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Temperature influences host-instar selection in an aphid parasitoid: a support for the relative fitness rule.

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Introduction

Organisms should adopt decisions that maximise their lifetime fitness, according to the environment they face. Consequently, parents should avoid laying eggs or rearing offspring in conditions where high mortality of progeny may occur (Eriksson & Götmark 1982, Blaustein et al. 2004). For example, parasitoid females reduce the number of hosts parasitized when predators (Takizawa, Yasuda & Agarwala 2000) or hyperparasitoids are present in the habitat (Höller et al. 1994, Petersen et al. 2000) or avoid laying eggs in low-quality hosts (Vinson 1998). However under some conditions, females may adopt risk-prone behaviours and reproduce in habitats where the survival of their progeny is compromised. For example, drosophila parasitoid *Leptopilina heterotoma* having a short-life expectancy tend to increase self-superparasitism following a decrease in barometric pressure, a climatic parameter associated with deteriorating foraging conditions, (Roitberg et al. 1993). The female accepts a lower immediate fitness return, a consequence of self-superparasitism, because her prospect of fitness gain later in life is reduced.

Recently, Giraldeau and Boivin (2008) proposed a relative fitness rule for foraging parasitoids, based not only on the quality of the environment but also on female physiological condition. This rule states that "animals that do not expect to match the average expected fitness of the population will suffer a cost because they will lose representation in the next generation, perhaps even disappear. Consequently, the chances of avoiding the genetic cost for such an organism are maximised by adopting risk-prone reproduction options." Parasitoid females should thus adopt risk-prone reproduction options when expecting a deficit in reproductive success due to their intrinsic

characteristics, especially body size. To our knowledge no study has yet experimentally investigated this relative fitness rule. Giraldeau and Boivin (2008) suggested testing this prediction using female parasitoids that are phenotypically different. For instance, smaller females with lower fecundity and reduced capacity to find new host patches are expected to be more risk-prone than larger females.

The Temperature-Size Rule (Atkinson 1994: Angilletta and Dunham 2003) states that ectotherms generally grow larger at lower temperature. Accordingly, parasitoids of different size can be produced at different developmental temperatures (Colinet et al. 2007). Females developing at high temperature are smaller, have fewer eggs at emergence and lower capacities to find new host patches; they are thus expected to engage more risk-prone behaviour than larger females that developed at cooler temperatures. Alternatively to this hypothesis, cold-developed insects are expected to have a higher metabolic rate than warm-developed individuals when tested in a common environment because of temperature compensation following the Metabolic Cold Adaptation theory (Wohlschlag 1960; Clarke 1993). Cold-developed females should therefore use their energetic resources faster, live shorter (Le Lann et al. 2011) and thereby have fewer reproduction opportunities than females developing at higher temperature when foraging at a common temperature. This alternative hypothesis implies that cold-developed females should be more risk-prone than warm-developed females because they are time-limited.

Temperature affects reproductive success of parasitoids during both larval development and adult life. Life expectancy typically decreases as temperature increases in ectotherms (e.g., Loeb & Northrop 1917; Moiroux et al. 2013). Females foraging in a hot climate

have less time available for oviposition, and consequently a lower expected reproductive success than females living in a cooler environment. They should thus adopt more risk-prone behaviours.

Risk-prone reproduction behaviours in parasitic wasps include oviposition in the presence of superior competitors (Vayssade et al. 2012), hyperparasitoids (Höller et al. 1994) or predators (Takizawa, Yasuda & Agarwala 2000), self-superparasitism (Roitberg et al. 1993) or oviposition in hosts suboptimal for larval development (Henry, Gillespie & Roitberg 2005). This last decision may have strong consequences on reproductive success as ovipositing in suboptimal hosts can lead to an emergence rate close to zero (Henry et al. 2005) and low quality hosts should thus be avoided in optimal conditions.

