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ORIGINAL ARTICLE

Short-term population differences in the genetic architecture of life history traits related to sexuality in an aphid species

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One of the most important factors that determine the evolutionary trajectory of a suite of traits in a population is the structure of the genetic variance–covariance matrix (G). We studied the cyclically parthenogenetic aphid *Rhopalosiphum padi*, whose populations exhibit two types of reproductive lineages respectively specialized in sexuality (that is, cyclically parthenogenetic lineages) and in asexuality (that is, obligate parthenogenetic lineages). We compared the quantitative genetics of life histories in these two lineage types. Our results suggest that both, the elements and the whole structure of the resulting G matrices differ in the very short term, between lineage types. This would involve the evolution toward different evolutionary optima in the same population, depending on whether sexual or asexual lineages predominate. Since sexual and asexual lineages vary seasonally in their abundance, a fluctuating selective regime has been proposed for this species, which would contribute to the maintenance of the reproductive polymorphism that these populations exhibit.
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Introduction

One of the most important factors that determine the evolutionary trajectory of a suite of traits in a population is the structure of the genetic variance–covariance matrix (G) (Steppan *et al*., 2002). The genetic variances and covariances among traits define a set of constraints under which selection operates, and determine the evolutionary optima a population could attain (Begin and Roff, 2003; Jones *et al*., 2003; Begin *et al*., 2004). Also, the structure of the G matrix is itself modified by evolutionary forces such as selection, mutation and drift (Steppan *et al*., 2002; Begin and Roff, 2003; Jones *et al*., 2003). Hence, in a population the G matrix is the final result of a combination of ecological/evolutionary processes (Steppan *et al*., 2002; Begin and Roff, 2003). Empirical classical quantitative genetics (that is, analyzing one or two traits at a time), in general support this view (Falconer and Mackay, 1997; Roff, 1997; Lynch and Walsh, 1998), but the definite proof of G matrix explanatory power will become established after the existence of good empirical knowledge about the patterns of complex (that is, many traits) G matrix variation across populations, species, phenotypes and environments (Steppan *et al*., 2002; Begin and Roff, 2003).

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Clonal designs simplify greatly quantitative genetic experiments since the genetic variance for any quantitative trait can be readily estimated by partitioning the phenotypic variance into its within- and between-lineage components, and an analogous treatment is valid for genetic covariances between traits (Lynch and Walsh, 1998; Pfrender and Lynch, 2000). It is surprising, however, that only few quantitative genetic studies have been performed on clonal organisms (Lynch and Deng, 1994; Deng and Lynch, 1996; Pfrender and Lynch, 2000). One of these works explored the genetic (co)variance structure in life histories of an asexually reproducing aphid, *Myzus persicae* (Vorburger 2005). Unexpectedly, a total absence of evolutionary trade-offs was found between major life history traits across several asexually reproducing lineages, which in other words means that all life history traits can be maximized at the same time. Hence, considerable insight could be obtained using clonal organisms as model systems by exploring the G matrix of life histories (both its elements and the whole G matrix) across populations. For instance, genetic correlations between life history traits such as fecundity, male production and/or age at maturity could reveal evolutionary trade-offs (that is, negative genetic correlations) that appear during some conditions (Pfrender and Lynch, 2000). On the other hand, genetic correlations between life history traits and lineage mortality could reveal costs of a given strategy in a given moment. We explored this problem in the aphid *Rhopalosiphum padi* populations with coexisting lineages specialized either in cyclical or obligate parthenogenesis (Halkett *et al*., 2005). For that, we measured on a pool of cyclical parthenogens (here referred as 'sexual' lineages for sake of simplicity)

and obligate parthenogens (here referred as asexual lineages) of *R. padi* from a single area, sex-related traits that are only expressed under specific conditions (see the Methods section). These sexual and asexual lineages were representative of those found at a larger scale (for example, across the scale of France) as previous works showed that sexual lineages constitute panmictic populations over large geographic scales (Loxdale and Brookes, 1988; Simon *et al*., 1996; Delmotte *et al*., 2002) and that asexual lineages also could have a wide geographic distribution (Delmotte *et al*., 2002).

Given that ambient temperature have profound effects on insect life histories (Begin *et al*., 2004), here we compared quantitatively sexual and asexual lineages across two temperature regimes: (1) by determining how the reproductive status of these lineages affects their respective life history strategies, (2) by exploring how rearing temperature interacts with reproductive mode in its effects on life history means and (3) by assessing how the genetic (co)variances of life histories (broad-sense heritabilities and genetic correlations) varies between the two types of lineages.

