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Disentangling plasticity from local adaptation in diapause expression of parasitoid wasps from contrasting thermal environments: a reciprocal translocation experiment

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Abstract

An important question in evolutionary ecology is to understand the drivers of phenotypic variations in contrasted environments. Disentangling plasticity from evolutionary responses in such contexts allows a better knowledge of how organisms adapt their phenotypes to changing climates. Various aspects of the seasonal ecology of insect populations are essential for their persistence in the environment, including their capacity to overwinter. Phenotypic plasticity should allow insects to adjust their locally adapted diapause levels to actually experienced environmental conditions. Using an outdoor reciprocal translocation experimental design, we compared diapause expression of Canadian and French populations of aphid parasitoid species of the genus *Aphidius* in both their respective and foreign bioclimatic regions, thus mostly varying temperature conditions under similar latitude (i.e. same photoperiod). From June to December 2016, diapause and mortality levels were recorded every two weeks. We found both genotypic (populations' origins) and environmental effects (experimental locations) on diapause reaction norms of parasitoid species. The incidence of diapause was higher in Canadian populations (up to 90%) than French populations (<20%) at either location, suggesting local adaptations to harsh (Canadian populations) or mild (French populations) winter climatic conditions in their area of origin. Phenotypic plasticity played an important role in mediating diapause incidence at different temperatures but similar photoperiods, as diapause was induced at higher levels in Canada than in France, independently of parasitoid's origin. We conclude that both plastic and evolutionary responses could be involved in the adaptation of parasitoids' overwintering strategies to different thermal environments and to ongoing climate warming.

Keywords: Climate change, Translocation Experiment, Transplant, Adaptation, Reaction Norms, Parasitoids

Introduction

Understanding the basis of phenotypic variations across varying environments is an important question in evolutionary ecology. Reaction norms (RN) describe the degree to which a genotype (G) responds, in plastic way, to environmental changes (E), in a manner that G x E interactions can be measured (Via and Lande, 1985; Scheiner, 1993). This implies that organisms' trait expression, and *in fine* their fitness, can change with the environmental conditions at which they were selected (determining the level of the RN) and which they actually experience (slope of the RN) (Ayrinhac et al., 2004; Nussey et al., 2007). Organisms can respond to environmental changes through genetic evolution or plasticity (Parmesan, 2006; Sgrò et al., 2016). Disentangling the relative effects of plastic and evolutionary responses to environmental changes is crucial if we aim at predicting how organisms will face ongoing global change, including climate change (Gienapp et al., 2008; Merilä and Hendry, 2014). Transplant (i.e. translocation) experiments of populations between contrasted environments provide interesting ways to study RN and to infer organisms' responses to climate changes by comparing their performance at different locations (Kawecki and Ebert, 2004; Hoffmann and Sgrò, 2011).

Facultative diapause is a well-documented example of developmental plasticity, allowing insects to cope with variable environments (Nylin and Gotthard, 1998). Insects from temperate regions typically enter diapause in response to decreasing photoperiod that reliably indicates unfavorable conditions to come (Tauber et al., 1986). However, the photoperiodic response is often modulated by temperature and other environmental factors (Danks, 1987) and climate warming would diminish the reliability of photoperiod as a predictor of winter onset, leading to potential phenological mismatches (Bale and Hayward, 2010; van Dyck et al., 2015; Forrest, 2016). It is thus necessary to separate the respective effects of photoperiod and temperature when studying diapause reaction norms across environmental gradients. Few studies have examined the consequences of photoperiod-based adaptations, such as diapause, when organisms face new climates (Grevstad and Coop, 2015).

Timing is of the essence; too early or too late diapause induction can lead to impair insect fitness and induce mortality (Sgrò et al., 2016). Insect populations minimize such timing costs by adapting diapause incidence and initiation to local environmental seasonal variations (Danks, 1987). Therefore, for a given insect species, there are geographic clines in diapause expression; winter diapause being induced earlier and at lower environmental threshold in northern populations (Winterhalter and Mousseau, 2007; Hut et al., 2013). A few transplant experiments in the context of diapause study have been conducted (e.g. Chen et al., 2014) but, to our knowledge, no previous study on diapause RN has held the photoperiodic environment constant while varying the thermal environment. The experimental design described below allows disentangling local adaptations and plasticity in diapause expression without confounding the effects of temperature and photoperiod.