In this paper, we investigated the relative role of developmental and foraging temperature on acceptance of low-quality hosts by the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae) parasitizing the potato aphid *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphididae). For koinobiont aphid parasitoids, second and third nymphal instars usually represent high quality hosts whereas fewer progeny emerges from eggs laid in first or fourth nymphal instars (Colinet et al. 2005; Henry et al. 2005). Under laboratory conditions, *A. ervi* females were reared at low, medium or high temperature and next allowed to oviposit on the four host nymphal instars at one of these temperatures. We expected to observe more risk-prone behaviours, i.e. higher parasitism rate in non-optimal aphid nymphal instars, in (i) females foraging at high temperature because of reduced female longevity, in (ii) warm-developed females following the body size-related prediction, and (iii) cold-developed females following the prediction based on metabolic compensation.

Material & Methods

Insect colonies

Aphidius ervi is a solitary koinobiont parasitoid of several aphid species of economic importance. A few weeks prior to the tests, an *A. ervi* colony was initiated with individuals bought from BioBest Canada Company (Leamington, Canada). Parasitic wasps were reared in cages on the potato aphid *Macrosiphum euphorbiae* at $20\pm1°C$, $60\pm10\%$ RH, 16L: 8D photoperiod. The aphid colony was established with individuals collected from potato fields in the vicinity of Québec City, Canada, and was maintained on potato plants, *Solanum tuberosum* Linnaeus, cultivar "Norland" under the same conditions.

Preliminary experiment

To confirm that observation of a sting is relevant to evaluate host-instar acceptance by *A. ervi*, we determined if the probability of a sting resulting in the deposition of an egg was similar between host nymphal instars, as observed by Henry *et al* (2005). Five 48h-old *A. ervi* mated females were each allowed to attack eight aphids from each four nymphal instar. Aphids were removed after one sting and reared on a potato leaf for 48h at $20\pm1°C$, $60\pm10\%$ RH, 16L: 8D. After this period, 25 aphids per nymphal instar were randomly selected and dissected in a drop of Ringer's solution to check for parasitoid eggs. There were significantly fewer aphids that contained eggs than aphids that were stung (z = 3.114, p < 0.001), with 65 to 70% of attacked aphids being parasitized.

However, this pattern was similar across host instar (GLM, z = 0.608, p = 0.517). Observation of a sting can therefore be used to assess host-instar acceptance by *A. ervi*.

Experimental design

To measure the influence of developmental and foraging temperature on host selection behaviour in *A. ervi*, we first reared parasitoids at three different temperatures: 12, 20 and 28±1°C. These temperatures were selected because 20°C is the optimal temperature for rearing while 12 and 28°C are close to the extremes at which *A. ervi* remains active when foraging (Gilchrist 1996). Fifty parasitoid couples were each placed in a Petri dish at 20±1°C for five hours with 30 N2 aphids placed on a potato leaf. After this period, 10 presumably parasitized aphids per parasitoid couple were reared at 12, 20 and 28±1°C on a potato plant. Once parasitized aphids turned into mummies, they were placed individually in gelatine capsules until parasitoid emergence. Emerged female parasitoids were then kept for 24 hours in a Petri dish containing moistened cotton and honey along with a male from the same treatment at the same temperature they experienced during development. This period allowed females to mate and mature eggs (Le Lann *et al.* 2010).

The next day, the host selection behaviour of *A. ervi* females was characterized for each of the four aphid nymphal instars (N1 to N4) in a climate room (60±10% RH). Seven treatments were established to examine the relative role of developmental and foraging temperatures on host selection: (1-3) females foraging at the same temperature as the one they experienced during their development (i.e., 12, 20 and 28°C; named 12-12, 20-20 and 28-28 treatments, respectively); (4-5) females reared at 20°C and foraging at 12 or

28°C (20-12 and 20-28 treatments, respectively); (6-7) females reared at 12°C and 28°C and foraging at 20°C (12-20 and 28-20 treatments, respectively).

