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Effect of developmental temperatures on *Aphidius colemani* host-foraging behavior at high temperature

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ABSTRACT

Temperatures experienced by insects during their adult life often differ from developmental temperatures. Yet, developmental thermal acclimation can play an important role in shaping physiological, morphological, and behavioral traits at the adult stage. We explored how three rearing temperatures (10, 20, and 28 °C) affected host-foraging behaviors and associated traits under warm conditions in the parasitoid *Aphidius colemani*, a key model in behavioral ecology and an important natural enemy of aphids. Developmental time was longer at lower temperatures, resulting in bigger emerging parasitoids, with higher egg-loads. Parasitism rates, emergence rates, and parasitoid survival (once placed at high temperature) were the highest for parasitoids developed at 20 °C. When exposed to 28 °C, the expression of all behavioral items (time spent walking searching for hosts, number of antennal and ovipositor contacts with hosts) was higher for parasitoids reared at 20 °C, followed by those reared at 10 °C, then those reared at 28 °C. Finally, we showed that parasitoid residence time on aphid patches was determined by both developmental temperatures and the number of host encounter without oviposition, representative of the resource quality. We revealed that developing at 28 °C did not lead to increased adult performance at this temperature, probably because of complex interactions and trade-offs between developmental costs at high temperature and optimal foraging behaviors (e.g., parasitoid size and host-handling capacities). Our results strengthen the idea that thermal developmental plasticity may play an important role in insect behavioral responses to varying temperatures, and is important to consider in the context of climate change.

1. Introduction

As poikilothermic organisms, insects are extremely dependent on the temperature of their environment. Temperature variations affect the physiology, immunity, and metabolic rates of insects (Chown and Terblanche, 2007; Irlich et al., 2009), as well as seasonal or daily activity timings (Danks, 1987), and various behaviors such as walking speed, flight, foraging, and mating (Huey and Kingsolver 1989; Matthews and Matthews 2009; Jerbi-Elayed et al. 2015a,b). Temperature also influences their development rate, resulting in bigger insects produced at low temperatures (Atkinson, 1994), which is consequently affecting behaviors and several fitness-related life history traits usually associated with size, such as fecundity and longevity (Colinet et al., 2007; Van der Have and De Jong, 1996). In addition, temperature deeply impacts how species interact with each other, and thermal variations may alter the outcomes of such interactions in terms of ecosystem functioning (Bale et al., 2002; Barton and Ives, 2014; Hance et al., 2007; Harvey, 2015; Tougeron et al., 2019).

There is no doubt that, in a climate change context, insects are increasingly exposed to both high temperatures exceeding their upper thermal physiological limits, and to high temperature variations among generations or over the lifespan of an individual (Deutsch et al., 2008; Kingsolver et al., 2011). Many recent studies discuss in detail how exposure to temperature warming, temperature fluctuations at variable scales and climatic extremes impose constraints on insect life-histories and behaviors (Colinet et al., 2015; Harvey et al., 2020; Iltis et al., 2021). The ability of natural populations to respond to such environmental changes depends on the evolution of thermal tolerance traits and

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thermal limits, their thermal behavioral and physiological plasticity, and subsequent matches and mismatches with interacting species (Calosi et al., 2008; Chen et al., 2019; Damien and Tougeron, 2019; Parmesan, 2006; Tylianakis et al., 2008). Therefore, understanding the variety of adaptive mechanisms and plastic responses of insects to different temperatures is relevant both in theoretical thermal biology, for example for the conservation of insect populations facing climate change, and in applied ecology, for example in the context of biological pest control (Buckley et al., 2017; Rodrigues and Beldade, 2020; Sgrò et al., 2016).

Thermal acclimation is generally defined as the plastic adjustment of behavioral and physiological traits in response to changes in temperature, and different forms can be expressed over different time scales (e.g., developmental acclimation, rapid hardening) depending on the timing and the length of the temperature exposure (e.g., long-term warming, transient heat shock) (Angilletta, 2009). Empirical evidences exist on the effects of thermal acclimation of insects in both natural and laboratory experiments (Alford et al., 2012; Enriquez et al., 2018; Kellermann et al., 2017; Ma and Ma, 2012). Animals acclimated to a given temperature have, in theory, enhanced behavioral and physiological performances at that temperature when compared to animals acclimated to other temperatures (Chown and Terblanche, 2007; Hoffmann et al., 2003; Lagerspetz, 2006). Adaptive physiological thermal plasticity may play an important role in insect response to climate change, because it could help buffering the effects of experienced high temperatures (Sgrò et al., 2016; Somero, 2010), even if the generality and the role of such beneficial acclimation hypothesis in climate change adaptation of insects is long time debated (Terblanche and Hoffmann, 2020; Wilson and Franklin, 2002; Woods and Harrison, 2002).

Yet, as in most organisms, experienced temperatures during the adult life often differ from developmental temperatures, which can create behavioral and physiological response mismatches between the acclimation temperature (i.e., developmental plasticity) and the actual experienced temperature by adults (i.e., adult phenotypic plasticity) (Santos et al., 2021; Terblanche and Chown, 2006). Parasitoid insects are interesting models to explore how insect interactions vary with temperatures, because they can adapt their host-foraging behaviors depending on environmental conditions, such as variations in host quality or in temperature (Goubault et al., 2004; Langer et al., 2004; Le Lann et al., 2008; Wajnberg et al., 2008; Le Lann, et al. 2011a,b; Benelli et al., 2014). Parasitoids are key models in behavioral ecology, however, few studies address the implication of rearing temperatures and of developmental thermal plasticity on host-foraging behaviors (Moore et al., 2020; Wu et al., 2011). When facing temperature increase and heat shocks, parasitoids not only have to adjust their own response, but they also have to deal with changes in host quality, population dynamics and host patch distribution, in a way that temperature extremes could induce trophic chain interaction disruption and community breakdown (Hance et al., 2007; Harvey et al., 2020).

