hatched larvae (less than 24h), randomly selected with a brush from the source population, were individualized with paintbrush in Petri dishes (Ø 35 mm) and assigned to one of the three temperature treatments. Each larva was monitored for eight days which corresponds to the complete duration of larval stage for *E. balteatus* (Bargen 1998). The larvae were fed *ad libitum* by providing randomly 50 mixed ages of *A. pisum* (reared at 20 °C ± 1°C) in Petri dishes (containing filter paper to moisten the area) each day until they reach the pupal stage. Petri dishes were cleaned (also for the remaining aphids) and watered on filter paper daily and covered with perforated Parafilm™ to prevent the larvae from escaping. The mass and body length of each larva were daily monitored throughout the larval development using an analytical balance (Kern ABT 120-5DM, Kern, Germany) and a graduated binocular magnifier, respectively. The number of consumed aphids by each larva was recorded daily and the adult emergence rate was calculated in the same temperature and humidity conditions than for the larvae.

### 2.3. Statistical analysis

We tested the dependency link using the Spearman rank correlation test between each considered quantitative variable: number of consumed aphids, body length, and mass of *E. balteatus* larvae. To compare our temperature treatments, analysis of variance (ANOVA) or Kruskal-Wallis tests for nonparametric datasets (i.e. nonrespect of the normality condition tested by Shapiro-Wilk's test) were conducted on all our quantitative variables throughout the duration of the experience, per day of the experiment and for the last measurement of each larva. We computed *post-hoc* tests of Tukey from parametric tests or *post-hoc* tests of Dunn for nonparametric tests with Bonferroni correction with *dunn.test* R package<sup>1</sup>. To assess larvae mortality, we conducted a Log-Rank test on generated Kaplan-Meier survival curves followed by multiple comparisons with Bonferroni correction with *survival* and *survminer* R packages<sup>2,3</sup>. We used Fisher's exact test on adult emergence rate, with Fisher's pairwise test with Yates correction to compare the three temperature treatments. All statistical treatments were performed with R software (version 4.0.1)<sup>4</sup>, with alpha level set at p < 0.05.

## 3. Results

Throughout the eight days of measurements, the variables of larval mass and body length were highly correlated (*rho*

<sup>1</sup> Dinno A (2017) *dunn.test*: Dunn's Test of Multiple Comparisons Using Rank Sums [online]. Website <https://cran.r-project.org/package=dunn.test> [accessed 01 April 2021].

<sup>2</sup> Kassambara A, Kosinski M, Biecek P (2021) *survminer*: Drawing Survival Curves using “ggplot2” [online]. Website <https://cran.r-project.org/package=survminer> [accessed 01 April 2021].

<sup>3</sup> Therneau T (2020) *\_A Package for Survival Analysis in R\_*. R package version 3.1-12 [online]. Website <https://cran.r-project.org/package=survival> [accessed 01 April 2021].

<sup>4</sup> R Core Team (2020) *R : A Language and Environment for Statistical Computing* [online]. Website <https://www.r-project.org/> [accessed 01 April 2021]

= 0.97;  $p < 0.01$ ) and followed the same development curve during the whole development (Figure 1 A-B). During the first four days of development, the body mass and body length were significantly highest for larvae reared under 26 °C. Inversely, for the last three days, these measures were higher for those reared at 20 °C (Figure 1 A-B; Table 1). The mean time spent by individuals to reach the pupal stage was significantly shorter at 26 °C compared to other temperatures (Table 2). At this point, the last measures on larvae before pupation indicated larger and heavier individuals at 20 °C compared to 26 °C (Table 2).

The daily aphid consumption rate was higher at 26 °C compared to the two other temperatures (Table 2), because of a shorter larval development coupled to a higher consumption rate during the two first days (Figure 1C). However, the mean total quantity of aphids consumed during the whole development under the three temperature regimes is similar (Table 2). From the fourth day of experiment, we observed a decline in aphid consumption during the larval development without consideration of the temperature (Figure 1C, Table 1).

*E. balteatus* larvae have a lower probability to survive at 26 °C than at 23 °C ( $\chi^2 = 7.30$ ;  $P = 0.03$ ) (Figure 2), with only 50% of larvae reaching the pupal stage. A deleterious effect of the highest tested temperature was detected by Fisher's pairwise test on the adult emergence rate, with only 24% of successful emergence at 26 °C, significantly lower than those observed at 20 °C (57%) and 23 °C (64%) (Table 2).