This study focused on parasitoid species of the genus *Aphidius* (Hymenoptera: Braconidae); *Aphidius ervi* (Haliday) present in both North America and Europe, and the sister species *Aphidius rhopalosiphi* (Haliday) from Europe / *Aphidius avenaphis* (Fitch) from North America. Photoperiod and temperature interact to induce diapause in these species (Brodeur and McNeil, 1989; Tougeron et al., 2017b). The aim of this study was to investigate and compare the RNs of diapause expression in multivoltine populations of aphid parasitoids from contrasted winter climate areas (eastern Canada *vs.* western France) in outdoor semi-experimental conditions across the season for diapause induction. In this longitudinal translocation experiment, we tested parasitoids' species and population responses to summer, fall and winter climatic conditions to which they were, or not, adapted, in order to measure the degrees of local adaptation and plasticity in diapause expression. In their native environment, Canadian parasitoids start to enter winter diapause in mid-July and 100% incidence is reached before lethal frosts occur (Brodeur and McNeil, 1994). In contrast, in western France some parasitoid species can remain active throughout winter, at least part of the population, due to mild temperatures and host availability throughout the year (Krespi et al., 1997; Andrade et al., 2016).

We hypothesized that; (i) Canadian populations enter diapause at higher levels and earlier in the season than French populations, due to

adaptations to conditions of their area of origin; (ii) Diapause levels are higher and parasitoids enter diapause earlier in Canada than in France, regardless of the origin of the parasitoid population, due to phenotypic plasticity to local temperatures; (iii) Mortality levels are higher for parasitoid populations tested in the foreign location.

Material & Methods

Meterological data

Minimum, mean and maximum temperatures were recorded every hour throughout the experiment using LOG32 data logger (Dostmann, Germany) in France and HOBO data logger (Onset, MA, USA) in Canada directly placed in one of the outdoor experimental cages Bugdorm-4S (32x32x32 cm, Taichung, Taiwan). Cages did not produce any greenhouse effect since mean temperature was similar to outdoor weather stations close to the experimental sites (mean ±SE difference between inside and outside the cages of 0.35 ±0.24 °C over the experimental session). Temperatures for each date of outdoor releases were averaged using data of the following 14 days to have reliable information on climatic conditions experienced by developing parasitoids.

Biological material

Three parasitoid species of the English grain aphid (*Sitobion avenae* (Fabricius) (Homoptera: Aphididae)) were used: *A. ervi* (present in both France and Canada), *A. rhopalosiphi* (strictly Eurasian species) and *A. avenaphis* (strictly North American species). The two latter species are phylogenetically, ecologically and morphologically closely related species and are considered as sister species (Kos et al., 2011; Tomanović et al., 2013). Although they are two different species, *A. rhopalosiphi* was considered as the French population and *A. avenaphis* as the Canadian population. By this way, we were able to compare the plastic response of two populations of a same species (*A. ervi*), and of two close species that have evolved in different bioclimatic areas (*A. rhopalosiphi* and *A. avenaphis*). Four parasitoid populations were collected from cereal fields in 2015 and the colonies were started with about 50 individuals for each population. One population of *A. ervi* was collected in Québec, Canada (45.58°N, 73.24°W) and the other was collected in Brittany, France (48.11°N, 1.67°W). *Aphidius rhopalosiphi* parasitoids were collected in Brittany, France, and *A. avenaphis* parasitoids were collected in Saskatchewan, Canada (52.21°N, 106.66°W). Parasitoid colonies were maintained in climatic chambers at 20°C, 16:8 h LD photoperiod and 75% Relative Humidity (RH) on cereal aphids colonies (*S. avenae*) collected either in Brittany (for the maintenance of and experiments on French parasitoid populations) or in Québec (for Canadian parasitoid populations). All the experiments were conducted within the 2 years after parasitoid culture establishments.

Experimental design

Experiments were conducted every 14 days from 20th June to 5th December, 2016 in outdoor mesocosms in Montréal 45.55 °N, 73.55 °W (QC, Canada) and Rennes 48.11 °N, 1.65 °W (Brittany, France), thus providing approximately the same photoperiodic regime (similar latitude) in both locations across the season. In France, experiments were not performed from 4th July to 29th August (4 experimental dates) because no winter diapause was expected prior to this period and to avoid measuring summer diapause (Krespi et al., 1997; Tougeron et al., 2017b). The first observation (20th June) was done in France to obtain a common starting point with Canada. We were not able to obtain data for the Canadian population of *A. ervi* tested on October 24, nor for *A. avenaphis* tested on August 29 in France.