Residence time on patch of resources (e.g., hosts or food) is a major element to consider, because it determines how organisms optimize the number of exploited resources per unit of time, and ultimately the gain of exploiting such patches distributed in the environment (Charnov et al., 1976). In parasitoids, the internal motivational status of females are influenced by many biotic and abiotic parameters such as host quality, female physiological and morphological characteristics, and temperature, which in turn affects host exploitation behaviors and patch residence time (Fletcher et al., 1994; Boivin et al., 2004; Goubault et al., 2005; Wajnberg 2006; Le Lann et al., 2011b, 2014; Moiroux et al., 2016). For example, increasing temperature during host-searching generally leads to more efficient host-searching behavior (Zamani et al., 2006), probably as a result of increasing metabolic rate.

In this study, we focused on the generalist aphid parasitoid *Aphidius colemani* (Hymenoptera: Braconidae), which is a koinobiont parasitoid originating from Northern India and Pakistan and now distributed worldwide after its introduction in more temperate regions. It is used in mass release biological control programmes since 1992 in many European countries (Hance et al., 2017). It is the principal parasitoid of major pests such as *Aphis gossypii* on cotton and Cucurbitaceae, or *Myzus persicae* on various cultivated plants. It is likely that populations reared for biocontrol are now adapted to lower temperatures than that of their evolutionary history in subtropical regions; they are generally reared at an intermediate temperature of around 20 °C, and have therefore to deal with heat stress when they are released in warmer conditions in the flied or in greenhouses (Jerbi-Elayed et al., 2021). Understanding the consequences of this type of temperature change on the behavior of natural enemies helps finding efficient biological control solutions and may avoid the failure of some biological control programs (Furlong and Zalucki, 2017; Hance et al., 2007) and may additionally responds to theoretical question in relation with global warming (Colinet et al., 2015; Harvey, 2015; Jeffs and Lewis, 2013).

The goal of our study was to measure the effects of different developmental rearing temperatures on parasitoid fitness-related traits, and on parasitoid host-foraging behaviors when exposed to high temperature at the adult stage. Several variables were measured to account for the complexity of decision-making processes in parasitoids. We predicted that female parasitoids acclimated at high temperatures during immature stages have the most efficient host-foraging behavior at high temperature.

2. Material & methods

2.1. Biological material and thermal treatments

Aphids and parasitoids were obtained from Viridaxis SA (Charleroi, Belgium). *Myzus persicae* were reared on artificial diet (Jerbi-Elayed et al. 2015a,b). Three cultures of *A. colemani* were established, and parasitoids were reared either at 10, 20 or 28 °C, under a 16:8 h LD photoperiod regime and 50% relative humidity level, in climate-controlled rooms. Once parasitoids emerged from the mummies, all subsequent experiments were done at 28 °C, under the same photoperiod and humidity conditions. The test temperature of 28 °C was chosen because it is at the limit of most temperate insect thermal tolerance range, and it corresponds to thermal conditions likely experienced in the field where this species is released in some parts of the world, such as in Tunisia (Jerbi-Elayed et al. 2015a,b).

2.2. Pre-behavioral assays life-history trait measurements

48h-old mated and fed parasitoid female was put in presence of 50 aphid third instar larvae during 3 h at 20 °C. All potentially parasitized aphids were directly transferred under one of the three temperature treatments. The day they were formed, mummies were individualized in micro-tubes and kept under their respective treatments. Parasitoid adult emergence from the mummies was recorded twice a day (at 8:00 and 18:00), and parasitoids were sexed upon emergence. The proportion of emergence was calculated by dividing the number of emerging individuals by the total number of mummies obtained during the same contact series. Development time was calculated for each parasitoid as the number of days between oviposition and emergence of the adult.

To measure longevity, naive and unmated parasitoids of each sex, aged of <24h, and from each temperature rearing treatment, were placed in microtubes at 28 °C, with cotton soaked in water (N=35/32, 33/33, 51/35 females/males, for 10, 20, and 28 °C developmental temperatures, respectively). Parasitoids were observed three times a day, and their longevity was recorded (precision of a few hours). Once all parasitoids had died, the length of female right hind leg tibia was measured, which is a standard measure to estimate the size of parasitoids. To do so, we took pictures of the tibia using a camera (Panasonic, Super Dynamic, WV-CP450) mounted on a stereo microscope (× 4, Leica MZ6), and measures were taken using the ImageJ software (Rasband, W.S., US National Institutes of Health, Bethesda, MD, USA).

2.3. Host-foraging behavior at high temperature

Behaviors of parasitoid females aged of 4–12 h, from each temperature rearing treatment, were observed in a climate-controlled chamber at 28 °C and 50% relative humidity on a light table (273 lux) (N=35, 33, and 36, for 10, 20, and 28 °C developmental temperatures, respectively). Females were individually placed in presence of 25 third instar larvae of *A. gossypii* on a piece of cucumber leaf of ≈12 cm^2, in the center of a 9 cm diameter arena delimited by a red circle representing the limits of patch and covered by a transparent plastic box (15 x 25 x 9.5 cm) for observation. For each female (i.e., each behavioral assay), the following behaviors were observed and recorded using the J watcher software (v.0.1): entrance into the patch, antennal contact with a host, walking, ovipositor contact with a host, oviposition, exit from the cluster. The maximum observation time was 30 min, and a female was considered to have left the cluster permanently when she spent more than 1 min out of the red circle. We obtained the time spent in the cluster, the time spent walking, and the frequency of antennal and ovipositor contacts per unit of time.

