

Contrasting performances of generalist and specialist *Myzus persicae* (Hemiptera: Aphididae) reveal differential prevalence of maternal effects after host transfer

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Abstract

Transgenerational maternal effects on performance (r_m) after host transfer were evaluated in the generalist aphid *Myzus persicae* s.s., and in its subspecies specialized on tobacco, *M. persicae nicotianae* Blackman. We tested whether the performance of these taxa, when reared separately on optimal and suboptimal hosts (as sources of different maternal background) and then transferred to optimal hosts, experienced variations along four successive generations. Additionally, to compare the tolerance of both taxa to stress following host transfers, developmental instability (fluctuating asymmetry and body abnormalities) along the four generations was assessed. Taxon, rearing host, and generation affected the performance after host transfer. In the generalist, there was a significant improvement of r_m along generations when transferred from suboptimal to optimal host and a significant decrease when transferred from optimal to optimal host; in the specialist, no increase or decrease occurred in any host transfer treatment. Transfer from suboptimal to optimal hosts caused higher losses of remaining replicates along generations than transfers from optimal to optimal hosts, and the specialist showed higher losses than the generalist. The only significant effect detected in comparisons involving fluctuating asymmetry values was that of taxon on length of siphunculi. Frequency of body abnormalities was not affected by treatments. Collectively, these results show a transgenerational weakening of maternal effects in the generalist but not in the specialist aphid, and suggest that rearing the latter in a suboptimal host causes not easily reversible changes that further give rise to constraints in performance.

Keywords: performance, maternal effects, ecological specialization, fluctuating asymmetry, green peach aphid, tobacco aphid

Introduction

In many organisms, the environment experienced in previous generations has a profound impact on contemporary phenotypic expression; in particular, environmental

conditions experienced by a mother can determine the phenotype of her offspring (Mousseau, 1998). In such cases, this so-called maternal effect (Mousseau & Dingle, 1991a,b; Fox *et al.*, 1995; Mousseau & Fox, 1998; Hunter, 2002), can evolve as adaptive transgenerational phenotypic plasticity (Mousseau & Dingle, 1991a; Mousseau, 1998; Mousseau & Fox, 1998; Hunter, 2002), whereby the mother can programme a developmental switch in her offspring which tunes them to a future environment predicted by cues such as humidity, temperature, food quality, presence of natural

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enemies, population density and photoperiod (Fox *et al.*, 1995; Fox & Mousseau, 1998; Hunter, 2002).

Diapause and wing polymorphism are among the best studied examples of maternal effects in insects and have been demonstrated to be adaptive and likely to be adaptive, respectively (reviewed by Tauber *et al.*, 1986; Mousseau & Dingle, 1991a,b; Fox & Mousseau, 1998). Among insects, aphids are a group of particular interest when studying transgenerational adaptive maternal effects on account of their telescopic reproduction, where the parthenogenetic female carries within herself three generations of embryos (Dixon, 1998) and, thus, her transgenerational influence encompasses at least three generations (Mousseau & Dingle, 1991a). Maternal influence is among the mechanisms known to trigger the production of winged morphs on parthenogenetic females (reviewed by Braendle *et al.*, 2006); and both maternal host-plant condition and crowding may also induce progeny to enter diapause (reviewed by Tauber *et al.*, 1986). The host plant, in particular, is an important environmental variable since it represents a spatially and temporally heterogeneous resource in terms of quality and availability (Fox *et al.*, 1995); for example, both poor and high quality hosts may cause inhibition of wing induction (Müller *et al.*, 2001). Previous laboratory studies on the performance of aphids which have experienced host transfer have shown that some aphid clones show a low initial performance on the newly colonized host which improves through generations (Mackenzie & Guldmond, 1994; Via, 1991; De Barro *et al.*, 1995; Douglas, 1997; Caballero *et al.*, 2001; Gorur *et al.*, 2005). Some authors have suggested that the cause of this performance improvement is a weakening of maternal effects (influence of the rearing host) (De Barro *et al.*, 1995; Douglas, 1997; Caballero *et al.*, 2001), and some claim that genetic differences related to host adaptation play a major role (Via, 1991; Mackenzie & Guldmond, 1994; De Barro *et al.*, 1995).

