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Differential thermal performance curves in response to different habitats in the parasitoid *Venturia canescens*

Vincent Foray · Patricia Gibert · Emmanuel Desouhant

Abstract Environmental variability is expected to be important in shaping performance curves, reaction norms of phenotypic traits related to fitness. Models predict that the breadth of performance curves should increase with environmental variability at the expense of maximal performance. In this study, we compared the thermal performance curves of two sympatric populations of the parasitoid *Venturia canescens* that were observed under contrasting thermal regimes in their respective preferred habitats and differing in their modes of reproduction. Our results confirm the large effect of developmental temperature on phenotypic traits of insects and demonstrate that thelytokous and arrhenotokous wasps respond differently to temperature during development, in agreement with model predictions. For traits related to fecundity, thelytokous parasitoids, which usually occur in stable thermal conditions, exhibit specialist performance curves, maximising their reproductive success under a restricted range of temperature. In contrast, arrhenotokous parasitoids, which occur in variable climates, exhibit generalist performance curves, in keeping with the hypothesis "jack of all temperatures, master of none".

Keywords Phenotypic plasticity · Reaction norm · Temperature · Parasitoid · Generalist and specialist strategies · Environmental variability

Introduction

Phenotypic plasticity, the capacity of organisms to produce different phenotypes according to the environment, is well-recognised as a potential response to environmental variability (Chevin et al. 2010; Ernande and Dieckmann 2004; Lind and Johansson 2007; Pigliucci 1996). It is less clear how the reaction norm, the set of phenotypes that an individual or a genotype expresses over an environmental gradient (Woltereck 1909), affects ecological distribution and the coexistence of populations or species (Griffith and Sultan 2006; Sultan 2001). This question is receiving increasing attention in the context of biological invasions, especially in response to global warming (Chevin et al. 2010; Chown et al. 2010; Richards et al. 2006). It is generally assumed that phenotypic plasticity allows for maintenance of fitness-related traits by expressing beneficial phenotypes in a broader range of environments, resulting in a broader ecological niche (Van Tienderen 1991). According to the sensitivity of their fitness-related traits to environmental conditions, organisms may be described as generalists or specialists. Most theoretical and experimental studies on the sensitivity of fitness to environmental conditions or on factors promoting specialist and/or generalist strategies (Gilchrist 1995; Lynch and Gabriel 1987; Moran 1992; Van Tienderen 1991) make the assumption, "jack of all trades, master of none". This

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phrase is intended to mean that the ability to perform in a broad range of environments can be "achieved only at the sacrifice of maximal performance" (Huey and Hertz 1984). Specialist individuals are therefore expected to outperform generalists under a restricted range of environmental conditions, i.e., the optimal conditions, while generalists should be favoured when the environment is variable or unpredictable.

Testing the "jack of all trades, master of none" hypothesis would ideally require a comparison of performances curves, which are a special case of reaction norm for phenotypic traits related to fitness (Angilletta 2009; Huey and Kingsolver 1989; Huey and Stevenson 1979), of generalists and specialists conspecifics. Such curves are generally concave and are characterised by two parameters: a maximum, i.e., the optimal environmental value, at which the individual performance is maximised, and a breadth, which measures the equitability of fitness over the environmental gradient (Lynch and Gabriel 1987). Natural selection shapes the trade-off between maximum and breadth to optimise the inter-environmental fitness, the average fitness over all possible environmental conditions. Under the hypothesis of trade-off between the maximal performance and the breath of the performance curve, optimality models predict the relationship between these parameters and environmental conditions: (1) optimum performance should coincide with the mode of the environmental conditions and (2) breadth should increase with the variability of environmental conditions (Gilchrist 1995; Lynch and Gabriel 1987; Moran 1992). Thus, generalists maintain their fitness in a wide range of environments, while specialists perform well only in their optimal environment, with decreasing performance outside these restricted conditions.

