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Joffrey Moiroux, Guy Boivin, Jacques Brodeur. Ovigeny index increases with temperature in an aphid parasitoid: Is early reproduction better when it is hot?. Journal of Insect Physiology, 2018, 109, pp.157-162. 10.1016/j.jinsphys.2018.06.001 . hal-02020945

HAL Id: hal-02020945

<https://univ-avignon.hal.science/hal-02020945>

Submitted on 15 Feb 2019

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Ovigeny index increases with temperature in an aphid parasitoid: is early reproduction better when it is hot?

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Conflicts of interest: none

Abstract. Studying relative investment of resources towards early and delayed reproduction is central to understand life history evolution since these traits are generally negatively correlated and traded-off against several other fitness components. For this purpose, ovigeny index (OI), which is calculated as the fraction of the maximum potential lifetime egg complement that is mature upon female emergence, has been developed in insects. Despite the central role of temperature on life history evolution in ectotherms, its influence on ovigeny index has never been tested. Adaptive models imply that OI should increase with temperature because of changes in body size, but the same influence may be expected considering physiological effects of temperature on egg maturation rate or amount of energy available. We investigated in the aphid parasitoid *Aphidius ervi* the influence of temperature experienced by the immature and/or the adult (from 12°C to 28°C) on ovigeny index and oviposition behaviour. As predicted, OI increased between 16 and 28°C, i.e. females were able to reproduce earlier as temperature increased but this was traded off against a lower delayed reproduction. The highest OI was however observed at 12°, probably because this temperature was too low for females to mature eggs. Females that developed at 20°C and were transferred as adult at 24°C and 28°C had the highest ovigeny index and laid more eggs during the early oviposition period while those transferred at 16°C laid more eggs at the end of their life. Our results suggest that ovigeny index is not only influenced by body size –i.e. the adaptive explanation- but also by adult egg maturation rate, lifespan or amount of energy available –i.e. a physiological and adaptive explanation.

Keywords. *Aphidius ervi*; fecundity; life history; oviposition behaviour; synovigeny; trade-off.

Highlights

- Ovigeny index (OI) has been developed to study timing of reproduction in insects.
- OI = ratio of the mature egg load upon emergence to the lifetime fecundity.
- We investigated the influence of temperature on OI in an aphid parasitoid.
- OI increased with temperature between 16 and 28°C but was the highest at 12°C.
- OI thermal variations were the consequence of physiological and adaptive changes.

Introduction

Life history theory aims at understanding how natural selection and other evolutionary forces shape organisms in the face of their environment (Roff 1992, Stearns 1992). This theory is based on the study of fitness components, so-called life history traits, such as age at maturity, number and size of offspring, progeny sex ratio or lifespan, that are assumed to be optimised in a given environment (Roff 2002). Among those traits, early reproduction is central since it is generally traded-off against several other fitness components such as future reproduction (e.g. Desouhant et al. 2005, Harshman and Zera 2007, Stearns 1989), survival (Jervis et al. 2007, Papaj 2000), or mobility (Papaj 2000), because of limited resources (de Jong and van Noordwijk 1992). Investigating environmental and intrinsic factors that constrain timing of reproduction is thus crucial to understand how species evolved and to help make prediction on potential evolution in a changing world.

Different approaches have been developed to investigate reproductive strategy. For oviparous insects which are able to mature eggs during their development and/or during adult life, Jervis et al (2001) proposed an ovigeny index which is calculated as “the fraction of the maximum potential lifetime egg complement that is mature upon female emergence into the environment”. An ovigeny index of 1 indicates that all eggs are mature upon emergence, such organisms being called pro-ovigenic, while an index of 0 applies to females that emerge with no mature oocytes. A continuum exists between these two extremes, and females that produce eggs during their reproductive life are called synovigenic; although this term may sometimes refer only to females with an ovigeny index of 0, females with an index between 0 and 1 being considered as “partly synovigenic”. This ovigeny index has been first proposed to investigate the diversity of egg maturation strategies found in insects (Jervis et al. 2001). It offers the benefit of linking resource capital (i.e. larval resources carried-over to adult), income (through adult feeding) and

expenditure (i.e. egg production and somatic maintenance) (Jervis et al. 2003). Several studies showed that such an index is an interesting tool to study life history evolution since it is related with other biological characteristics such as lifespan (Jervis et al. 2007), female mobility or degree of polyandry (Jervis et al. 2005). When considering egg maturation strategy as a keystone in life history evolution, parasitoids -i.e. insects that lay their eggs on or in the bodies of other insects, the larva feeding on its host and eventually killing it (Godfray 1994) - are very interesting as they are generally unable to synthesise lipids as adults (Visser et al. 2010). Resources used for early reproduction will thus never be regained for delayed reproduction or for other traits.