Rearing experience has been shown to affect selection abilities of insects (Szentesi & Jermy, 1990). For example, data has been presented in support of generalist and specialist aphid taxa differing in their host selection speed and efficiency, with specialists taking faster and more efficient decisions than generalists, when reared and tested on their respective host plants (Bernays & Funk, 1999; Funk & Bernays, 2001; Vargas *et al.*, 2005). However, this faster selection by specialists did not occur when aphids were evaluated on hosts different from their rearing hosts (Tosh *et al.*, 2003; Troncoso *et al.*, 2005). These results suggest that the extent of maternal effects as well as their transgenerational influence is related to the degree of host specialization. In this work, we evaluated whether the performance and developmental instability of a generalist and a specialist aphid, reared on optimal and suboptimal hosts (as sources of different maternal background, from now on referred to as rearing hosts) and then transferred to optimal hosts (as sources of different degrees of stress), experienced variations along four successive generations. The aphids chosen for this study were the green peach aphid, *Myzus persicae* s.s. (Blackman & Eastop) (Hemiptera: Aphididae), a generalist aphid that uses peach, *Prunus persica* L. (Rosaceae) as its primary host and more than 400 plant species from different families as secondary hosts (Blackman & Eastop, 2000), and a form of *M. persicae* s.s. associated to tobacco (Brain, 1940), with distinctive biological and genetic traits which allow it to be treated as the subspecies, *M. persicae nicotianae* (Blackman

& Eastop) (Blackman & Eastop, 2006). We expect that: (i) the performance of both taxa on optimal hosts will be lower when transferred from suboptimal host than from optimal host, and the recovery of performance levels will be different in the generalist than in the specialist; and (ii) developmental instability will be greater when aphids are transferred from the suboptimal rearing host to the optimal test host, will be greater in the specialist than in the generalist, and will decrease along the four successive generations.

Materials and methods

Insects and plants

Aphids of both taxa were collected from parthenogenetic populations in agricultural fields in the neighbourhood of Talca, Chile (*M. persicae* s.s. from sugarbeet *Beta vulgaris* L., and *M. persicae nicotianae* from tobacco *Nicotiana tabacum* L., cv. BY 64). Aphid taxa were separated on the basis of morphometrical multivariate analysis; clonal characterization of the colonies was achieved with microsatellite markers (Fuentes-Contreras *et al.*, 2004). A colony of the only clone of *M. persicae nicotianae* present in Chile (Fuentes-Contreras *et al.*, 2004), and a polyclonal colony of *M. persicae* s.s. were established in the laboratory. Optimal and suboptimal hosts were chosen after a study of the performance (r_m) of the two taxa on different hosts. Cabbage was designated as the suboptimal host for both the generalist and the specialist, and sweet pepper and tobacco the optimal hosts for these taxa, respectively. Colonies were maintained at $20 \pm 2^\circ\text{C}$, and 16L:8D photoperiod for more than ten parthenogenetic generations before the beginning of the experiments. Plants of cabbage, sweet pepper and tobacco were grown under the same conditions as aphids.

