

Heritability of defence and life-history traits in the two-spotted spider mite

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ABSTRACT

Background: Two-spotted spider mites hide against predatory mites in a web of self-produced sticky silk. The proteins invested in this shelter may reduce investment in reproduction.

Questions: Do spider mite populations harbour genetic variation for web production, thereby enabling a response to selection by predation? Is adaptation affected by genetic trade-offs with life-history traits? The data were also used to test a central hypothesis in quantitative genetics, that heritability indicates a trait's importance for fitness and is positively correlated with the amount of additive genetic variation across traits.

Method: Using a mother–daughter breeding design, we determined the narrow-sense heritability and coefficients of additive genetic and residual variation (CV_A and CV_R) for web production and six life-history traits. In addition, we examined correlations between heritable traits for genetic trade-offs.

Conclusions: Web production exhibited heritability of 50% and a high CV_A . Thus, web production is not a fixed defence-related trait, and probably has the potential to evolve. Two life-history traits (oviposition rate and total adult offspring) revealed significant heritable variation. Results were inconclusive regarding genetic trade-off with web production. The life-history data demonstrate a positive relationship between heritability and CV_A , which supports the hypothesis that the relationship of traits with fitness influences their amount of heritable variation.

Keywords: elimination-selection hypothesis, *Tetranychus urticae*, trade-off, variance compounding.

INTRODUCTION

Most species of spider mites in the subfamily Tetranychinae produce silken threads, but the quantity produced and the way in which silk is used differ markedly among species (Saito, 1985). The two-spotted spider mite, *Tetranychus urticae*, has one of the highest rates of silk production, spinning silken threads whenever it moves around (Saito, 1985). The adults and their offspring live within the web, which has been shown to be successful as a defence

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against predatory mites (Sabelis, 1985; Sabelis and Bakker, 1992). The sticky and chaotic web impedes the movement of predatory mites, which may even become stuck and die. Some predator species cannot enter an area with *T. urticae* webbing (such as *Amblyseius andersoni*), whereas others (such as the specialist predator of *T. urticae*, *Phytoseiulus persimilis* Athias-Henriot) are less hindered unless the web has become very dense, which occurs when spider mites over-exploit their host plant (Sabelis, 1985).

We assume that the fitness effects of producing silk depend on the level of predation. Thus, when predation is high, good defensive abilities will contribute greatly to individual fitness. Hence, selection on web production may be strong. The first question to arise is whether there is potential for web production to evolve. A second, related question is whether the evolution of web production is influenced by genetic trade-offs. The production of silk to create a web requires mites to metabolize large amounts of amino acids (Hazan *et al.*, 1975). Given the limited amount of resources an individual can procure and utilize, production of silk may come at a cost to other fitness-determining traits, such as growth and reproduction. Amino acids are metabolized via different biochemical pathways. The determination of the flux of amino acids through these pathways may have a genetic basis and this may generate a genetic trade-off between traits (Zera and Zhao, 2006).

The questions above can be addressed by a quantitative genetic approach (Falconer and Mackay, 1996). To address whether web production has the potential to adapt to predation pressure, we assessed the similarity between parent and offspring and calculated two measures of the amount of additive genetic variation (V_A) in the population: the narrow-sense heritability and the coefficient of additive genetic variation. The narrow-sense heritability, h^2 , estimates the share of the phenotypic variation in a population that is additive genetic and thereby the potential strength of a response to selection (Falconer and Mackay, 1996), since selection acts on the total phenotypic variation, whereas adaptation emerges from selection on genetic variation only. The coefficient of additive genetic variation, CV_A , estimates V_A scaled by the trait mean, which enables comparison between traits (Houle, 1992). To examine the second question, whether genetic trade-offs exist between web production and life-history traits, the correlations between traits with heritable variation were determined (Falconer and Mackay, 1996).