Temperature is considered to play a central role in life history evolution in insects (e.g. Abram et al. 2016 a, Angilletta et al. 2002, Chown and Terblanche 2006), including timing of reproduction. Ismail *et al.* (2012) observed for example that cold storage resulted in a higher early fecundity in the parasitoid *Aphidius ervi*, but those females were exposed to stressful temperatures which may be quite different from field temperatures. To the best of our knowledge, influence of non-stressful temperatures on ovigeny index has never been tested in insects, although temperature-dependent egg maturation received some attention in Lepidoptera (Berger et al. 2008). Non-stressful temperatures may have several influences on parasitoid reproduction strategy. First, higher egg maturation rate may occur because of higher metabolic rate with increasing temperature (Berger et al. 2008, Brown et al. 2004, Moiroux et al. 2012). Second, such influence of temperature on insect physiology implies that more energy is needed to sustain metabolism (Brown et al. 2004); the amount of energy available for delayed reproduction would thus decrease and the ovigeny index increase. Third, lifespan is known to commonly decrease as temperature increases because of higher metabolic rate (Brown et al. 2004, Nylin and Gotthard 1998). Organisms should thus invest more resources in early

reproduction at high temperature to lay eggs before reaching average lifespan (Olsen et al. 2004). Finally, body size, which generally decreases with increasing developmental temperature in arthropods (Atkinson 1994), may influence ovigeny index. Ellers and Jervis (2003) proposed theoretical models to link ovigeny index with body size. Although initial egg load and lifetime potential fecundity typically increase with body size, ovigeny index is expected to decrease with increasing body size as a result of a lower relative increase in initial egg load compared to the relative increase in the maximum potential complement of eggs (Ellers and Jervis 2003). The adaptive explanation, proposed by these authors, is that small, short-lived females perceive the environment as more stochastic than large, longe-lived females because they sample fewer host patches. In a stochastic environment, individuals should allocate a larger proportion of resources to initial egg load (Ellers et al. 2000), small females should thus allocate a larger portion of resources to initial egg load than large females. Thorne et al. (2006) confirmed this negative relationship between body size and ovigeny index in the *Drosophila* parasitoid *Aphaereta genevensis*, considering intraspecific variability in body size, while Fischbein et al. (2013) found a constant relationship between these two traits in the woodwasp parasitoid *Ibalia leucospoides*.

Based on direct physiological influence of temperature on egg maturation rate or resources available and on indirect influence through changes in lifespan or body size, small-warm developed females living at high temperature should be more pro-ovigenic and reproduce earlier than females that developed and live at lower temperature. We tested this prediction by investigating the influence of developmental and adult temperature on ovigeny index and oviposition behaviour in a synovigenic parasitic wasp, the aphid parasitoid *Aphidius ervi* (Sequeira and Mackauer 1994), which is known to be unable to synthesize lipids as adult (Visser et al. 2010). We measured the influence of temperature on ovigeny index and oviposition

behaviour in *A. ervi* by rearing females at five temperatures, from 12°C to 28°C, during their entire life. We also distinguished the effects of developmental temperature and adult temperature by transferring females that developed at optimal temperature (20°C) to different temperatures. Such protocol would help to understand if ovigeny index and oviposition behaviour are mainly determined by body size or metabolic rate. If body size alone explains changes in ovigeny index, we should observe no difference between transferred females. Any change in oviposition behaviour and ovigeny index would thus result from a change in egg maturation rate and/or resources available and/or lifespan, which are all dependent on metabolic rate (Berger et al. 2008, Brown et al. 2004). Such study should help to predict how climate change (IPCC 2014) may influence parasitoid and aphid population dynamics, and may be useful to develop better conditions for mass-rearing parasitoids commonly used for biological control (Boivin et al. 2012).

Material & Methods

Insect colonies. *Aphidius ervi* is a solitary koinobiont parasitoid that attacks several aphid species. Our colony was established with individuals bought from BioBest Canada Company (Leamington, Canada). Parasitoids were reared in cages on the potato aphid *Macrosiphum euphorbiae* at $20\pm1^{\circ}\text{C}$, $60\pm10\%$ RH, 16L: 8D photoperiod. The aphid colony was initiated with individuals collected from potato fields near Québec City, Canada, and maintained on potato plants, *Solanum tuberum*, cultivar “Norland” under the same conditions.

Ovigeny index.