Only a few empirical studies, mainly restricted to plant models, support such a conceptual framework (Griffith and Sultan 2006; Sultan et al. 1998). For instance, in *Polygonum* plants that occur in a habitat with highly variable competition for light, the reaction norm of seed production is more stable than that observed in the less variable habitat (Griffith and Sultan 2006). A study of the performance curves expressed by ectotherms in response to thermal variability represents an opportunity to test whether the hypothesis "jack of all trades, master of none" is corroborated in animals. In ectotherms, environmental temperatures influence the biochemical reactions taking place in the organism, with direct consequences for life history traits (Hochachka and Somero 2002). Several comparative studies show, generally through a latitudinal or altitudinal analysis, a correlation between the optimal thermal value and the mean temperature of the habitat, both at intra- and inter-specific levels (Angilletta 2009 for a review). For example, in the striped marsh frog (*Limnodynastes peronii*), the optimal

temperature for locomotion is lower in cool–temperate populations than in tropical populations (Wilson 2001). However, evidence for population-level divergence in the breadth of thermal performance curves is less common. Recently, Liefting et al. (2009) showed that populations of *Drosophila serrata* from a temperate climate, where temperature is highly variable, exhibit a more stable developmental rate over a thermal gradient than populations from a stable tropical climate. In the same way, an artificial selection experiment on parasitization capacity of *Trichogramma pretiosum* at different temperatures highlighted that the resulting changes in the norm of reaction of parasitization capacity follow the "jack of all trades, master of none" hypothesis (Carrière and Boivin 2001).

In this study, we test whether the breadth of thermal performance curve increases with the environmental variability of thermal conditions in an ectotherm. The ecology of the parasitoid *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) makes it an ideal model to test these predictions. In this species, we found two reproductive modes that undergo contrasting thermal regimes in their respective preferred habitats (Amat et al. 2006; Schneider et al. 2002). Arrhenotokous (called "sexual") wasps live exclusively in natural conditions such as forests and orchards, where temperature varies on a daily and seasonal basis. In contrast, thelytokous ("asexual") wasps occur preferentially in anthropogenic environments (i.e. granaries and mills) characterised by relatively stable and moderate temperatures. Nevertheless, thelytokous and arrhenotokous wasps are sometimes found in sympatry in the field (Amat 2004; Schneider et al. 2002). From a genetical point view, arrhenotokous and thelytokous populations are considered like distinct entities; even if occasional gene flows between both reproductive modes cannot be completely ruled out (Schneider et al. 2002). We predict that arrhenotokous individuals will exhibit stable fitness values irrespective of thermal conditions, while the performance of thelytokous wasps will be negatively affected by low and high thermal conditions. Assuming a trade-off between maximal performance and breadth of the performance curve, thelytokous wasps should outperform arrhenotokous wasps at the intermediate temperature.

The generation of performance curves requires analysis of phenotypic traits relevant to individual fitness (Richards et al. 2006). In parasitoids, traits enhancing oviposition contribute to lifetime reproductive success (Godfray 1994; Wajnberg et al. 2008); we focused on fecundity and longevity to compare the performance of arrhenotokous and thelytokous wasps. Size and developmental rate, usually affected by temperature, were also measured. The suitability of all measured traits as estimators of wasp performance will be discussed.

Materials and methods

Biological material and cultures

V. canescens is a Mediterranean endoparasitoid of lepidopteran larvae, principally Pyralidae (Salt 1976). Hosts are attacked from their second to fifth instar and, as *V. canescens* is a koinobiont parasitoid, continue to grow when parasitised. The larval parasitoid delays its development until the host reaches its final instar (Harvey et al. 1994). *V. canescens* is a "solitary parasitoid", meaning that only one parasitoid larva can develop per host. Several generations occur over the season of activity for adults which extend from May to October. *V. canescens* is also synovigenic, meaning that females emerge with a stock of mature eggs available to be laid; that stock increases during the adult's lifetime as oocytes mature (Jervis et al. 2001). *V. canescens* females produce small and yolk-poor eggs (Le Ralec 1995), but this nutrient deficiency is offset by the egg's ability to absorb nutrients from the host's blood (i.e. hydropic eggs). Egg resorption, whereby some of the nutrients invested in individual eggs are re-allocated to maintenance in some synovigenic parasitoids (Jervis and Kidd 1986; Richard and Casas 2009; Rosenheim et al. 2000), does not occur in this species (Eliopoulos et al. 2003), as is to be expected of an hydropic egg producer (Jervis et al. 2001). Like other hymenopteran species, *V. canescens* has a haplodiploid sex determination system; unfertilised eggs produce haploid males, whereas fertilised eggs produce diploid females. Additionally, two reproductive modes occur in *V. canescens*: arrhenotokous parthenogenesis, in which haploid males are produced from unfertilised eggs, and thelytokous parthenogenesis, in which thelytokous females produce diploid females from unfertilised eggs, leading to the absence of males (Beukeboom et al. 1999). This latter mode is unlikely induced by endosymbiotic bacteria (Mateo Leach et al. 2009; V. Foray, unpublished data).

