

Influence of Temperature on Flight, Walking and Oviposition Capacities of two Aphid Parasitoid Species (Hymenoptera: Aphidiinae)

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Revised: 28 January 2015 / Accepted: 13 February 2015 /
Published online: 27 February 2015
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Abstract The cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) is one of the major pests of many greenhouse crops. The aphid parasitoids, *Aphidius colemani* Viereck and *Aphidius matricariae* (Haliday) (Hymenoptera: Braconidae: Aphidiinae) have been considered good agents for the biological control of *A. gossypii*. In Mediterranean area, these parasitoids can currently be released under elevated temperature conditions. However, few findings on their behavior changes with temperature are available. In this study, we analyze the consequence of constant temperatures ranging from 20 to 32 °C on the flight, walking and oviposition capacities of *Aphidius colemani* and *Aphidius matricariae*. Our results revealed that flight capacity is clearly influenced by temperature. The optimal temperatures for flying are 20 and 25 °C for *A. colemani* and *A. matricariae*, respectively. For both species, we observed an increase in the walking capacity but a decrease in the reproductive potential at higher temperatures. Furthermore, regardless of the tested temperature, the mummy production rate was always higher in *A. colemani* than in *A. matricariae*. These results indicate that *A. colemani* is more suitable than *A. matricariae* for the biological control of *A. gossypii* in Mediterranean environments.

Keywords *Aphidius colemani* · *Aphidius matricariae* · flight · walking · mummy production · elevated temperatures

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Introduction

Temperature is the main barrier for the establishment of exotic species in a novel environment (van Lenteren et al. 2006). This limitation is especially true for ectothermic organisms, such as insects, because of their limited ability to regulate body temperature (Bale and Hayward 2010). Brutal fluctuations in temperature or regular exposure to elevated temperatures during a portion of the day constitute major stressors that may reduce the potential activity of non-adapted ectotherm insects (Sørensen and Loeschcke 2007; Chown and Terblanche 2006). These stressors are particularly important when such sensitive organisms are used for biological control and the daily maximum temperature regularly exceeds the thermal optima, which results in unsuccessful pest control (Boivin et al. 2006; van Lenteren et al. 2006). This outcome may occur in several Mediterranean ecosystems where the temperature currently exceeds 40 °C in the afternoons during the summer. The sub-lethal effect of temperature can have severe consequences on the population dynamics and fitness of ectothermic organisms (Feder and Kerbs 1998; Fasolo and Kerbs 2004, Hance et al. 2007). As a consequence, elevated temperatures play a role in species distribution (Mellanby, 1939, Deutsch et al. 2008) and can result in mortality because of behavior inactivation that leads to an inability to find food resources or breed successfully (Gwennan et al. 2010). Temperature influences the dispersal ability of insects, including flight initiation and maintenance (Taylor 1963; Walter and Dixon 1984; Suverkropp et al. 2001) as well as walking and oviposition capacities (Prinsloo et al. 1993; Suverkropp et al. 2001). An understanding of the mobility and dispersal capacity of entomophagous arthropods is essential for the implementation of biological control strategies (Bourchier and Smith 1996; Zappalà et al. 2012;). In this context, flight and walking behaviors are the main factors that determine the searching capacity of aphid parasitoids and influence their level of parasitism (Langer et al. 2004). For example, in the case of a mass release, parasitoids must first disperse from their release point to the infested leaves (Pickett and Pitcairn 1999) and may undergo heat stress if they move from a lab rearing temperature of approximately 20 °C (Personal communication, Thierry Hance) to 30 °C or higher.

Understanding the consequences of this type of temperature change on the behavior of natural enemies may explain the failure of biological control programs and will help in finding more adequate solutions (Boivin et al. 2006; Hance et al. 2007).

With its worldwide distribution, the cotton aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) is one of the major pests of many protected and open field crops (Havelka 1978; Kersting et al. 1999; Heinz et al. 2004; Carletto et al. 2009). It is a polyphagous species that is widely distributed in tropical, subtropical and temperate regions (Kersting et al. 1999; Carletto et al. 2009) but is particularly adapted to elevated temperatures (Xia et al. 1999). For instance, in Tunisia and other Mediterranean countries, *A. gossypii* is reported to be an important aphid pest of Cucurbitaceae cultivated in greenhouses and of citrus (Ben Halima Kamel and Ben Hamouda 1993; Boukhris-Bouhachem 2011; Campolo et al. 2014). Chemical control has been widely used and is considered the only valuable tool for controlling aphids over a long period (Parrella et al. 1999). However, insecticide resistance due to recurrent use is a growing concern, as is the occurrence of off-target