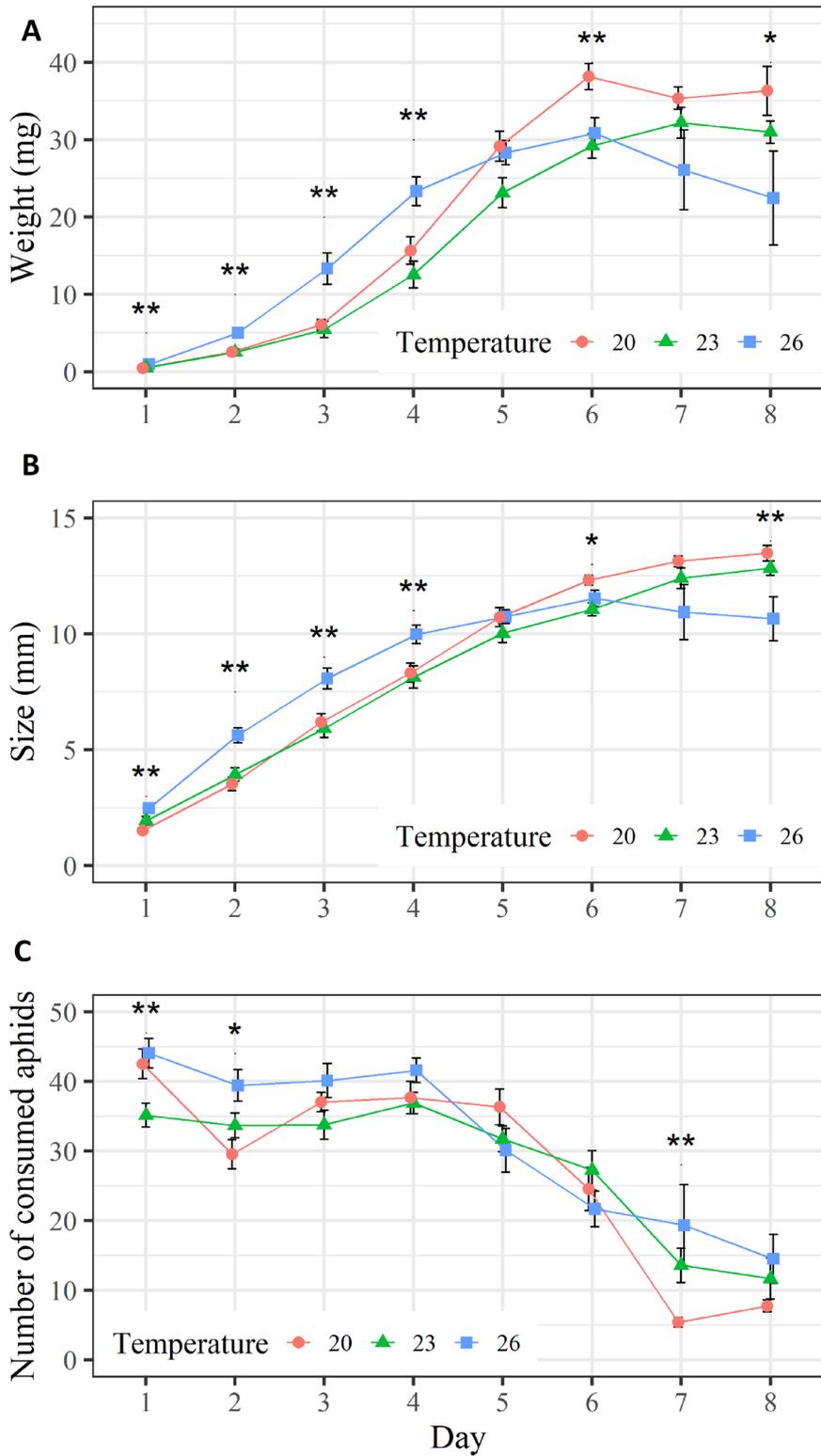
#### 4. Discussion

Our study reports no differences in measurements of the larval weight and body length, the aphidophagous potential, and the mortality, pupation and emergence rates between 20 °C and 23 °C. Contrariwise, 26 °C has a deleterious effect (despite the fact that individual voracity is identical) on the fitness-related parameters of *E. balteatus*. As the metabolic rate of insects increases with higher temperature, it leads to an acceleration of larval development (Trudgill et al. 2005), which is confirmed by other studies on *E. balteatus* larval development (Hart et al. 1997, Hong and Hung 2010), which also resulted in smaller final body lengths (Atkinson, 1994). Despite this rapid gain in larval body length and mass observed at 26 °C during the first days, these individuals entered their pupal stage being smaller and lighter. High temperatures may also impair the quality of digestion and may prevent efficient conversion of the food consumed into body mass which may be due to a less efficient activity of enzymes for the assimilation of nutrients (Bochdanovits and De Jong 2003).

