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Environmental effects on the detection of adaptation

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Abstract

Detecting adaptation involves comparing the performance of populations evolving in different environments. This detection may be confounded by effects due to the environment experienced by organisms prior to the test. We tested whether such confounding effects occur, using spider-mite selection lines on two novel hosts and one ancestral host, after 15 generations of selection. Mites were either sampled directly from the selection lines or subjected to a common juvenile or to a common maternal environment, mimicking the most frequent environmental manipulations. These environments strongly affected all life-history traits. Moreover, the detection of adaptation and correlated responses on the ancestral host was inconsistent among environments in almost 20% of the cases. Indeed, we did not detect responses unambiguously for any life-history trait. This inconsistency was due to differential environmental effects on lines from different selection regimes. Therefore, the detection of adaptation requires a careful control of these environmental effects.

Introduction

The environment experienced by individuals or their mothers can affect the expression of life-history traits later on (Mousseau & Fox, 1998; Lindstrom & Kokko, 2002; West-Eberhard, 2003). These effects may depend on the quality of the past environment. For example, individuals that experience a high-quality environment as juveniles may have an advantage as adults over individuals growing in low-quality environments (Lummaa & Clutton-Brock, 2002). In addition, effects of the immediate past environment hinge on the similarity between the past and the current environment. For instance, individuals exposed to a stressful environment may learn to avoid or cope with that stress, thereby having an advantage over naïve individuals (Chivers *et al.*, 1996; Agrawal *et al.*, 2002; Nomikou *et al.*, 2003; but see Leroi *et al.*, 1994). Moreover, a harsh environment may induce a generalized response to other threats, such as the attack of a particular herbivore inducing a response in the plant that deters other herbivore species as well (Bostock, 2005). Conversely, growing in a particular environment may reduce the later performance in another environment or the performance of the next generation (Stillwell & Fox, 2005). Maternal and juvenile environments may also interact in complex ways to shape life-history traits in the adults (Stillwell & Fox, 2005; Kaplan & Phillips, 2006).

Despite many studies on short-term changes in life-history traits in response to the environment, little is known about the way these environmental effects affect the detection of adaptation. Adaptation can be defined as genetic changes of populations evolving in a novel environment. Evidence for these evolutionary changes comes from comparing the performance of populations having evolved in different environments. But a requisite of testing adaptation is to compare the performance between populations after removing effects of the different environments *per se*; otherwise, one would confound plasticity and genetic (evolutionary) effects. Only a few studies have dealt with this question. Watson & Hoffmann

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(1996) found that the response to selection for cold resistance in *Drosophila* was less marked if individuals had been previously acclimatized to cold temperatures. Thus, maternal and juvenile environments may modify the performance of an organism in the environment where the population has evolved. Maternal and juvenile effects of the ancestral environment may also affect the performance of organisms evolving in a novel environment. For example, Bettencourt *et al.* (1999) showed that acclimation to specific temperatures modified the correlated responses of *Drosophila melanogaster* populations selected at different temperatures. As detecting adaptation to a novel environment involves the comparison of performance of organisms selected in the novel environment to that of organisms from the ancestral environment, environmental maternal and juvenile effects may confound the detection of such adaptation.

This issue pertains in particular to studies of local adaptation. Such studies involve comparing the performance of laboratory or field populations evolving in different environments, either in each others' environment (reciprocal transfer experiments) or in a common environment (common garden experiments) (Kawecki & Ebert, 2004). In such studies, populations can be sampled directly from the environment where they have been selected, a procedure that is used both in laboratory and in field populations (Ahonen *et al.*, 2006; Koskella & Lively, 2009; Xue *et al.*, 2009). Another treatment that is mostly applied to natural plant populations is to collect (seed) maternal families in the field and grow them in a common (juvenile) environment (Stowe, 1998; Caballero *et al.*, 2001; Jimenez-Ambriz *et al.*, 2007). Finally, populations can spend a whole generation in a common (maternal) environment before being tested (Bettencourt *et al.*, 1999; Doroszuk *et al.*, 2006; Lopes *et al.*, 2008). This procedure is most commonly used in laboratory populations, usually more amenable to such manipulations (Kawecki & Ebert, 2004). It is also the most desirable manipulation to adopt, as it ensures that all populations are exposed to similar environmental effects before testing for adaptation. However, this manipulation is not always achievable, as it depends on the characteristics of the species under study. For example, it is difficult to conceive that most tree species will be amenable to such manipulation. Hence, a concordance between the different measures on the detection of adaptation (with or without common environments) would be desirable if firm conclusions are to be drawn. Despite its obvious relevance for adaptation studies, such concordance has never been sought. This is the subject of this study.