Thelytokous and arrhenotokous populations used in this experiment were trapped in orchards during the summers of 2006 and 2007, respectively, near Valence (France, North: 44°58′34″, East: 4°55′66″). Since thelytokous wasps thrive in anthropic habitats, some traps were placed at proximity of granaries (Ahmad 1936; Amat 2004). Hosts used for parasitoid development, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), were maintained in the laboratory on wheat semolina. Hosts and parasitoids were reared in a controlled environment: 25 ± 1°C, 70 ± 5% RH and 12:12 (L/D). The experiments were conducted in 2008, and arrhenotokous and thelytokous populations were maintained in the laboratory during about 10 and 25 generations respectively before the experiment.

Experimental design

The experiment was arranged in two steps. First, hosts were parasitised by arrhenotokous or thelytokous *V. canescens* females (henceforth, "mothers") and then placed at three different developmental temperatures. In the second step, we measured phenotypic traits potentially related to fitness in the female *V. canescens* emerging from these hosts (henceforth, "daughters") to plot thermal performance curves for each reproductive modes. Thus, the performance curves corresponded to population reaction norms (for another example, see Liefting and Ellers 2008), rather than to genotype reaction norms.

1. Parasitisation and developmental conditions

   The parasitoid mothers were randomly chosen from rearing boxes. They were isolated at their emergence and put in boxes (300×300×300 mm) with food (honey diluted 1:2 in water on a piece of cotton wool). Each box contained six females of the same reproductive mode; the boxes with arrhenotokous females also contained 12 virgin males of the same age to favour matings. After 24-h, each female was transferred individually to boxes (170×160×60 mm) containing three host patches. The patches consisted of petri dishes (Ø, 52 mm) filled with semolina and containing 25 third-instar *E. kuehniella* larva. To obtain semolina covered by kairomones, which are produced by host mandibular gland secretions, the patches were prepared 1 week before being offered to the parasitoids. These kairomones induce searching behaviour in female parasitoids (Castelo et al. 2003). Each female was free to lay in any of the three patches over the course of 48 h and had access to food. The sex ratio is nearly 1:2 in the arrhenotokous population (Metzger et al. 2008); hence, we used in this experiment twice as arrhenotokous females as thelytokous females (72 and 36 females, respectively) in order to obtain a sufficient and roughly the same number of daughters for the two reproductive modes. Three females died before the end of the 48-h parasitism period (two thelytokous females and one arrhenotokous) and were removed from the dataset.

   The patches with parasitised hosts were then randomly distributed in three identical incubators (LMS-cooled incubator), in which the temperature was regulated at 17°C, 25°C and 30°C (±1°C). In the three incubators, the photoperiod was identical (12:12, D/L), as was relative humidity (range=10–20%, recorded with a data logger (EasyLog USB), data not shown). The patches were inspected every day at 30-min intervals between 8:00 and 11:30 p.m. to collect wasps at their emergence. In total, 228

parasitoid females were collected, representing the two reproductive modes and three developmental conditions, for use in the following analysis.

2. Reaction norms of fitness-related traits to developmental temperature

To assess the impact of developmental temperature on phenotypic traits related to fitness, we performed measurements on the daughters of both reproductive modes. Arrhenotokous males were excluded from the analysis to avoid confounding effects of sex, so comparisons between the two reproductive modes were performed only on females. Each day after emergences, daughters were assigned randomly to two groups. In group 1, we measured fecundity at emergence. In group 2, we measured longevity and maximal egg load. For daughters of the two groups, we also measured developmental rate (i.e. inverse of the development time) and body size. Body size was estimated by the left hind tibia length, using the positive correlation between dry body mass and hind tibia ($r^2=0.72$, $P<0.0001$, data not shown). Left hind tibia was measured after dissection under a microscope with the software Motic Images Plus 2.0.