A final issue that we investigated relates to a controversy in quantitative genetics about the relationship between fitness and V_A (Stirling *et al.*, 2002). Classical theory states that natural selection shapes the amount of V_A of a trait: if a trait is important for fitness, selection acts strongly on that trait and consequently erodes much of the V_A in the population (Falconer and Mackay, 1996). In that case, across traits both heritability and CV_A are negatively correlated with the trait's importance for fitness and positively correlated to each other. This mechanism is known as the 'elimination-selection hypothesis' (Stirling *et al.*, 2002). In contrast, the amount of V_A in a trait can also be shaped by how integrated the trait is (Price and Schluter, 1991; Houle, 1992). This so-called 'variance compounding hypothesis' (Stirling *et al.*, 2002) states that a trait further down the causal pathway from genes to phenotype (Price and Schluter, 1991) (and thus more highly integrated) accumulates more genetic variation and also more environmental variation. However, how integrated the trait is affects V_A less than it affects the residual variation V_R (e.g. Houle, 1992; Kruuk *et al.*, 2000; Merilä and Sheldon, 2000), which incorporates both environmental variation and the non-additive genetic variation. Since $h^2 = V_A / (V_A + V_R)$, this results in a lower heritability for traits that are more highly integrated. Thus, according to the variance compounding hypothesis, greater integration leads to a higher CV_A (and a higher coefficient for residual variation, CV_R) but a lower h^2 . Consequently, h^2 and CV_A are

negatively correlated. We evaluated the relationships between h^2 and CV_A and CV_R across traits of the two-spotted spider mite to assess the role of variance compounding and selection in shaping the genetic architecture of this population.

MATERIALS AND METHODS

Tetranychus urticae was collected in the dunes of Castricum in the Netherlands in July 2005. More than 150 females were collected from spindle shrubs (*Euonymus europaeus*), along a 50-m transect. These females were used to establish a laboratory population in a climate room at 23°C, 60% humidity, and a 16:8 h light/dark photoperiod. Mites were reared on the first leaves of common bean (*Phaseolus vulgaris*), placed flat on wet cotton wool on top of water-soaked sponges. Common bean is a very suitable host plant for *T. urticae* (Helle and Sabelis, 1985; Agrawal *et al.*, 2002). The experiment began when the spider mites had been reared in the laboratory for three generations.

Web quantification

Adult females were placed on bean leaf discs (1.5 cm diameter), 24 h before the experiment. The leaf discs were punched from the first leaves of 2-week-old bean plants with the main vein of the leaf in the centre of the disc. Only two discs were punched from a leaf, nearest to the starting point of the vein. This was done to ensure that leaf discs had veins of similar size and structure. *Tetranychus urticae* uses protrusions on the leaf surface to attach silk, thereby creating a three-dimensional structure of the web. By using flat leaf discs with similarly structured veins, the conditions for web formation were standardized among females.

After 24 h, approximately 500 sand particles [of equal shape and size (63–90 μm)] were sprinkled over the surface of each leaf disc, using a fine brush. The three-dimensional structure of the web ensures that some particles land on and stick to the silk, whereas others end up on the leaf surface. The numbers of particles on the leaf surface and attached to the silken threads of the web were counted. Here, web production is defined as the ratio of the number of particles in the web to the total number in the web and on the leaf surface. This estimate is related to the amount of web: since more females produce more webbing, we examined the relationship between number of females (1, 3 or 5) and the index of web production. A linear regression of web production on the number of females produced a significant, positive relationship ($F_{1,35} = 57.6$, $P < 0.001$) with a high degree of fit ($R^2 = 0.62$) (N.S.H. Tien, data not shown).

Heritability experiment

The heritability of six life-history traits (oviposition rate, development rate, juvenile survival and number of adult sons, daughters, and total offspring) and web production were determined using a single-parent, single-offspring design. The trait values were measured in mothers and daughters and linear regression was used to determine the heritability (Falconer and Mackay, 1996). The experiment was carried out in two blocks. A cohort of eggs was created from about 60 females that laid eggs on a bean leaf for a period of 24 h. Thereafter, the females were removed and their offspring maintained on leaf discs in the climate room. Individual females (the ‘mothers’) aged 14 days (age in days since egg deposition) were

placed on leaf discs and left there for 24 h to allow them to lay eggs and produce web. After this time, the amount of web was quantified and the eggs counted. The females were placed on a new (upside facing up) leaf disc for 24 h, after which they were removed. For these offspring, we determined development rate, juvenile survival, and number of adult offspring. The number of individuals per stage (egg, larva, protochrysalis, protonymph, deutochrysalis, deutonymph, teleiochrysalis, and adult) was counted on day 12. Females in the teleiochrysalis stage were isolated with two unrelated males to mate. On day 13, most individuals were either adult or teleiochrysalis, at which stage sex can be determined. If uncertainty remained, individuals were maintained until mature so that sex could be determined unambiguously. On day 14, one adult female (the ‘daughters’) was collected per mother and all measurements were repeated with these females.