One hour before the beginning of the observation, a potato leaf (ø 4cm) was taped on a piece of paper and 60 apterous aphids were placed on it, 15 from each nymphal instar. Concurrently, parasitoid females were acclimatized to the experimental temperature for one hour. Females were next introduced in the experimental arena (ø 26cm, h 8.5 cm) and their behaviour was monitored using a camera (Panasonic WV-BD400) and next analyzed with The Observer XT software (Noldus, Wageningen, The Netherlands). Twenty-five females per treatment were observed and the frequency of the following behaviours was determined: successful oviposition (sting), failed oviposition (unsuccessful oviposition attempt due to aphid behavioural defence), host rejection (parasitoid contact with a motionless aphid not followed by an attack) and misplaced attack (sting attempt on a section of the potato leaf with no aphid). This latter behaviour is rarely taken into account in similar studies but was frequently observed in some treatments and could indicate a neural disruption induced by temperature. Handling time was measured and included duration of host antennation, oviposition and time to recover from behavioural defence. We did not replace parasitized aphids because superparasitism was rare under our experimental conditions (<5%, J. Moiroux, unpublished data). The numbers of successful ovipositions, failed ovipositions and host rejections were pooled to calculate the number of encounters per host nymphal instar. An attack rate per host nymphal instar was also calculated, i.e. the sum of successful and failed ovipositions on a given nymphal instar divided by the number of encounters.

The observation stopped when the parasitoid remained motionless for more than 15 minutes or left the patch for more than one minute at 28°C, 2 minutes at 20°C and 6 minutes at 12°C, these durations being proportional to the relationship between temperature and walking speed for *A. ervi* females (Gilchrist 1996). At the end of the experiment, parasitoid females were frozen and their tibia length was measured under a microscope with the µScope Microscopy Software (PixeLINK®, Ottawa, Canada). Hosts from a given treatment were sorted by nymphal instar, placed on a potato plant and reared at 20±1°C, 60±10% RH, 16L: 8D photoperiod until parasitoid emergence. Mummification rate, emergence rate and tibia length of *A. ervi* progeny were determined to assess the suitability of each aphid nymphal instar for parasitoid larval development. We only considered tibia length of female progeny because no males emerged from N4 aphids and a sexual dimorphism in body size exists in *A. ervi* (Sequeira & MacKauer 1993).

Longevity

Females reared at 12, 20 and 28°C and not used in the previous experiment were placed at emergence at 20°C, 60±10% RH, 16L: 8D in 12 cm cubic cages containing moistened cotton and honey to measure their longevity. Mortality was recorded twice a day, in the morning and evening.

Statistical analyses

The effect of both developmental temperature and foraging temperature on body size of parasitoid females was analyzed with a two-way ANOVA, data being normally distributed.

We compared the number of successful and failed ovipositions and the number of host rejections using Generalized Linear Models (GLM) with developmental temperature, foraging temperature and host nymphal instar as fixed factors and the number of encounters as a covariate, considering a Poisson distribution of data. Attack rate was compared using a Generalized Linear Model (GLM) with developmental temperature, foraging temperature and host nymphal instar as fixed factors, considering a binomial distribution of data. The number of misplaced attacks was analysed using a GLM with developmental and foraging temperature as fixed factors. We also performed GLM with developmental temperature, foraging temperature and host nymphal instar as factors to test for differences in handling time, mummification rate, emergence rate and progeny tibia length. The survival package provided by R software was used to test for differences in longevity between females that developed at different temperatures, using a Weibull distribution. All statistical analyses were carried out using R software version 2.14.1 (R Development Core Team, 2011).

Results

Developmental temperature significantly influenced *A. ervi* female size (F= 7.14, p < 0.001), tibia length decreasing with increasing temperature (12°C = 0.76 ± 0.06 mm, 20°C = 0.67 ± 0.05 mm, 28°C = 0.56 ± 0.05). In contrast, no difference in parasitoid size was associated to foraging temperature (F= 0.49, p = 0.806).

The attack rate was significantly influenced by host nymphal instar (z = 4.118, p = 0.012), developmental temperature (z =5.907, p < 0.001), foraging temperature (z = 6.252, p < 0.001), the interaction between nymphal instar and developmental temperature (z = 3.816, p = 0.031) and the interaction between nymphal instar and foraging temperature (z = 3.057, p = 0.043). Second and third nymphal instars were more frequently attacked than first and fourth nymphal instars. Females that developed at 28°C attacked first and fourth nymphal instars more frequently than females that developed at 12 and 20°C, and females foraging at 28°C attacked N4 aphids more frequently than females foraging at lower temperatures.

