



Colder is better: The differential effects of thermal acclimation on life history parameters in a parasitoid fly



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ABSTRACT

In this article, we assessed the effect of the rearing temperature on life history traits of the poorly known fly *Phasmovora phasmophagae* (Diptera: Tachinidae), a parasitoid of *Agathemera crassa* (Phasmatodea: Agathemeridae) in order to: i) test the effect of ambient temperature on life history traits and ii) assess the potential trade-off between reproduction and survival. Parasitoids were obtained from a population of hosts located in the Andes range of central Chile. Upon emergence from the host parasitoids were randomly allocated to three thermal treatments (15 °C, 22.5 °C and 30 °C) and several life history traits were measured. We recorded higher survival at 15 °C and 22.5 °C and a lower survival at 30 °C. We found differences for both body mass and head width among thermal treatments. In females, body mass was higher at 15 °C than at 30 °C. An effect of breeding temperature and sex was observed only for developmental time. In addition, males reared at different temperatures during the pupal stage and held as adults at 22.5 °C, exhibited no differences in longevity between treatments. A significant effect of temperature on the mass of ovaries and lipid was recorded in females. These patterns suggest a trade-off between reproduction and survival. Overall, data seem to support the “colder is better” hypothesis, because Andean parasitoid *P. phasmophagae* inhabiting and experimentally reared in colder environments have a higher performance in all environments.

1. Introduction

Life-history traits such as survival, growth rate, fecundity, and age at maturity are considered indirect measurements of an organism's fitness in nature (Stearns, 1992; Ricklefs and Wikelski, 2002; Roff, 2002). The variation of these phenotypic traits is mediated by environmental influences such as temperature. Variations in the thermal regime are particularly relevant for ectothermic animals, since temperature has both direct and indirect effects upon physiological and ecological processes. Thermal constraints are particularly important in determining the life history of invertebrates inhabiting seasonal environments, where the animals are periodically exposed to extreme conditions. On the other hand, the classic trade-offs between reproduction and survival constrain the simultaneous evolution of both traits (Stearns, 1992), where allocation to reproduction may compromise future survival (Tallamy and Denno, 1982; Colinet et al., 2007). A measure of the trade-offs between these traits is the allocation to ovarian structure (Price, 1975) and lipid storage, see Zera and Larsen (2001). According to the temperature-size rule (reviewed in

Blanckenhorn et al., 2004 and Scheihing et al., 2011), theoretically, high temperatures increase growth rate and shorten developmental time, favoring smaller body size in adults (Atkinson, 1994; Atkinson and Sibly, 1997; Klapwijk et al., 2010). Alternatively, low temperatures are associated with the development of larger body sizes, which could lead to higher survival (Ellers et al., 1998; Colinet et al., 2007). Particularly in parasitoid insects, body size and developmental time are key components of life history strategies (Colinet et al., 2007). Body size is positively correlated with other traits that affect fitness such as longevity and fecundity (Charnov and Skinner, 1984; Waage and Godfray, 1985; King, 1989). In endoparasitoids, a close relationship with their hosts until the last larval instar depends mainly on the amount of accumulated reserves during this phase (Feener and Brown, 1997; Godfray, 1994).

Regarding the effect of temperature on development, there are alternative hypotheses to explain that the fitness advantage in adults is maximized as a result of development under low (colder is better), intermediate (optimal development) and high temperatures (hotter is better) (Leroi et al., 1994; Atkinson, 1994; Zamudio et al., 1995; Huey

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and Berrigan, 1996). In this context, acclimation is considered a mechanism of physiological adaptation, where adult performance is maximized when individuals develop under the same thermal environment in which juveniles were reared (beneficial acclimation) (Leroi et al., 1994; Zamudio et al., 1995).