General procedure and preliminary experiment on lifespan. Ovigeny index is defined as the initial egg load divided by potential lifetime fecundity (Jervis *et al.* 2001). Since these two variables cannot be measured on a given individual, it is necessary to pair different females to calculate the index. In our experiment, we paired sisters to reduce genetic variability between individuals used for calculation of ovigeny index. Moreover, only paired sisters that had similar tibia length were used for calculation (Thorne *et al.* 2006). Initial egg load can be measured by dissecting females at emergence while estimation of potential lifetime fecundity requires an experimental design in which females can mature eggs throughout their life, providing them oviposition opportunities (Vayssade *et al.* 2012). To estimate the influence of non-stressful temperatures on potential lifetime fecundity, *A. ervi* females were reared at different temperatures, were offered aphids at one third (early oviposition) and two third (late oviposition) of their average lifespan, and were dissected one day before average lifespan. Since longevity changes with temperature in most ectotherms (e.g. Atkinson 1994, Colinet *et al.*

2007), we first calculated average lifespan of *A. ervi* at the five tested temperatures. Parasitoids were randomly collected from our laboratory colony and females were allowed to parasitise 25 second instar aphids in a Petri dish (Ø90 mm) at 20±1°C. Those parasitised aphids were reared on potato plants at 12, 16, 20, 24 or 28±1°C until mummification. This thermal range was chosen as it corresponds to the linear part of *Aphidius ervi* thermal curve for locomotor activity (Gilchrist 1996) and mainly for development time, although 28°C was a suboptimally high temperature for this parameter (Moiroux et al., unpublished data). Mummies were then individually placed in gelatine capsules until parasitoid emergence, which was observed twice daily (at 8:00 and 18:00). Thirty emerging females per temperature were placed separately in a Petri dish (Ø90 mm) containing moistened cotton and honey with a male. They were reared at their developmental temperature and mortality was checked twice daily (at 8:00 and 18:00). Females' average lifespan was next used to determine ages of early and late oviposition and age of dissection at the five temperatures (Table 1).

Initial egg load, potential lifetime fecundity and ovigeny index: influence of developmental and adult temperature. Parasitoids were randomly collected from the colony and fifteen couples were each placed for a day with 60 second instar aphids in a Petri dish (Ø90 mm) at 20±1°C. Parasitised aphids from a cohort were divided into 4 groups of 10 aphids that were reared on potato plants at 12, 16, 20, 24 or 28±1°C, respectively. The remaining 10 aphids were reared at 20±1°C for a second experiment. This experimental design allowed allocating sisters among temperatures in order to avoid lineage effect. Once parasitised aphids turned into mummies, they were placed individually in gelatine capsules until parasitoid emergence, which was observed every two hours from 07:30 to 18:30, aphid parasitoids rarely emerging at night. At emergence, two females per mother (i.e., 30 females per temperature) were frozen and their

hind tibia length measured under a stereomicroscope using PixeLINK® μScope Microscopy Software (Ottawa, Canada). To measure initial egg load, these females were next placed in a drop of Ringer's solution on a microscope slide and dissected under a stereomicroscope to count the number of mature eggs, which were distinguished from immature ones by their shell-like chorion and their lemon-shaped size (Völkl and Stadler 1991). To measure potential lifetime fecundity, the remaining females were placed in a Petri dish (Ø90 mm) containing moistened cotton and honey together with a male from the same thermal treatment until they reached one third of their average lifespan. Females were then allowed to parasitise 60 second-instar aphids placed on a potato leaf in a Petri dish for 4 hours at 20°C. Those aphids were then reared at $20\pm1^\circ\text{C}$ until mummification. The number of mummies was divided by an average mummification rate measured at 20°C (i.e. 0.765, J. Moiroux, unpublished data) to evaluate the number of eggs laid by parasitoids. After this early oviposition period, *A. ervi* females were once again isolated with a male at their developmental temperature until they reached two third of their average lifespan, and the same oviposition procedure was conducted. Parasitoids were thus offered 120 aphids throughout their lifetime, which is closed to the maximum lifetime fecundity measured by Ismail *et al.* (2012) in this species. After this late oviposition, females were kept at their developmental temperature with a male in a Petri dish containing moistened cotton and honey until they reached one day before average lifespan. Females were then frozen and their tibia and the number of mature eggs in their ovaries were measured as described above. The number of eggs laid during early and late oviposition was added to the egg load measured in ovaries to calculate the potential lifetime fecundity of each female. An ovigeny index was next calculated by dividing initial egg load by the potential lifetime fecundity of a sister with a similar tibia length.

Potential lifetime fecundity and ovigeny index: influence of adult temperature. To discriminate between the influence of temperature encountered during the entire life vs. adult life, parasitoid females emerging from the 10 remaining aphids reared at 20°C in the previous experiment were placed following emergence at 12, 16, 24 or 28±1°C. The same procedure as the one described above was performed to calculate potential lifetime fecundity and ovigeny index. Ages of early and late oviposition and age at dissection were the same than for individuals tested in the previous experiment at a given temperature.