Four days before each date of outdoor releases, fifteen parasitoid females and five males from each population, less than 48-h-old, were taken from the colony and placed during 24 h in three different plastic tubes (h=10cm, ⌀=3cm) at a ratio of 5 females for 3 males for mating and with a dilution of honey for feeding. Parasitoid females were then placed in three fine netting Bugdorm-4S cages in presence of 200 to 300 second and third instar larvae *S. avenae* aphids of the same size and originating from the same cohort on a wheat pot for 60 to 72 h, with a dilution of honey, at 20°C, 16:8 h LD. Parasitism rate was about 40%. Female parasitoids were then removed from the cages and the three wheat pots with parasitized aphids were put together in a new fine netting cage. The four cages (one per population), protected from rain by a plastic roof, were put outside in a semi-

shaded place. This procedure was repeated every two weeks in both locations.

Twice a week, the formation of mummies (i.e. dead aphid containing a parasitoid prepupa or pupa) was checked in each cage. Mummies were collected from the plants, individually put in 1.5 mL plastic microtubes with a tiny hole on the top for venting and left in their respective cages. Adult emergence from the mummies was checked three times a week and mummies from which no parasitoid emerged within 15 days after the last adult emergence were dissected (or 45 days after mummy formation when no emergence occurred in a cage). Contents from mummies' dissections were categorized as dead parasitoids (immature and adult stages) or gold-yellow diapausing prepupae (Tougeron et al., 2017b). Diapause incidence was calculated as the number of diapausing prepupae relative to the number of emerged individuals (thus excluding dead individuals). Mortality rate refers to the number of dead parasitoids inside the mummies relative to the total number of mummies. Mean diapause and mortality levels were calculated and analyzed from 12th September to 5th December (i.e. over the experimental dates in common between France and Canada).

Statistical analyses

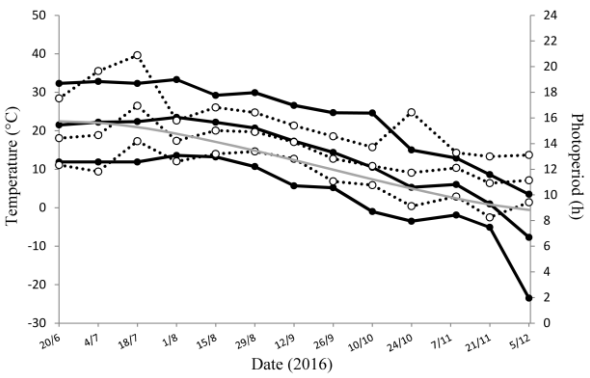
The number of days since the beginning of the experiment was used in the models as a "date" factor. A global model was first created: for each species separately (*A. ervi,* and the sister species *A. rhopalosiphi* / *A. avenaphis*), a Generalized Linear Model (GLM, quasi-binomial family to account for data overdispersion) was fitted to the data to test for differences in diapause incidence over the season (number of individuals in diapause *vs.* not in diapause) on the following explanatory variables: parasitoid origin, tested location, the date and their two-ways interactions. The same procedure was used to analyze mortality levels. Significant differences in diapause incidence between populations at a same location were interpreted as genetic variation (local adaptation) for the expression of diapause. On the other hand, significant differences in diapause incidence between locations for a given parasitoid population were interpreted as plastic variation of diapause (Winterhalter and Mousseau, 2007). A Spearman correlation test was done to analyze the links between photoperiod and minimal temperatures in France and Canada, since minimal temperatures are likely to be the best predictor of diapause increase over the season. A Gaussian GLM was applied to analyze the evolution of minimal temperatures over the experimental season using the date, the tested location and their interaction as explanatory variables. The significance of each explanatory variable was tested with the 'Anova' function from the package *car* in R which performs an analysis of variance of type II (R Core Team, 2017), using a F statistic for diapause and mortality quasibinomial data, and a likelihood-ratio (LR) test using a chi-square statistic for meteorological data.