In all the three temperature treatments, the decrease of voracity (Figure 1C) over the time was unexpected and hard

to explain because not in agreement with former studies carried out on *E. balteatus*, where a higher consumption was observed in late instar larvae (Ankersmit et al. 1986, Tenhumberg and Poehling 1995, Hindayana et al. 2001, Hong and Hung 2010). One potential explanation to these observations could be that placing the aphids inside the Petri dish without a piece of host plant to feed on can cause stress affecting their nutritious quality, which in turn might affect the development of syrphid larvae.

Because the final larval body length plays an essential role in the longevity and fertility of adults of several insect groups (Bochdanovits and De Jong 2003, Lee and Roh 2010), we can conclude that a constant rearing temperature of 26 °C is unsuitable for the development of *E. balteatus*. The low metabolic conversion that we hypothesized earlier can be the cause of this weak survival ability. Moreover, extreme temperature episodes could be negative for the predation efficiency of *E. balteatus* and, therefore, for its use as a biological control agent. Hart et al. (1997) suggested that the temperature limit for *E. balteatus* to complete its development cycle must be between 25 °C and 30 °C, but regional adaptations (i.e. ecotype) could also influence the development cycle of *E. balteatus* (Tenhumberg and Poehling 1995). Also, we worked with constant average temperatures which could under or overestimate values for larval development traits compared to natural populations, which are influenced by fluctuating daily temperatures (Carrington et al. 2013, Colinet et al. 2015, Speights and Barton 2019). Indeed, in their natural habitat, temperatures vary more or less strongly during the day and according to the season and the location of the larval population (Ragland and Kingsolver 2008). Thus, syrphid larvae continually have to adjust their physiology to these changing thermal conditions. Jensen's inequality explains the nonlinearity of these physiological responses and thermal performance curves (Jensen 1906). These curves are asymmetrical for fluctuating temperatures: effects are limited when temperatures decrease, and are more pronounced when temperatures increase (Martin et al., 2008). Furthermore, the divergence of these experiments into constant versus fluctuating temperatures depends on the degree of thermal sensitivity of the population and the magnitude of the temperature fluctuation over small or long periods (Foray et al. 2014). In the field, the energy costs generated by *E. balteatus* populations in the warm part of the daily cycle is probably higher than those resulting from the cooler daily period, especially for thermosensitive populations such as those belonging to higher latitudes of temperate regions (Williams et al. 2012, Verheyen and Stoks 2019). Hence, incorporating fluctuating temperatures in our experimental design would have allowed a better understanding of what would be the population dynamics of this important auxiliary insect under global warming in Belgium.



**Figure 1.** Mean values ( $\pm$  S.E.) for mass (A), body length (B), and pea aphid (*Acyrtosiphon pisum*) consumption rate (C) of *Episyrrhus balteatus* larvae per day of experiment depending on rearing temperature. Dot shapes correspond to temperature treatments: circle to 20 °C (red), triangle to 23 °C (green), and square to 26 °C (blue). After post-hoc tests with Bonferroni correction, the character ‘\*’ corresponds to one significant pairwise comparison, ‘\*\*’ corresponds to two significant pairwise comparisons among the temperature treatments. Details of the mean values and statistical test outcomes per day of the experiment are given in Table 1.

**Table 1.** Mean weight, body length, and number of aphids consumed ( $\pm$  S.E.) by *E. balteatus* larvae reared under different temperature treatments. Letters following the values represent post-hoc comparisons for each day of the experiment with Bonferonni correction. N column corresponds to the number of replicates per day and temperature treatment after removing the loss of individuals caused by the mortality of first instars of the first day and every following day. Results of ANOVA or Kruskal-Wallis tests are also shown with the degree of freedom (*df*) at 2, their respective F statistic or  $\chi^2$  and their *p*-value.