effects on other arthropods and the environment in general (Desneux et al. 2007). This issue has stimulated the research and development of aphid biological control methods (Van Lenteren and Woets 1988; Parrella et al. 1999; Boivin et al. 2012). Two aphid parasitoids, *Aphidius colemani* Viereck and *A. matricariae* (Haliday) (Hymenoptera: Braconidae: Aphidiinae) are considered good agents for the biological control of *A. gossypii* (Bennison 1992, Van Steenis and El-Khawass 1995, Goh and Yoo 1997) and are already used against other aphid species (Van Lenteren and Woets 1988; Goh and Yoo 1997; Toussidou et al. 1999). Previous studies showed the effects of temperature on the development rate, survival, parasitism rate, and sex ratio of *A. colemani* and *A. matricariae* (Rabasse and Shalaby 1980; Van Steenis 1993; Miller and Gerth 1994), but to the best of our knowledge, no study has focused on the effect of temperature on the essential behaviors linked to host searching and efficacy of parasitism. Our aim was to compare the flight, mummy production and walking capacities of *Aphidius colemani* and *Aphidius matricariae* at different temperatures ranging from 20 to 30 °C.

Material and Methods

Insect Culture

Aphis gossypii was obtained from citrus orchards in Tunisia in September 2010 and reared on cucumber (*Cucumis sativus*) in wooden cages (0.3 m³) under long-day conditions (16 h L: 8 h D) at 20 °C and 60 % relative humidity (RH).

Both parasitoid species (*A. matricariae* and *A. colemani*) were obtained from Viridaxis SA (Belgium). To obtain standardized individuals, patches of 50 standardized 3-day-old *Myzus persicae* were offered to a mated female parasitoid for 4 h at 20 °C. After parasitism, the females were removed, and the aphids were reared on an artificial diet following the method described by Cambier et al. (2001) until mummification under long-day conditions (16 h L: 8 h D) at 20 °C and 60 % RH. Mummification was monitored every day, and mummies were transferred to centrifuge tubes (1.5 mL, Eppendorf, Germany). Emergence was monitored every day, and parasitoids were used in the experiments at 1 day old.

Flight Capacity

The flight capacity was recorded at 20, 25 and 30 °C and under 55 %±2.3 % RH. Ten parasitoids (5 males+5 females), reared at 20 °C as previously described, 1 day old and fed, were placed in a 3.5 cm diameter Petri dish at the bottom of an upright, opaque cylinder with a 9 cm width and 20 cm height based on the protocol developed by Langer et al. (2004).

To prevent parasitoids from walking off, the Petri dish was surrounded by water. The inner part of cylinder was painted with a light film of Fluon® beforehand so that the parasitoids could only reach the top of the cylinder by flying. A transparent sticky lid was placed at the top of the cylinder. Insects were attracted to the top by the light of a 7500 lux light source. The number of parasitoids glued to the lid (meaning they had flown) was recorded after 24 h. Thirty replicates were performed for each temperature.

Walking Capacity

The walking capacity of the two parasitoid species was tested at 20 °C, 25 °C, and 30 °C. Because mating experience can significantly reduce locomotion activity in parasitoids (Pompanon et al. 1999), all tested females were virgin. Isolated females ($N=19$) were placed in the center of a Petri dish ($\varnothing=5.5$ cm) in a constant temperature chamber. Their behavior was recorded with an analogic camera focused on the set-up. Pictures were extracted from each film every 5 s, and then three sets of 13 images (one minute) were sampled at the beginning (7th minute), middle (11th minute) and end (16th minute). These three sets of 13 pictures were analyzed using the data processing program Image J (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, MD, USA, <http://rsb.info.nih.gov/ij/>, 1997–2008), which attributed spatial coordinates to each individual. By computing these locations, we estimated the total distance walked by the tested individuals during each of the three minutes for the two species at the three tested temperatures (20 °C, 25 °C, and 30 °C). Furthermore, we estimated the time spent in movement during each of the three analyzed minutes for each individual. By dividing the total distance walked by the time in movement, we calculated the average speed of each tested individual. This average speed was used as a walking capacity indicator. Experiments were conducted between 14:00 and 17:00 pm, at 35 ± 2.3 % RH, and under a 9000 lux light source.