Host stage (z = 3.383, p < 0.001), developmental temperature (z = 2.388, p = 0.017) and the interaction between developmental temperature, foraging temperature and host nymphal instar (z = -3.47, p < 0.001) significantly influenced the number of successful ovipositions by *A. ervi*. Second and third nymphal instars were more frequently parasitized than other instars. First nymphal instars were more frequently parasitized by females that developed at 28°C than females that developed at 12°C (p = 0.018) or 20°C (p < 0.001), with no difference between these two treatments (p = 0.617). The numbers of second and third nymphal instars parasitized by *A. ervi* were the highest in the 20-20 and

20-28 treatments and the lowest in the 28-28 treatment. Fourth nymphal instars were the most frequently parasitized in the 20-28 treatment, second in the 12-12 treatment and no difference was observed between the other treatments (Figure 1A).

The number of failed ovipositions varied with host age ($z = 2.573$, $p = 0.010$) and the interaction between developmental and foraging temperature ($z = 2.457$, $p = 0.014$). Parasitoids failed more frequently to parasitize N4 aphids than other host ages and females from the 28-28 treatment were less successful than other females (Figure 1C), especially when attacking N4 aphids.

Host nymphal instar ($z = 5.758$, $p < 0.001$), developmental temperature ($z = 6.559$, $p < 0.001$) and the interaction between developmental temperature and host nymphal instar ($z = -2.803$, $p = 0.005$) significantly influenced the number of host rejections. First nymphal instars were more frequently rejected than other host nymphal instars in all treatments. Rejections of N1 were most frequent in females that developed at 20°C and less frequent in females that developed at 28°C (Figure 1B).

The number of misplaced attacks was significantly influenced by developmental temperature ($z = 3.917$, $p < 0.001$), foraging temperature ($z = 3. 514$, $p < 0.001$) and the interaction between these two factors ($z = 4.712$, $p < 0.001$). It was the highest in the 12-12 treatment and higher for females that developed or foraged at 12°C than for females from other treatments (Number of misplaced attacks, mean ± se; 12-12: 9.9 ± 0.9; 20-20: 1.0 ± 0.4; 28-28: 1.0 ± 0.5; 20-12: 5.7 ± 0.6; 20-28: 0.7 ± 0.3; 12-20: 4.4 ± 0.7; 28-20: 1.7 ± 0.4).

Host handling time was influenced by host nymphal instar ($z = -2.751$, $p = 0.027$), and the interaction between nymphal instar, developmental and foraging temperature ($z =$

3.989, p < 0.001). Parasitoids took more time to attack N4 aphids than other instars, N1 aphids being attacked the most quickly. Females from the 20-28 treatment handled hosts faster than other females, while handling time was the longest for females from the 28-28 treatment (Figure 2). Handling time decreased with developmental temperature for females foraging at 20°C.

Development

Mummification rate (z = 3.761, p < 0.001) and emergence rate (z = 3. 012, p = 0.003) of *A. ervi* were only influenced by host age (Table 3), being highest in N2 aphids, intermediate in N3 and lowest in N1. Size of *A. ervi* progeny was influenced by host nymphal stage (F = 4.117, p = 0.012). Parasitoids laid in N3 aphids were bigger than parasitoids laid in other nymphal instars, with parasitoids laid in N1 aphids being the smallest (Table 1).

Longevity

Developmental temperature significantly influenced longevity of parasitoid females (Survival analysis, $\chi 2$ = 48.07, p = 0.013). When transferred to 20°C at emergence, wasps that developed at 12°C (longevity = 8.76 • ± 1.48 days, mean • ± SE) lived significantly shorter than wasps that developed at 20°C (15.43 • ± 2.17 days) and 28°C (12.86 • ± 1.93 days), with no difference being observed between the last two treatments (p = 0.247).

Discussion

Temperature affects body size, initial egg load and basal metabolic rate during *A. ervi* larval development, as well as their life expectancy during adult life. Following the relative fitness rule proposed by Giraldeau and Boivin (2008), we predicted that (1) warm-developed parasitoid females should adopt more risk-prone behaviours than females that developed at lower temperature because of their smaller body size and egg load; (2) cold-developed females should adopt more risk-prone behaviours than females developed at warmer temperature when foraging in a common environment because of metabolic compensation; (3) females foraging at high temperature should adopt more risk-prone behaviours than females foraging at lower temperature because of reduced longevity. The first and third predictions are supported by our results as *A. ervi* (1) females that developed at high temperature attacked low-quality hosts more frequently than other females and (2) females foraging at high temperature attacked low-quality hosts more frequently than those foraging at lower temperature. The second prediction was not supported, as females that developed at cold temperature attacked similar proportions of less suitable hosts than females that developed at intermediate temperature.