After each behavioral assay, aphids were kept during three days in rearing cages (0.031 m^3) on cucumber plants at 20 °C. This is long enough to allow egg hatching and early larval development within the host, but short enough to avoid cannibalism between developing larvae (Chow and Mackauer, 1986; McBrien and Mackauer, 1991). Each aphid was then dissected in a saline solution under binocular microscope (x4) to count the number of parasitoid larvae. The numbers of parasitized and superparasitized (i.e., parasitized by more than one larva) aphids were recorded. The number of aphids still alive before dissection was also noted to see if mortality could be due to multiple attacks by the parasitoid. Parasitism rate was calculated as: number of parasitized aphids/25.

2.4. Post-behavioral assays life-history trait measurements

After behavioral assays, parasitoid females were individually frozen at −20 °C. The next day, they were dissected in saline solution under binocular loupe (x6.3), and the number of mature eggs present in their ovaries were counted. The total number of eggs was calculated as the sum of the number of mature eggs present in the ovaries during dissection and the number of parasitoid larvae found in the aphids. The right hind leg tibia length was also measured as described above, to try linking egg-load with parasitoid size.

2.5. Statistical analyses

The R 3.0.1 software (R Development Core Team, 2013) was used for statistical analyses. Model assumptions (e.g., error distribution, scaled Schoenfeld residuals for survival analyses) were assessed visually. Emergence percentages were compared among temperature treatments with a two-sided comparison of proportions, followed by pairwise comparisons. A one-way ANOVA was used to test the effect of developmental temperatures on tibia length. Generalized linear models (GLMs) were used for the analysis of all other measured variables. A Poisson distribution with a log link function was used to test for the effect of developmental temperatures on following variables: number of antennal contacts, number of ovipositor contacts, number of actual oviposition, frequency of antennal contacts, frequency of ovipositor contacts, number of parasitized aphids, and number of eggs. The effect of parasitoid size on the number of eggs was also tested. A Gamma distribution with an inverse link function was used for cumulative time spent walking, and the interaction with the sex of the parasitoid was added as an explanatory variable to analyse developmental duration and longevity. The significance of each term in the GLMs was assessed using the *Anova* function from the package *car* and a Wald statistic (Fox and Weisberg, 2011), and GLMs were followed by Tukey post-hoc tests using the *glht* function from the *mulctomp* package (Hothorn et al., 2008) for pairwise comparison between levels of each treatment. Comparisons were done among temperatures for each sex separately for longevity, and between sexes for each temperature separately for developmental duration.

To determine the variables influencing parasitoid residence time in aphid patches, we used Cox models fitted to our data using the *survival* package (Therneau, 2021), which have been proposed to be the most suitable for such analysis (Wajnberg, 2006). What is actually analyzed is the probability of a female staying in the patch at any time during the experiment. Preliminary analyses allowed retaining the rearing temperature, the number of encounters without laying eggs (ovipositor contact), and the interaction between these two variables as significant effects. According to Wajnberg (2006), for each tested explanatory variable; a value >1 for the exponential of the model regression coefficient means an increase in the probability to leave the patch (i.e., reduced residence time), and a value <1 means the opposite. The *sjPlot* package computing estimated marginal means (predicted values) (Lüdecke, 2018) was used to visualise and interpret interaction effects in the patch residence time analysis; the “survival probability” (here, corresponding to the probability of staying in a patch) was calculated.

3. Results

3.1. Life-history trait measurements

Emergence rates were different among rearing temperatures (proportion test, $\chi^2 = 22.53$, df = 2, $p < 0.001$); 55.8, 76.9, and 61.7%, at 10, 20, and 28 °C, respectively. We found differences in emergence rates between 20 and 28 °C ($\chi^2 = 13.71$, df = 1, $p < 0.001$), between 10 and 20 °C ($\chi^2 = 19.43$, df = 1, $p < 0.001$), but not between 10 and 28 °C ($\chi^2 = 1.29$, df = 1, p = 0.25).

Developmental temperatures significantly influenced the developmental duration of parasitoids (both sexes considered, $\chi^2 = 23935$, df = 2, $p < 0.001$). Individuals developing at 10 °C took longer to complete their egg-to-adult developmental cycle, followed by those at 20 °C and 28 °C (Fig. 1A). The development duration was globally not different between sexes ($\chi^2 = 0.76$, df = 1, p = 0.38), but there were sex-specific effects of temperature on developmental durations ($\chi^2 = 9.4$, df = 2, $p < 0.01$); parasitoid females reared at 28 °C took longer to develop than males, but it was not the case at other temperatures (Table 1). Developmental temperatures also significantly influenced the developmental duration of females that were used for the behavioral study ($\chi^2 = 13408$, df = 2, $p < 0.001$).

Rearing temperature had an effect on female tibia length (F = 464.8, df = 2, $p < 0.001$). Individuals developing at 10 °C were the largest (Fig. 1B). Development time also had a significant positive effect on the tibia size of parasitoid females ($\chi^2 = 6.76$, df = 1, $p < 0.01$, $R^2 = 0.84$).

Total egg number (egg load + egg laid) was different between temperature rearing treatments ($\chi^2 = 989.9$, df = 2, $p < 0.001$), and females reared at 10 °C had the highest number of eggs. We found differences between 10 and 20 °C ($z = -23.16$, $p < 0.001$), 10 and 28 °C ($z = -25.7$, $p < 0.001$), and light differences between 20 and 28 °C ($z = -3.30$, $p < 0.01$) (Fig. 1C). Size also positively influenced egg numbers ($\chi^2 = 169.95$, df = 1, $p < 0.001$, $R^2 = 0.32$).