Thermal plasticity has rarely been studied during metamorphosis (Stevens, 2004). In insects, immature stages are very sensitive to temperature variations (Steigenga and Fisher, 2009), mainly during the pupae stage, which represents the phase where metamorphosis occurs (Davidowitz et al., 2003). The latter is due to hormonal interactions operating in this stage of development, which can be also altered by changes in temperature (Davidowitz et al., 2003). For instance, Amic et al. (2008) studied the variability in responses to thermal stress in parasitoid wasp (*Aphidius picipes*) by testing the effect of an increasing duration of cold stress, concluding that this regime could result in rapid adaptive changes. Also, Blanford et al. (2003) suggested that fluctuation in ambient temperatures, through its non-linear impact on parasite virulence and host defense, may contribute to the lack of evidence for frequency-dependent selection in natural ecosystems (Thomas and Blanford, 2003). In this study, we assessed the effect of ambient temperature on the life history in an insect of a highly seasonal environment. Since temperature may play an important role on ecological interactions, we were particularly interested in the Andean *Phasmodora phasmophagae* Cortés (1968) (Diptera: Tachinidae), a parasitoid fly of *Agathemera crassa* Blanchard, 1851 (Phasmatodea: Agathemeridae). Specifically, we tested: i) the effect of ambient temperature during the pupal stage and ii) the potential trade-off between reproduction and survival. In this seasonal environment, the climate is dry and warm during summer and cold/snowy during winter. Our natural history observations (Veloso, unpubl. results) revealed that during winter, larvae of the first instar remain in the host and more than 80% of host are parasite. Parasite load ranged from one to more than 20 larvae.

2. Methods

2.1. Rearing of parasitoids

Parasitoids were obtained from a population of hosts located in the Andes range of central Chile (Lagunillas: 33°36' S, 70°17' W; 2300 m a.s.l.). The hosts were taken to the laboratory and maintained in a common garden condition (20 ± 2 °C and natural photoperiod). As parasitoids emerged as a third-instar larvae and immediately became pupae, they were collected from the bottom of the cage by hand and randomly allocated to three thermal treatments, in individual glass containers in thermoregulated chambers (Hi Tech Instrument RGX 250), at 15 °C, 22.5 °C or 30 °C (± 0.5 °C), with $50 \pm 5\%$ relative humidity and a photoperiod LD=12:12. When pupae became adult, they were kept at 22.5 ± 0.5 °C, and under the same conditions of humidity and photoperiod described above. Selected temperatures fall within the range of ambient temperatures observed in the natural environment of the parasitoid (see Kalin-Arroyo et al., 1985).

2.2. Measuring life history traits

The developmental time from pupa to adult was recorded. However, the number of individuals at 30 °C was increased due to the low survival to adult stage, which produced an unbalanced comparison between treatments for other variables. Body mass of all individuals was measured using an electronic analytical balance (PRECISE XB 120 A; ± 0.00005 g) and adult longevity was also recorded. Head width was used as a measure of body size and recorded with a digital caliper (MITUTOYO ± 0.005 mm). Dry mass of ovaries were used as a measure of fertility (Price, 1975). Females were sacrificed one day after emergence as an adult, time required for maturation of ovarioles and to avoid eggs in the oviduct. Abdominal dissection was performed to obtain ovaries and oviduct, dried at 60 °C to constant mass and weighed using an electronic analytical balance (± 0.00005 g).

Mass of body fat is considered a measure of energy reserves, and therefore is used as a proxy of maintenance and survival (Colinet et al., 2007; Zera and Larsen, 2001). Female bodies used for the extraction of ovaries, were milled and the powder was stored in packages of filter paper and dried at 60 °C to constant mass. Total lipids were extracted by a Soxhlet system with petroleum ether as solvent. Final mass was calculated as the difference between the initial and the final mass of the filter paper, weighed using an electronic analytical balance (± 0.00005 g).

2.3. Statistical analyses

To determine the effect of temperature on pupal stage survival, a nonparametric chi-square (X^2) test was performed. We used two-way ANOVA to analyze the effect of temperature treatment and sex, on the duration of the pupal stage and adult body mass. We used a one-way ANOVA to assess the survival of adult males. Changes in ovarian mass and lipid reserves were tested by ANCOVA using body mass as a covariate. The *post-hoc* Tukey's test was also used (Zar, 1996). All analyzes were performed using STATISTICA 7.0.

3. Results

A significant effect of breeding temperature on survival was observed ($X^2 = 65.7$, $df = 2$; $p < 0.001$). Indeed, we recorded higher survival at 15 °C (94.1%, $n = 68$) and 22.5 °C (92.6%, $n = 68$), and lower survival at 30 °C (48.4%, $n = 128$). Differences for both body mass and head width among thermal treatments (Tables 1, 2) were found. Also, differences between sexes were observed for body mass. In females, indeed, differences at 15 °C and 30 °C were observed, whereas in males, head width was different only at 30 °C (Tables 1, 2). In addition, an effect of breeding temperature and sex was observed only for developmental time (Tables 1, 2). For longevity, it was observed that males reared at different temperatures during the pupal stage and held as adults at 22.5 °C, exhibited no significant differences among treatments (Table 1).