Wasps assigned to group 1 were frozen individually at $-20°C$ after their emergence. They were then dissected, and mature eggs from the whole egg complement were counted under the microscope to estimate fecundity at emergence. Newly emerged daughters assigned to the second group were placed individually in plastic vials (Ø, 30 mm; h, 70 mm) with a piece of cotton wool soaked with 2 mL of water. They were maintained under controlled conditions at $25\pm1°C$, $70\pm5\%$ RH, 12:12 D/L and kept without host stimulus until their death. The tubes were inspected at 2-h intervals from 8:00 a.m. to 6:00 p.m. in order to record the time of death. When death occurred at night, 1:00 a.m. (the median time between 6:00 p.m. and 8:00 a.m.) was considered the time of death (Desouhant et al. 2005). The time lapse between emergence and death was used as an estimator of longevity. After death, wasps were dissected and mature eggs from the whole egg complement were counted under the microscope. Mature egg load at death was used as an estimator of maximum egg load.

Statistical analyses

Our protocol created non-independent data because a mother wasp could have more than one daughter assigned to the same group. Therefore, statistical analysis were performed with generalised linear models (Nelder and Weddenburn 1972), including a generalised estimat-ing equation (GEE; Liang and Zeger 1986) to deal correctly with the non-independent data. An exchangeable working matrix was applied in the GEE. A gamma distribution (inverse link function) was used to analyse longevity and egg loads was analysed by means of a Poisson distribution (log link function). A Gaussian distribution (identity link function) was used to analyse body size and developmental rate. The two explanatory variables were reproductive mode (qualitative) and develop-mental temperature (quantitative). We also integrated a quadratic effect of developmental temperature to better fit the shape of the performance curve. To remove any effect of animal size from egg load and longevity measurements, tibia length was always introduced as the first explanatory variable (Pelosse et al. 2010). Explanatory variables were selected by backward elimination of nonsignificant effects from the full models using Wald's test (W). All data analyses and graphics were done using R 2.12.1 (R Development Core Team 2010).

Results

As expected, developmental temperature had a major effect on phenotypic traits of *V. canescens* females and some traits exhibited a significant interaction of developmental tem-perature and reproductive mode.

Size and developmental rate

Developmental temperature influenced parasitoid adult size significantly ($W=86.54$, $P<0.0001$) and presented a signif-icant quadratic relation ($W=95.97$, $P<0.0001$). Females that developed at $30°C$ were about 10% smaller than females that developed at the two other temperatures (Fig. 1a). There were no significant differences in size between thelytokous and arrhenotokous females ($W=0.11$, $P=0.74$). Similarly, the interaction between the variables "reproductive mode" and "developmental temperature" was not significant (linear effect, $W=0.03$, $P=0.87$; quadratic effect, $W=0.01$, $P=0.93$). The correlation parameter of the working matrix was significant ($\alpha=0.14$, $P=0.001$), indi-cating that females tend to be more similar in size to their sisters than to unrelated females.