Methods

Biological system

The aphid *R. padi* encompasses sexual and asexual lineages that can coexist in the same area, and are representative of both reproductive modes across the whole geographic range of *R. padi* (Simon *et al*., 1991; Rispe *et al*., 1999; Figure 1). The sexual lineages reproduce parthenogenetically in summer on many species of *Poaceae* including cereals, and sexual reproduction takes place on a winter-specific host, which is *Prunus padus* L. in Europe. In *R. padi* (and in the sexual lineages), the shift from parthenogenetic to sexual reproduction is triggered by decreasing day length and temperature (Dixon and Glen, 1971). Parthenogenetic females exposed to such stimuli produce gynoparae (parthenogenetic females that give birth exclusively to sexual females) then males, both of which fly to the winter host (Figure 1). Sexual females produced by gynoparae mate with males upon maturation and lay diapausing cold-resistant eggs. Asexual lineages reproduce continuously on summer hosts so that sexual and asexual lineages can be distinguished in winter and beginning of spring when living on separate hosts (Figure 1). Sexual and asexual lineages exhibit considerable genetic differentiation at several allozyme and microsatellite loci (Simon *et al*., 1996; Delmotte *et al*., 2002), although gene flow between these two has been detected at low level, probably mediated by the residual production of males in some asexual lineages (Halkett *et al*., 2005, 2006).

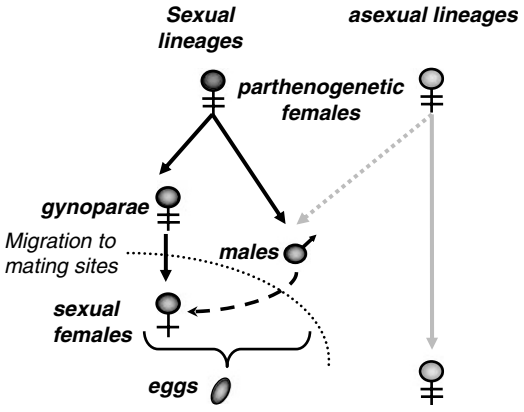

Figure 1 Life cycle variation in *Rhopalosiphum padi* (modified from Halkett *et al*., 2006). In 'sexual lineages', the life cycle encompasses several parthenogenetic generations and a single sexual one and is achieved on two types of hosts: the summer host, which involves many *Poaceae* species and the winter host, which is the bird cherry tree or *Prunus padus*. Rounds of parthenogenetic generations occur mostly during summer on *Poaceae*. By the end of summer, the production of sexual forms starts and involves gynoparae (that is parthenogenetic females that produce sexual females only) and males. Both forms then fly to winter hosts where sexual reproduction occurs and frost-resistant eggs are laid. Eggs hatch by the end of winter and after few parthenogenetic generations on the winter host, sexual lineages migrate to the summer hosts. In asexual lineages, the whole life cycle is completed on the summer hosts only. Hence, sexual and asexual populations are separated in winter by their host. Note that some asexual lineages are able to produce few males whose contribution to gene flow between sexual and asexual populations is unclear (dashed line).

Experimental protocol

Aphids were collected on individual trees of *P. padus*, in the vicinity of Rennes (Brittany, France). Each of these individuals was sampled on a distinct twig just after egg hatching. This sample was considered as containing the sexual lineages. In the previous winter, another sample of individuals was collected in the same local area in various fields of *Poaceae* (wheat, barley and oat). As these individuals were overwintering asexually on summer hosts, they were considered as asexual lineages. After collection, sexual and asexual lineages were isolated and reared under conditions ensuring continuous parthenogenetic reproduction (L:D 16:8, 20 °C). Each individual thus initiated a clonal line that was reared during six months (~20 generations) prior to biological experiments. After this period, each lineage was tested for its response to conditions that normally induce the production of sexual forms using standard methods (Simon *et al*., 1991). Under these conditions, sexual lineages are expected to produce gynoparae and males, while asexual lineages would produce mainly asexual forms although the production of males may also occur at some extent (Simon *et al*., 1991). Given that we were interested in the (co)variances of sex-related traits, we submitted each lineage to standard conditions for sex induction. These experiments were carried out using two replicated ambient temperatures (10 and 15 °C), while the photoperiodic regime was identical (L:D 12:12). Hence, we had a total of 43 sexual lineages per two temperatures with three replicates per treatment (~258 individuals) and 53 asexual lineages per two temperatures with three replicates per treatment (~318 individuals). In each of these focal individuals, and during sexual induction, we measured four life history traits: longevity (number of days elapsed from birth to death), fecundity (total number of individuals produced during lifetime), age at first reproduction (number of days elapsed from birth to the first offspring) and mortality (number of dead offspring during the life of the focal individual). In addition, we recorded the number of each type of morph (gynoparae, males or parthenogenetic females) in the