In this article, we use experimental populations of the herbivorous two-spotted spider mite, *Tetranychus urticae*, evolving on different novel host plants to measure adaptation and its correlated responses (i.e. performance on the ancestral host) to address how juvenile and maternal environments affect the detection of long-term adaptation. Using a cucumber-adapted laboratory population of spider mites, we have previously shown that when mites were placed in common maternal environment prior to being tested, they displayed significant adaptation to novel host plants within 15 generations, but not for all life-history traits (Magalhães *et al.*, 2007a). Indeed, whereas juvenile survival and fecundity on the novel hosts increased significantly on lines selected on those hosts, no significant changes were detected in developmental time or in longevity. This adaptation did not entail a measurable cost in the ancestral environment, cucumber (Magalhães *et al.*, 2009). Here, we ask whether such conclusions still hold if we expose mites to different environments prior to testing adaptation or its cost. We perform tests on populations selected on two different host plants (tomato and pepper) to increase the generality of our findings.

Material and methods

Stock cultures

Two-spotted spider mites (*Tetranychus urticae* Koch) were cultured in large numbers (>10 000) on cucumber plants (approximately 4 weeks old, provided twice per week) in a climate-controlled room (25 °C). Spider mites were originally collected from a cucumber greenhouse (variety Ventura) in Pijnacker, the Netherlands, in May 1994 and kept on that same variety in a climate chamber at the University of Amsterdam. The culture at the University of Montpellier (used in this study) was established in April 2004 from approximately 10 000 individuals of the population at the University of Amsterdam. Plants were sown once per week and cultured in a herbivore-free room under controlled conditions (25 °C). Cucumber plants (variety Ventura) were provided by Rijkzwaan in France, tomato plants (variety Moneymaker) were provided by Gebroeders Eveleens in the Netherlands, and pepper plants (variety pikante reuzen) were obtained from the University of Wageningen.

Selection regimes

Selection lines of spider mites were established in March 2005 by placing 300 adult mated females from the base population on a detached leaf of cucumber, tomato or pepper. The petiole of each leaf was placed in a small vial (circa 5 cm in diameter and 3 cm in height) with water. The vial was covered with a plastic lid with a few holes for the petioles. The leaf and the vial were maintained in a larger plastic box (circa 20 × 20 × 10 cm) closed with a lid with a central hole covered with gauze to allow ventilation. The lid was sealed with parafilm, and each box was placed in a tray containing water with a small quantity of soap to isolate the selection lines from one another. New leaves were added twice per week and old leaves were discarded when completely devoid of mites. There were five selection lines (SL; replicate populations),

hereafter called C-lines, P-lines or T-lines, depending on whether mites evolved on cucumber, pepper or tomato, respectively, evolving on each plant species [cucumber, tomato or pepper, hereafter called selection regimes (SR)]. Populations evolved under each selection regime during 15 generations. Because the base population has been collected and reared on cucumber, cucumber is the ancestral host, whereas tomato and pepper are novel hosts for this population.

Experimental design

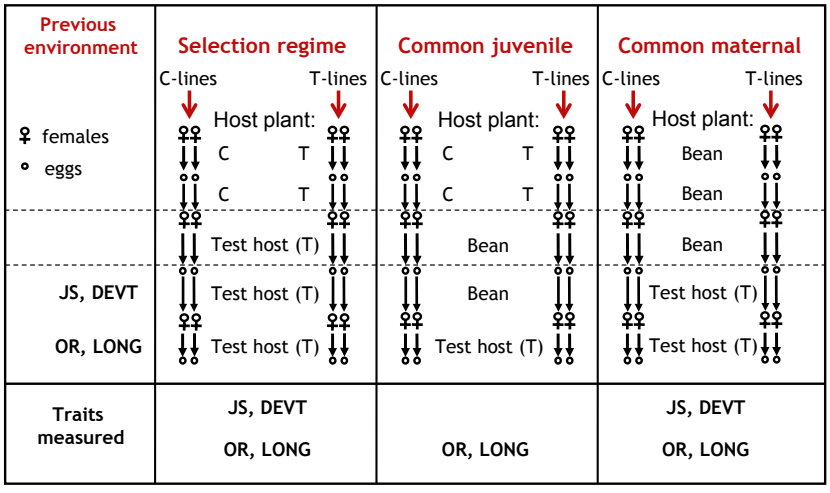
General procedure

Experiments were performed in a climate-controlled room at approximately 25 °C. Life-history traits of mites from each selection line were measured on detached leaves of one of the three host plant species (cucumber, tomato and pepper, hereafter 'test host'), placed on water-soaked cotton wool inside a plastic tray (20 × 10 × 5 cm). Developmental time and survival to adulthood were assessed by placing eggs of mites from each selection line on leaves of each test host. Eggs were transferred to leaves of each plant on the day they were laid. There were several leaves per selection line, corresponding to different days of egg laying. Every 4 days during the first 12 days and every other day thereafter, we recorded the individuals that died on the leaf, drowned in the water or became adults. Subsequently, mated females of each selection line were placed on a separate leaf of each test host, and oviposition rate was measured by counting the eggs laid every 3 days during 12 days or until the female died. In this way, we obtained one estimate of oviposition rate per selection line. Leaves were replaced after each counting. The number of females used varied among SL and with time, ranging from 10 to 40 per population. In three of five lines per selection regime, the experiment was prolonged until all females died, to measure total oviposition rate and longevity (except for cucumber populations on tomato, for which only two lines were tested).