Weight (mg)							ANOVA/Kruskal-Wallis test; df = 2	
Day	20 °C	N	23°C	N	26°C	N	F-stat / $\chi^2$	p-value
1	0.46 $\pm$ 0.06a	19	0.49 $\pm$ 0.15a	22	0.96 $\pm$ 0.13b	17	$\chi^2 = 13.41$	<0.01
2	2.55 $\pm$ 0.29a	19	2.51 $\pm$ 0.41a	22	5.01 $\pm$ 0.51b	17	$\chi^2 = 16.14$	<0.01
3	6.05 $\pm$ 0.68a	19	5.45 $\pm$ 1.06a	22	13.32 $\pm$ 2.01b	17	$\chi^2 = 18.29$	<0.01
4	15.64 $\pm$ 1.76a	19	12.55 $\pm$ 1.75a	22	23.33 $\pm$ 1.86b	17	F-stat = 9.22	<0.01
5	29.13 $\pm$ 1.94a	19	23.11 $\pm$ 1.93a	22	28.29 $\pm$ 1.58a	16	F-stat = 3.26	<0.05
6	38.13 $\pm$ 1.69a	19	29.17 $\pm$ 1.58b	20	30.83 $\pm$ 2.00b	12	F-stat = 8.28	<0.01
7	35.34 $\pm$ 1.41a	12	32.2 $\pm$ 1.99a	14	26.07 $\pm$ 5.15a	3	F-stat = 2.49	0.1
8	36.30 $\pm$ 3.16a	4	30.97 $\pm$ 1.44ab	6	22.45 $\pm$ 6.05b	2	F-stat = 4.52	<0.05
Body length (mm)							ANOVA/Kruskal-Wallis test; df = 2	
Day	20 °C	N	23°C	N	26°C	N	F-stat / $\chi^2$	p-value
1	1.56 $\pm$ 0.14a	19	1.94 $\pm$ 0.18a	22	2.47 $\pm$ 0.16b	17	$\chi^2 = 13.20$	<0.01
2	3.53 $\pm$ 0.28a	19	3.93 $\pm$ 0.29a	22	5.63 $\pm$ 0.32b	17	F-stat = 12.86	<0.01
3	6.18 $\pm$ 0.37a	19	5.92 $\pm$ 0.40a	22	8.08 $\pm$ 0.46b	17	F-stat = 7.83	<0.01
4	8.33 $\pm$ 0.42a	19	8.13 $\pm$ 0.48a	22	9.98 $\pm$ 0.40b	17	F-stat = 4.93	0.01
5	10.72 $\pm$ 0.41a	19	10.03 $\pm$ 0.41a	22	10.74 $\pm$ 0.29a	16	$\chi^2 = 1.63$	0.44
6	12.32 $\pm$ 0.21a	19	11.06 $\pm$ 0.28b	20	11.53 $\pm$ 0.35ab	12	$\chi^2 = 13.54$	<0.01
7	13.13 $\pm$ 0.23a	12	12.39 $\pm$ 0.44a	14	10.93 $\pm$ 1.19a	3	$\chi^2 = 5.49$	0.06
8	13.48 $\pm$ 0.34a	4	12.83 $\pm$ 0.31b	6	10.65 $\pm$ 0.95b	2	F-stat = 8.18	<0.01
Aphid consumption							ANOVA/Kruskal-Wallis test; df = 2	
Day	20 °C	N	23°C	N	26°C	N	F-stat / $\chi^2$	p-value
1	42.53 $\pm$ 2.11a	19	35.14 $\pm$ 1.73b	22	44.06 $\pm$ 2.11a	17	$\chi^2 = 16.56$	<0.01
2	29.53 $\pm$ 2.09a	19	33.68 $\pm$ 1.79ab	22	39.41 $\pm$ 2.28b	17	$\chi^2 = 10.31$	<0.01
3	37.05 $\pm$ 1.40a	19	33.77 $\pm$ 2.10a	22	40.12 $\pm$ 2.42a	17	$\chi^2 = 5.86$	0.05
4	37.68 $\pm$ 2.32a	19	36.91 $\pm$ 1.54a	22	41.59 $\pm$ 1.78a	17	$\chi^2 = 4.57$	0.10
5	36.32 $\pm$ 2.56a	19	31.73 $\pm$ 1.85a	22	30.13 $\pm$ 3.16a	16	$\chi^2 = 4.8$	0.09
6	24.53 $\pm$ 3.06a	19	27.25 $\pm$ 2.82a	20	21.67 $\pm$ 2.55a	12	$\chi^2 = 1.53$	0.47
7	5.42 $\pm$ 0.70a	12	13.57 $\pm$ 2.48b	14	19.33 $\pm$ 5.84b	3	$\chi^2 = 13.20$	<0.01
8	7.75 $\pm$ 0.85a	4	11.67 $\pm$ 2.93a	6	14.50 $\pm$ 3.50a	2	$\chi^2 = 3.33$	0.19