Table 1 Number of lineages and number of individuals assayed, corresponding to each combination of temperature and population

Treatment	*No. of lineages*	*Age (days)*	*Long (days)*	*Mort*	*Males*	*Fec*	*Part*	*Gyn*
Asexual, 10 °C	53	21.1 ± 0.18 (159)	76.3 ± 1.07 (159)	6.9 ± 0.35 (159)	6.5 ± 0.35 (159)	47.5 ± 1.04 (159)	34.2 ± 1.01 (159)	0 (159)
Asexual, 15 °C	55	12.7 ± 0.09 (165)	59.9 ± 0.91 (165)	3.27 ± 0.22 (165)	3.27 ± 0.22 (165)	66.7 ± 1.30 (165)	61.6 ± 1.52 (165)	0 (165)
Sexual, 10 °C	43	18.3 ± 0.20 (116)	69.6 ± 1.52 (122)	1.2 ± 0.14 (122)	12.3 ± 0.64 (122)	25.5 ± 0.80 (122)	0 (122)	12.0 ± 0.90 (122)
Sexual, 15 °C	43	9.5 ± 0.17 (112)	41.6 ± 1.03 (128)	3.3 ± 0.28 (128)	11.7 ± 0.62 (128)	27.1 ± 0.67 (128)	3.8 ± 0.38 (128)	8.2 ± 0.48 (128)

Abbreviations: Age, age at first reproduction; Fec, total number of individuals; Gyn, number of gynoparae; Long, longevity; Males, number of males; Mort, mortality (number of dead individuals in the whole progeny); Part, number of parthenogenetic females.

offspring of each female of *R. padi* lineages in response to sex-inducing conditions (Figure 1; Table 1).

Statistics I: quantitative genetic parameters

Common statistical analyses were performed using Statistica 6.0 software (StatSoft, 2001). Our breeding design based on clonal lineages, with the trait of interest assayed in the progeny, allowed us to estimate two variance components: G, the (broad-sense) genetic variance, and E, the specific environmental variance or residual variance. To account for the unbalanced design (that is, slightly different numbers of individuals per lineage), we used a restricted maximum likelihood-based method, the animal model (MTDFREML software) procedure (Boldman *et al*., 1995). Iterations were continued until the differences in successive likelihood were less than 0.00001. We iterated the analysis in the full model (GE) and several starting values were assayed to ensure the solution being actually a global maximum of the likelihood. Also we tested the pure environmental model by constraining the G parameter of the full model to zero, which gives a new likelihood value. The statistical significance of the G component was assessed using likelihood-ratio tests (LRT), where critical χ^2 is selected with degrees of freedom equal to the number of parameters dropped from the model (that is, d.f. = 1; $\chi^2_{crit} = 3.841$). Genetic covariances and correlations were estimated in a similar fashion, but including pairs of traits in a multivariate version of the animal model software (Boldman *et al*., 1995). We also present asymptotic standard errors (that is, their values should be considered just approximate since they are estimated based on large samples).

Statistics II: G matrices comparisons

We defined four experimental treatments according to the combinations of the two temperatures and the two types of lineages (sexual and asexual). The resulting G matrices were compared first by using the Flury hierarchical method. This procedure is a principal component approach to the comparison of matrices (Flury, 1988) whose application to G matrices was developed by Phillips and Arnold (1999). The method, based on maximum likelihood compares two or more matrices and determines their structural differences based on comparisons in a hierarchical fashion. This progression tests (following this order) (1) unrelated structure, indicating that matrices do not share any eigenvector, (2) partial common principal component, indicating that matrices share some eigenvectors, (3) common principal components, indicating that matrices share all eigenvectors, but not eigenvalues, (4) proportionality, indicating that matrices share all eigenvectors and eigenvalues all differing by the same constant and (5) equality, indicating that matrices share all eigenvector and eigenvalues. An LRT is calculated for each model against the model of 'unrelated structure' (the 'jump-up' approach, see Phillips and Arnold, 1999; Steppan *et al*., 2002). A randomization is performed to test the null hypothesis that the model fits the data significantly better than the unrelated structure. We performed 5000 randomizations, where in each iteration, lineages were randomly assigned to the group being compared. We used the software CPCrand (Phillips and

Arnold, 1999) to perform the Flury hierarchical comparisons applied to G matrices. Because the asexual lineages did not produce any gynoparae and the sexual lineages, reared at 10 °C did not produce any parthenogenetic females, we excluded these traits from the four G matrices that were compared (Table 1). We also compared the G matrices by the Jackknife–multivariate analysis of variance (MANOVA) method. This procedure, developed by Roff (2002, 2006) uses the Jackknife procedure to produce a distribution of pseudovalues of matrix elements within each group. These pseudovalues are produced by deleting each sampling unit (lineages, in this case) in turn. The final data matrix is arranged such that the columns comprise the pseudovalues of each covariance and the rows are the results of the deletion of a given lineage (Roff, 2006).