Web production is quantified as the fraction of sand particles caught in the web produced in 24 h. Oviposition rate is quantified as the number of eggs produced in the same period. Juvenile survival is the fraction of eggs that survive to day 13 [i.e. up to the stage of deutonymph, of which at least 99% survive to adulthood (N.S.H. Tien, unpublished data)]. Development rate is calculated similar to Egas and Sabelis (2001): the stages are numbered (egg = 1, protochrysalis = 2, protonymph = 3, deutochrysalis = 4, deutonymph = 5, teleiochrysalis = 6, and adult = 7) and the development rate is the average stage number of the offspring reached on day 12.

Heritability and covariance statistics

All analyses were performed using the software ‘R’ (R Development Core Team, 2006). Heritability is determined by performing a linear regression on the trait value of the daughter, with the trait value of the mother and the blocks as explanatory variables. Heritability is calculated as: $h^2 = 2b$, where b is the slope of the regression on the trait value of the mother. The standard error of the heritability is: $\text{s.e.}(h^2) = 2\text{s.e.}(b)$ (Roff, 1997). The P -value of the heritability is calculated by removing the explanatory variable ‘mother’ from the model and comparing the two models using an F -test.

The traits were analysed using linear regression, with a normal error distribution. However, juvenile survival and web production are fractions and therefore do not comply with the assumptions of a normal error distribution. To confirm the probability estimates of the regression model, these traits were also analysed with logistic regression and a (quasi)binomial error structure. Two other traits, the number of sons and development rate, also did not comply with the assumptions of a normal error distribution. Therefore, the number of adult sons was also regressed with a Poisson error distribution and development rate was re-analysed using a Kruskal-Wallis test.

The coefficients for additive genetic variation and residual variation were calculated as: $CV_A = 100\sqrt{V_A}/\bar{x}$ and $CV_R = 100\sqrt{(V_P - V_A)}/\bar{x}$, where \bar{x} = the trait mean and $V_A = h^2 V_P$ (Houle, 1992). If $h^2 < 0$, then both h^2 and CV_A are set to 0 (as in Houle, 1992).

Only for traits with (marginally) significant heritability did we investigate the genetic correlation with other heritable traits (Schwaegerle and Levin, 1991). The covariance of one trait in the daughter and the other trait in the mother, and vice versa, was examined by determining the Pearson’s correlation coefficient. If there is a significant and negative correlation in both directions, an index for the genetic trade-off can be calculated, as in Falconer and Mackay (1996, Ch. 19). However, no such correlations were found in our data set.

For the tests regarding both heritabilities and the correlation coefficients, a power analysis was performed. The power of the test was $1 - \beta_{(1)}$, where $\beta_{(1)}$ is the probability of the normal deviate $Z_{\beta(1)} = (z - z_\alpha) \sqrt{n - 3}$ (Zar, 1999, Ch. 19). For determining the power of the regressions (for calculating the heritabilities), the correlation coefficient r was extracted from the results of the two-factor regression model (Zar, 1999, Ch. 17).

RESULTS

The linear mother–daughter regression of web production was nearly significant and led to an estimate of the narrow-sense heritability, h^2 , of 0.50 (s.e. = 0.28, $P = 0.08$) (see Table 1). The regression of juvenile survival was significant ($P = 0.002$), but examination of the distribution of residuals revealed an outlier. When re-analysed with a Kruskal-Wallis test, which is more robust to outliers (Quinn and Keough, 2006), the relationship was no longer significant ($\chi^2 = 18.2$, d.f. = 13, $P = 0.15$). Also, by removing this outlier in the logistic regression, significance was lost (from $P < 0.001$ to $P = 0.30$). Therefore, although the cause for this outlier was unknown, the heritability of juvenile survival was calculated from data excluding the outlier. Consequently, the heritability was not significant ($h^2 = 0.22 \pm 0.26$, $P = 0.42$; Table 1) and the power of the regression model was high ($1 - \beta = 0.93$). The estimates of heritability for both development rate and number of adult sons were negative ($h^2 = -0.20 \pm 0.34$ and $h^2 = -0.26 \pm 0.18$, respectively) and non-significant, but the power of the regressions regarding each trait was low (Table 1). Significant heritability was found for oviposition rate ($h^2 = 0.75 \pm 0.23$, $P = 0.002$) and the total number of adult offspring ($h^2 = 0.46 \pm 0.22$, $P = 0.04$). Nearly significant heritability was observed for number of adult daughters ($h^2 = 0.32 \pm 0.18$, $P = 0.09$). Linear regression with a normal error distribution and alternative statistical models that were more appropriate for the data (see Materials and Methods) revealed similar P -values for all traits (Table 1).