Oviposition Activity

Oviposition behavior was tested for one-day-old mated females at 20, 25 and 30 °C, under a photoperiod of 12 h light and 55 ± 2.3 % RH. To ensure they were mated, each female was left for 24 h at 20 °C with two males and fed with water+honey (50:50). Females ($N=15$) were then individually transferred to a small pot containing a cucumber plant infested with approximately 100 third instar nymphs of cotton aphid under different temperature conditions (20, 25 or 30 °C). The infested plant was renewed every day until the death of the female. The parasitoids were removed, and aphids were reared at 20 °C and 60 ± 2.3 % RH under a 16 h L: 8 h D regime until mummies were formed. The total amount of mummies produced during the entire experiment divided by the number of days the females lived was used as the mummy production rate.

Statistical Analysis

Two-way ANOVA and Bonferroni post-hoc tests were used to compare the flight capacity and the mummy production rate among the temperatures and parasitoids species. A three-way ANOVA was performed to test the potential influence of (1) the species (*A. colemani* and *A. matricariae*), (2) the temperature (20, 25, or 30 °C), and (3) the time when the measures were recorded (seven minutes after the start of the experiment and then eleven and sixteen minutes after the start) in determining the parasitoid walking capacity.

Statistical analyses were performed using R (version 2.14.1, Copyright (C) 2011). All tests were applied under two-tailed hypotheses, and the significance level p was set at 0.05.

Results

Flight Capacity

The results of two-way ANOVA revealed that flight capacity is influenced by temperature ($F_{2,174}=14.12, P<0.001$) but does not differ between the two species ($F_{1,174}=2.24, P>0.05$). However, a significant correlation between parasitoid species and temperature was observed ($F_{2,174}=8.02, P<0.001$). Therefore, we used the Bonferroni procedure to detect differences in flight capacity in the same species at different temperatures. For *A. colemani*, the optimal temperature for flying was 20 °C (Bonferroni Test: 20 °C vs 25 °C: $t=2.52, P<0.05$; 20 °C vs 30 °C: $t=3.41, P<0.01$; 25 °C vs 30 °C: $t=0.88, P>0.05$) (Fig. 1). At this temperature, a mean of 4.43 ± 0.454 adult females were trapped on the sticky lid. For *A. matricariae* the optimal temperature for flying was 25 °C, with a mean of 4.36 ± 0.366 (Bonferroni Test: 20 °C vs 25 °C: $t=2.52, P<0.05$; 20 °C vs 30 °C: $t=3.10, P<0.01$; 25 °C vs 30 °C: $t=5.62, P<0.001$) (Fig. 1).

Walking Capacity

Using a three-way ANOVA, we tested the influence of the species, temperature and time at which the measures were recorded on the walking capacity. Temperature significantly influenced the parasitoid walking capacity ($F_{3,267}=6.80, P=0.001$) (Fig. 2). Additionally, we did not observe any significant difference between the two species ($F_{1,267}=0.48, P=0.49$) or the three minutes of experiment ($F_{2,267}=0.28, P=0.76$) (Fig. 2). However, we observed a significant correlation between the temperature and the species ($F_{2,267}=3.72, P=0.025$). We observed a relatively constant average speed for *A. matricariae* as the temperature increased (4.46 mm/sec). For *A. colemani*, however, we observed a peak in activity at 30 °C (5.42 mm/sec) (Fig. 2).

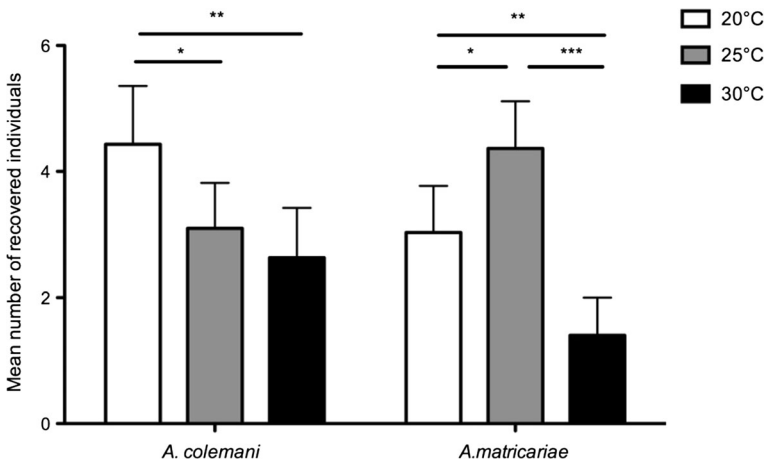


Fig. 1 Flight activity: Mean number of individuals trapped on the sticky lid ($N=10\times30$) at three temperatures. Symbol (***) (**), (*) indicates respectively $P<0.0001, P<0.01$ and $P<0.05$