Effect of previous environments on the detection of adaptation

To assess the effects of maternal and juvenile environments on the detection of adaptation, mites were

(a) Tests of environmental effects on adaptation to a novel host



(b)

	C-lines	P-lines	T-lines
On pepper	Adaptation P	Adaptation P	-
On tomato	Adaptation T	-	Adaptation T
On Cucumber	Cost P/Cost T	Cost P	Cost T

Fig. 1 (a) Experimental protocol to detect adaptation and adaptation cost with different previous environments. Here, we show as an example the protocol to detect adaptation to tomato. Performance of selection lines on tomato (T-lines) and control lines on the ancestral host cucumber (C-lines) is measured on the test host (in this case tomato) after one of three different previous environments [sequence of host plants on which females lay eggs or offspring develop: tomato (T), cucumber (C) or bean]. To detect a cost of adaptation, the lines were tested on the ancestral host, cucumber. Performances were measured using the following traits: juvenile survival (JS). developmental time (DEVT). oviposition rate (OR) and longevity (Long). (b) Overview of the comparisons made. To detect the adaptation on pepper, the performance of pepper lines (P-lines) on pepper (P) was compared with that of cucumber lines (C-lines). To detect the adaptation on tomato, the performance of tomato lines (T-lines) on tomato (T) was compared with that of cucumber lines (C-lines). A cost of adaptation to pepper was tested by comparing the performance of C-lines and P-lines on cucumber (C), whereas a cost of adaption to tomato was tested by comparing the performance of C-lines and T-lines on C.

exposed to three different environments (hereafter named 'previous environments') before measuring their life-history traits on each host plant ('test host') (Fig. 1a). Bean is a very favourable environment for spider mites (Agrawal *et al.*, 2002; Pietrosiuk *et al.*, 2003; Gotoh *et al.*, 2004); therefore, we used this host plant in some previous environments as a way to homogenize maternal or juvenile environment without changing the genetic composition of each evolved line. The adult environment of tested individuals was not manipulated; hence in all cases, it corresponded to the test host.

Selection environment
Thirty adult female mites per selection line were placed on leaves from one of the three test hosts (10 mites on each) to oviposit during 1 day. The number of eggs laid was subsequently equalized to obtain approximately 30 eggs on each test host. Life-history traits were then measured as described earlier. Thus, these mites had maternal effects from their selection regime and experienced each test host as juveniles.

Common juvenile environment
Thirty adult females per selection line laid eggs on bean during 1 day. Subsequently, mated females that had developed from those eggs were collected and placed on each test host. The oviposition rate and adult survival of these females were then measured as described earlier. Thus, these individuals had maternal effects of their selection regime but a common environment (bean) as juveniles. In this environment, we did not measure juvenile traits, as mites were on bean during that period. Differences in responses detected between this treatment and treatment 1 reveal the effects of the juvenile environment in detecting adaptation in the adult traits (oviposition and longevity).

Common maternal environment
Thirty females from each selection line were placed on bean to lay eggs for 1 day. The resulting offspring completed their development on bean and, when reaching adulthood, 30 mated females laid eggs of their own on another bean leaf for 1 day. These eggs were then placed on each test host and life-history traits were recorded as described earlier. These mites had thus a common maternal environment (bean) and the test host as juvenile environment. Hence, differences in responses between this treatment and treatment 1 would reveal the effect of the maternal environment on the detection of adaptation. The data on the performance of all lines in treatment 3 (common maternal environment) are already published (Magalhães *et al.*, 2007a, 2009).

Statistical analysis

All analyses were carried out using SAS software. To test whether the previous environment had an effect on the detection of adaptation or of its potential cost on the ancestral host, we performed mixed analyses of variance (procedure MIXED) for all traits except survival, for which the analysis was carried out using the PHREG procedure. Adaptation was tested by comparing the performance on a novel host (tomato or pepper) of lines evolving on that host and of lines evolving on the ancestral host (cucumber). A correlated response to adaptation was tested with a comparison of the performance of those same lines on the ancestral host (Fig. 1b). The statistical model in both comparisons had SR, previous environment (PE) and the interaction SR × PE as fixed factors and line nested within selection regime [SL(SR)] and the interaction SL(SR) × PE as random factors. This random interaction was deleted from the model if its variance estimate was null. For oviposition rate, because we had a single measure per line, we did not obtain an estimate for SL(SR) and for SL(SR) × PE. This trait was log-transformed before the analyses, to comply with the assumptions of parametric tests. If an interaction SR × PE yielded a *P*-value above 0.25, it was removed from the model, as recommended by, for example, Doncaster & Davey (2007), but its value is reported in Table 1. If the *P*-value for the interaction SR × PE was below 0.05, this indicated that the PE affected the detection of adaptation or its cost. In this case, we studied the effect of SR conditional on previous environment (LSMEANS statement with option SLICE). If SR was overall significant without a significant interaction SR × PE, this indicated that adaptation or its cost was present independently of the PE used. If the PE was significant in the adult traits (for which three PEs were used), we used the CONTRAST statement to test for pairwise differences between PEs.