Developmental temperature significantly affected the lifespan of parasitoids once placed at 28 °C (both sexes considered, $\chi^2 = 70.53$, df = 2, $p < 0.001$); all parasitoids reared at 20 °C lived the longest (around 18 days more than those reared at any other temperature). The sex of the parasitoid also affected lifespan (regardless of the temperature, $\chi^2 = 6.97$, df = 1, $p < 0.01$); males lived longer than females (53.5 ± 1.7 h, and 47.5 ± 1.3 h, for males and females, respectively). There were no sex-specific effects of developmental temperature on parasitoid lifespan ($\chi^2 = 1.94$, df = 1, p = 0.38) (Table 2).

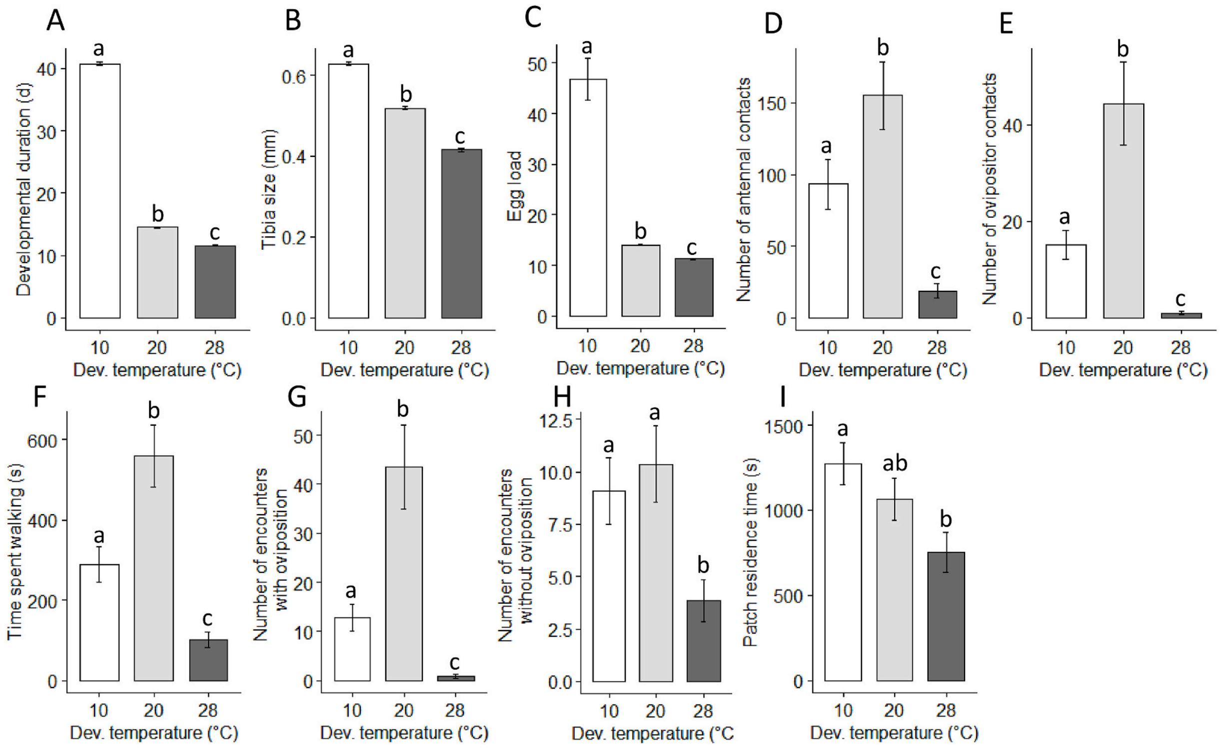

Fig. 1. Effect of parasitoid developmental temperature (10, 20, or 28 °C) on means (±SE): A. developmental duration, B. tibia length, C. egg load, D. number of antennal contacts at 28 °C, E. number of ovipositor contacts at 28 °C, F. time spent walking in the host patch at 28 °C, G. number of encounter with oviposition at 28 °C, H. number of encounter without oviposition at 28 °C, I. patch residence time at 28 °C. Lower script letters indicate significant differences (<0.05) between temperature treatments.

Table 1
Developmental duration (d) of male and female parasitoids, from egg to adults, according to developmental temperatures. Statistical results show pairwise comparisons between sexes, for each developmental temperature.

T (°C)	Sex	N	Mean developmental duration (d) (±SE)	Z value	P value
10	Female	70	42.61 ± 0.34	−0.07	0.94
	Male	33	40.79 ± 0.41		
20	Female	66	14.26 ± 0.10	0.22	0.82
	Male	33	14.48 ± 0.08		
28	Female	87	11.54 ± 0.07	3.21	<0.01
	Male	35	11.34 ± 0.08		

Table 2
Longevity (h) of male and female parasitoids according to developmental temperatures. Different lower script letters indicate statistical differences ($p<0.05$) among developmental temperatures, for each sex.

T (°C)	Sex	N	Mean longevity (h) (±SE)
10	Female	35	44.63 ± 2.74 a
	Male	33	44.91 ± 2.06 a
20	Female	33	57.70 ± 1.82 b
	Male	33	68.21 ± 2.55 b
28	Female	51	42.86 ± 1.70 a
	Male	35	47.74 ± 2.61 a

3.2. *Behavioral assays at high temperature*

Developmental temperature had an effect on the number of antennal contacts at 28 °C ($\chi^2 = 2807.4$, df = 2, $p < 0.001$). Individuals reared at 20 °C had the highest number of antennal contacts, followed by those reared at 10 °C and 28 °C (10 vs. 20 °C, z = 22.7, $p < 0.001$; 10 vs. 28 °C, z = −37.9, $p < 0.001$; 20 vs. 28 °C, z = −51.6, $p < 0.001$) (Fig. 1D).