Optimal thermal conditions

When *A. ervi* females developed and foraged at 20°C, their optimal thermal conditions, they preferentially parasitized second and third nymphal instar aphids and avoided first and fourth nymphal instars. He & Wang (2006) also observed a preference for intermediary nymphal instars for *A. ervi* parasitizing the pea aphid *Acyrthosiphon pisum*.

We observed that mummification rate, emergence rate and body size of progeny were the highest when *A. ervi* developed in N2 and N3 hosts. Host selection by *A. ervi* females is thus optimal at 20°C. Avoidance of first and fourth nymphal instar may result from a combination of factors including lower nutritional quality of small hosts (Vinson & Iwantsch 1980), increased resistance in larger/older hosts (Li et al. 2002) and more efficient behavioral defence by fourth instar aphids that lower their profitability to parasitoids (Barrette et al. 2009).

Developmental temperature

We observed that female parasitoids developing at high temperature (28-28 and 28-20 treatments) and having a lower initial egg load (Moiroux et al. submitted), increased their attack rate on first and fourth nymphal instars, despite an emergence rate ranging from 2 to 4% in these hosts. Females thus took the risk of ovipositing in hosts where their progeny faced a high mortality rate. The higher number of failed ovipositions in N2 to N4 instars observed for 28-28 females may partly explain higher acceptance of N1 hosts. However, 28-20 females succeeded as much as females that developed at lower temperatures to oviposit in N2 to N4 aphids but still attacked N1 aphids. This suggests that females attacked first nymphal instar not because they were unable to parasitize other instars but rather to increase the number of oviposition opportunities. This result is in contradiction with the prediction that egg-limited parasitoids, i.e. warm-developed females in our study, should accept only high quality hosts for oviposition (Mangel 1989, Heimpel, Rosenheim & Mangel 1996). Time-limitation, which is expected to result in acceptance of low-quality hosts (Mangel 1989), is also unlikely to explain our results

since 28-20 females lived as long as 20-20 females, and longer than 12-20 females. The relative fitness rule (Giraldeau & Boivin 2008) however helps to explain our results. Warm-developed females were smaller than females from other treatments, emerged with a lower initial egg load and less energetic resources required for egg maturation (Giron & Casas 2003) and foraging activity (Nation 2008). According to the fitness rule, these small females may expect a lower reproductive success than the overall population and should therefore adopt risk-prone behaviours, i.e. oviposition in less suitable hosts. A small female is expected to have a lower fitness than a large female because of lower fecundity and smaller capacity to find and attack hosts. To increase their relative fitness, an optimal decision woud be to parasitize a maximum number of hosts as rapidly as possible, relying on occurrence of a sudden high mortality event, such as a heat wave or a storm.

The lower attack rate of low-quality hosts by females from the 12-20 treatment in comparison to females that developed at higher temperature and foraged at 20°C does not support the alternative prediction that temperature compensation in cold-developed organisms (Wohlschlag 1960; Clarke 1993) should increase risk-prone behaviours. The shorter longevity and handling time we observed for females that developed at low temperature both suggest that metabolic compensation occurs in *A. ervi*, as observed for the closely related species *Aphidius rhopalosiphi* (Le Lann et al. 2011). It is thus unlikely that the pattern observed for 12-20 females resulted from the absence of temperature compensation. If parasitoids assess their expected reproductive success through egg load and life expectancy, the higher initial egg load in females that developed at low

temperature may compensate for the lower life expectancy when foraging at intermediate temperature and may thus influence risk-sensitive decision-making.