Determination of performance along successive generations

Aphids from the established colonies (*M. persicae* s.s. reared on cabbage and sweet pepper, *M. persicae nicotianae* reared on cabbage and tobacco) were transferred to their respective optimal host and studied over four generations. Four host transfer treatments were established: (i) transfer of *M. persicae* s.s. from optimal to optimal host ($Mp_{O \rightarrow O}$); (ii) transfer of *M. persicae* s.s. from suboptimal to optimal host ($Mp_{SO \rightarrow O}$); (iii) transfer of *M. persicae nicotianae* from optimal to optimal host ($Mpn_{O \rightarrow O}$); and (iv) transfer of *M. persicae nicotianae* from suboptimal to optimal host ($Mpn_{SO \rightarrow O}$). For each treatment, three adult apterae were placed on plants at the 4- to 6-leaf stage in tobacco or at the 14- to 16-leaf stage in sweet pepper. The aphids were allowed to reproduce for 24 h and then adults were removed. Five of the newly born nymphs on each plant (first generation, G_1) were left undisturbed for a fixed number of days for each taxon (four days for *M. persicae* s.s. and five days for *M. persicae nicotianae*) and the rest removed. After this time, one nymph per plant was haphazardly selected to be monitored and the other four were removed. Survival and fecundity were evaluated daily. The number of days from birth to first reproduction (T) and fecundity of individual females in the subsequent T days were used to calculate the intrinsic rate of natural increase (r_m) according to Wyatt & White (1977). Starting the day in which each adult aphid began to reproduce, the progeny was counted and removed daily with the exception of nymphs produced on the third

reproductive day, which were not removed. Five of the nymphs born in the third reproductive day (G_2) were left undisturbed for a fixed number of days for each taxon (see above) and the rest removed. After this time, one nymph per plant was haphazardly selected to be monitored and the other four were removed. Survival and fecundity were evaluated daily. Starting the day in which each adult aphid began to reproduce, the progeny was counted and removed daily with the exception of nymphs produced on the third reproductive day, which were not removed. They constituted the third generation (G_3) and were reared using the protocol described above. The same protocol was used for G_4 . For all four generations the same plant was used in order to avoid the stress produced to the nymphs by the change of plant to measure their performance. The experiment began with 30 replicates for each treatment, but the number decreased as the generations progressed.

Two-way ANOVA with repeated measures was used to evaluate the effects on r_m of aphid taxon (generalist vs. specialist), rearing host (optimal vs. suboptimal), and generation (first to fourth, corresponding to the repeated measures). Post-hoc comparisons were performed using Tukey HSD test modified for unbalanced samples (StatSoft, 2006). Student t-tests were used to compare the r_m of the first generation of aphids transferred from suboptimal to optimal hosts with the respective r_m on the rearing suboptimal host. Pearson product moment correlations were used to evaluate the significance of eventual relationships between r_m and generation. Data passed the tests of parametric analysis assumptions for each procedure and all analyses were performed with STATISTICA 6 (StatSoft, 2001). To analyse differences in aphid mortality during the period of study, the total number of remaining replicates within treatments were counted after each generation, and rates of loss of replicates were compared using a 2×2 factorial ANCOVA (Lowry, 2006).

Assessment of developmental stability

Adults (age = $2T$) whose performance had been evaluated were individually stored in 70% ethanol and later mounted on slides as described by Blackman & Eastop (2000). The length of the third antennal segments and the siphunculi (abdominal tubes) were measured according to Ilharco & van Harten (1987), with a binocular microscope (magnification $40\times$). These traits were chosen based on previous studies in which they showed sensitivity to stressing conditions, as expressed in significant fluctuating asymmetry values (Gorur, 2004; Liu *et al.*, 2005). In particular, Liu *et al.* (2005) indicated that the third antennal segment is one of the parameters most sensitive to host variations and hence an ideal trait, likely due to its function in host-plant volatile detection. Both traits were measured three times and then evaluated for measurement error, antisymmetry, directional asymmetry, and trait-size dependence of fluctuating asymmetry values, following procedures suggested by Palmer (1994).

Fluctuating asymmetry values (FA) were estimated using the index FA_5 , $FA = \sum (R - L)^2 / N$, where L and R represent the length of the left and right traits, respectively (Palmer & Strobeck, 1986; Palmer, 1994). Two-way ANOVA with repeated measures was used to compare differences in FA values of each taxon on different host transfers through generations.

Table 1. Summary of two-way ANOVA with repeated measures performed to evaluate the effect of maternal effect on the intrinsic rate of increase between taxa and across generations.