Results

Abiotic factors

Photoperiod and minimal temperatures were highly correlated ($p<0.001$, $r_2=0.85$ and $r_2=0.89$ in France and Canada, respectively) (Figure 1). Minimal temperatures were on average 6.5°C lower in Canada than in France (GLM, LR=5.8, df=1, $p<0.05$) and decreased over the season in both locations (GLM, LR=57.7, df=1, $p<0.001$) although they decreased faster in Canada (-0.17°C/day, $R^2=0.77$) than in France (-0.09°C/day, $R^2=0.66$) (GLM interaction effect, LR=5.3, df=1, $p<0.05$). Temperatures in France were more buffered (lower min-max amplitude) than temperatures in Canada. Negative temperatures were only encountered a few days in late November in France (down to -2.5°C during the night) while several frost events (down to -23.5°C) occurred almost every day in Canada from early October. First snow fall occurred on 20th November in Canada. There was no snow in France during the time of this experiment. Day length at 46.50°N (similar in both experimental locations) decreased from 15.7 h to 8.8 h between the 20th June and the 5th December.

Figure 1: Minimum, mean and maximum temperatures (°C) in Montréal, QC, Canada (solid lines) and Rennes, Brittany, France (dotted lines) from 20th June to 5th December, 2016. Data shown at each date is the average of temperature data for the 14 days following this date. Photoperiod at 46.50°N is shown for each date (grey line).



Diapause incidence

For every species, Canadian populations had overall higher mean diapause levels than French ones when tested in Canada and in France (Table 1, Figure 2). There was no significant interaction between the origin of the parasitoid populations and the tested locations for any species (Table 1), meaning that differences in diapause incidence between parasitoid populations were consistent across locations (Figure 2). Additionally, diapause incidence increased over the season and this effect was independent of the population origin, but not of the tested location, as it increased faster in Canada than in France (Table 1, Figure 3a). Data for each date (number of mummies collected, number of diapausing parasitoids, and number of dead individuals) can be found in Supplementary Material S1.

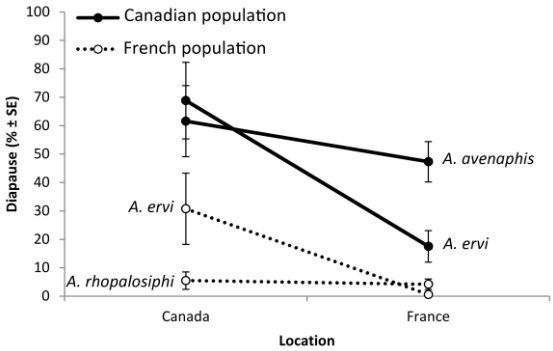
Table 1: Generalized Linear Models (GLMs) on the effect of origin-locations and photoperiod and their interaction on diapause incidence and mortality levels of *A. ervi* (n=1416 mummies in Canada and n=762 in France) and *A. rhopalosiphi* / *A. avenaphis* (n=1469 in Canada and n=2231 in France). The F-value and p-values are presented. Degree of freedom (df) is 1 for each test. NS=non-significant.

Species		*Aphidius ervi*			*Aphidius rhopalosiphi / A. avenaphis*		
Factor		F	p		F	p	
Diapause incidence	Origin	66.9	**<0.001**	***	72.5	**<0.001**	***
	Location	129.0	**<0.001**	***	2.1	0.16	NS
	Date	205.9	**<0.001**	***	33.5	**<0.001**	***
	Origin x Location	0.2	0.68	NS	0.6	0.45	NS
	Origin x Date	0.5	0.48	NS	1.8	0.19	NS
	Location x Date	14.6	**<0.001**	***	13.5	**<0.001**	***
Mortality levels	Origin	1.8	0.18	NS	0.95	0.34	NS
	Location	9.3	**<0.01**	**	15.7	**<0.001**	***
	Date	17.6	**<0.001**	***	18.1	**<0.001**	***
	Origin x Location	3.2	**0.06**	NS	8.9	**<0.01**	**
	Origin x Date	0.8	0.40	NS	1.0	0.31	NS
	Location x Date	3.5	0.07	NS	3.8	0.06	NS