Results

Comparisons of means

Lineage means showed considerable intra-lineage variance, especially in mortality and male production. However, clear patterns of differentiation according to temperature and reproductive mode were evident in most traits, excepting longevity and mortality (Figures 2–4). Treatment comparisons showed a significant multivariate interaction between temperature and lineage type (Wilk's $\lambda = 0.586$; $F_{5,186} = 26.2$; $P < 0.001$, MANOVA). Univariate analyses of variance (ANOVAs) yielded significant interactions for longevity ($F_{1,190} = 23.1$; $P < 0.001$, ANOVA), mortality ($F_{1,190} = 70.0$; $P < 0.001$, ANOVA), male production ($F_{1,190} = 9.7$; $P = 0.002$, ANOVA) and fecundity ($F_{1,190} = 44.5$; $P < 0.001$, ANOVA). The only trait that presented a nonsignificant interaction between reproductive mode and temperature was age at first reproduction ($F_{1,190} = 0.98$; $P = 0.2$, ANOVA). The *post hoc* tests (Tukey) revealed that all groups differed significantly ($P < 0.05$) both in age at first reproduction and longevity (Figures 2 and 5). The Tukey comparison revealed that the sole groups that did not differ significantly ($P > 0.05$) in total fecundity (Figures 2 and 5) were sexual lineages at 10 °C compared with the same lineages at 15 °C. Nonsignificant differences among lineage type were found between temperature treatments for both parthenogenetic female and male production (Figures 3 and 5). For mortality, the sole pair of treatments that did not differ significantly ($P > 0.05$) was the comparison between lineage type, reared at 15 °C (Figures 2 and 5), suggesting that mortality was more affected by temperature than by lineage type. In sexual lineages, the number of gynoparae depended significantly on temperature (Figures 4 and 5). Overall, the means comparison (Figure 5) suggested that traits related with generation time (age at maturity, longevity) showed more effects of ambient temperature, whereas

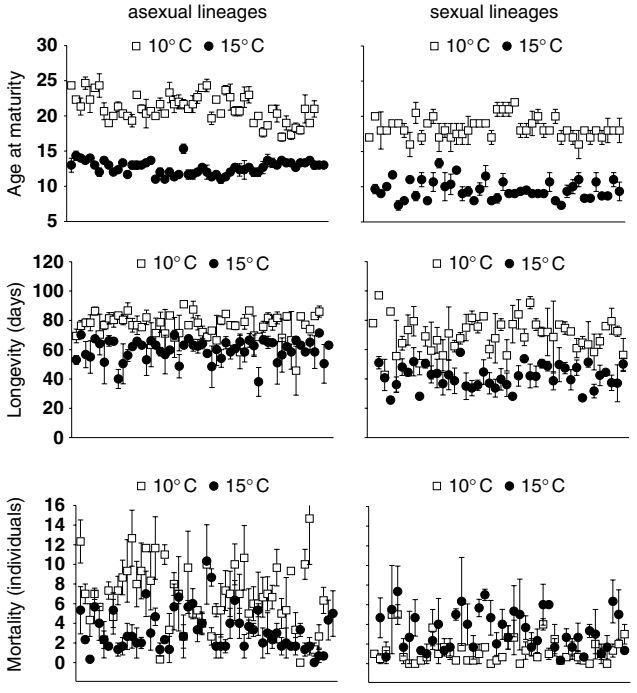

Figure 2 Lineage means (±s.d.) for age at maturity, longevity and mortality. Each symbol represents a different lineage raised either at 10 or 15 °C and obtained from either sexual or asexual populations.

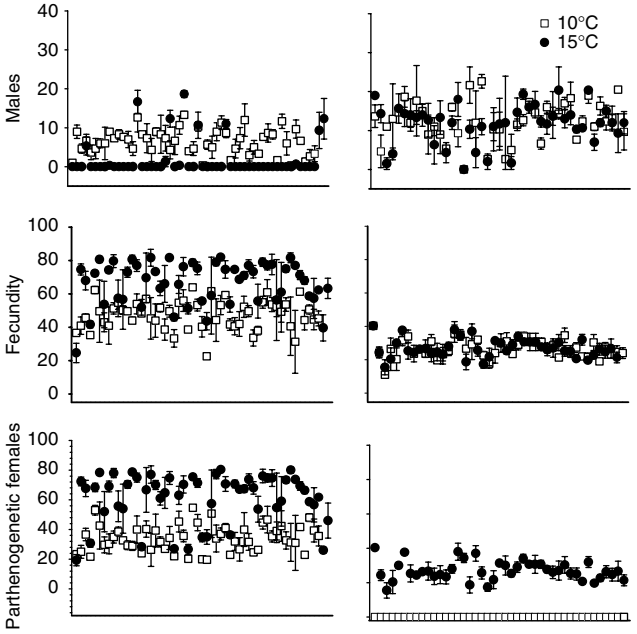

Figure 3 Lineage means (±s.d.) for male production, total fecundity and parthenogenetic female production. Each symbol represents a different lineage raised either at 10 or 15 °C and obtained from either sexual or asexual populations.