Source of variation	d.f.	MS	F	P
Intercept	1	44.659	7014.65	<0.001
Taxon	1	0.132	20.72	<0.001
Host transfer	1	0.243	38.13	<0.001
Taxon \times Host transfer	1	0.001	0.17	0.681
Error	73	0.006		
Generation	3	0.006	3.87	0.010
Generation \times Taxon	3	0.002	1.07	0.365
Generation \times Host transfer	3	0.002	1.42	0.237
Generation \times Taxon \times Host transfer	3	0.007	4.91	0.002
Error	219	0.002		

Morphological abnormalities observed were quantified in each treatment. Frequencies of abnormalities in generalist and specialist aphids were compared with a Fisher exact test (Zar, 1996).

Results

The results revealed significant overall effects of taxon, rearing host, and generation on the intrinsic rate of natural increase (r_m). Most importantly, these factors showed a significant interaction (table 1), indicating that the performance of the generalist and specialist aphids after host transfer depends on their original provenance (optimal or suboptimal hosts), and that the maternal background operates differentially along generations (fig. 1). The only biologically meaningful post-hoc comparison which was significant occurred in the first generation of *M. persicae* s.s. between host transfer treatments ($P = 0.013$, fig. 1). Additionally, when comparing the r_m value of the first generation of the generalist and specialist aphids from suboptimal

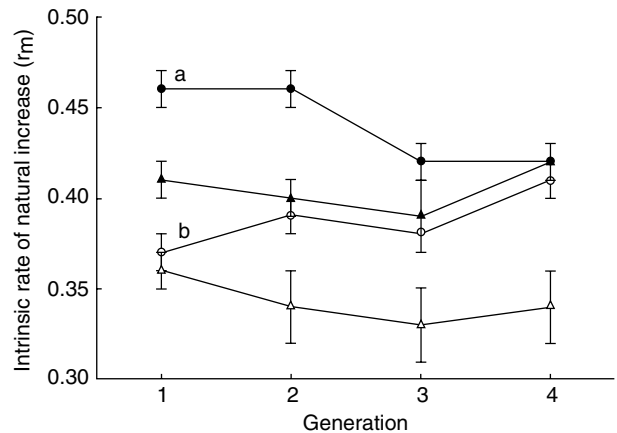


Fig. 1. Intrinsic rates of natural increase (r_m) of *Myzus persicae* s.s. reared on the optimal (●) and suboptimal (○) hosts, and of *M. persicae nicotianae* reared on the optimal (▲) and suboptimal (△) hosts, and then tested on the optimal host over four generations. The letters indicate significant differences between host transfer treatments of *M. persicae* s.s. at the first generation.

Table 2. Summary of 2×2 factorial ANCOVA performed to compare the rates of replicate loss between treatments across generations (fig. 2).

Source of variation	d.f.	MS	F	P
Taxon	1	0.132	20.72	<0.001
Host transfer	1	0.243	38.13	<0.001
Taxon \times Host transfer	1	0.001	0.17	0.681
Error	73	0.006		
Test of homogeneity of regressions				
Between regressions	3	17.900	13.26	<0.001
Remainder	12	1.350		
Error	15	4.660		

rearing host transferred to optimal hosts, with r_m values on the respective suboptimal hosts, the generalist showed a clearly significant increase ($t = -5.49$, $P < 0.001$) while the specialist did not ($t = -2.02$, $P = 0.056$). The latter P value was considered non-significant because no further tendency to increased performance was observed along generations.

The values of r_m for the generalist aphid from the suboptimal rearing host increased significantly along generations ($r = 0.209$, d.f. = 91, $P = 0.04$); however, there was a significant decrease of r_m in the generalist aphid from the optimal rearing host ($r = -0.384$, d.f. = 99, $P < 0.01$). No significant increase or decrease was found for the specialist either from the optimal or suboptimal rearing hosts ($r = 0.028$, d.f. = 63, $P = 0.83$, and $r = -0.101$, d.f. = 51, $P = 0.48$, respectively).