Developmental temperature also affected the number of ovipositor contacts at 28 °C ($\chi^2 = 871.8$, df = 2; $p < 0.001$). Individuals reared at 20 °C had the highest number of ovipositor contacts, followed by those reared at 10 °C and 28 °C (10 vs. 20 °C, z = 21.3, $p < 0.001$; 10 vs. 28 °C, z = −15.6, $p < 0.001$; 20 vs. 28 °C, z = −22.1, $p < 0.001$) (Fig. 1E). However, developmental temperature did not influence the frequency of antennal contacts ($\chi^2 = 3.28$, df = 2, p = 0.19), nor the frequency of ovipositor contacts ($\chi^2 = 1.49$, df = 2, p = 0.47), at 28 °C.

Developmental temperature had an effect on total time spent walking at 28 °C ($\chi^2 = 30.59$, df = 2, $p < 0.001$). Females growing at 20 °C spent the longest time walking (i.e., searching for hosts) followed by those that grew at 10 °C and 28 °C (10 vs. 20 °C, z = −2.6, $p < 0.05$; 10 vs. 28 °C, z = 3.8, $p < 0.001$; 20 vs. 28 °C, z = 5.1, $p < 0.001$) (Fig. 1F).

Developmental temperature had a significant effect on the number of encounters followed by oviposition at 28 °C ($\chi^2 = 912.5$, df = 2, $p < 0.001$). It was the greatest for parasitoids reared at 20 °C (10 vs. 20 °C, z = 22.6, $p < 0.001$; 10 vs. 28 °C, z = −14.6, $p < 0.001$; 20 vs. 28 °C, z = −21.6, $p < 0.001$) (Fig. 1G).

Developmental temperature had a significant effect on the number of encounters without oviposition at 28 °C ($\chi^2 = 100.87$, df = 2, $p < 0.001$). Females reared at 10 and 20 °C had similar numbers of encounters without oviposition (z = 1.7, p = 0.21), and there were differences with females reared at 28 °C (10 vs. 28 °C, z = −8.4, $p < 0.001$; 20 vs. 28 °C, z = −9.8, $p < 0.001$) (Fig. 1H).

Rearing temperature influenced the number of parasitized ($\chi^2 = 504.03$, df = 2, $p < 0.001$) and superparasitized aphids ($\chi^2 = 307.76$, df = 2, $p < 0.001$), at 28 °C. For assays with parasitoid females reared at 10 °C, the number of parasitized aphids was 0.77 ± 1.7 (mean ± SE) aphids, the number of superparasitized aphids was 0.17 ± 0.56, for a total parasitism rate of 3.08% ± 0.07. For assays with parasitoid females reared at 20 °C, these values were 8.27 ± 7.37, 4.6 ± 5.29, and 33.09% ± 29.5, respectively. No aphids were parasitized by females reared at

28 °C.

3.3. Patch residence time

Rearing temperature ($\chi^2 = 6.42$, df = 2, p = 0.04, Fig. 1I), the number of encounters without oviposition ($\chi^2 = 22.5$, df = 1, $p < 0.05$), and the interaction between these two variables ($\chi^2 = 6.7$, df = 2, $p < 0.05$, Fig. 2) had an effect on parasitoid residence time in host patches at 28 °C, as detailed below (Table 3).

Females reared at 28 °C were 2.80 times more likely to leave the aphid patch at any time than females reared at 10 °C (z = 2.8, $p < 0.05$), and there was no significant difference in this tendency between 20 and 10 °C (z = 1.3, p = 0.39), nor between 20 and 28 °C (z = 1.5, p = 0.31), regardless of the number of host encounter without oviposition (Fig. S1). Each host encounter without oviposition increased—with a marginally non-significant effect—the probability that a female parasitoid stayed in the patch (i.e., multiplies the probability of leaving by 0.95), for 20 and 28 °C, compared to 10 °C (Fig. S2). However, the effect of the number of host encounter without oviposition on residence time at 28 °C differed according to parasitoid developmental temperature. The negative effect of host encounter without oviposition on the probability of leaving the patch was stronger for rearing temperature of 28 °C than for the other rearing temperatures, as determined by the comparison of regression slopes, and interaction effect in the model (Fig. 2).

4. Discussion

Contrary to our initial hypothesis, a high temperature (28 °C) during development affected a series of life history traits such as survival and the rate of emergence which had direct negative consequences on the ability to parasitize at this same temperature. Surprisingly, it was the intermediate temperature during development that best prepared the parasitoids for high temperature efficiency. In fact, the temperature of 20 °C corresponds to an overall thermal optimum which ensures a better physiological state and therefore a better capacity to react to stress. In addition, we revealed the interplay between developmental temperatures and the number of hosts encountered without oviposition on parasitoid residence time on host patches. These behavioral aspects are rarely tested in relation to developmental conditions. Overall, our results strengthen the idea that developmental temperature plays an important role in modulating insect physiological, morphological and behavioral traits at the adult stage (Atkinson, 1996; Fraimout et al., 2018).