On the other hand, a significant effect of temperature on the mass of ovaries was recorded (Tables 1, 2). The highest values were in females reared at 15 °C and 22.5 °C, and the lowest values in females reared at 30 °C. Also a significant effect of breeding temperature on the mass of lipid in females was recorded (Tables 1, 2). The largest reserves of lipids accumulate at 15 °C and 30 °C, whilst at 22.5 °C lipid accumulation was significantly lower.

4. Discussion

Temperature can cause variation in annual survival rate and fecundity, leading to a negative correlation between survival rate and fecundity among populations in different thermal environments (Adolph and Porter, 1993; Zippay and Helmuth, 2012). In this context, Thomas and Blanford (2003) reviewed the thermal effect on insect-parasite ecological interactions. They reported a range of possible influences of temperature on these interactions, including effects on latent periods of infection, expression of latent disease, parasite mortality, replication and virulence, as well as host resistance. Interestingly, they observed that most studies reveal non linear effects in line with an interaction between host and pathogen thermal sensitivity. In addition, ambient temperature variability can result in noticeably different effects from those predicted under constant temperatures (Bozinovic et al., 2013a, 2013b; Klapwijk et al., 2010). In this study, independently of thermal treatments, and contrarily to previous reports (Cortés, 1968), we observed sexual dimorphism in body size with larger females. In addition, females but not males, exhibit the largest mass at 15 °C, indicating an effect of temperature. A similar pattern was observed in developmental time in both sexes, being negatively associated with ambient temperature (Karan et al., 1998; Folguera et al., 2007; Colinet et al., 2007), which supports the "temperature-size rule" (Atkinson, 1994; Atkinson and Sibly, 1997). This rule proposes that low temperatures induce slower developmental time and larger body sizes. Nevertheless, in

Table 1

Results after a one and two-way ANOVA as well as an ANCOVA test for morphological and life history traits of *Phasmovora phasmophagae*. SS: sum of the square; MS: mean square.

Trait	Source	SS	df	MS	F	p
Body mass	Sex	0.006463	1	0.006463	466.970	< 0.001
	Temperature	0.000134	2	0.000067	4.842	0.008
	Sex*temperature	0.000119	2	0.000059	4.294	0.015
	Error	0.002533	183	0.000014		
Head width	Body mass (covariate)	1.63467	1	1.63467	224.543	< 0.001
	Sex	0.00047	1	0.00047	0.065	0.799
	Temperature	0.31744	2	0.15872	21.802	< 0.001
	Sex*temperature	0.02750	2	0.01375	1.889	0.154
	Error	1.131768	181	0.00728		
Development time	Sex	56.8	1	56.8	26.61	< 0.001
	Temperature	33,655.4	2	16,827.7	7880.83	< 0.001
	Sex*temperature	6.4	2	3.2	1.50	0.226
	Error	390.8	183	2.1		
Male longevity	Temperature	0.47	2	0.238	0.296	0.744
	Error	58.6	73	0.803		
Ovaries mass	Body mass (covariate)	0.000002	1	0.000002	26.22818	< 0.001
	Temperature	0.000002	2	0.000001	10.24540	< 0.001
	Error	0.000006	77	0.000001		
Female lipid reserves	Body mass (covariate)	0.000004	1	0.000004	3.140	0.081
	Temperature	0.000019	2	0.000009	7.989	< 0.001
	Error	0.000081	69	0.000001		

Table 2

Morphological and life history traits of *Phasmovora phasmophagae* at different thermal treatments. Values are mean ± SE. Different letters associated with temperature and sex means indicate significant differences (p < 0.05) as indicated by Tukey *post-hoc* comparisons when the ANOVAs are significant.

Trait	Thermal treatments (°C)		
	15	22.5	30
Sample size (males/females)	36/28	30/33	37/25
Body mass (g)			
Females	0.0286 ± 0.0005 ^a	0.0261 ± 0.0009 ^{ab}	0.0249 ± 0.0010 ^b
Males	0.0150 ± 0.0003 ^c	0.0140 ± 0.0005 ^c	0.0152 ± 0.0004 ^c
Head width (mm)			
Females	2.51 ± 0.02 ^a	2.46 ± 0.03 ^a	2.66 ± 0.02 ^a
Males	2.13 ± 0.01 ^b	2.17 ± 0.03 ^b	2.25 ± 0.02 ^c
Development time (days)			
Females	43.9 ± 0.4 ^a	18.3 ± 0.1 ^b	12.6 ± 0.1 ^c
Males	42.4 ± 0.3 ^a	17.2 ± 0.2 ^b	12.0 ± 0.1 ^c
Male longevity (days)			
Sample size	32	29	15
	3.59 ± 0.16	3.75 ± 0.12	3.6 ± 0.3
Ovaries mass (mg)			
Sample size	28	32	21
	0.0011 ± 0.00004 ^a	0.001 ± 0.00006 ^a	0.0006 ± 0.00008 ^b
Female lipid reserves (mg)			
Sample size	28	28	17
	0.0079 ± 0.0001 ^a	0.0067 ± 0.0002 ^b	0.0076 ± 0.0003 ^a