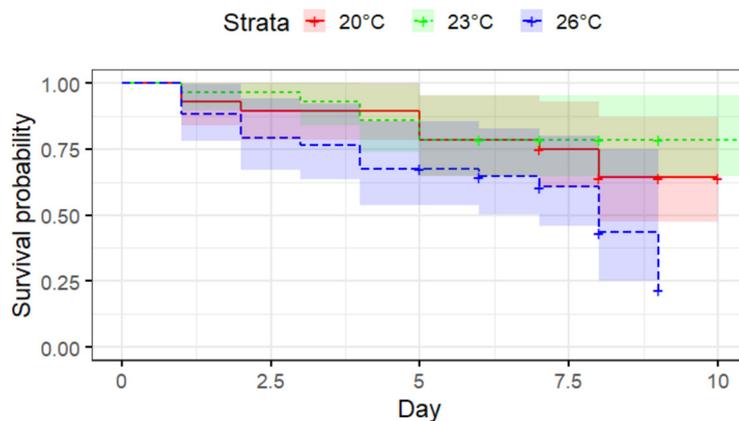
Nevertheless, we can assume that the Belgian climate with higher fluctuating temperatures with high amplitudes (Ramon et al. 2020) would be even more damaging for the larvae than those that developed at constant temperatures of 26 °C.

## 5. Conclusions

Our study reflects that elevated temperatures, like those expected in Belgium under a global warming scenario, could alter larval development of *E. balteatus* as well as its survivability and adult emergence, while the effects on

**Table 2.** Mean of larval measurements ( $\pm$  S.E.) of *E. balteatus* reared under different temperature treatments. Letters following the values represent post-hoc comparisons for each day of the experiment with Bonferonni correction. N column corresponds to the number of replicates or observations. Results of ANOVA or Kruskal-Wallis tests are also shown with the degree of freedom (*df*) at 2, their F statistic or  $\chi^2$  and their p-value.

Measures	20°C	N	23°C	N	26°C	N	F-stat / $\chi^2$	p-value
Last larval weight (mg)	35.75 $\pm$ 1.39a	19	32.52 $\pm$ 1.21ab	21	30.88 $\pm$ 1.46b	17	F-stat = 3.28	<0.05
Last larval body length (mm)	12.74 $\pm$ 0.22a	19	12.4 $\pm$ 0.29a	21	11.45 $\pm$ 0.24b	17	F-stat = 6.3	<0.01
Total of consumed aphid per larva	212.68 $\pm$ 6.64a	19	207.82 $\pm$ 6.74a	22	213.94 $\pm$ 5.94a	17	$\chi^2$ = 0.46	0.79
Daily aphid consumption	31.2 $\pm$ 5.6a	130	30.59 $\pm$ 4.6a	150	36.59 $\pm$ 5.15b	101	F-stat = 12.52	<0.01
Days to reach pupal stage	6.84 $\pm$ 0.17a	19	6.86 $\pm$ 0.19a	22	5.94 $\pm$ 0.25b	17	$\chi^2$ = 9.59	<0.01
Adult emergence ratio (%)	57a	21	63a	22	24b	17	NA	<0.05



**Figure 2.** Kaplan-Meier survival curves of *Episyrphus balteatus* larvae reared under 20 °C (red color and filled line), 23 °C (green color and tiny dashed line), and 26 °C (blue color and large dashed line). Shade-colored areas indicate a 95% confidence interval computed from the medians of Kaplan-Meier survival curves.

adult fitness have not been explored in this work. Higher temperatures induce higher rate of larval development and aphid consumption with the expectations of shorter generation time. Nevertheless, the evolution of aphid consumption was similar between the different temperature treatments with a surprising decrease of daily ingested aphid over the days of the experiment. For future studies, taking the interaction of other abiotic components of climate change into account such as CO<sub>2</sub> atmospheric concentration or rainfall will allow consolidating the understanding of *E. balteatus* larval predation. Also, many more scientific efforts should be addressed in the responses of other trophic levels (i.e. prey or parasitoid) regarding the key role of climate change in the context of IPM.

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#### Author contributions

Grégoire Noel, Jéssica Caetano, Solène Blanchard, and Frédéric Francis designed the experiment. Jéssica Caetano conducted all the laboratory experiments. Jéssica Caetano and Solène Blanchard maintained the hoverfly and aphid rearing. Grégoire Noel and Jéssica Caetano analysed the data. Grégoire Noel and Frédéric Francis supervised the work. Frédéric Francis secured the budget and provided the laboratory, rooms, and materials. Grégoire Noel wrote the first draft of the manuscript. All authors read and approved the manuscript.

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