In detail, mean diapause levels over the season were higher for *A. ervi* tested in Canada than in France for both the Canadian-origin populations (68.8 ±13.5% *vs.* 17.5 ±5.5%) and the French-origin population (30.7 ±12.5% *vs.* 0.6 ±0.5%), but this effect varied with the tested date because differences between locations were only seen at the end of the season (Figure 2, Figure 3a). Mean diapause levels over the season were 61.6 ±12.5% *vs.* 47.3 ±7.1% in *A. avenaphis* (Canadian species) and 5.5 ±3.1% *vs.* 4.2 ±1.8% in *A. rhopalosiphi* (French species), in Canada *vs.* France, respectively. Although there was overall no mean diapause differences between locations in these species, a location effect was observed for a few dates at the end of the season, especially for *A. avenaphis* (Figure 2, Figure 3a). In Canada, diapause peaks (i.e. maximum incidence over the season) occurred one month earlier (24th October) for Canadian populations than for French populations (21st November). In both Canada and France, first entrance in winter diapause was observed earlier for Canadian-origin parasitoids (as early as 20th June) than for French-origin parasitoids (not

earlier than 26th September, except for *A. rhopalosiphi* on 20th June which may have entered in summer diapause, as discussed below) (Figure 2a).

Figure 2: Mean percent reaction norms of diapause incidence (% ± SE) of Canadian (full line) and French (dotted line) populations of *A. ervi* and *A. rhopalosiphi* / *A. avenaphis* reared under outdoor conditions either in Canada or in France. For each population origin, more than 600 and 350 mummies were collected in Canada and France, respectively.



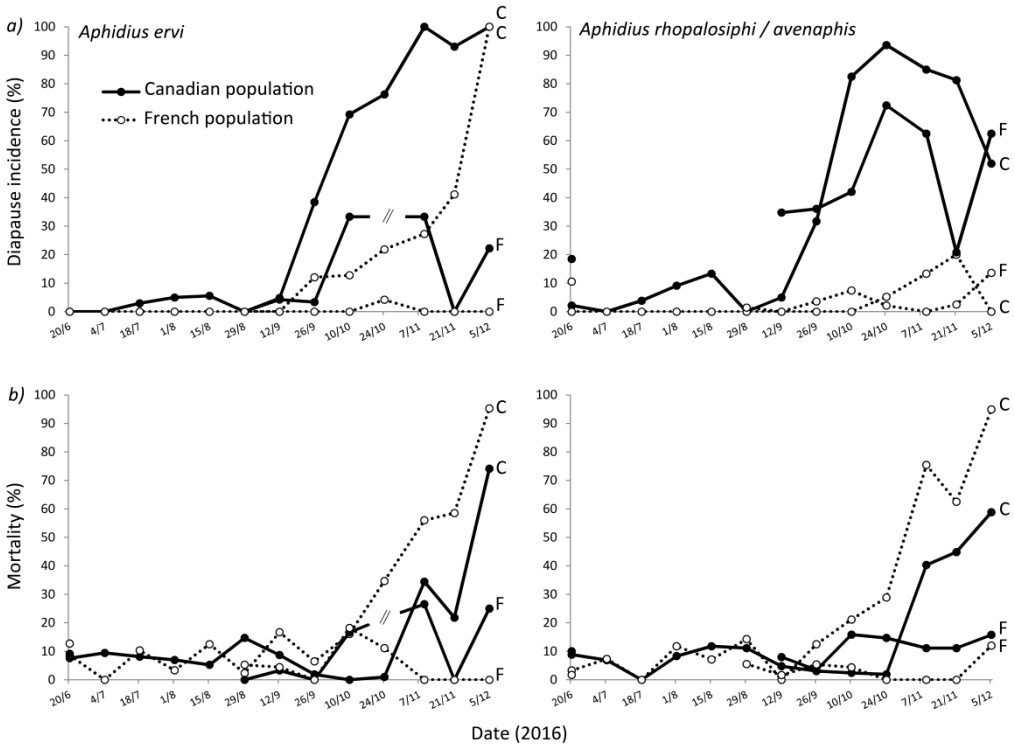
Mortality levels

From late October to early December, mortality levels of each species increased similarly for both populations' origins and locations (Table 1, Figure 3b). Mortality levels were significantly higher in Canada (between 59% and 95% mortality in early December) than in France (between 0% and 25% in early December) (Table 1, Figure 3b). However, the effect of the location on mortality differed depending on the origin of the parasitoid population, although this interaction was only marginally non-significant in *A. ervi* (Table 1). Notably, in France, end-season mortality levels were higher for Canadian parasitoid populations than for French populations. Reversely in Canada, end-season mortality levels were higher for French populations than for Canadian populations, for any species or group of species (Figure 3b).