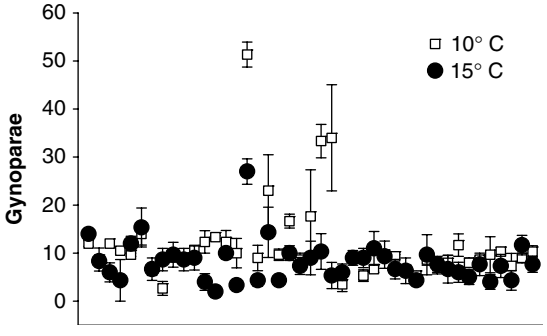

Figure 4 Lineage means (±s.d.) for gynoparae production. Each symbol represents a different sexual lineage raised either at 10 or 15 °C. In the asexual lineages, no gynoparae was produced.

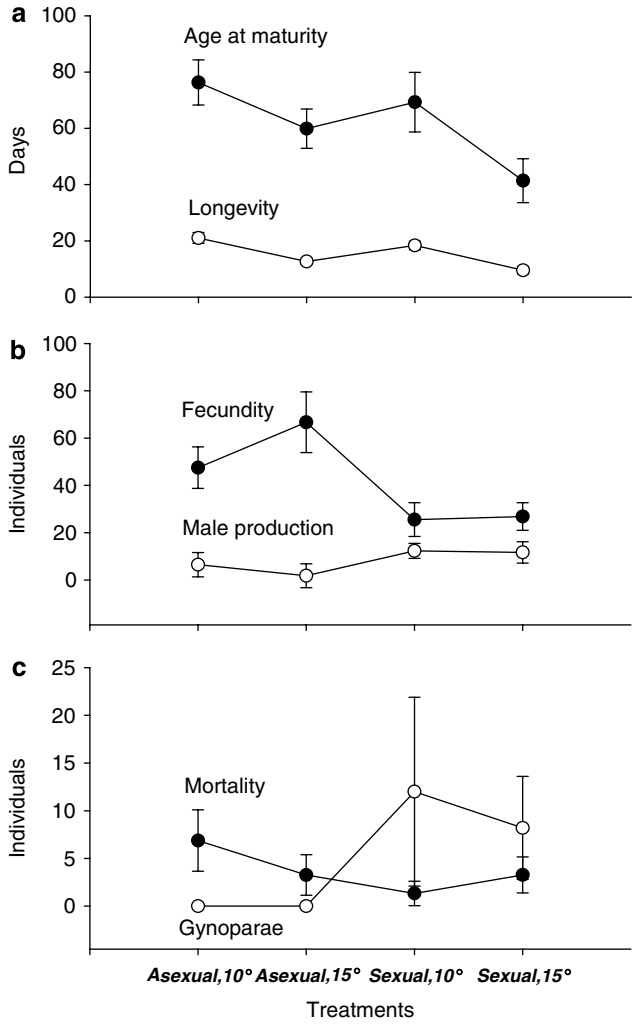

Figure 5 Means (± s.d.) comparisons across populations and temperature. (**a**) Traits related to generation time (age at maturity and longevity); (**b**) traits related with fecundity (total fecundity and male production) and (**c**) gynoparae production and mortality. Note that for asexual lineages, no gynoparae was produced and for sexual lineages there was no production of parthenogenetic individuals at 10 °C. Asexual, 10°, asexual lineages reared at 10 °C; Asexual, 15°, asexual lineages reared at 15 °C; Sexual, 10°, sexual lineages reared at 10 °C; Sexual, 15°, sexual lineages reared at 10 °C. See Figure 1 for details of the life cycle.

traits related with fecundity (production of different reproductive morphs) showed more effects of lineage type (Figure 5).