Results

Effects of varying the previous environment on life-history traits

Several life-history traits were significantly affected by the main factor 'Previous environment' (Table 1). For juvenile survival, two of the four comparisons (T- vs. C-lines on T, and P- vs. C-lines on C) were significantly affected by this factor. For these two comparisons, mites with a maternal environment corresponding to that of their selection regime had higher juvenile survival than mites with bean as a common maternal environment (Table 1; Fig. 2). The same pattern was found in the other two comparisons, although not significantly so (Fig. 2). For developmental time, the only comparison that yielded a significant effect of the previous environment was that between P- and C-lines on pepper, in which the developmental time was shorter when mites were in the selection environment (Tables 1 and 2). Oviposition rate was significantly affected by the previous environment for all comparisons except that

Table 1 Results of the analysis of traits at generation 15. We analysed specifically the comparisons that would allow to test for adaptation and its potential associated cost. P: pepper; C: cucumber; T: tomato. SR: selection regime; PE: previous environment; juvenile survival: average fraction surviving to adulthood; developmental time: time from egg to adult, in days; oviposition rate: mean oviposition rate in the first 12 days; longevity: average age of death. *F*: Fisher's *F*; dff: degrees of freedom of the factor tested; dfe: degrees of freedom of the error. Whenever the SR × PE interaction had a *P*-value higher than 0.25, the model without the interaction is given, and the significance of the interaction is given between brackets. *P*-values below 0.05 are highlighted in boldface. Only fixed effects are shown.

	Traits	Juvenile survival		Developmental time		Oviposition rate		Longevity	
Comparison	Previous environment	χ^2	*P*	$F_{dff,dfe}$	*P*	$F_{dff,dfe}$	*P*	$F_{dff,dfe}$	*P*
Adaptation									
P vs. C on P	SR	**3.98**	**0.046**	$F_{1,7} = 0.61$	0.46	$\mathbf{F_{1,8} = 10.47}$	**0.012**	$F_{1,4} = 0.17$	0.70
	PE	0.48	0.49	$\mathbf{F_{1,7} = 11.37}$	**0.012**	$\mathbf{F_{2,16} = 4.03}$	**0.038**	$\mathbf{F_{2,10} = 20.45}$	**0.0003**
	SR × PE	1.79	0.18	$F_{1,7} = 1.7$	0.23	$\mathbf{F_{2,16} = 4.00}$	**0.039**	($F_{2,8} = 0.76$)	(0.50)
T vs. C on T	SR	**23.00**	**<0.0001**	$F_{1,7} = 2.65$	0.15	$\mathbf{F_{1,7} = 6.38}$	**0.039**	$F_{1,5} = 1.52$	0.27
	PE	**13.46**	**0.0002**	$F_{1,7} = 0.67$	0.44	$\mathbf{F_{2,16} = 32.84}$	**<0.0001**	$\mathbf{F_{2,8} = 12.06}$	**0.004**
	SR × PE	(0.15)	(0.70)	($F_{1,7} = 0.01$)	(0.94)	($F_{2,14} = 0.41$)	(0.67)	($F_{2,6} = 0.32$)	(0.74)
Cost of adaptation									
P vs. C on C	SR	0.406	0.52	$\mathbf{F_{1,8} = 6.44}$	**0.035**	$F_{1,8} = 1.13$	0.32	$F_{1,4} = 2.78$	0.17
	PE	**3.89**	**0.049**	$F_{1,8} = 0.35$	0.57	$F_{2,18} = 2.93$	0.079	$F_{2,9} = 2.70$	0.12
	SR × PE	(0.22)	(0.64)	$\mathbf{F_{1,8} = 8.56}$	**0.019**	($F_{2,16} = 1.42$)	(0.27)	($F_{2,7} = 0.44$)	(0.66)
T vs. C on C	SR	**6.91**	**0.008**	$\mathbf{F_{1,7} = 5.92}$	**0.045**	$F_{1,7} = 1.00$	0.35	$F_{1,4} = 0.58$	0.49
	PE	3.64	0.057	$F_{1,7} = 1.07$	0.33	$\mathbf{F_{2,16} = 7.74}$	**0.0045**	$F_{2,9} = 2.13$	0.17
	SR × PE	**6.93**	**0.009**	($F_{1,7} = 0.77$)	(0.41)	($F_{2,14} = 0.37$)	(0.70)	($F_{1,7} = 1.42$)	(0.30)