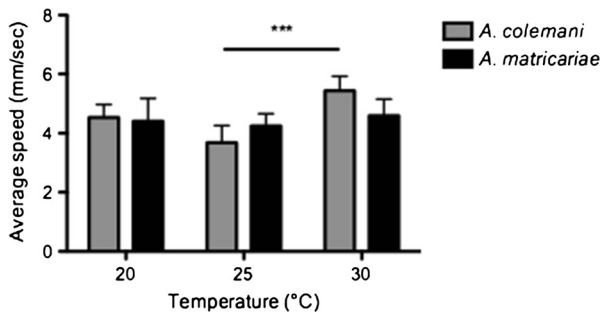


Fig. 2 Average speed (mm/s) of *A. colemani* and *A. matricariae* ($N=19$) at three temperatures

Oviposition Activity

The two species demonstrated different mummy production rates ($F_{1,80}=111.30$, $P<0.001$) (Table 1), which was always higher for *A. colemani* than *A. matricariae*. Furthermore, temperature significantly influences this parameter ($F_{2,80}=4.54$, $P=0.01$) (Table 1). *Aphidius colemani* demonstrated a significant decrease in mummy production with the increase in temperature (Bonferroni Test: 20 °C vs 25 °C: $t=1.80$, $P>0.05$; 20 °C vs 30 °C: $t=2.74$, $P<0.05$; 25 °C vs 30 °C: $t=0.84$, $P>0.05$) (Table 1). Conversely, no temperature influence on mummy production was observed for *A. matricariae* (Bonferroni Test: 20 °C vs 25 °C: $t=0.16$, $P>0.05$; 20 °C vs 30 °C: $t=1.52$, $P>0.05$; 25 °C vs 30 °C: $t=1.30$, $P>0.05$) (Table 1).

Discussion

Temperature had a clear impact on the locomotor activities and mummy production rate of *A. matricariae* and *A. colemani*, but differences were observed between the two species.

The optimal temperature for flight appears to be 20 °C for *A. colemani*. *Aphidius matricariae*, however, demonstrated the most flight activity at 25 °C. Under our conditions, both species were reared at 20 °C, which corresponds to the current temperature used in commercial insectaries (Personal communication, Thierry Hance). In cases of a mass release, particularly under greenhouses, exposure to elevated temperatures, from 25 °C to 30 °C, probably occurs frequently and corresponds to a brutal heat shock without any acclimation, which can lead to a failure in control. Under these conditions, *A. matricariae* will likely fly better than *A. colemani*. However, flight activities observed under lab conditions do not necessarily reflect true flight activity in the field. For other species, this behavior can be affected by other abiotic factors, such as atmospheric pressure, wind and rainfall, or by physiological conditions such as age, mating and egg laying status (Juillet 1964; Elzen et al. 1987; Messing et al. 1997; Blackmer and Cross 2001; Gu and Dorn 2001). Flight activity concerns inter-patch behavior related to optimal foraging strategy, dispersal and mate searching. At elevated temperatures, we predict that fewer patches will be explored, which can lead to a failure in host control. To address this concern, an increase in the number of release points may

Table 1 Number of mummies / day produced by *A. colemani* and *A. matricariae* at three constant temperatures (Different letters: a, b, and c in the same column indicates significantly different between the two parasitoid species at various constant temperatures)

Species	Temperature (°C)	Number of mummies / day
<i>A. colemani</i>	20	50.38±3.4 a
	25	40.22±7.31 ab
	30	35.5±4.59 b
<i>A. matricariae</i>	20	11±1.93 c
	25	10.23±2.51 c
	30	2.88±1.72 c

be an alternative but may have important consequences on costs and the potential adoption of the method by producers (Fournier and Boivin 2000). Acclimation or a change in the rearing temperature may be other valuable solutions that exploit the phenotypic plasticity of the species.