Statistical analyses. We used the survival package provided by R software to test for differences in longevity between the five thermal treatments, using a Weibull distribution.

The effect of developmental temperature on body size of parasitoid females was analysed with an ANOVA, as data were normally distributed. We compared initial egg load using a Generalised Linear Model (GLM) with temperature as fixed factor and tibia length as a covariate, considering a Poisson distribution of errors. GLMs were also used to compare the number of eggs laid at early and late oviposition periods, the number of eggs counted in ovaries at the end of life, and the lifetime potential fecundity using thermal treatment as fixed factor and tibia length as a covariate. Females tested in the first and second experiment were treated altogether in these analyses, to compare the influence of temperature on reproductive parameters during the whole life vs. adult life. Ovigeny index was compared using an ANCOVA with temperature as fixed factor and average tibia length of paired sisters as a covariate. We used the multcomp package, available in R software, to perform post hoc tests following a GLM. All statistical analyses were carried out using R software version 2.14.1 (R Development Core Team, 2011).

Results

Parasitoid longevity significantly decreased as temperature increased (Survival analysis, $\chi^2 = 41.36$, $p < 0.001$; Table 1). Female ages of early and late oviposition and age of dissection deduced from longevity measures are presented in Table 1 for the five temperatures.

Developmental temperature significantly influenced *A. ervi* female body size (ANOVA, $F = 675.5$, $p < 0.001$); tibia length decreased with increasing temperature (Table 2). Body size differed between treatments, except for females that developed at 16°C which were similar in size to females that developed at 12 and 20°C.

Initial egg load was significantly influenced by the interaction between developmental temperature and body size (GLM, $\chi^2 = 10.27$, $p = 0.021$), body size (GLM, $\chi^2 = 21.04$, $p < 0.001$), but not by temperature alone (GLM, $\chi^2 = 0.027$, $p = 0.412$). Small warm-developed females (i.e. 24 and 28°C treatments) emerged with more eggs – relatively to their body size – than larger females, while no significant difference was observed between females that developed at 12, 16 and 20°C (Table 2).

Number of eggs laid during early and late oviposition, egg load measured one day before average lifespan, and lifetime fecundity were significantly influenced by thermal treatments, body size and the interaction between thermal treatment and body size (Table 3). The number of eggs laid during early oviposition increased with temperature experienced during immature and adult phases and with decreasing body size, while the number of eggs laid during the last oviposition period was the lowest at 12°C-developed females, the highest at 16- and 20°C-developed females and intermediary at 24- and 28°C-developed females. Egg load measured at the end of life and lifetime fecundity decreased as immature and adult temperature increased and as body size decreased between 16 and 28°C, but the lowest values were detected at 12°C. Those relationships were observed considering both temperature alone and the interaction

between temperature and body size. We did not observe any significant differences between females from experiment 1 which experienced different temperatures during their lifetime, and females from experiment 2 which experienced different temperatures only as adults, except for the number of eggs counted at the end of life which was higher in females that developed at 20 °C and were transferred at 12, 24 and 28°C than females that respectively developed and were reared as adults at 12, 24 and 28°C (Figure 1).

Ovigeny index was significantly influenced by thermal treatments (ANCOVA, $F = 18.77$, $p = 0.003$), body size (ANCOVA, $F = 36.04$, $p < 0.001$) and the interaction between these two variables (ANCOVA, $F = 41.30$, $p < 0.001$). It increased between 16 and 28°C, but was the highest at 12°C (Figure 2). We observed linear negative relationships between body size and ovigeny index for each temperature, except at 12°C. The intercept of the model temperature*body size was significantly higher at 28 and 24°C than at 20 and 16°C. Females that developed at 20°C and next transferred at 12, 24 or 28°C had respectively a lower ovigeny index than females kept at 12, 24 or 28°C for their whole life, while no difference was observed between females kept at 16°C and those transferred from 20 to 16°C (Figure 3).

Discussion

We investigated in an aphid parasitoid the influence of non-stressful temperature experienced by the immature and the adult on ovigeny index and oviposition behaviour. We considered a thermal range which mainly corresponds to the linear part of *A. ervi* thermal curve. We expected to observe a higher ovigeny index in females reared throughout their life at high temperature than in cold-developed females living at low temperature as adult, because of higher metabolic rate (Berger et al. 2008, Brown et al. 2004) or smaller body size (Ellers and Jervis 2003). Our results partly support this prediction since the ovigeny index increased between 16 and 28°C although we also observed the highest value in females reared at the lowest temperature (i.e. 12°C). Females that developed at 20°C and were transferred as adult at 24°C and 28°C had the highest ovigeny index and laid more eggs during the early oviposition period while those transferred at 16°C laid more eggs at the end of their life. These results suggest that ovigeny index is not only influenced by body size but also by adult egg maturation rate, lifespan or amount of energy available.