Foraging temperature

Developmental temperature clearly influenced oviposition decisions of parasitoids foraging at a common temperature. Foraging temperature also strongly influenced host selection by *A. ervi* females. Parasitoids foraging at high temperature (20-28 and 28-28 treatments) attacked low-quality hosts more frequently than adult females experiencing lower temperature. They attacked N4 aphids at a similar rate and more frequently than in other treatments but 20-28 females were more successful than 28-28 females as they were fast enough to avoid kicks from N4 aphids. Although both foraging at 28C, females from these two treatments experienced different profitability (Barrette et al. 2009) because handling time and oviposition success varied with developmental temperature. These results support the hypothesis that foraging females associate high temperature to short life expectancy and thus low reproductive success, resulting in risk-prone behaviours. Roitberg et al. (1993) observed a similar result in *Leptopilina heterotoma* females which superparasitized more frequently when exposed to a probability of decreased life expectancy, simulated by a rapid drop in atmospheric pressure as observed before a storm.

Aphidius ervi females from the 12-12 treatment rejected hosts very rarely compared to females from all other treatments. Furthermore, the number of misplaced attacks was the highest in the 12-12 treatment. This suggests that an alteration of the host selection

behaviour, including host-instar discrimination, occurred at low temperature, as observed in cold stored *Anaphes victus* females (van Baaren, Outreman & Boivin 2005). Effects of cold temperature on nervous system would explain the acceptance of all aphid nymphal instars by 12-12 females although we cannot reject the hypothesis of a behavioural change with low temperature. Developmental and foraging temperatures may be both involved in this alteration, as we observed an increased number of misplaced attacks in 12-20 and 20-12 treatments.

PerformanceOur experimental design allowed us to test the classical physiological hypothesis that performance is maximal at the temperature at which an organism is acclimated. Our results concur with other studies in which no beneficial effect was associated to acclimation (e.g., Leroi, Bennett & Lenski 1994; Gibert, Huey & Gilchrist 2001), as females from the 12-12 and 28-28 treatments parasitized fewer hosts than females from other treatments. Our results however support the optimal developmental temperature hypothesis (Cohet & David 1978) that states that ectotherms that developed at intermediate temperatures perform well at a wider range of temperatures than individuals developed at extreme temperatures. *Aphidius ervi* females reared at 20°C indeed performed better than females from other treatments, independently of foraging temperature, as observed by Gibert et al. (2001) in *Drosophila melanogaster*.

Conclusion

An increasing number of studies have identified potential consequences of global warming on trophic relationships and the structure and stability of communities. Temporal and spatial species associations between trophic levels may be sensitive to the expected increase in mean temperature and frequency of extreme climatic events (Parmesan 2006). Functional and numerical responses have also been shown to be temperature-dependent (e.g., Sentis et al. 2012) and other behavioural components are should be taken into account when investigating consequences of climate change on interacting species. We present evidence that developmental and foraging temperatures are both involved in host selection and risk-sensitive decision-making in parasitoids. For instance, an increase in developmental and/or foraging temperature resulted in acceptance of less profitable hosts, which could have detrimental consequences on parasitoid populations in natural and managed ecosystems. Our study underlines the necessity to further investigate the influence of temperature on behaviour to understand how organisms and communities will cope with global warming.

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Table 1. Mummification rate, emergence rate and tibia length of female progeny measured on parasitoids from seven thermal treatments where *Aphidius ervi* females were allowed to parasitize 60 *Macrosiphum euphorbiae* aphids of four different instars. Mean ± s.e.