Developmental rate increased significantly with devel-opmental temperature ($W=388.7$, $P<0.0001$; Fig. 1b). The developmental temperature presented a quadratic effect in interaction with the reproductive mode (interac-tion with quadratic effect, $W=8.1$, $P=0.005$), with arrhe-notokous females developing faster at $30°C$ than thelytokous ones (Fig. 1b). The correlation parameter of the working matrix was also positive and significant ($\alpha=0.13$, $P=0.02$)
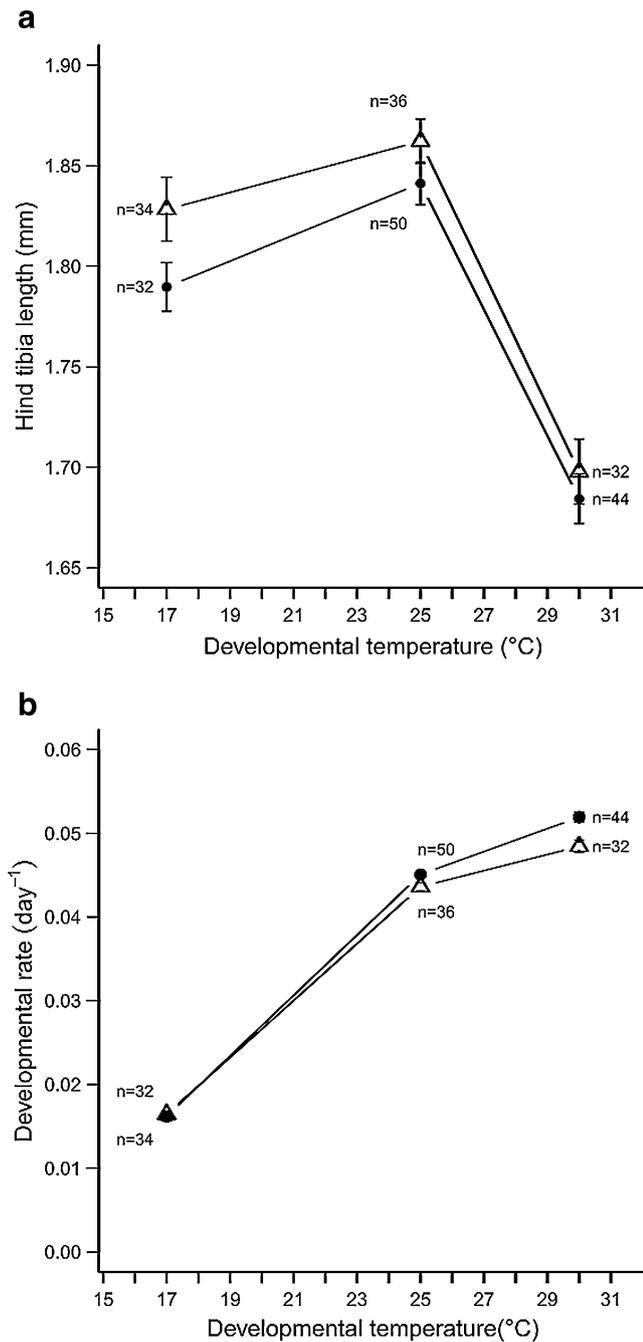
a

b

Fig. 1 Thelytokous (*open triangles*) and arrhenotokous (*filled circles*) females **a** hind tibia length and **b** developmental rate (mean±SE) according to the developmental temperature. Sample size is denoted by "*n*"

Longevity

After we removed the positive effect of body size ($W=7.8$, $P=0.005$), developmental temperature and reproductive mode were shown to have a strong effect on females' longevity ($W=19.32$, $P<0.0001$ and $W=30.7$, $P<0.0001$, respectively). Developmental temperature had a signifi-

cant quadratic effect on females' longevity ($W=12.90$, $P=0.0003$); longevity increased with developmental temperature, but this relationship slowed with increasing temperatures (Fig. 2). The interaction between reproductive mode and developmental temperature was not significant, so parallelism between thelytokous and arrhenotokous reaction norms was not rejected (interaction with linear effect, $W=2.88$, $P=0.09$; interaction with quadratic effect, $W=3.07$, $P=0.08$). At every developmental temperature, arrhenotokous females lived about 20% longer than thelytokous ones (Fig. 2).