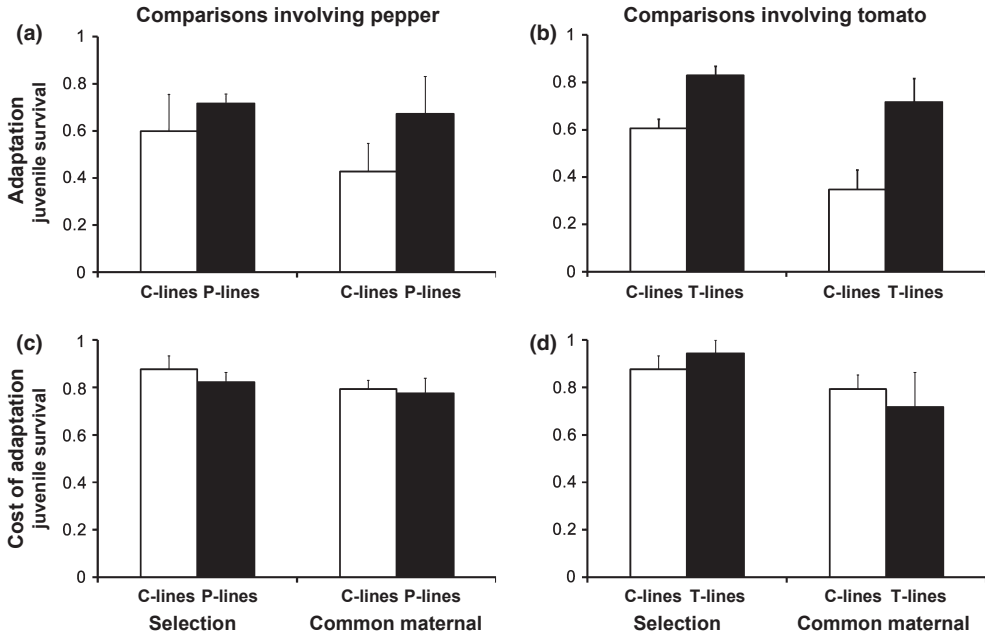


Fig. 2 Analysis of local adaptation for juvenile survival. (a, c): C-lines (white bars) vs. P-lines (black bars) on pepper (a) and cucumber (c). (b, d): C-lines (white bars) vs. T-lines (black bars) on tomato (b) and cucumber (d). Selection: all mites were reared in their selection environment; common maternal: all mites spent one generation on bean prior to testing. Shown is the proportion of individuals surviving to adulthood. Vertical bars correspond to standard errors among lines.

of P- and C-lines on cucumber (Table 1, Fig. 3). Overall oviposition rate was lower when mites had a common maternal environment (T- vs. C-lines on T, contrast common maternal vs. common juvenile: $F_{1,14} = 49.61$, $P < 0.0001$; common maternal vs. selection environment: $F_{1,14} = 37.52$, $P < 0.0001$; T- vs. C-lines on C,

Table 2 Developmental time and longevity (the traits that did not respond to selection) for all lines (mean ± standard error). Given are the values that allow to test for adaptation and its potential associated cost on each previous environment.

	Selection env.			Common juvenile environment			Common maternal environment		
Trait	C-lines	P-lines	T-lines	C-lines	P-lines	T-lines	C-lines	P-lines	T-lines
Developmental time									
On cucumber	15.9 ± 0.18	17.34 ± 0.06	16.98 ± 0.01	–	–	–	16.56 ± 0.1	16.4 ± 0.08	17.02 ± 0.18
On pepper	19.07 ± 1.68	17.04 ± 0.82	–	–	–	–	20.8 ± 0.31	20.51 ± 0.31	–
On tomato	18.6 ± 0.37	–	16.41 ± 0.38	–	–	–	19.51 ± 0.25	–	17.24 ± 0.72
Longevity									
On cucumber	36.08 ± 3.04	32.03 ± 1.38	35.41 ± 1.41	34.18 ± 1.95	39.38 ± 3.71	41.44 ± 2.92	33.45 ± 0.37	34.4 ± 3.14	33.06 ± 2.78
On pepper	41.14 ± 4.49	29.37 ± 1.47	–	24.97 ± 0.48	26.31 ± 1.33	–	34.88 ± 1.09	35.37 ± 2.17	–
On tomato	30.22 ± 3.04	–	31.93 ± 1.5	22.02 ± 1.56	–	23.73 ± 1.79	29.38 ± 3.29	–	34.7 ± 2.86