	Host stage			
	N1	N2	N3	N4
Mummification rate	0.05 ± 0.03 a	0.31 ± 0.08 b	0.23 ± 0.06 b	0.08 ± 0.04 a
Emergence rate	0.02 ± 0.01 a	0.27 ± 0.05 b	0.16 ± 0.04 c	0.04 ± 0.02 a
Tibia length of female progeny (mm)	0.51 ± 0.03 a	0.64 ± 0.04 b	0.69 ± 0.05 c	0.56 ± 0.03 d
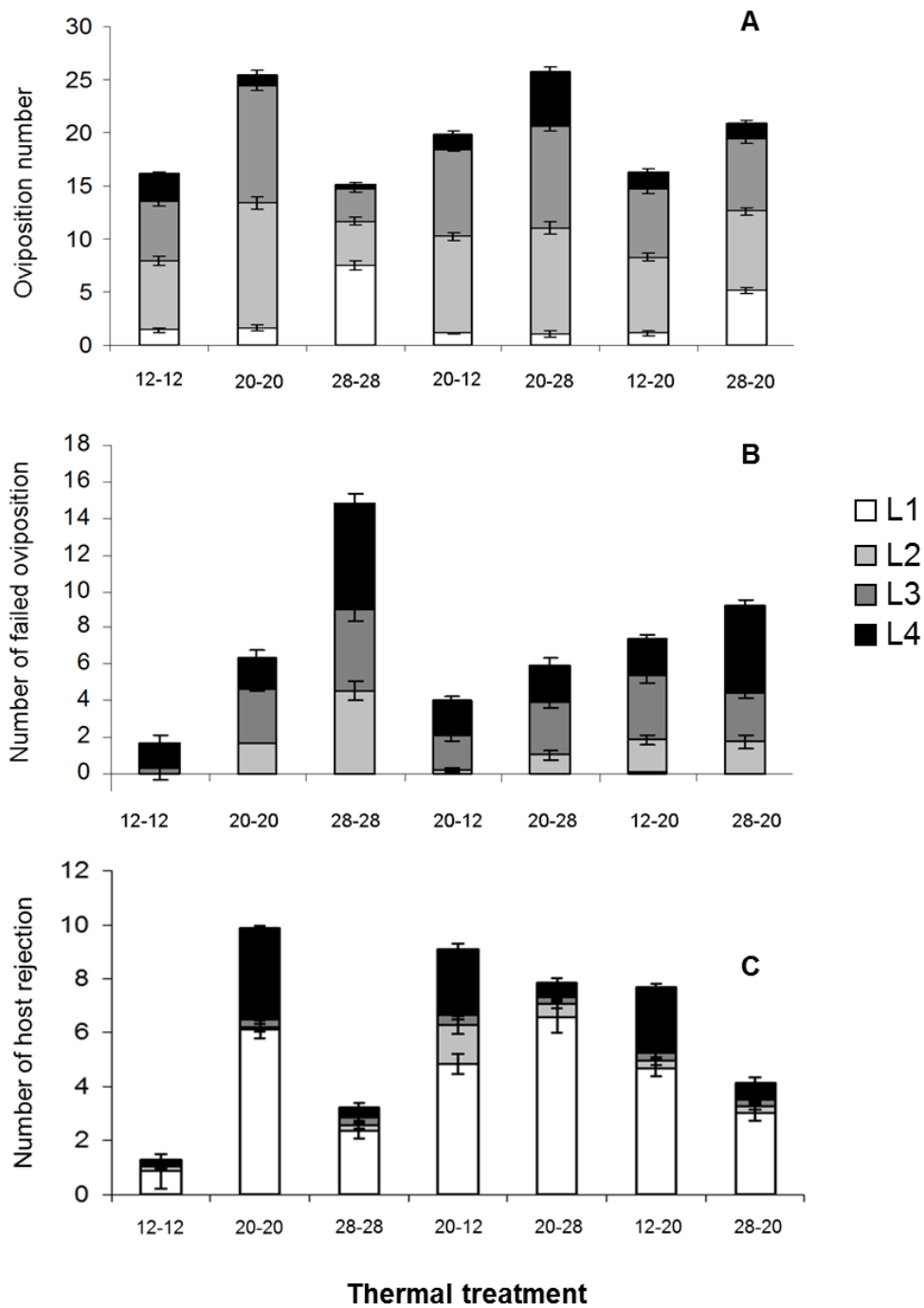
Figure 1. Mean (± s.e) number of (A) successful ovipositions (B), failed ovipositions and (C) host rejections in each of the four nymphal instar of *Macrosiphum euphorbiae* by *Aphidius ervi* females exposed to seven thermal treatments.
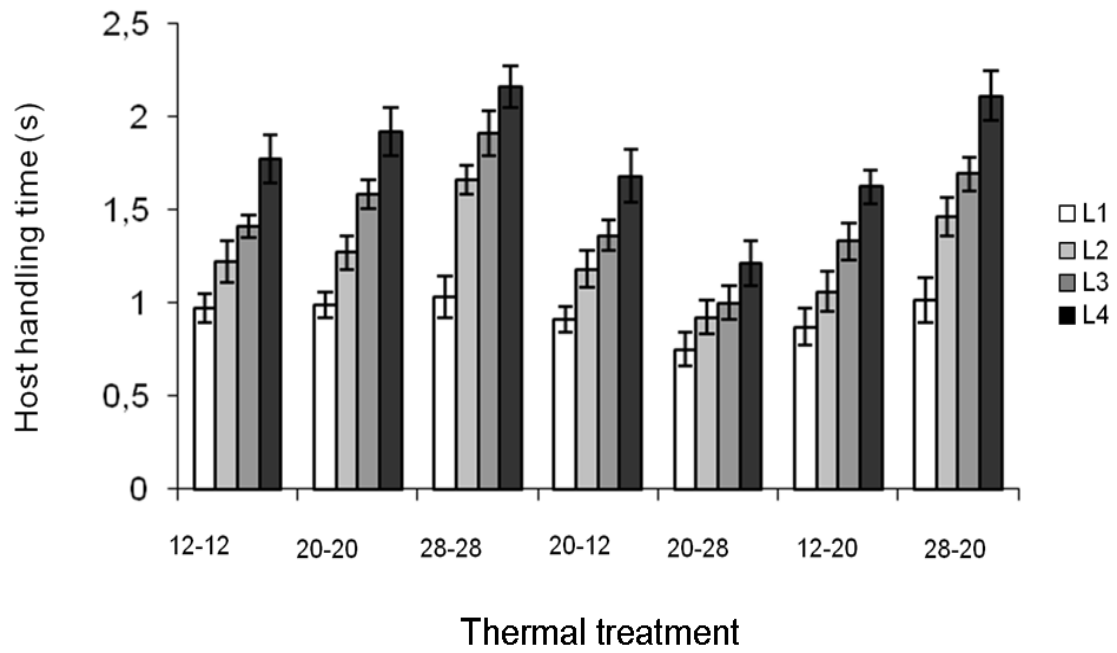
Figure 2. Mean (± s.e) handling time of *Aphidius ervi* females attacking *Macrosiphum euphorbiae* aphid hosts of four different nymphal instars in seven thermal treatments.