Broad-sense heritabilities and genetic correlations

Broad-sense heritabilities were significant in most cases, being nonsignificant for all populations only in longevity (Table 2). In general, both types of lineages exhibited similar heritabilities (Table 2). Several broad-sense genetic correlations resulted significantly different from 0 (Table 2). Genetic correlations indicated that sexual lineages with higher age at maturity also presented higher mortality. Also at 15 °C, sexual lineages with higher longevity also presented higher male production (Table 2). For the pool of asexual lineages, negative genetic correlations with mortality suggested that asexual lineages with higher production of parthenogenetic females had higher survival. In asexual lineages, total fecundity was largely influenced by parthenogenetic female production, as deduced from the large positive genetic correlation between both traits. On the other hand, the same reasoning on sexual lineages suggested that total fecundity was largely affected by gynoparae production (Table 2).

G matrices comparisons

Matrix comparisons by Flury's method and jump-up approach (that is, at each step in the hierarchy, the hypothesis is tested against the hypothesis of unrelated structure) showed significant departure from equality hypothesis (LRT = 291.1, $P < 0.0001$) and from proportionality hypotheses (LRT = 273.7, $P < 0.0011$), but not from common principal components hypothesis (LRT = 29, $P = 0.24$), which suggests that the matrices differ but share their principal component structure. The G matrices comparison through the Jackknife–MANOVA methods showed that the two types of lineages differ significantly (Wilk's $\lambda = 0.68$; $F_{45,524} = 1.59$; $P < 0.01$). Temperature did not significantly affect matrices neither in sexual lineages (Wilk's $\lambda = 0.86$; $F_{15,70} = 0.75$; $P = 0.72$), nor in asexual ones (Wilk's $\lambda = 0.78$; $F_{15,92} = 1.70$; $P = 0.07$). After pooling data collected under the two temperature regimes, the comparison between the sexual lineages and the asexual lineages matrices was significant (Wilk's $\lambda = 0.51$; $F_{15,178} = 11.23$; $P < 0.001$). The whole MANOVA (that resulted from the four matrices comparison) remained significant: (1) after excluding only the sexual lineages raised at 10 °C: Wilk's $\lambda = 0.70$; $F_{30,268} = 1.73$; $P = 0.013$ and (2) after excluding only the sexual lineages raised at 15 °C: Wilk's $\lambda = 0.69$; $F_{30,268} = 1.79$; $P = 0.009$). However, after performing the same procedure (that is, to remove one combination population/temperature at a time) in the asexual lineages, results changed to nonsignificant when excluding sexual lineages raised at 10 °C: Wilk's $\lambda = 0.76$; $F_{30,248} = 1.22$; $P = 0.21$ and after excluding the asexual lineages raised at 15 °C: Wilk's $\lambda = 0.75$; $F_{30,244} = 1.24$; $P = 0.19$.

Discussion

The published empirical works dealing with comparative quantitative genetics (sensu Steppan *et al*., 2002) remain scarce and restricted to a few model organisms. In a growing progression of complexity, G matrices of wild species have been studied first by estimating and interpreting its components on morphological and life history traits (that is, 'classical' quantitative genetics: Cheetham *et al*., 1994, 1995; Vorburger, 2005; Akimoto, 2006); second, by including physiological traits but in a single population (Caruso *et al*., 2005; Nespolo *et al*., 2005); third, by including and comparing two or more populations but restricted to morphology and life histories (Pfrender and Lynch, 2000; Begin *et al*., 2004). New levels of complexity have been handled by studies that analyzed two or more species (Begin and Roff, 2003), studies that compared the neutral (molecular) level of divergence with the quantitative genetic divergence through G matrix comparison (also in morphology and life histories, see Lynch *et al*., 1999; Cano *et al*., 2004), and studies that included complex traits such as geometric

Table 2 Broad-sense heritabilities and genetic correlations among life history traits (±asymptotic s.e.) of sexual and asexual lineages of *Rhopalosiphum padi*