Adaptive and physiological explanation. The proportion of the maximum potential lifetime egg complement that is mature upon female emergence, i.e. ovigeny index, is expected to have evolved in parasitoids in response to environmental variables such as host spatial distribution (Ellers and Jervis 2004) and life history traits such as egg size (Ellers and Jervis 2004) or body size (Ellers and Jervis 2003). The increase in ovigeny index that we observed in *A. ervi* between 16 and 28°C supports predictions proposed by Ellers et al. (2003) who stated that small parasitoids –those which developed at high temperatures in our study- should allocate more of resources to early reproduction, thereby increasing ovigeny index, as they experience a more stochastic environment because they sample fewer patches than the larger females with a longer

life span. This prediction has previously been confirmed in a *Drosophila* parasitoid (Thorne et al. 2006) and has been suggested by Abram et al. (2016 b) who observed that small *Telenomus podisi* females shifted resource allocation to early reproduction compared to larger females. Such negative relationship between ovigeny index and body size is also partly supported when *A. ervi* females were kept at a given temperature their entire life; but may be limited to species with a low ovigeny index as proposed by Fischbein et al. (2013) who did not observe this relationship in a species with a high index.

Results from our second experiment in which females developed at 20°C and were transferred at a different temperature following adult emergence suggest that others factors than body size influence ovigeny index. Indeed, we observed an increase in ovigeny index with temperature experienced by adult females with similar body size. Moreover, females kept throughout their life at a given temperature had similar ovigeny index than females that developed at 20°C and were transferred at the same given temperature. Body size alone thus cannot explain temperature-dependent variations in ovigeny index in *A. ervi*.

Variations in ovigeny index are generally considered to be adaptive but temperature-mediated variations may be mainly physiological and result from the increase in metabolic rate with increasing temperature observed in ectotherms (Brown et al. 2004, Clarke 2006). A higher metabolic rate implies a higher consumption rate of energy and consequently fewer resources available for other life history traits, including reproduction. Such effect would result in a higher ovigeny index since females exposed to high temperatures would have less resources to mature additional eggs. Moreover, egg maturation rate is expected to increase with metabolic rate and thus with temperature (Berger et al. 2008); females will thus mature eggs faster at high temperature and have a higher ovigeny index. Temperature-mediated egg maturation rate may partly explain variations in ovigeny index in *A. ervi*, as observed in Lepidoptera (Berger et al.

2008). This hypothesis is partly supported by our results, especially the highest ovigeny index observed in *A. ervi* females which developed at 12°C, or in females that developed at 20°C and were transferred at 12°C. It is likely that egg maturation was slowed down at low temperature and few eggs were produced during adult life, resulting in the highest ovigeny index. Similar results were observed by Ismail *et al.* (2012) who exposed *A. ervi* to cold storage, resulting in an increase in early fecundity.

Physiological and adaptive explanations are not mutually exclusive. Life expectancy decreases with increasing metabolic rate, and thus with temperature, in insects (Nylin and Gotthard 1998), including *A. ervi* (Table 1). Females should thus allocate more resources to early reproduction -as indicated by the higher number of eggs laid during the early oviposition period (i.e. at one third of average lifespan) in females transferred to the highest temperatures- in order to maximise reproduction before dying. This higher investment in early reproduction would however be paid off by a lower quantity of resources available for survival and other life history traits (Harshman and Zera 2007, Papaj 2000). Such physiological and adaptive hypothesis may partly explain why females which were kept throughout their life at a given temperature had similar ovigeny index than females that developed at 20°C and were transferred at the same given temperature.

Behavioural variations. In this study, variations in timing of reproduction were both physiological and behavioural since warm-developed females laid more eggs early in life (i.e. one third of average lifespan) while females which developed and lived at 16 or 20°C laid more eggs at later age (i.e. two third of average lifespan). Females that developed at 20°C and were transferred at 24 or 28°C as adults also shifted their egg laying early in life, proportionally to their lifespan. Several non-exclusive mechanisms may explain such behavioral changes with

temperature, as proposed by Abram et al. (2016 a) who recently developed a conceptual framework to unify thermal physiology and behavioural plasticity. Parasitoids may first change their behaviour according to changes in metabolic rate, which may inform females about their lifespan, or egg maturation rate, a direct physiological effect of temperature (Berger et al. 2008). Such mechanism is referred as a medium-term kinetic effect (Abram et al. 2016 a), i.e. insects change their behaviour according to temperature-dependent physiological changes. Parasitoids may also integrate temperature as an environmental cue for decision-making. Females may perceive hot environment as a risky one and thus lay their eggs early in life. Amat el al. (2006) observed for example that parasitoid females laid more eggs following a sudden change in temperature, and proposed that such integrated mechanism may explain their results.