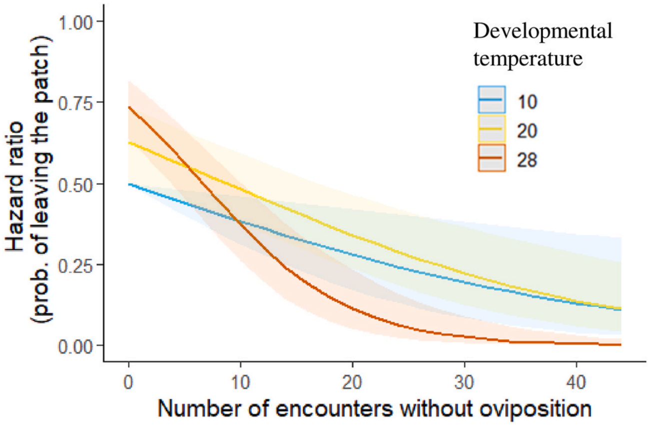

Fig. 2. Estimated marginal means of hazard ratios (i.e., probability of leaving the host patch, at 28 °C, retrieved after Cox regression coefficients), as a function of the number of host encounters without oviposition, and for each developmental temperature of parasitoid females. The number of encounters by parasitoids without laying eggs leads to an increase in the probability of females to stay in the patch (a decrease in the probability of leaving), and the effect is stronger for females reared at 28 °C.

Table 3
Statistical results from Cox model on parasitoid residence time in host patches at 28 °C, depending on developmental temperature, the number of host encounter without oviposition decision, and the interaction between both factors. Note that the developmental temperature of 10 °C is taken as a reference variable in the analysis. Regression coefficients, standard errors (SE), and exponential of regression coefficients (exp(coef)) are provided. An exp(coef) >1 indicates an increase in the probability to leave the patch (i.e., reduced residence time), and a value <1 means the opposite, compared to 10 °C.

Variable	Coef	SE	exp (coef)	Z value	P value
Temperature 20 °C	0.51	0.39	1.66	1.3	0.18
Temperature 28 °C	1.03	0.37	2.80	2.8	**<0.01**
Encounter without oviposition	−0.04	0.02	0.95	−1.9	0.05
Temperature 20 °C x encounter without oviposition	−0.01	0.03	0.99	−0.4	0.72
Temperature 28 °C x encounter without oviposition	−0.11	0.04	0.90	−2.5	**<0.05**

On a practical level, these results are interesting in terms of the possibility of application in biological control in agroecosystem conditions even at high temperature, because mass rearing of aphid parasitoids is generally carried out at a temperature of around 20 °C, but parasitoids may be released under warmer conditions. However, our results show the limits in the possibility of using some form of acclimatization to improve resistance to this type of heat stress, as it was pointed out in other species (Terblanche and Chown, 2006). On a more fundamental aspect, insects face heat stresses at different scales as they have to withstand transient heat waves, at varying amplitudes and frequencies, as well as gradual increase in temperature in the context of climate warming (Harvey et al., 2020; Ma et al., 2021). Depending on the scale at which temperature change affects them, insects may not necessarily show the same type of adaptive responses (Angilletta, 2009). In the long term, adaptation to temperature warming may be achieved through changes in distribution, phenology, and through genetic or plastic adjustments in behavior and physiology (e.g., long-term thermal acclimation) (Andrew and Terblanche, 2013). However, it is still not clear how insects may deal with short-term climatic extremes, for example over the course of one generation, as they could either simply tolerate the stress, die or suffer from reduced fitness, use thermoregulatory behaviors to seek shelters, or develop plastic physiological responses to heat stress (Harvey et al., 2020). Developmental acclimation, as shown in this study, or rapid heat hardening (e.g., Mutamiswa et al., 2018) could play a role in such adaptive responses to unpredictable transient periods of extreme heat. Considering temperatures occurring during insect ontogenesis in terms of thermal biology (i.e., developmental plasticity) is crucial because it can affect upper thermal limits for survival or reproduction when insects are exposed to transient heat stress (Bowler and Terblanche, 2008; Jerbi-Elayed et al., 2021; Santos et al., 2021).

4.1. Direct effects of developmental temperature

The lowest emergence levels of *A. colemani* were recorded in mummies formed at non-optimal low and high temperatures (10 and 28 °C), suggesting that those are actually stressful thermal conditions for proper parasitoid development, ultimately causing death of the insect before emergence from the mummy. In a closely related species, *Aphidius rhopalosiphi*, rearing temperatures of 25 °C also drastically decreased emergence levels (Jerbi-Elayed, unpublished data). In contrast, in *A. colemani*, Colinet et al. (2007) found that emergence levels were not dependent on the temperature experienced during juvenile development, at 12, 15, 18 and 25 °C. Multiples factors could explain such differences among studies, such as humidity levels, light exposure, host quality, diet quality, and parasitoid population origin.

As predicted by the temperature-size rule (Atkinson, 1994), and confirmed in several parasitoid species, including aphid parasitoids (Colinet et al., 2007; Le Lann et al., 2011b), the size of *A. colemani* at emergence (i.e., adult size) is directly linked to development time, which is in turn negatively corelated with developmental temperature. The longest development time was noted at 10 °C and was about 40 days, resulting in the longest parasitoid tibia sizes (about 0.8 mm long). Longer development durations are usually not an advantage, because it increases the risk of exposure to various biotic and abiotic conditions, such as predators, parasites, pathogens or heat or cold chocs, in addition to delaying reproduction (Nijhout et al., 2010; Roff, 1993).

At the opposite, larger size achieved by longer developmental duration at lower developmental temperature would be an advantage for *A. colemani* fecundity. In our study, the highest number of eggs was found in parasitoid females that had developed at 10 °C, which is also reported in many insect species in which female size is positively correlated with fecundity (Blanckenhorn, 2000; Ellers et al., 2001; Honěk, 1993). In *A. rhopalosiphi*, females reared at 10 °C seem to invest their resources more in quality egg production (e.g., more and bigger eggs) than in the maintenance of somatic functions (Le Lann et al., 2011b). However, the advantage of low temperatures on fecundity is not always true, because in some cases females have larger eggs, but in smaller quantities compared to those reared at high temperatures, such as in the butterfly *Bicyclus anynana*. In such cases, the investment of resources for egg production is higher at high temperatures (Steigenga and Fischer, 2007).