	Asexual lineages		*Sexual lineages*	
	10 °C	*15 °C*	*10 °C*	*15 °C*
Age	**0.53 ± 0.08*** (550.0)**	**0.45 ± 0.09*** (103.0)**	0.09 ± 0.10 (0.3)	**0.39 ± 0.10*** (35.0)**
Age—Long	**0.08 ± 0.02* (4.2)**	0.66 ± 0.60 (0.9)	−0.68 ± 1.30 (1.4)	−0.16 ± 0.38 (1.1)
Age—Mort	0.02 ± 0.22 (1.2)	−0.12 ± 0.21 (0.2)	**0.99 ± 0.24*** (129.0)**	0.46 ± 0.50 (1.0)
Age—Males	−0.12 ± 0.21 (2.3)	0.20 ± 0.16 (1.21)	−0.32 ± 0.37 (1.6)	0.24 ± 0.27 (0.1)
Age—Part	−0.32 ± 0.23 (1.0)	−0.12 ± 0.18 (0.01)	—	0.10 ± 0.23 (1.7)
Age—Fec	**−0.41 ± 0.25*** (791.7)**	−0.11 ± 0.20 (0.02)	0.56 ± 0.47 (1.9)	−0.37 ± 0.25 (3.0)
Age—Gyn	—	—	0.68 ± 0.57 (2.2)	−0.38 ± 0.22 (2.7)
Long	0.03 ± 0.08 (1.9)	0.05 ± 0.08 (0.01)	0.08 ± 0.10 (0.8)	0.12 ± 0.10 (1.8)
Long—Mort	0.34 ± 0.77 (2.0)	−0.02 ± 0.59 (0.09)	−0.68 ± 0.74 (0.6)	0.02 ± 0.74 (0.1)
Long—Male	0.52 ± 0.63 (1.1)	0.40 ± 0.56 (0.8)	0.05 ± 0.65 (0.01)	**0.78 ± 0.26*** (49.0)**
Long—Part	−0.06 ± 0.96 (0.5)	−0.10 ± 0.50 (0.1)	—	0.02 ± 0.36 (0.5)
Long—Fec	0.40 ± 0.64 (0.1)	−0.10 ± 0.55 (0.9)	0.17 ± 0.41 (0.8)	0.47 ± 0.33 (1.0)
Long—Gyn	—	—	0.18 ± 0.40 (0.9)	−0.27 ± 0.39 (0.3)
Mort	**0.29 ± 0.09*** (55.0)**	**0.43 ± 0.14*** (13.0)**	**0.36 ± 0.12*** (35.0)**	0.08 ± 0.09 (0.1)
Mort—Male	**0.61 ± 0.21*** (742.8)**	**0.73 ± 0.12*** (58.0)**	−0.21 ± 0.28 (1.1)	−0.48 ± 0.48 (0.8)
Mort—Part	**−0.53 ± 0.24* (4.5)**	**−0.78 ± 0.11*** (31.0)**	—	0.41 ± 0.45 (1.9)
Mort—Fec	0.13 ± 0.32 (0.1)	−0.06 ± 0.31 (0.01)	0.07 ± 0.26 (0.3)	0.27 ± 0.49 (1.1)
Mort—Gyn	—	—	0.06 ± 0.23 (0.8)	0.19 ± 0.45 (0.1)
Male	**0.29 ± 0.09** (5.9)**	**0.75 ± 0.09*** (99.0)**	**0.27 ± 0.10*** (39.0)**	0.25 ± 0.10 (3.5)
Male—Part	−0.40 ± 0.28 (0.33)	**−0.82 ± 0.07*** (121.0)**	—	0.33 ± 0.24 (0.9)
Male—Fec	0.27 ± 0.30 (0.5)	0.25 ± 0.25 (0.1)	−0.41 ± 0.29 (3.1)	0.31 ± 0.27 (0.9)
Male—Gyn	—	—	**−0.73 ± 0.15*** (51.0)**	−0.27 ± 0.27 (1.5)
Part	**0.22 ± 0.09* (3.9)**	**0.58 ± 0.07*** (88.0)**	—	**0.45 ± 0.09*** (109.0)**
Part—Fec	**0.73 ± 0.14*** (68.0)**	**0.96 ± 0.02*** (401.1)**	—	0.33 ± 0.24 (1.9)
Part—Gyn	—	—	—	−0.21 ± 0.22 (2.1)
Fec	0.16 ± 0.09 (0.011)	**0.39 ± 0.08*** (41.1)**	**0.46 ± 0.10*** (48.0)**	**0.28 ± 0.10*** (15.0)**
Fec—Gyn	—	—	**0.91 ± 0.06*** (120.0)**	**0.51 ± 0.20*** (34.0)**
Gyn	—	—	**0.67 ± 0.10*** (31.0)**	**0.40 ± 0.10*** (51.0)**

Abbreviations: Age, age at first reproduction; Fec, total number of individuals; Gyn, number of gynoparae; Long, longevity; Males, number of males; Mort, mortality (number of dead individuals in the whole progeny); Part, number of parthenogenetic females.
Significant values are indicated in bold, after a likelihood-ratio test with 1 degree of freedom (χ^2 values are presented in parenthesis with: *$P<0.05$; **$P<0.01$ and ***$P<0.001$).

morphometrics in the G matrix comparison (Monteiro *et al*., 2002). Altogether, these works suggest that the structure of the G matrix is considerably stable over ecological time. However, given that sexual reproduction is the commonest mode of reproduction in metazoans, the evidence for the stability of G matrices has been obtained mostly from sexually reproducing organisms. Contrasting with previous studies, we found that in cyclically parthenogenetic organisms, the reproductive mode can provoke large differences in the genetic architecture of life histories at small temporal and spatial scale.