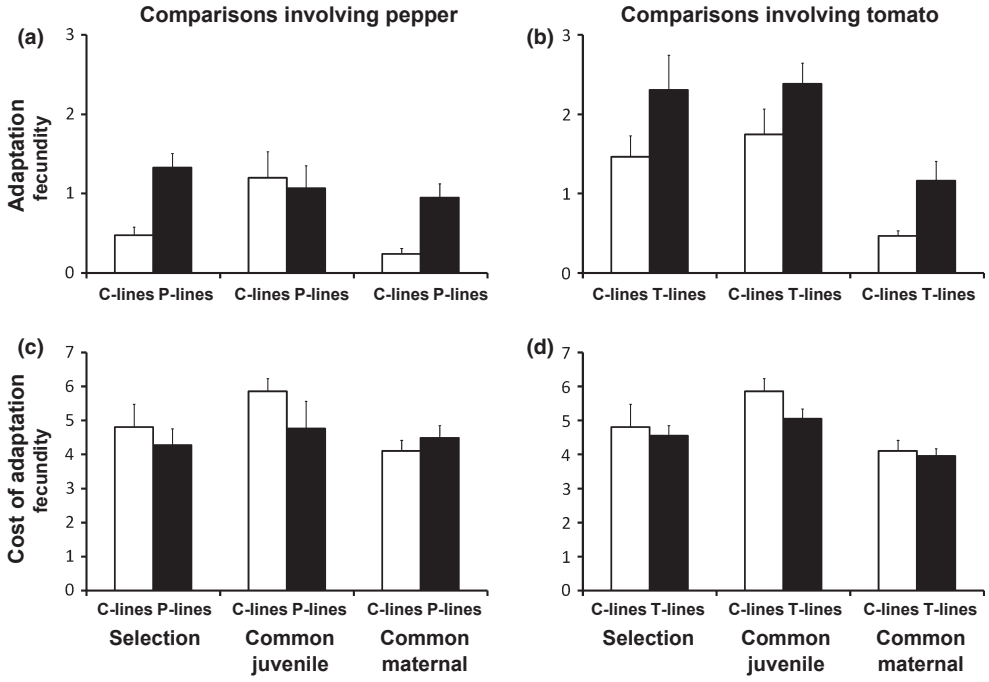


Fig. 3 Analysis of local adaptation for oviposition rate. (a, c): C-lines (white bars) vs. P-lines (black bars) on pepper (a) and cucumber (c). (b, d): C-lines (white bars) vs. T-lines (black bars) on tomato (b) and cucumber (d). Selection: all mites were reared in their selection environment; common juvenile: all mites were reared on bean as juveniles; common maternal: all mites spent one generation on bean prior to testing. Shown is the mean oviposition rate (number of eggs per day) during the first 12 days of egg laying. Vertical bars correspond to standard errors among lines.

contrast common maternal vs. common juvenile: $F_{1,14} = 55.79$; $P < 0.0001$; common maternal vs. selection environment: $F_{1,14} = 41.7$, $P < 0.0001$), although the difference was not always significant for the comparison P- vs. C-lines on pepper (P- vs. C-lines on P, contrast common maternal vs. common juvenile: $F_{1,16} = 7.82$, $P = 0.013$; common maternal vs. selection environment: $F_{1,16} = 3.33$; $P = 0.087$). In contrast, no differences were found between mites who had bean as a common juvenile environment and mites from the selection environment (contrast selection environment vs. common juvenile: P- vs. C-lines on P, $F_{1,16} = 0.94$, $P = 0.346$; T- vs. C-lines on T: $F_{1,14} = 0.84$, $P = 0.374$; T- vs. C-lines on C: $F_{1,14} = 1.02$, $P = 0.327$). For longevity, only the comparisons between T- and C-lines on tomato and between P- and C-lines on pepper were significantly affected by the previous environment (Table 2). Indeed, mites from the common juvenile environment had the shortest longevity (Table 2, contrast statement for the T- vs. C-lines on T comparison: common juvenile vs. common maternal: $F_{1,8} = 19.66$, $P = 0.002$; common juvenile vs. selection environment, $F_{1,8} = 15.47$,

$P = 0.004$; common maternal vs. selection environment: $F_{1,8} = 0.33$; $P = 0.582$).

Does the previous environment affect the detection of adaptation? (i.e. the effect of SR × PE on T or P)

Juvenile traits

Compared with lines evolved on the ancestral host (C-lines), lines evolved on the novel hosts (P-lines and T-lines) had higher juvenile survival on that host, irrespective of the previous environment experienced by the mites (Table 1, Fig. 2a,b). However, when adaptation was tested in each environment separately, we found that adaptation was not detected on pepper, irrespective of the previous environment ($\chi^2 = 2.12$, $P = 0.15$ and $\chi^2 = 1.55$, $P = 0.21$ for mites experiencing the selection and the common maternal environment, respectively). Developmental time on the novel hosts was not different between C-lines and P-lines on pepper, but the *P*-value for the interaction between selection regime and previous environment was < 0.25; hence, it was kept in the model. There were no significant differences among SR for developmental time on tomato, irrespective of the previous environment (Tables 1 and 2).

