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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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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.

1. Introduction

Life history theory aims at understanding how natural selection and other evolutionary forces shape organisms in the face of their environment (Roff, 1992a,b; 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, 1992b). Among those traits, early reproduction is central since it is generally traded-off against several other fitness components such as future reproduction (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

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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 (Abram et al., 2016a; 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).

2. Material & methods

2.1. 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 ± 1 °C, 60 ± 10% 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.

2.2. Ovigeny index

2.2.1. 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 (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 s 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. 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).