Fecundity at emergence and maximum egg load

Parasitoid size influenced positively both fecundity at emergence ($W=8.25$, $P=0.004$) and maximum egg load ($W=8.17$, $P=0.004$). After removing the body size effect, developmental temperature and reproductive mode had an interactive effect on the fecundity of newly emerged females (interaction with linear effect, $W=8$, $P=0.005$ and interaction with quadratic effect, $W=7.2$, $P=0.007$). Thelytokous females reached maximum fecundity when they had developed at 25°C, with, on average, 58 mature eggs at 25°C and only 30 and 26 mature eggs at 17°C and 30°C, respectively. In contrast, the fecundity of arrhenotokous females was relatively stable regardless of temperature treatment, with 30, 38 and 22 mature eggs on average after development at 17°C, 25°C and 30°C, respectively (Fig. 3a).
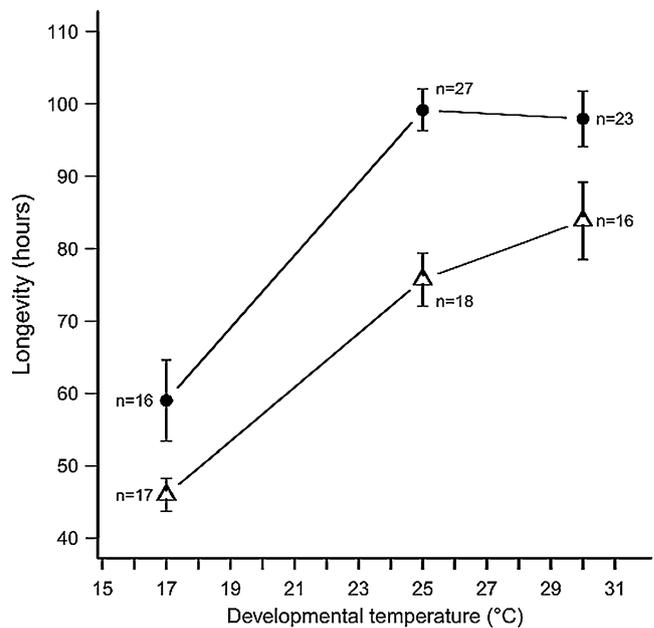

Fig. 2 Longevity of thelytokous (*open triangles*) and arrhenotokous (*filled circles*) females (mean±SE) according to developmental temperature. Effect of body size on longevity is not represented in this figure and does not change the shape of the reaction norms. Sample size is denoted by "*n*"
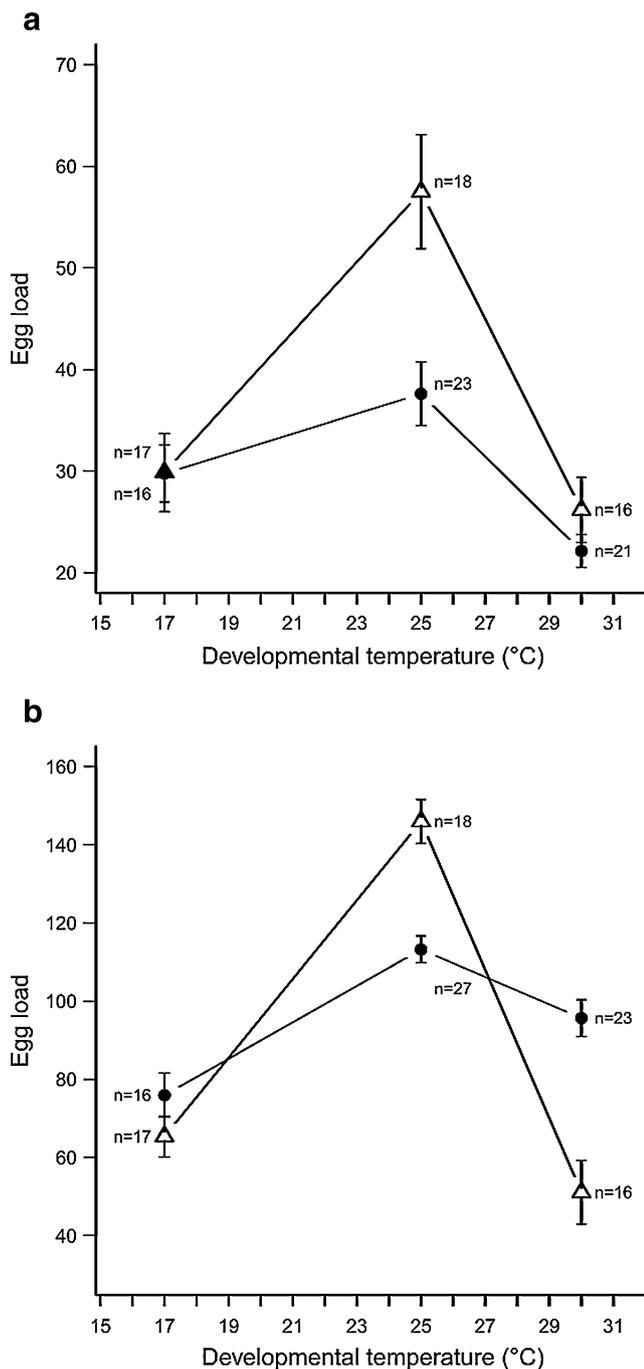
a