Adult traits

On pepper, the detection of adaptation in the oviposition rate was significantly affected by the previous environment (significant SR × PE, Table 1). Indeed, this trait was significantly higher in P-lines than in C-lines when mites were reared in their selection regime ($F_{1,16} = 8.09$, $P = 0.012$) or when they had a common maternal environment ($F_{1,16} = 10.19$, $P = 0.006$), but not when they had a common juvenile environment ($F_{1,16} = 0.19$, $P = 0.671$; Table 1; Fig. 3a,b). On tomato, there was no significant effect of the interaction between selection regime and previous environment. However, significant differences at the 5% level in oviposition rate among T-lines and C-lines were detected when mites were reared in a common maternal environment ($F_{1,14} = 6.29$, $P = 0.025$), whereas these differences were not significant or only marginally significant when they were reared in the other environments ($F_{1,14} = 4.15$, $P = 0.061$ and $F_{1,14} = 2.51$, $P = 0.135$ for mites from the selection and the common juvenile environment, respectively). No differences were found in the longevity of all lines in all environments, irrespective of the previous environment experienced (Tables 1 and 2).

Does the previous environment affect the detection of a cost to adaptation? (i.e. the effect of SR × PE on C)

Juvenile traits

On cucumber, juvenile survival did not differ between C-lines and P-lines, irrespective of the previous environment (Table 1; Fig. 2c,d). In contrast, the juvenile survival of mites from T-lines was higher than that of mites from C-lines when their mothers were reared on their selection host (i.e. the selection environment, $\chi^2 = 5.97$, $P = 0.015$), but not when their mothers were reared on bean ($\chi^2 = 0.94$; $P = 0.33$; Table 1; Fig. 2c,d). Mites from T-lines and P-lines developed more slowly than mites from C-lines when they were reared in their selection environment ($F_{1,8} = 12.23$, $P = 0.008$), but not when they experienced a common maternal environment ($F_{1,8} = 0.05$, $P = 0.128$; Tables 1 and 2). On tomato, the previous environment did not affect the detection of a cost of adaptation for developmental time (Tables 1 and 2).

Adult traits

No differences were found in the oviposition rate or in longevity of all lines in all environments, irrespective of the previous environment experienced (Tables 1 and 2; Fig. 3c,d).

Discussion

In this study, we measured adaptation in replicate selection lines of spider mites on tomato and on pepper. By varying the previous (maternal or juvenile) environments to which test individuals were exposed, we addressed the question of how these environments affect the detection of long-term adaptation. Overall, we found that the environment experienced by the mites affected the detection of adaptation (i.e. a significant previous environment × selection regime interaction) in approximately 20% of the comparisons we made.

Phenotypic plasticity and maternal effects

The environment experienced by the mites tested or by their mothers considerably affected the trait values on all selection regimes. Indeed, the offspring of mothers subjected to a common maternal environment (bean) had lower juvenile survival, longer developmental time and lower oviposition rate than the offspring of mothers from the selection environment (see Table 2). This suggests that maternal effects from mothers reared on pepper, tomato or cucumber led to higher performances on these hosts than maternal effects from mothers reared on bean. Hence, the maternal effects from one host plant were not only beneficial on that host plant, but also beneficial on other host plants. Other studies have also found that maternal effects from one environment can be beneficial in another (Stillwell & Fox, 2005). However, our result is surprising in the sense that bean is a high-quality environment for spider mites (Agrawal *et al.*, 2002; Pietrosiuk *et al.*, 2003; Gotoh *et al.*, 2004); hence, maternal effects were expected to lead to an increased performance of the offspring. In other organisms such as *Drosophila melanogaster* and *Daphnia magna*, maternal effects from environments of high quality have also led to a poorer performance of the offspring than maternal

effects from environments of low quality (Prasad *et al.*, 2003; Mitchell & Read, 2005). Hence, the quality of the habitat where mothers live is not necessarily correlated with the quality of the maternal effects that they transmit to their offspring.

When mites were reared in a common juvenile environment composed of bean, they had not only the highest oviposition rate of all treatments, but also the lowest longevity. This indicates that the environment experienced by juveniles might determine the variation of juvenile traits, which will then cascade down to the adult traits (Metcalfe & Monaghan, 2001; Rivero *et al.*, 2001; Tschirren *et al.*, 2009). Moreover, this result suggests that resource allocation to life-history traits in these mites varies with the environment that they experience as juveniles. There are at least two possible interpretations for this. First, it is possible that bean as a juvenile environment is indeed an environment of better quality than the other host plants and that investment in higher oviposition rate is the optimal strategy; hence, mites that developed on bean would benefit from the 'silver spoon effect' (Reid *et al.*, 2003; Monaghan, 2008). Above a certain threshold value, it may not be possible to increase oviposition rate without decreasing longevity (Sabelis, 1991), which would explain why populations raised on bean would have a lower longevity than others. In line with this hypothesis, it has been previously shown that longevity was not under selection in this system (Magalhães *et al.*, 2007a). Alternatively, it may be that different juvenile environments are of similar quality but induce a different pattern of resource allocation to each life-history trait, a pattern also found in other studies (Ellers & vanAlphen, 1997; Hellriegel & Blanckenhorn, 2002; Wilkin & Sheldon, 2009).