our case this response seems to be associated with sex. On the other hand, no effect of temperature on longevity was observed. However, data of the percentage of emergence to adults indicate that 30 °C seems to be close to the upper tolerance limit in this species, because less than 50% individuals reared at this temperature survived. Alternatively, almost 100% of individuals emerged to adults at 15 °C and 22.5 °C. Thus, this species exhibits an increase in performance with a decrease in temperature, which

seems to support the hypothesis “colder is better” (Atkinson and Sibly, 1997).

Phasmovora phasmophagae seems to exhibit a pro-ovigenic reproductive strategy (Jervis et al., 2008). Thus, the reproductive allocation should be determined during its pre-adult development, consequently potential fecundity appears as an environmental-dependent physiological response during the pupal stage. Here we found that adult females of *P. phasmophagae* showed highest values of ovarian mass at 15 °C, in comparison to 30 °C. On the other hand, regarding a trade-off between reproduction and storage (Stearns, 1992; Ellers and Van Alphen, 1997; Ellers et al., 2000; Jervis et al., 2003; Colinet et al., 2007), we observed that low temperatures allow this species to perform better in reproduction and survival. Thus, ambient temperature during pupae development seems to affect the variability in the trade-off between these traits. Indeed, allocation to ovary mass may have a cost on storage for future maintenance. Nevertheless, a decrease in temperature during development increases fitness as a consequence of a higher allocation to energy storage, again supporting the “colder is better” hypothesis (Leroi et al., 1994; Atkinson, 1994; Zamudio et al., 1995; Huey and Berrigan, 1996).

Climatic changes are likely to result in substantial alterations of the distribution and population of vectors of insect-borne pathogens. Specifically, description of the effect of temperature shifts on the life history traits, and trade-offs of vectors is needed to define how such temperature changes could impact the epidemiological patterns of vector-borne diseases, as well as biodiversity patterns. For instance, Ciota et al. (2014) studied the effect of temperature on developmental time, immature survival, adult survival, size, blood feeding, and fecundity of populations of *Culex* mosquitoes. They demonstrated that temperature affects all life-history traits, yet also that the extent of this effect is at times incongruent among temperatures. Furthermore, Kuo et al. (2006) tested the effect of temperature on life history traits of *Rhopalosiphum maidis*. These leaf aphids showed population growth adapted to a wider range of high temperatures in warm regions. Also, Foray et al. (2011) compared the thermal performance curves of two sympatric populations of the parasitoid *Venturia canescens*, recorded under contrasting thermal regimes in their habitats and differing in their modes of reproduction. These authors observed an important effect of developmental temperature, demonstrating that thelytokous and arrhenotokous wasps respond differently to temperature during development. In addition to traits related to fecundity, thelytokous parasitoids, which inhabit stable thermal environments,

exhibit specialist performance curves, maximizing their reproductive success under a restricted range of temperatures. In contrast, arrhenotokous parasitoids, which inhabit variable climates, exhibit generalist performance curves. These examples indicate that acclimation to varying thermal environments depends on the temporal pattern of environmental changes, and the physiological tolerance and capacities of species and populations. Nevertheless, it is important to recognize the potential impacts changes in thermal variation on a scale that pertains directly to organisms (Blanford et al., 2003; Bozinovic et al., 2011, 2013a; Clavijo-Baquet et al., 2014; Estay et al., 2014). Indeed Carrington et al. (2013) showed that fluctuating temperature can alter *Aedes aegypti* vector competence for dengue viruses, as well as many life-history traits. Thus, new experiments that assess not only the effect of average values of environmental variables, as we did here, but also the effect of actual environmental variation in physiological traits, are important for inferring ecological responses, especially in extreme environments. Indeed, the geographic region, as well as intra and inter-population habitat specific differences, must be taken into account when testing the effect of temperature on insect populations (Robinet and Roques, 2010).

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