Most relationships between web production and life-history traits were (slightly) negative, whereas all relationships among the life-history traits were positive (Table 2). Most correlations between traits were non-significant, but the power of analysis for almost all combinations was too low ($\beta < 0.5$) to reject the presence of genetic correlations. Positive coefficients were found to be (marginally) significant in both mother–daughter and daughter–mother correlations (see Table 2) for the number of total adult offspring and female adult offspring. This makes sense because female adult offspring is a part of the total adult offspring and both traits have heritable variation.

The scatter plot of heritability against CV_A showed a clear positive relationship (Fig. 1a), whereas h^2 and CV_R showed no consistent relationship (Fig. 1b). When using a linear regression (despite the small data set) with CV_R and CV_A as explanatory variables, the model was significant ($F_{2,3} = 22.94$, $P = 0.02$), but only CV_A had a significant effect on heritability ($CV_A = 0.02 \pm \text{s.e.} = 0.004$, $P = 0.01$). This effect remained when CV_R was removed from the model.

DISCUSSION

We explored the genetic architecture of web production and various life-history traits of the two-spotted spider mite in search of (1) trait heritabilities and genetic trade-offs and (2) the relationship between h^2 and both CV_A and CV_R .

Table 1. Descriptive statistics, heritabilities, and variance components

Trait	Mean	n	Var	Model	P	h^2	s.e.	CV_A	CV_R	Power
Oviposition rate	8.02	110	6.64	Normal	0.002	0.76	0.22	28.02	15.75	0.96
Juvenile survival	0.90	94	0.02	Normal	0.42	0.22	0.26	7.93	14.92	0.93
				Logistic	0.35					
Development rate	5.92	96	0.14	Normal	0.57	-0.20	0.34	0	9.37	<0.5
				K-W	0.44					
Number of adult sons	1.56	96	1.81	Normal	0.16	-0.26	0.18	0	86.02	0.56
				Poisson	0.23					
Number of adult daughters	5.64	96	3.54	Normal	0.09	0.32	0.18	18.88	27.53	0.74
Number of adult offspring	7.20	96	4.67	Normal	0.04	0.46	0.22	20.35	22.05	0.87
Web production	0.17	110	0.004	Normal	0.08	0.50	0.28	27.02	27.02	0.84
				Logistic	0.07					

Note: Values are the average of the trait over both generations (Mean), total number of individuals measured (n), variance of the trait over both generations (Var), types of model used (Model), P -value in the regression model (P), narrow-sense heritability (h^2), standard error of h^2 (s.e.), coefficient of additive genetic variation (CV_A) and of residual variation (CV_R), and the power of the two-factor regression model ($1 - \beta$). 'Normal' = linear regression with a normal error distribution, 'Logistic' = logistic regression with a (quasi)binomial error distribution, 'Poisson' = Poisson regression, 'K-W' = Kruskal-Wallis test. The negative heritabilities were set to zero in further analyses.

Table 2. The Pearson correlation coefficient and its significance (*P*-value, in italics) of traits with (marginally) significant heritability estimates

Trait	Daughter				
	Oviposition	#Daughters	#Offspring	Web	
Mother	Oviposition	—	0.29	0.28	−0.008
		—	<i>0.05</i>	<i>0.05</i>	<i>0.96</i>
	#Daughters	0.2	—	0.42	−0.172
		<i>0.17</i>	—	<i>0.003</i>	<i>0.24</i>
	#Offspring	0.09	0.27	—	−0.006
	<i>0.56</i>	<i>0.06</i>	—	<i>0.97</i>	
Web	0.07	−0.16	−0.001	—	
	<i>0.63</i>	<i>0.91</i>	<i>0.99</i>	—	

Note: The trait in the mothers is correlated with a trait in the daughters and vice versa. ‘Oviposition’ = oviposition rate, ‘#Daughters’ = number of adult daughters, ‘#Offspring’ = number of total adult offspring, ‘Web’ = web production. Power of analysis: $1 - \beta \leq 0.51$ in all cases except for the combination #Daughters (Mother) and #Offspring (Daughter), where $1 - \beta = 0.85$.