Conclusion and significance to biological control. To our knowledge, this study is the first to explore influence of non-stressful temperatures on ovigeny index in parasitoids. In *A. ervi*, ovigeny index fluctuated from 0.24 at 24°C to 0.53 at 12°C, i.e. an estimated range of 0.29. Such large temperature-mediated range should favour the selection of egg maturation strategy adapted to different climates, as suggested by Moiroux et al. (2010) who observed pro-ovigenic and synovigenic populations originating from contrasting climates in a *Drosophila* parasitoid, *Leptopilina boulardi*. Predicted global warming (IPCC 2014) may therefore rapidly select for a higher ovigeny index in the next decades since our results suggest that early reproduction is better when temperature increases. However, it will remain difficult to disentangle the physiological effects of temperature via metabolic rate on ovigeny index from adaptive allocation of resources when studying thermal response in ectotherms.

This plasticity in the ovigeny index could be used in biological control programmes. Different strains of parasitoids could be produced by varying immature developmental temperature

according to the need of growers: a first strain developing at high temperature and characterised by a high ovigeny index that would result in a rapid impact at reducing pest populations, traded-off against a lower lifetime fecundity and lower longevity, and a second strain developing at low temperature and characterised by a low ovigeny index that would have a more long-term impact on pest populations. Such possibility should however be investigated further since a higher immature temperature may decrease ability of *Aphidius ervi* to successfully parasitise aphids (Moiroux et al. 2015). Moreover, photoperiod should be considered in such studies since this environmental factor is known to influence reproduction in parasitoids (e.g. Sagarra *et al.* 2000).

Acknowledgements. We are grateful to Cécile Gerardin for help during this study. This research was part of the project “Impact of climate change on synchronism between pests and their natural enemies” supported by the Consortium on Regional Climatology and Adaptation to Climate Change, OURANOS (Québec, Canada), and the Fonds vert of the Québec Ministry of Agriculture, Fisheries and Food.

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1 Table 1. Average lifespan (Mean \pm s.e.), age of early and late oviposition, and age of dissection
2 used for measurements of potential lifetime fecundity when *Aphidius ervi* females were reared at
3 five temperatures. Different letters mean significant differences between thermal treatments.

4	Temperature (°C)	Average lifespan (days)	Age of early/late oviposition	Age of dissection
5	12	15.6 \pm 1.5 a	5/10	14
6	16	14.9 \pm 1.2 a	5/10	14
7	20	11.4 \pm 1.2 b	4/8	10
	24	9.1 \pm 1.0 c	3/6	8
	28	6.9 \pm 0.7 d	2/4	6

9 Table 2. Tibia length (1) and initial egg load of *Aphidius ervi* females reared at five temperatures, tibia
 10 length (2) of individuals used for estimating potential lifetime fecundity, and tibia length (3)
 11 of individuals transferred from 20°C to other temperatures upon emergence. Different letters mean
 12 significant differences between thermal treatments, considering body size as covariate for initial egg
 load. Mean \pm s.e.

Temperature (°C)	Tibia length (1) (mm)	Initial egg load	Tibia length (2) (mm)	Tibia length (3) (mm)
12	0.80 \pm 0.05 a	45.3 \pm 4.4 a	0.79 \pm 0.05 a	0.69 \pm 0.06 b
16	0.75 \pm 0.05 ab	45.6 \pm 3.6 a	0.74 \pm 0.04 ab	0.70 \pm 0.05 b
20	0.71 \pm 0.04 b	42.4 \pm 3.1 a	0.71 \pm 0.05 b	-
24	0.56 \pm 0.05 c	45.5 \pm 3.3 b	0.57 \pm 0.05 c	0.70 \pm 0.05 b
28	0.46 \pm 0.06 d	48.5 \pm 3.0 c	0.45 \pm 0.04 d	0.71 \pm 0.04 b

13 Table 3. Results of generalized linear models testing the influence of body size, temperature and interaction between these two factors on reproductive parameters measured on *Aphidius ervi* females reared at five different temperatures.