Discussion

We provide evidence, using parasitoid insects, that both plasticity and local adaptations can be involved in insect response to varying climates. Our translocation study allowed separating the effects of local adaptations from those of plasticity on diapause incidence. As predicted, aphid parasitoid populations originating from the harsh winter area (Canada) expressed higher levels of diapause than populations from the mild winter area (France), when tested either in France or in Canada. This first pattern reflects parasitoid adaptations to climatic conditions of their respective area of origin (genotypic effect, G). Diapause incidence was overall higher for parasitoids tested in Canada than in France, especially for *A. ervi*. This second pattern highlights plastic responses of diapause expression under different thermal environments (environmental effect, E). To the same extent, insect thermal reaction norms usually are determined by both basal genetic response to temperatures (local adaptation) and acclimation (plastic response) to experienced temperatures (Noh et al., 2017). There was however no GxE interactions, as the plasticity following the change in environment was expressed by both Canadian and French parasitoids in a similar fashion. Such results are similar to patterns observed along latitudinal gradients. For example northern populations of the parasitoid *Nasonia vitripennis* (Hymenoptera: Pteromalidae) enter diapause earlier and at higher incidence than southern populations because of local adaptations of plastic responses to seasonal photoperiodic and thermal changes (Paolucci et al., 2013).

Figure 3: Percent seasonal levels of diapause (number of diapausing prepupae / total number of mummies, excluding dead individuals) (*a*), and mortality within the mummies (*b*), recorded every two weeks from 20th July to 5th December, 2016 in the Canadian (solid lines) and French (dotted lines) parasitoid populations of *left*: *Aphidius ervi* and *right*: *Aphidius avenaphis* / *Aphidius rhopalosiphi*. Letters on the right of each panel indicate where the experiments were conducted: Canada (C) and France (F). Slashes (//) correspond to a lack of data (see Material and methods).



We observed that, at a given date (i.e. a specific photoperiod) and for a given location (i.e. a specific temperature regime), Canadian parasitoid populations entered diapause at higher levels than French populations. In France, Canadian populations entered diapause at important levels (up to 27.8% for *A. ervi* and 61.8% for *A. avenaphis*) even if temperatures were warm enough for continuous development and adult survival (developmental thresholds are around +3°C in this genera; Sigsgaard, 2000; Zamani et al., 2007), suggesting a strong genetically determined photoperiodic effect in harsh winter populations. On the other hand, French parasitoids expressed overall low diapause levels in both Canada and France, suggesting a weak response to environmental cues. We showed that *A. ervi* had higher level of plasticity to environmental changes (i.e. location effect with higher RN slopes, see Figure 2) than the other "sister-species". The response to environmental change in *Aphidius* parasitoids' diapause could thus be different between species and could depend on their respective responses to environmental cues (temperature and photoperiod). For example in the laboratory, it was shown that *A. ervi* diapause incidence was influenced by photoperiod x temperature interaction but not *Aphidius avenae* diapause which is triggered by these cues independently of each other (Tougeron et al., 2017b). Furthermore, in the French population of *A. rhopalosiphi* held in France, around 10% of the individuals entered diapause in June. This suggests the expression of summer diapause initiated in the offspring when female parasitoids encounter competitors for host resources, under summer like conditions (Krespi et al., 1997; Tougeron et al., 2017a).

As in many arthropod species, both temperature and photoperiod interact to induce diapause in aphid parasitoids (Brodeur and McNeil, 1989; Tougeron et al., 2017b), but it is difficult to disentangle them because these stimuli are highly correlated . Nevertheless, the relative importance of photoperiod and temperature at inducing diapause can differ between insect populations

of a same species because the reliability of these stimuli may vary among regions (Piercey and Maly, 2000; Pruisscher et al., 2017). Northern populations normally enter diapause under strict photoperiodic control and earlier than southern populations in which diapause may be more sensitive to modulation by temperature (Hut et al., 2013). Our results suggest that parasitoids from mild winter climates may be relatively more sensitive to temperature than to photoperiod to enter diapause. This would allow parasitoids to match more accurately their overwintering strategy to actual winter temperatures.