b

Fig. 3 Thelytokous (*open triangles*) and arrhenotokous (*filled circles*) females **a** fecundity at emergence and **b** maximum egg load (mean± SE) according to developmental temperature. Effect of body size on egg load is not represented and does not change the shape of the reaction norms. Sample size is denoted by "*n*"

Maximum egg load of wasps showed a similar expression pattern: arrhenotokous and thelytokous females had significantly different reaction norms (interaction with linear effect, $W=43.1$, $P<0.0001$; interaction with quadratic effect, $W=43.7$, $P<0.0001$). Thelytokous females reached maximum fecundity when they developed at 25°C, with an

average of 146 mature eggs at 25°C and only 65 and 51 mature eggs at 17°C and 30°C, respectively. In contrast, variation in maximum egg load of arrhenotokous females over the thermal gradient was slight, with on average 76, 113 and 96 mature eggs at 17°C, 25°C and 30°C, respectively (Fig. 3b).

Discussion

The comparison of the developmental temperature performance curves of conspecific parasitoids from contrasting habitats corroborates the hypothesis "jack of all trades, master of none" for *V. canescens*, and the shape of the performance curve responds to the level of environmental variability. Arrhenotokous female wasps, which undergo natural climatic variations, exhibit a generalist performance curve; thelytokous wasps, which thrive in stable habitats, exhibit a specialist performance curve.

We measured performance using various life history traits expected to be related to fitness. Results concerning developmental rate and traits related to fecundity are in accordance with our predictions and exhibit a significant developmental temperature by reproductive modes interaction. In parasitoids, maximal egg load, i.e. the potential number of eggs available to be laid during a lifetime, is a proxy for the number of offspring. This trait is under selective pressure, as egg load influences reproductive behaviours (Casas et al. 2000; Sirot and Bernstein 1996). When they develop at intermediate temperature (25°C), *V. canescens* thelytokous females have a higher egg load at emergence and death than arrhenotokous ones. This trend is in agreement with results previously found at 25°C in studies conducted in *V. canescens* with both types of reproductive modes maintained the same number of generations in laboratory conditions (Barke et al. 2005; Pelosse et al. 2007), suggesting that it does not result from an adaptation of thelytokous wasps to thermal laboratory conditions. Beyond these restricted environmental conditions (i.e. around 25°C), the pattern changes. At low developmental temperature, there is no difference in egg load; and at high temperature, arrhenotokous females outperform thelytokous ones. In the same token, at high temperature, the developmental rate of arrhenotokous females is faster than that of thelytokous ones, even though they express the same developmental rates when they developped at the two others temperatures. In solitary parasitoids, a faster developmental rate is expected to confer an advantage for the access to hosts (Godfray 1994). This faster developmental rate in arrhenotokous wasps at high temperature could compensate for the absence of difference in egg load at emergence when wasps were reared at 30°C.

Maximum egg load constitutes an estimation of the potential fecundity, allowing the comparison between the two reproductive modes in laboratory conditions, even if lifetime reproductive success of wasps is also affected by other ecological factors such as host and food distribution (Harvey et al. 2001). The number of eggs laid depends also on the longevity of wasps. In many insects, a trade off exists between fecundity (or egg load) and longevity (Roff 1992). For instance, in *Drosophila melanogaster*, reproduction decreases longevity (Sgrô and Partridge 1999). In *V. canescens*, longevity significantly increases with developmental temperature, and arrhenotokous females survive longer than thelytokous ones irrespective of the temperature (Fig. 2). At the temperature at which adult longevity was measured (25°C), arrhenotokous and thelytokous *V canescens* have the same basal metabolic rate (V. Foray, unpublished data), and thus the overall lower longevity of thelytokous females cannot be attributed to a higher metabolic rate relative to arrhenotokous females. Under the conditions of our experiment, fecundity across developmental temperatures is not traded off against a decrease in longevity because the maximum egg load, reached when females developed at 25°C, does not coincide with a lower longevity. The trade-off observed in many insects is due to the allocation of energy to eggs at the expense of longevity. In *V. canescens*, however, eggs are hydropic, and thus inexpensive in terms of energy used in production (Le Ralec 1995). The absence of trade-off in this species reinforces our conclusion drawn from egg load measures: at the boundaries of the temperature range we studied, arrhenotokous females should have greater fecundity than thelytokous females, as they have more eggs and more days to lay them.