Abstract

1. Organisms should adopt risk-prone behaviours when foraging under specific conditions. The relative fitness rule states that females should adopt risk-prone reproduction behaviours when expecting a deficit in reproductive success.

2. Temperature influences the reproductive success of ectotherms by affecting their (i) basal metabolic rate during immature development and egg load at emergence (ii) life expectancy as adult. Temperature should therefore modulate risk-sensitive decision-making of an organism. Using an aphid-parasitoid biological model, we tested under laboratory conditions the following three hypotheses: 1) females foraging at high temperature adopt more risk-prone behaviours than females foraging at lower temperature because of reduced life expectancy; 2) warm-developed females adopt more risk-prone behaviours than females reared at lower temperature because of lower initial egg load; (3) cold-developed females adopt more risk-prone behaviours than females reared at high temperature when foraging at the same temperature because of higher metabolic rate. We considered acceptance of low-quality host nymphal instar by the aphid parasitoid *Aphidius ervi* as a risk-prone behaviour.

3. Immature *A. ervi* females were reared at 12, 20 or 28°C and add access to the four nymphal instars of the potato aphid, *Macrosiphum euphorbiae* for oviposition at one of these temperatures. This protocol allowed the discrimination of the relative role of developmental and foraging temperature on oviposition decision. Host selection behaviour was continuously recorded during the exploitation of an aphid patch.

4. We observed that parasitoids foraging at high temperature attacked low-quality hosts (first and fourth nymphal instars) more frequently than females from other treatments and

that warm-developed females attacked first nymphal instars more frequently than females from other treatments. These results support our hypothesis that a decrease in the expected parasitoid reproductive success, indicated by a lower life expectancy or initial egg load, resulted in risk-prone behaviours. Cold-developed females did not attack non-optimal hosts more frequently than other females. This result does not support the hypothesis that higher metabolic rate results in risk-prone behaviours.

5. To our knowledge, this is the first experimental evidence that temperature influences host stage selection and risk-sensitive making-decision in parasitoids and the first study to support the relative fitness rule.