Half the phenotypic variation in web production in this population of two-spotted spider mites was of an additive genetic nature. Also, CV_A was relatively high (e.g. Houle, 1992; Kruuk *et al.*, 2000; Merilä and Sheldon, 2000; Stirling *et al.*, 2002; McCleery *et al.*, 2004). Thus, there seems to be potential for this population of two-spotted spider mites to respond to predation pressure by evolving increased web production. Although we observed no significant correlations between web production and any life-history trait, the lack of power of the analyses makes it impossible to rule out their presence. Most of the correlations were (slightly) negative and more research is needed to determine whether genetic trade-offs influence the evolution of web production.

The number of total adult offspring and the oviposition rate showed significant heritability ($h^2 = 0.46$ and 0.76 , respectively) and the number of adult daughters showed nearly significant heritability ($h^2 = 0.32$). For three life-history traits – development rate, juvenile survival, and number of adult sons – the heritability estimate was not significant. The power of the regression model for juvenile survival ($h^2 = 0.22 \pm 0.26$) was high ($1 - \beta = 0.93$), which supports the absence of significant heritability for this trait. The power of the regression models for development rate and number of adult sons was low and thus despite their negative heritability estimates ($h^2 = -0.20 \pm 0.34$ and $h^2 = -0.26 \pm 0.18$, respectively), the presence of (low) heritable variation cannot be excluded for these traits.

The oviposition rate (i.e. short-term fecundity of young females) had high heritability relative to the heritabilities of life-history traits reported by other authors (e.g. Mousseau and Roff, 1987; Stirling *et al.*, 2002), and a large amount of additive genetic variance (as in CV_A) compared with that of female reproduction traits reported for other species (e.g. Houle, 1992; Kruuk *et al.*, 2000; Merilä and Sheldon, 2000; McCleery *et al.*, 2004). Theory predicts that in species with a high intrinsic growth rate, such as *Tetranychus urticae*, a given proportional change in oviposition rate will have less of an influence on the intrinsic growth rate than the same proportional change in development rate (Caswell and Hastings, 1980). This would lead to weaker selection on oviposition rate than on development rate. Indeed, *Tetranychus* species exhibit low variability in development rate, and high variability in fecundity (Sabelis, 1991). In addition, we found that the

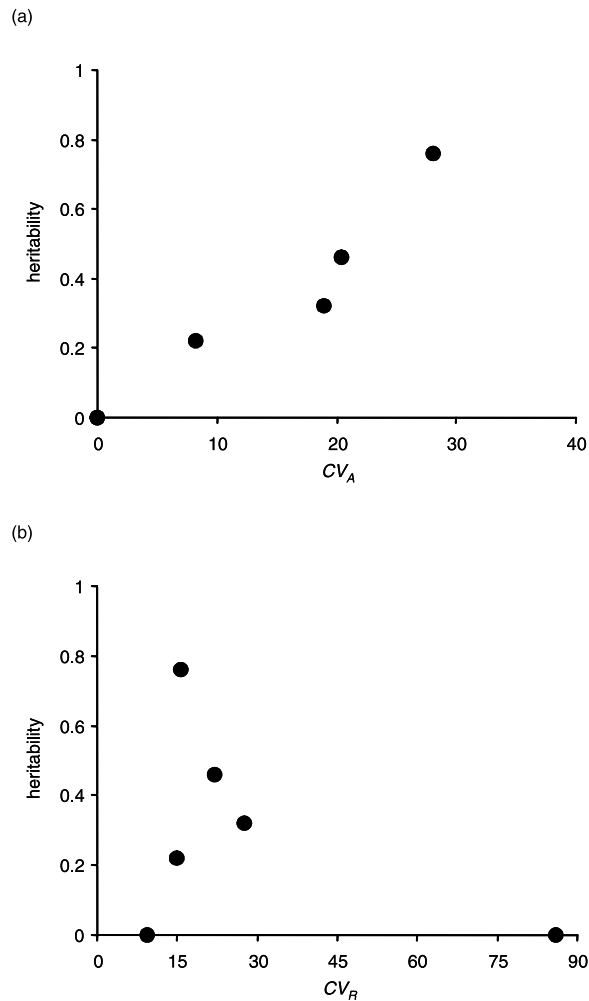


Fig. 1. The relationship between heritability and the coefficients of variation. Narrow-sense heritability is plotted against CV_A (a) and CV_R (b) for six life-history traits (see Table 1 for trait values). Note that point (0,0) in (a) has two overlapping data points.