In the laboratory, Tougeron et al. (2017b) observed very low diapause incidence in species of aphid parasitoids from mild winter climate. Under the most winter-like condition tested (14°C, 10:14 h LD), no diapause was expressed in *A. rhopalosiphi* while an average level of 11.2 ± 4.9% was observed in *A. ervi*. Here we demonstrate that, although mild winter populations of these two species express low diapause levels in both Canada and France, they have the capacity to enter diapause at higher levels through developmental plasticity when exposed to colder temperatures and lower photoperiods than when tested in the laboratory. Therefore, the capacity to enter diapause has not been "lost" in aphid parasitoid populations from mild winter climates, but diapause is not or little expressed in their area of origin because of advantageous climatic conditions. By contrast, our results confirm a selection process for low diapause induction thresholds (low temperature and day-length) and low plastic responses in populations from mild winter areas (Tougeron et al., 2017b), associated with changes in overwintering strategies (Andrade et al., 2016). This hypothesis is especially true for *A. ervi* which strongly responds to the change of thermal environment (i.e. when tested in Canada) while *A. rhopalosiphi*, a species that have favored a quiescence strategy over the diapause overwintering strategy a few decades ago (Tougeron et al., 2017b), do not exhibit such strong response to temperature. Similarly, in the pitcher-plant mosquito *Wyeomyia smithii* (Diptera : Culicidae), longer favorable season driven by climate-warming has led to the selection of lower critical photoperiod to enter diapause (Bradshaw and Holzapfel, 2001).

Several studies have used transplant experiments to move populations to warmer climates and investigate organisms' evolutionary and plastic responses to new environmental conditions (e.g. Andrew and Hughes, 2007; Logan et al., 2014; Nooten et al., 2014). Following transplant, the value of the most plastic traits rapidly changes while the value of traits strongly associated with local adaptations are not immediately modified (Charmantier et al., 2016; Kawecki and Ebert, 2004). For example, in the grasshopper *Melanoplus sanguinipes* (Orthoptera: Acrididae), body orientation toward a heat source is plastic to the temperature experienced by the insect while mobility and basking behaviours are determined by the climatic origin of the parental generation (i.e. locally adapted traits) (Samietz et al., 2005). For diapause, Chen et al., (2014) demonstrated that the moth *Hyphantria cunea* (Lepidoptera: Arctiinae), transferred from its temperate origin area to a subtropical location has the capacity to enter summer diapause to cope with warmer summers, thus highlighting a plastic developmental response. The moth however faced environmental conditions to which it was not adapted, and high mortality was observed (Chen et al., 2014).

When parasitized aphids were put outside in Canada at the end of the experimental season, most individuals died because of lethally cold temperatures. To the same extent, insects that do not enter diapause because of too high temperatures in fall may suffer high mortality from sudden cold spells in winter (Bale and Hayward, 2010). Higher mortality levels were observed for French populations tested in Canada, which may be poorly resistant to cold temperatures (Le Lann et al., 2011; Tougeron et al., 2016). Such high mortality highlights timing costs of being active too late in the season, but is not ecologically relevant to interpret because parasitoids are adapted to enter in diapause before the onset of lethal frosts. Canadian populations tested in France also incurred important mortality despite the relatively warm conditions across the experimental season. For Canadian populations in France, developmental costs might have occurred; temperatures were too hot to be sustainable in a diapause state. Indeed, mild winter temperatures lead to higher metabolic activity during the process of diapause, potentially increasing mortality in insects (Bosch et al., 2010; Williams et al., 2012; Xiao et al., 2016). These results strengthen the idea that there is a strong evolutionary pressure to enter early diapause in harsh winter climates, but not necessarily in mild winter climates where diapause can involve physiological (i.e. energy

consumption) and ecological costs (i.e. not exploiting available hosts in the environment).

From an applied perspective, studies on diapause expression among different parasitoid populations may help the biological control industry selecting appropriate strains for mass rearing. In the context of climate changes, animal populations will increasingly be exposed to environmental conditions to which they are not currently adapted. When populations face a new climate, the genetically-based photoperiod response is likely to be initially mismatched - until they adapt their response or modulate it through plasticity - because at a given location, photoperiod will not change whereas temperatures will (Grevstad and Coop, 2015). Increasing costs of diapause expression under an inappropriate thermal environment are thus to be expected (Bale and Hayward, 2010; Sgrò et al., 2016), for instance in case of unexpected cold spells in mild winter areas, although insects have great capacities to rapidly adapt to new thermal conditions. When species have to adapt to new environments, one could expect the reaction norm (i.e. the phenotypic response to the environment) to change genetically (Winterhalter and Mousseau, 2007; van Asch et al., 2012). Examples of genotypic changes when facing warmer climates (e.g. Bradshaw and Holzapfel, 2001; Logan et al., 2014) remain however less common than reports on plastic changes (Hill et al., 2002; Berteaux et al., 2004).

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