	Number of eggs laid at 1st oviposition	Number of eggs laid at 2nd oviposition	Egg load measured at dissection	Lifetime fecundity
Factors				
Body size	$\chi^2 = 24.07$, $p = 0.011$	$\chi^2 = 27.11$, $p = 0.011$	$\chi^2 = 31.24$, $p = 0.011$	$\chi^2 = 9.75$, $p = 0.023$
Temperature	$\chi^2 = 30.18$, $p = 0.002$	$\chi^2 = 34.09$, $p = 0.002$	$\chi^2 = 17.88$, $p = 0.027$	$\chi^2 = 36.47$, $p = 0.003$
Body size x Temperature	$\chi^2 = 12.27$, $p = 0.022$	$\chi^2 = 11.36$, $p = 0.038$	$\chi^2 = 20.44$, $p = 0.018$	$\chi^2 = 18.95$, $p = 0.017$

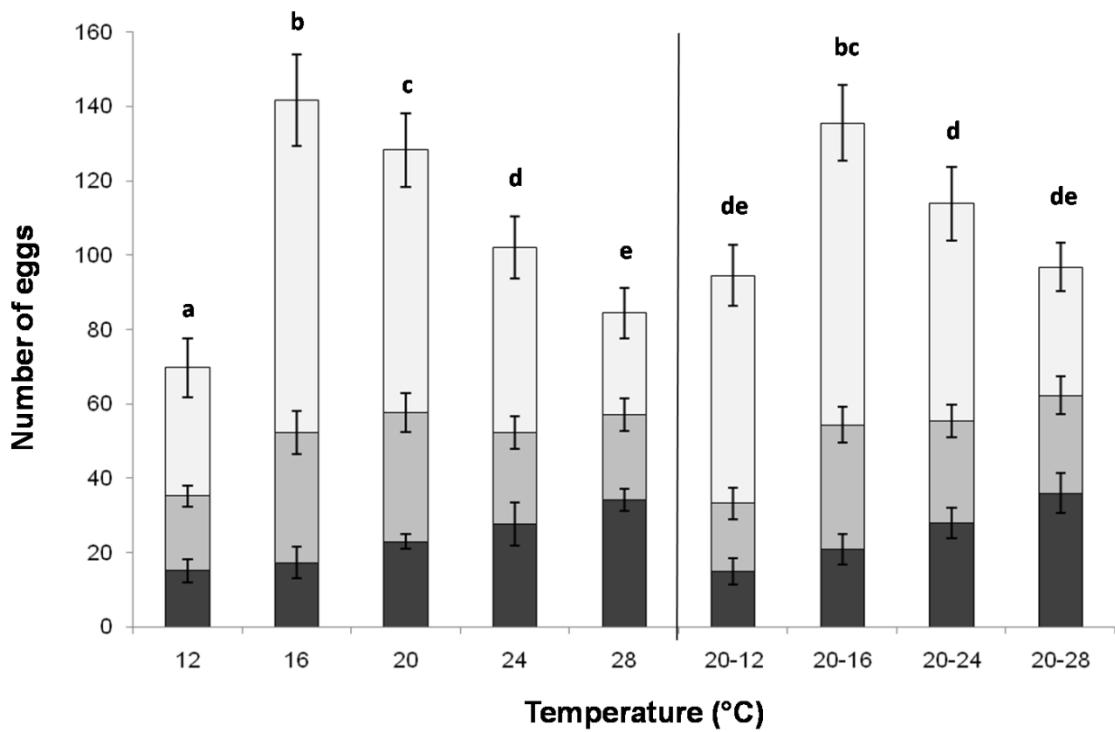
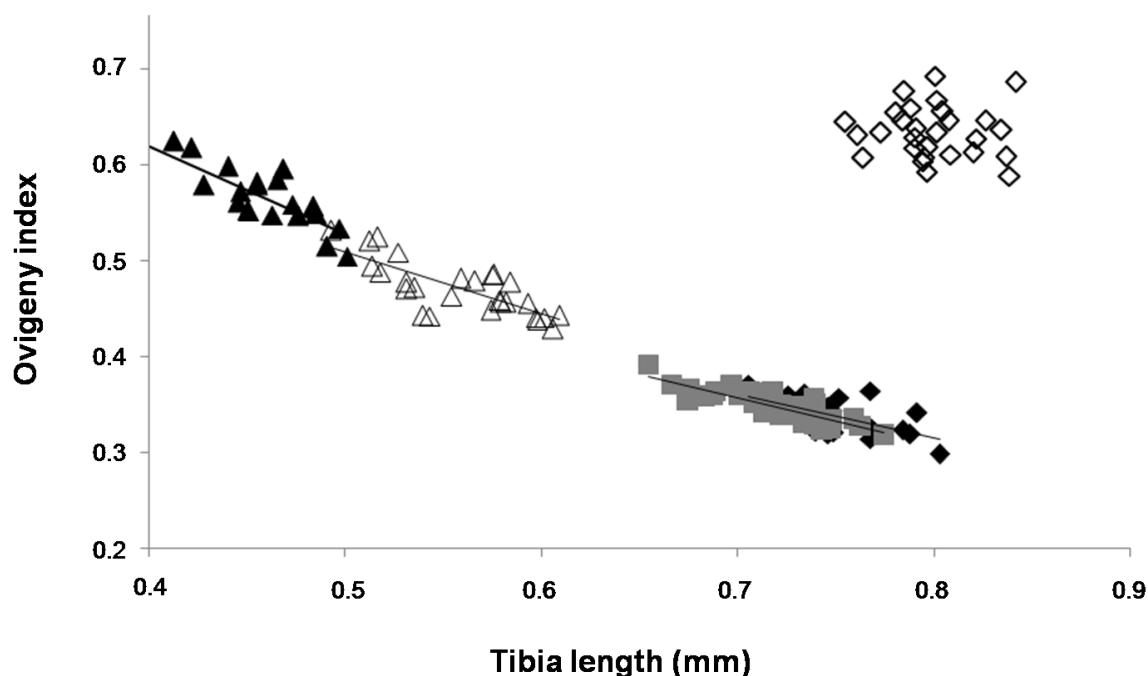
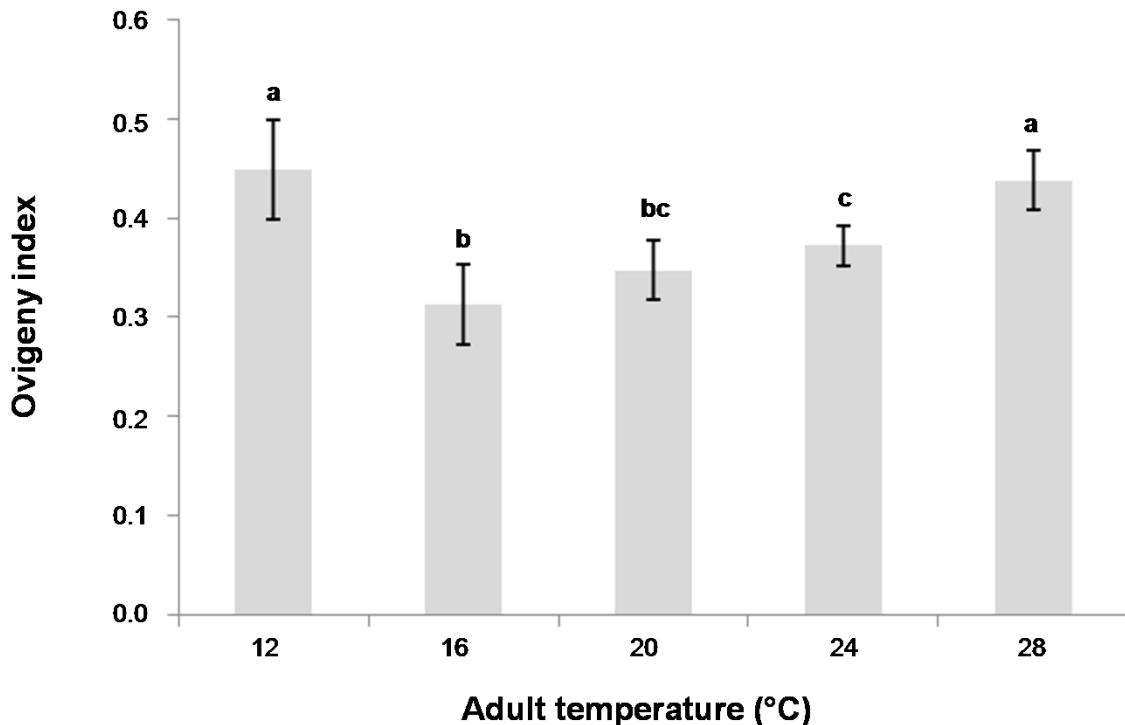


Figure 1. Number of eggs laid during early (dark grey) and late oviposition (light grey) period, and egg load measured in ovaries one day before average lifespan (white) for *Aphidius ervi* females reared at five temperatures throughout their life (left panel) or reared at 20°C and next transferred at a different temperature upon emergence (listed as 20-x, right panel). Different letters within each panel mean significant differences between thermal treatments for the potential lifetime fecundity, i.e. the sum of the three reproductive parameters cited above. Mean \pm s.e.



20 **Figure 2.** Relationship between ovigeny index and body size in *Aphidius ervi* females
 21 reared at five temperatures: 12°C (open diamonds, n=28), 16°C (filled diamonds, n=29),
 22 20°C (grey squares, n=29), 24°C (open triangles, n=27) and 28°C (filled triangles, n=23).
 Intercept was higher for females reared at 24 and 28 °C than females reared at 16 or 20°C.
 No significant relationship at 12°C.



23

24 a **Figure 3.** Ovigeny index in *Aphidius ervi* reared at 20°C and next transferred at 12
 25 (n=27), 16 (n=28), 20 (n=28), 24 (n=26) or 28°C (n=25) upon emergence. Different
 letters mean significant differences. Mean \pm C.I.