Environmental effects on the detection of adaptation

Of the 16 comparisons we made to detect adaptation or its associated cost, a significant interaction between selection regime and previous environment (SR × PE) was detected three times. However, it should be noted that discrepancies were found in two other cases when the interaction SR × PE was not significant. Namely, for juvenile survival on tomato, despite a nonsignificant SR × PE interaction (cf. Table 1), adaptation was detected when mites had a common maternal environment ($\chi^2 = 10.41$, $P = 0.001$) but not when they came from their selection environment ($\chi^2 = 2.27$, $P = 0.13$). This probably reflects a lack of statistical power. In those cases, it may be beneficial to test for adaptation using several previous environments, or by increasing the sample size in each environment, to increase the power of the analysis.

The number of discrepancies did not depend on the type of environments compared (common juvenile vs. selection or common maternal vs. selection environments). Moreover, differences among selection regimes were not preferentially detected in a particular environment. When for a given trait the main effect of the selection regime is significant and goes in the same direction whichever the previous environment, one can be confident that adaptive evolution has occurred. This was observed in the present study for juvenile survival between C-lines and either P-lines or T-lines in their respective novel environment and for oviposition between C-lines and T-lines on tomato (the significant interaction between previous environment and selection regime merely indicates that the magnitude of the difference varies with the previous environment). Conversely, when main effects of selection regimes on a trait are not significant irrespective of the previous environment, one can safely conclude that evolutionary change for this trait is unlikely to have occurred. In the present study, this was the case for longevity and developmental time of P- and T-lines on their respective host. Finally, when for a given trait there is no significant main effect of the selection regime, but there is a significant interaction between the selection regime and the previous environment, the decision on which previous environment to use, or which conclusion to draw, should be based on a biological reasoning.

Ideally, one should test adaptation in populations that have spent one or two generations in a common environment. This will ensure that all populations have undergone the same environmental manipulations prior to the test, which will magnify genetic differences among populations. However, even in this case, it is possible that environment-by-environment interactions (Rossiter, 1996) mask the detection of adaptation (that is, genotype-by-environment interactions). In this case, one should ensure that the common environment used is effectively neutral (i.e. it has the same effect in all populations), which is possible if in the populations used there is no genetic variance for fitness in that environment. This is, however, difficult to test experimentally. Another approach may be to test whether the reaction norm between the environments used in the selected lines and the common maternal environment used are parallel. This would ensure that introducing a common maternal environment before testing adaptation will not bias the detection of adaptation. However, using such a common maternal environment is not always possible, namely in organisms with long generations, such as several tree species. In that case, adaptation should be tested in several traits and preferably using several previous environments in order to increase the power of the analysis.

Consequences for host range evolution

We have previously shown that the host range of spider mites was expanded within a short timeframe (Magalhães *et al.*, 2007a, 2009). The results in this paper

indicate that mites exhibit high levels of phenotypic plasticity, in that their life-history traits are shaped by their maternal and juvenile environments. This plasticity may facilitate as well as hamper the initial establishment of populations in different environments (Jansen, 1985; Agosta, 2006). Our results show that maternal effects can indeed increase the performance of spider mites on their host plant; hence, they may foster the establishment of spider mites on a host similar to that of their mothers. However, the performance of spider mites on novel host plants was also positively affected by the maternal effects of mothers reared on other host plants (except for bean); hence, maternal effects do not necessarily favour host fidelity. On the other hand, when mites were reared on a host of good quality, their later oviposition rate on other hosts increased, which may also foster their establishment on novel host plants. Hence, most effects pertaining to the current environment experienced by mites detected in this study are expected to assist, rather than impede, host expansion. In addition, it has been shown before that spider mites pay no genetic cost of adaptation (Gould, 1979; Fry, 1990; Agrawal, 2000; Magalhães *et al.*, 2007a, 2009). In this context, it is important to notice that here we do find a slower developmental time of P-lines compared to C-lines on cucumber. However, we find this only when mites were reared in their selection environment, suggesting that this characteristic is not genetic but due to phenotypic plasticity. A lack of cost has also been found in other studies (Gould, 1979; Bell & Reboud, 1997; Caballero *et al.*, 2001; McCart *et al.*, 2005; Ahonen *et al.*, 2006; Lopes *et al.*, 2008). Therefore, our results suggest that there are as yet no intrinsic limits to spider mites being generalists. Thus, the occurrence of host races in natural populations (Tsagkarakou *et al.*, 1997; Weeks *et al.*, 2000; Magalhães *et al.*, 2007b) cannot at present be explained by a strong genetic trade-off in adaptation to different host plants or by limited phenotypic plasticity that would impede host colonization in the short term.

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