Previous genetic analyses of *R. padi* populations have revealed that they are composed by a variable proportion of sexual and asexual lineages coexisting in space at least during one season (Delmotte *et al*., 2003; Halkett *et al*., 2005, 2006). Phylogenetic and population genetic studies also showed that asexual lineages originated recently through various mechanisms leading to loss of sex in the sexual lineages (Simon *et al*., 2002; Delmotte *et al*., 2003). The higher viability of sexual lineages conferred by their ability to produce eggs resistant to frosts, together with the overwhelming growth rate of asexual lineages (Halkett *et al*., 2006), potentially explain the maintenance of this polymorphism in time as a dynamic adaptive landscape (sensu Wright, 1988). During very harsh winters, the extinction of asexual lineages is not unlikely as they are susceptible to low temperatures. Similarly, competitive displacements of the sexual lineages by asexual ones could also lead to extinction of the former. What avoids local extinction of one reproductive mode is probably the gene flow between sexual and asexual populations mediated by males frequently produced by asexual lineages (Halkett *et al*., 2005). Our computed genetic correlations provide an additional piece of information regarding the maintenance of these reproductive strategies. Although male production is an enhanced property of sexual lineages, male production exhibited significant heritabilities in both sexual and asexual lineages, indicating an evolutionary potential in this trait. This suggests that a range of reproductive strategies exists in between the two extremes corresponding to pure asexual and sexual reproduction. Most theoretical models consider only these two alternative reproductive strategies, on which general hypotheses on the maintenance of sex have been drawn. Here we add a new level of complexity as we found aphid lineages specialized in different levels of sex and gender investment. The full understanding of the factors maintaining sexual/asexual polymorphism in aphids would be benefited by considering a more quantitative variation in reproductive modes.

Also, in asexual lineages, mortality was negatively, genetically correlated with parthenogenetic female production and positively, genetically correlated with male production. In other words, asexual lineages that produced more parthenogenetic females exhibited substantial less mortality than those that produced more

males. This would be interpreted as a net selective advantage for asexual lineages. However, similar negative genetic correlations were absent in sexual lineages. Then, in terms of mortality there is a clear disadvantage of sex investment (through male production) for asexual lineages, but in the sexual lineages the few parthenogenetic offspring they produced when responding to inducing conditions do not appear to exhibit higher mortality.

Recombination is one of the most influential factors in genetic variances and covariances and the simplest rationale predicts that in a sexual population, genetic (co)variances should be higher (compared with a coexisting, simultaneous asexual population) because of higher recombination rate. The evidence from cyclically parthenogenetic organisms, however (that is, with both sexual and asexual reproduction) is contradictory (Lynch and Deng, 1994; Deng and Lynch, 1996; Via and Shaw, 1996; Pfrender and Lynch, 2000). The effects of sexual/asexual reproduction in the genetic (co)variances do not always follow the simple expectation of increase in genetic variation. Sometimes, clonal selection actually promotes the favorable combinations of alleles, increasing genetic disequilibria in the population which are disabled after sexuality (for example, Spitze *et al*., 1991; Deng and Lynch, 1996; Pfrender and Lynch, 2000). Hence, the identification of the precise causes of the differences that we detected in life history G matrices can be attributed either to the reproductive mode or to its consequences in the population (for example, selection), an issue that warrants further research.

There was also a differential effect of ambient temperature on life history means: Although generation time appeared to be equally affected by temperature both in sexual and asexual populations, fecundity appeared to be affected by temperature only in the asexual population. It is well known that rearing temperatures exert profound influences on ectotherms life histories (Berrigan and Charnov 1994; Sibly and Atkinson 1994; Huey *et al*., 1995; Madsen and Shine 1999). However, its effects on the genetic architecture are less known (Begin *et al*., 2004). Our results suggest that temperature did not have important effects on G matrices either directly or by interacting with lineage type.

According to Vorburger (2005), the absence of negative genetic correlations among life histories of asexual lineages of the aphid *M. persicae* represents a paradox. These findings contrast with our results, as we found significant and large negative genetic correlations (that is, age at maturity with fecundity, male production and parthenogenetic female production, fecundity and parthenogenetic female production and, fecundity and gynoparae production). Moreover, our results suggest that these genetic correlations are exceptionally labile: they can change both in magnitude and in sign at different temperatures and sexual/asexual lineages. The ultimate consequences of reproductive mode and ambient temperature can thus modify the structure of the G matrix and its elements, showing that both evolutionary trades-offs (negative genetic correlations) and evolutionary potentials (heritabilities and positive genetic correlations) can vary in the very short scale. Further research is needed to assess to what extent these G matrices are affected by nonadditive genetic variation and how genetic variance is differently expressed under different environmental conditions.

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