Surprisingly, even though flight is impeded at an elevated temperature, the maximum walking speeds for *A. colemani* and *A. matricariae* were observed at 30 °C. It seems that an elevated temperature increases the walking velocity of parasitoids, as shown in *Trichogramma* sp. (Boldt 1974; Suverkropp et al. 2001). These two behaviors (walking and flight) are therefore not affected in the same way. We can imagine that walking takes place at the leaf level and is perhaps less influenced by cuticular water loss because of the plant evapotranspiration at that level. Flight activity may be more costly in dry air because water loss through evaporation is important. Indeed, in arthropods, evaporation through the cuticle results in greater water loss than simply breathing (Edney 1977). Evaporation depends on the activity gradient between atmosphere and body water. Water represents 95–99 % of the molecules that make up the body (Danks 2000). The activity of water in the body is between 0.95 and 0.99 (Wharton 1985), and the atmospheric water activity in this case is approximately 0.5 (according to the 1985 Wharton activity atmospheric water=relative / 100 humidity). Because the activity of water in the body is higher (approximately double) than the atmospheric activity, significant evaporation is expected to occur.

There is very little information in the literature on the walking speed of *Aphidius* spp. Colinet and Hance (2009) observed a higher mean walking velocity for *A. colemani* males at 20 °C (6 mm/s) than we observed for females. In their study, however, walking was measured when males were exposed to females. Langer et al. (2004) observed velocities higher than 6 mm/s for *A. ervi* and *A. rhopalosiphi* at 22 °C. Generally, *Aphidius* spp. have a greater walking capacity than *Praon* spp., and the maximum speed was calculated at a temperature of 16 and 22 °C (Langer et al. 2004). Walking is an important factor of intra-patch searching behavior, and an increase in speed can improve the host encounter and consequently influence the patch residence time and parasitism. The high walking velocities observed for the two species under elevated temperature conditions indicates that parasitism may still be possible as long as the females are close to an aphid colony.

Elevated temperatures appear to have opposite effects on walking speed and mummy production, which is negatively affected by elevated temperatures in *A. colemani* (Table 1). Moreover, the number of mummies produced by *A. matricariae* was at least 5 times lower than the number produced by *A. colemani* at the three tested temperatures, even though *A. matricariae* flight activity is greater at higher temperature. This observation may be due to the higher searching rate of *A. colemani* than *A. matricariae* (Zamani et al. 2006) and the possibility that *A. gossypii* may be a less valuable host for *A. matricariae*. Interestingly, Zamani et al. (2007) observed a higher parasitism rate for *A. colemani* at 25 °C, but in this study, the initial rearing temperature was also 25 °C. For *A. matricariae*, their maximum parasitism rate was recorded at 20 °C. In our study, the maximum number of mummies produced was recorded at 20 °C for both species, which corresponds to the rearing temperature. However, our oviposition data were measured individually, and in the study by Zamani et al. (2007), it was measured for a group of 5 females. Zamani et al. (2012) also indicated that the maximum rates of fecundity for *A. colemani* were recorded at 25 °C, but this parameter was calculated for 15 females reared at 25 °C and was considered one replication. Concerning *A. gossypii* on cucumber, they also reached their maximum rate of increase at 25 °C ($r_m=0.556 \text{ day}^{-1}$), and this value dropped to 0.426 day^{-1} and 0.510 day^{-1} at 20 and 30 °C, respectively (Van Steenis and El-Khawass 1995). Similar results were reported by Aldyhim and Khalil (1993) on the squash *Curcubita pepo* and by Xia et al. (1999) on cotton. Thus, the optimal temperatures are the same for the parasitoids and their aphid host. Therefore, we predict that at least *A. colemani* should be able to control *A. gossypii* at 25 °C in the case of a mass release. The increase in walking velocity with temperature may compensate for the decrease in fecundity and give the parasitoids an advantage because aphid growth rate decreases at 30 °C. However, other components must be taken into consideration, such as a decrease in size of both the host and the parasitoid at higher temperatures and the potential consequences on handling time (Wu et al. 2011).

In conclusion, *A. colemani* appears to be more suitable than *A. matricariae* for the biological control of *A. gossypii* under greenhouses in a warm environment where the temperatures can rise above 30 °C during the day mostly because of its high rate of mummy production. Our results further our understanding of the difficulties involved in the biological management of *A. gossypii*, by combining these laboratory results with the trends in local agro-meteorological conditions. Additionally, further research is needed on the abiotic and biotic factors that influence the effectiveness of this species in a biological control context, especially on factors such as temperature and relative humidity fluctuations and unpredictable peaks of temperature.

Acknowledgments The present study was supported by a grant from the Ministry of High Education of Tunisia. *Aphidius colemani* was provided by Viridaxis S.A. This manuscript is publication number XXX of the Biodiversity Research Centre.

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