Thelytokous and arrhenotokous wasps express similar thermal reaction norms for adult size. The observed patterns according to temperatures tend to follow the "temperature size rule" (Atkinson 1994). As already described in other insect species, the relationship between size and temperature is non-linear, and size tends to reach a maximum and then decrease slowly at upper and lower temperatures (David et al. 1994; Davidowitz and Nijhout 2004; Karan et al. 1999). Our results could be explained by two non-exclusive hypotheses: either these traits are weakly correlated to the fitness of females, or they are under strong constraints. While it is generally assumed a positive correlation between size and fitness in insects (Honek 1993), field studies show that this relationship does not hold in the two parasitoid species *Aphaereta minuta* and *Trichogramma pretosuim* (Kazmer and Luck 1995; Visser 1994). Jointly, numerous studies have demonstrated, notably in *V. canescens*, the important influence of the host quality on parasitoid adult size and developmental time (Harvey and Vet 1997). These results highlight the importance of considering several components of perfor-

mance when testing the model's predictions. It could therefore be interesting to measure other fitness-related traits like larval survival to refine our estimation of the inter-environmental fitness.

The differences in the performance curves of wasps thriving in natural conditions and those living preferentially in anthropic conditions, raise the question of the adaptive value of these differences. In their preferred anthropic habitats, thelytokous wasps face stable thermal conditions, around 25°C, and high density of hosts (Ahmad 1936; Waage 1979). Under these conditions and in accordance with our observations, we expect that natural selection will lead to a specialist performance curve for egg load because this strategy maximises the efficiency of host exploitation. Under natural conditions, daily and seasonal thermal variability over the season of activity (May to October) is high (average temperature per month ranged from 7.4°C to 34.7°C in our field site during the last decade), leading the arrhenotokous females to adopt a generalist strategy; thermal variations over the season does not challenge their reproductive success. In spite of the lack of population replicates, our conclusion converges on those of previous studies conducted with several populations of *V. canescens*. In these works, behavioural (host patch exploitation behaviour, Thiel et al. 2006; information use while foraging, Lucchetta et al. 2007; travel time and flight capacity, Liu et al. 2009a,b) and physiological (egg production, Li et al. 2003) differences between arrhenotokous and thelytokous wasps result from adaptations to host and food distributions in their preferential habitat.

The existence of two strategies also has consequences at the population or community level when both reproductive modes occur in the same natural habitat. Our results suggest that arrhenotokous and thelytokous wasps have different potential thermal niches. This niche partitioning should promote the co-occurrence of the two reproductive modes in natural habitats (Amat 2004; Schneider et al. 2002). While it was established that thelytokous females are stronger competitors in host exploitation than arrhenotokous females (Amat et al. 2009; Lucchetta et al. 2007; Thiel et al. 2006), our study reveals that thermal conditions during development can offset this difference, even accounting for a sex ratio of 0.5 for arrhenotokous wasps. Particularly at high developmental temperatures, arrhenotokous females have a better fecundity than thelytokous ones. During the season of activity, the variations in the thermal conditions of development might alternately favour arrhenotokous and thelytokous individuals, leading to their coexistence in natural habitats by increasing intra-reproductive mode competition and reducing the competition between reproductive modes. These variations should create a storage effect, a fluctuation-dependent mechanism of coexistence (Chesson 2000). Further investigations are

still needed to test whether the differences observed in this study under laboratory conditions are maintained under more relevant ecological conditions; future experiments should account for the fluctuations of the temperature during the development and the simultaneous impacts of several environmental factors.

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