heritability of oviposition rate is higher than that of development rate in *T. urticae*. However, oviposition rate is a fitness-related trait and therefore the high heritability of this trait requires further explanation: Why did selection not erode heritable variation for this important life-history trait? There are several possible explanations, most of which are unlikely based on our data. First, only positive (and non-significant) correlations were observed with other heritable life-history traits. Thus, our study provides no evidence that genetic trade-offs impeded the evolution of oviposition rate. Second, there may be an inherited maternal effect, which is not related to the genetics of the spider mite, that involves cytoplasmic bacteria such as *Wolbachia* and *Cardinium* (Breeuwer and Jacobs, 1996; Gotoh *et al.*, 2007). These bacteria are transmitted from mother to offspring via the cytoplasm and can induce changes in oviposition rate (Vala *et al.*, 2000). Differences in infection status will then lead to

maternal differences in oviposition rate. Whether such an inherited maternal effect played a role remains to be determined. Third, a genotype \times environment interaction may affect heritability estimates in a novel environment, such as a laboratory (Weigensberg and Roff, 1996). However, laboratory estimates of heritability are generally good indicators of heritability in the field and they tend to be on average only marginally higher (Weigensberg and Roff, 1996). Also, the other life-history traits examined here do not have heritabilities as high as that of the oviposition rate. Therefore, the genotype \times environment effect is thought to be weak. In conclusion, oviposition rate seems to harbour a large amount of heritable variation, which is not expected for a trait assumed to be under strong directional selection. Our data do not provide an explanation for this high V_A .

A positive relationship between CV_A and heritability

Are the V_A -related parameters h^2 and CV_A a reflection of the importance of a trait with respect to fitness? According to the elimination-selection hypothesis, the importance for fitness determines the strength of selection acting on that trait and this selection will decrease V_A and thus also h^2 and CV_A . In contrast, the variance compounding hypothesis states that the amount of integration of a trait determines the amount of genetic and environmental variance and is negatively related to h^2 , but positively related to CV_A and especially CV_R .

The importance of the two mechanisms in explaining the amount of h^2 and CV_A differs between studies. The classical approach is to combine life-history traits (important for fitness) and traits that are deemed to be less important for fitness (morphological, physiological, and/or behavioural traits) (e.g. Gustafsson, 1986; Mousseau and Roff, 1987; Roff and Mousseau, 1987; Houle, 1992; Kruuk *et al.*, 2000; Merilä and Sheldon, 2000; McCleery *et al.*, 2004; Teplitsky *et al.*, 2009). Across these types of traits, a strong influence of variance compounding has been observed: the importance of the trait for fitness was negatively related to heritability (Gustafsson, 1986; Mousseau and Roff, 1987; Roff and Mousseau, 1987; Kruuk *et al.*, 2000; Merilä and Sheldon, 2000; McCleery *et al.*, 2004; Teplitsky *et al.*, 2009), but positively related to CV_R and not related or positively related to CV_A (Houle, 1992; Kruuk *et al.*, 2000; Merilä and Sheldon, 2000; McCleery *et al.*, 2004; Coltman *et al.*, 2005). This implies that h^2 and CV_A were shaped by the level of integration of the traits, rather than by the strength of their connection to fitness. This is as predicted by Price and Schluter (1991), who hypothesized that because life-history traits are furthest down the causal pathway from genes to phenotype, they accumulate the most variation (especially V_R) and have the lowest heritability. However, in a recent study on life-history and morphological traits in a wild bird population (Teplitsky *et al.*, 2009) and in a meta-analysis of behavioural traits (Stirling *et al.*, 2002), heritability was found to be positively related to CV_A and negatively related to CV_R . This implies that both variance compounding and selection play a role in shaping the heritability and CV_A in these cases.

In this article, we have considered only life-history traits, for which a clear and positive relationship between heritability and CV_A was observed, whereas no relationship with CV_R seemed present. These data support the elimination-selection hypothesis. Perhaps the narrow range of trait integration used (i.e. only life-history traits) helped to discern the influence of selection, as reported by Stirling *et al.* (2002), who considered only behavioural traits. In contrast to Stirling *et al.* (2002) and Teplitsky *et al.* (2009), we found no evidence for an influence of variance compounding. In conclusion, in this population of two-spotted spider mites, the additive genetic variation of life-history traits seems to have been shaped

by the importance of the traits for fitness and the consequent strength of selection on these traits.

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