We found that parasitoids developing at 20 °C had the longest life span, once placed at 28 °C. At the opposite, longevity decreased at 28 °C, for both parasitoids reared at 10 and 28 °C. It is likely that females developing at 10 °C would become time-limited, as their metabolic rate would be accelerated once placed at 28 °C, following the *Thermal Compensation Hypothesis (TCH)*. The TCH postulates that cold-adapted insects have higher metabolic rates than their warm-adapted counterparts, once exposed to relatively high temperatures (Clarke, 1993). The TCH has received some support in studies on fruit flies, but also in aphid parasitoids (Le Lann, et al. 2011a,b). According to Le Lann et al. (2011a, b), higher metabolic rates may result in a modification of the energy allocation between traits or functions, such as longevity and reproduction. In this regard, it is important to consider trade-offs that can occur among traits, such as between fecundity and longevity (Ellers et al., 2000). Finally, females reared at 28 °C are probably energy-limited, which can reduce their survival probability under heat stress (Jerbi-Elayed et al., 2015b). Desiccation during development could also be the phenomenon responsible for reduced lifespan at 28 °C, because evaporation by the cuticle induces strong water losses, even more than respiration (Edney, 2012). Individuals reared at 28 °C have a small quantity of body water, and are exposed to higher desiccation rates due to their important surface-to-volume ratio (Jerbi-Elayed, unpublished data). For parasitoids reared at 10 °C, the quantity of water remains high (Clarke 1993; Jerbi-Elayed, unpublished data) but longevity is still reduced. Considering the results at 10 °C, we suggest that the TCH and the high difference between developmental temperature and adult temperature (+18 °C) explain probably more the higher mortality observed than desiccation stress during development. However, we cannot exclude that different physiological alterations take place at high and low temperatures, and also that rate of water loss increases with higher metabolic rates, following the THC (Clarke 1993).

4.2. Host-foraging behaviors

Parasitoid females reared at 10 and 28 °C showed low motivation for host search compared to individuals reared at 20 °C. *Aphidius colemani* is a species that is not thought to be adapted to low temperatures, as it originally exhibits a subtropical distribution (Starý, 1970). Development at 10 °C would, therefore, affect its sensory structures as was observed in *A. rhopalosiphi* following exposure to 4 °C (Bourdais et al., 2006). This could be due to a poor ability to perceive chemical signals from hosts (e.g., kairomones) due to exposure to non-optimal temperatures. For example, in honey bees, temperature experienced during the pupal stage strongly influences the synaptic organization of the nervous system, which affects their adult behavior (Groh et al., 2004). In other parasitoid insects, such as *Anaphes victus* (Hymenoptera: Mymaridae), exposure to low temperatures during larval stage results in a change in host-seeking behavior, as females are unable to detect host quality signals (van Baaren et al., 2005). In *Microplitis demolitor* (Hymenoptera: Braconidae), exposure to cold during the pupal stage makes emerging females unable to detect odors (Hérard et al., 1988).

We expected that females reared at 28 °C would have better performed in exploiting aphid patches, but it was not the case. At the complete opposite, *A. colemani* females reared at 28 °C showed the lowest interest in searching for hosts (i.e., spent the lowest time walking), and in interacting with hosts with either the antennae or the ovipositor. This lack of interest toward the hosts led to low (for females coming from 10 °C) or null (for those coming from 28 °C) parasitism rates. We observed that parasitoid females reared at 10 °C spent a lot of time immobile in the aphid patch, but expressed little host searching behaviors, whereas females reared at 28 °C tended to rapidly leave the host patch, leading to low contact probabilities. As exposed by Wu et al. (2011), temperature could indirectly influence foraging efficiency through developmental effects. Indeed, high temperatures would result in smaller parasitoids, which would take more time handling aphid hosts than bigger parasitoids reared at lower temperatures (Wu et al., 2011). For females reared at 10 °C, they experience a high heat shock (+18 °C) when put back at 28 °C, which could explain why they may invest more in self-maintenance than in host exploitation behaviors.

In a context of temperature change, parasitoids not only are challenged by the need for physiological adjustments (egg load dynamics, longevity, changes in host quality), but also by the need for responding to changes in host population dynamics, patch structures and phenological shifts. Mismatches could occur in the activity timing of interacting hosts and parasitoids (Damien and Tougeron, 2019; Harvey, 2015), resulting in possible host shortage for parasitoids, and affecting their functional response. Even tiny temperature shifts can have cascading effects on food-webs and ultimately lead to community-level ’breakdowns’ (Harvey et al., 2020). For instance, the exposure of the primary parasitoid *Cotesia glomerata* to increased temperatures reduces the time window during which the idiobiont hyperparasitoids *Acrolyta nens* and *Gelis agilis* can parasitize cocoons of their hosts, resulting in reduced parasitism success under simulated heat wave conditions, especially for the less fecund species *G. agilis* (Chen et al., 2019). Koinobiont species such as aphid parasitoids may not be too heavily impacted by such mismatches, because they can parasitize all or at least several nymphal instars, although they may be constrained to attack suboptimal hosts under warmer regimes (Jeffs and Lewis, 2013; Tougeron et al., 2019).

In *A. colemani*, heat shock induces antennal asymmetry, which has consequences regarding mating (Jerbi-Elayed et al., 2015a). Although further studies are necessary to conclude on this point, it can be suggested that nervous structures involved in environmental perception are a possible cause of low host exploitation at 28 °C. Rearing *A. rhopalosiphi* 25 °C also has several consequences for host exploitation behavior when parasitoids are shifted back to 20 °C (Le Lann et al., 2011b). However, it should be mentioned that interspecific—and even inter-population—comparisons are difficult to make, given the high dependency of host-seeking behavior upon various biotic and abiotic factors, such as internal status of females, differences in nervous system, age, host quality, travel time between host patches, etc. (Wajnberg et al., 2008).

4.3. Residence time in host patches

Optimal residence time in a resource patch is an important determinant of fitness (Holyoak et al., 2008), especially for short-lived species such as parasitoids (Godfray, 1994; Wajnberg, 2006). In our study, the interplay between developmental temperature and host encounter without oviposition had a role in determining parasitoid residence time in aphid patches. Few studies so far have addressed how rearing temperatures affect host-foraging behavior (Wu et al., 2011) and residence time in resource patches. Parasitoid females tested in our experiment were naive, which means that they did not have past experience in patch exploitation, so they used their innate capacities to estimate marginal gain value on the explored host patch, which conditions residence time. In this regard, developmental temperatures are likely to have an effect on parasitoid decision-making, for example because, as discussed before, females being smaller when developing at 28 °C take longer to handle hosts.

Females reared at 10 °C taking the most time to finish their development stayed longer in host patches, followed by those reared at 20 °C, whereas parasitoids developed at 28 °C did leave the patch quickly. In practice, we already know that high temperature increases walking activities and thus probably modifies the time needed for patch exploration at 28 °C (Jerbi-Elayed et al. 2015a,b). Moreover, with respect to the thermal shift that parasitoids experienced, females reared at 28 °C did not face a change in thermal conditions, while females reared at 10 and 20 °C experienced a sudden increase in temperature, which could have been perceived by parasitoids as a signal of deteriorating climatic conditions. Such signal may be interpreted as an indicator of reduced egg-laying opportunities because costs of moving to exploit other patches becomes too high, and females decide to remain longer in the currently exploited host patch (Amat et al., 2006). In natural contexts, changes in abiotic conditions other than temperature, may also stimulate longer patch exploitation strategies, such as increased air pressure or rainfall (Fink and Völkl, 1995). Finally, in parasitic wasps, it has been suggested that perception of time is influenced by temperature, and would therefore influence patch time allocation and progeny investment (Parent, 2016). Variation in time perception depending on developmental temperatures could thus be an additional explanatory factor to our results.

In addition, we showed that each host encounter that did not lead to an oviposition decision actually increased the likelihood that a parasitoid will remain in the host patch. This suggests that *A. colemani* females follow an incremental pattern in their patch-exploitation decision-making; each examination of a host by antennal or ovipositor contacts followed by a rejection increased the tendency of the female to stay in the patch. These results are unexpected because it is common that parasitoid females are encouraged to leave patches after inconclusive encounters, in order to not “waste time” in a suboptimal host patch and try finding benefits elsewhere (Boivin et al., 2004; Wajnberg, 2006). The tendency to stay in a patch following host rejection was even more pronounced in females reared at 28 °C. Those females are limited in time since their longevity was reduced compared to females reared at 20 °C, and they also had the constraint of low egg availability, compared to females reared at 10 °C. Females could therefore stay in a patch to lay eggs, even if they consider it suboptimal, in order to maximize their adaptive value. In addition, even if a parasitoid encounters a host without decision to oviposit, it still represents a signal that other hosts could be available in this patch. This could explain why the number of host encounters without oviposition affected positively, although marginally, the probability that parasitoids stayed in the patch.

5. Conclusion

We demonstrated that strong links exist between developmental temperature, life-history traits, and exploitation behaviors of aphid patches by the parasitoid *A. colemani*. However, our results did not support the hypothesis that developmental acclimation at high temperature leads to better performance at 28 °C. Overall, parasitoids reared at 20 °C showed the highest motivation and efficiency in exploiting aphid patches. Our results can be partly explained by the various interactions among morphological and physiological characteristics of parasitoids with their behavior once placed at 28 °C. For example, rearing temperature influences parasitoid size, which in turns influences patch exploitation behaviors. Our results strengthen the idea that we need to consider what occurs during insect ontogenesis, in terms of thermal biology (Bowler and Terblanche, 2008). This study also reinforces the idea that it is important to consider not only the physiological responses of parasitoids, but also their interaction with other species, as heat stress may have consequences on the dynamic and structure of host-parasitoid multitrophic interactions (Harvey, 2015; Jeffs and Lewis, 2013; Tougeron et al., 2019).

In an applied perspective, parasitoid effects on aphid pest population dynamics depend on optimal decision-making by females exploiting host patches (Mills and Wajnberg, 2008). Our results show that considering developmental temperatures is crucial to determine how efficient biological control strategies can be achieved, depending on these complex decision-making processes. It is especially relevant for parasitoid mass release protocols, because commercial strains are often reared under constant 20 °C condition, while released parasitoids experience various thermal conditions. It is also relevant for improving our predictions about the efficiency of natural biological control in a climate-change context, because parasitoids face increasingly high thermal variations at different steps of their life-cycles (Hance et al., 2007; Tougeron et al., 2019). In this regard, the adaptive value of phenotypic and behavioral thermal plasticity when insects face high temperatures is still to be discussed.

CRediT roles

Conceptualization; M.J.-E., K.G.-L., T.H. Data curation; M.J.-E., K.T. Formal analysis; M.J.-E., K.T. Funding acquisition; K.G.-L., T.H. Investigation; M.J.-E. Visualization; K.T. Writing - original draft; K.T. Writing - review & editing; M.J.-E., K.T.

Data availability

Our dataset is freely and publicly available and has been deposited in Zenodo. It can be found at the following https://doi.org/10.5281/zenodo.4721086.

Declaration of competing interest

None.

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Appendix A. Supplementary data

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