Rates of loss of replicates along generations were significantly different between taxa as well as between host transfer treatments (table 2, fig. 2).

No significant effects were found within any of the treatments for measurement error, antisymmetry, directional asymmetry, and trait-size dependence of fluctuating asymmetry values. Taxon but not host transfer nor generation significantly affected fluctuating asymmetry values of siphunculi (table 3). FA values were significantly higher for *M. persicae nicotianae* (table 4). On the other hand, none of the factors studied significantly affected the FA values for third antennal segments (table 3). Finally, body abnormalities consisting of atrophied structures, antennal protuberances, and reduction of body size (dwarfism) occurred with low frequencies and without significant differences between generalist and specialist (Fisher exact test, $P = 0.30$).

Discussion

In the present study, the effects of host transfer treatments on aphid performance differed between the generalist and specialist aphids. In the optimal to optimal host transfer, r_m decreased along generations in the generalist on sweet pepper but not in the specialist on tobacco. The decreased performance of the generalist may be attributed to the accumulation of induced chemical defences in the plant arising from its interaction with the aphid; for instance, feeding by *M. persicae* s.s. has been shown to give rise to induced defences in sweet pepper (Tapia, 2006), and by *M. persicae nicotianae* to induced chemical defences in wild tobacco (Heidel & Baldwin, 2004). The insensitivity of the performance of *M. persicae nicotianae* to induced defences in

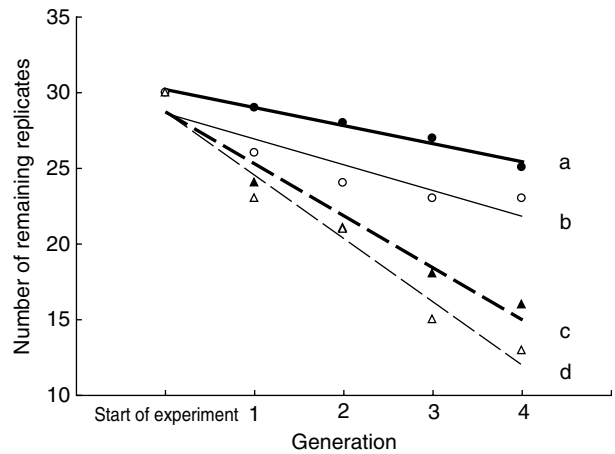


Fig. 2. Rate of replicate loss by the end of each generation of *Myzus persicae* s.s. reared on the optimal (●) and suboptimal (○) hosts, and of *M. persicae nicotianae* reared on the optimal (▲) and suboptimal (△) hosts, and then tested on the optimal host over four generations. Bold and thin regression lines correspond to 'optimal to optimal' and 'suboptimal to optimal' host transfer treatments, respectively; continuous and dashed regression lines correspond to the generalist and specialist taxon, respectively. Regression lines followed by a different letter differ at $P < 0.05$ (table 2).

tobacco may be attributed to the enzymatic detoxifying system it possesses (Cabrera *et al.*, 2005).

The generalist aphid reared on the suboptimal host was capable of progressively achieving higher performances after being transferred to the optimal host, r_m eventually becoming indistinguishable from that of an aphid which had been reared and transferred to the optimal host. In fact, an increase was already apparent when the performance of the first generation after transfer from the suboptimal to the optimal host was compared to the performance on the suboptimal rearing host, thus showing a fast recovery of the generalist after host transfer. On the other hand, the specialist reared on the suboptimal host was incapable of increasing its performance upon transfer to the optimal host, at least within four generations after host transfer. Furthermore, loss of replicates – equivalent to aphid mortality – along generations was higher in the specialist than in the generalist, and loss was highest in the suboptimal to optimal host transfers. These phenomena may arise from differential prevalence of maternal effects and phenotypic plasticity in the generalist and in the specialist. Thus, the generalist achieved higher levels of performance by progressively overcoming its maternal effects, while the specialist seemed unable to do it, which could also be taken as a commitment to its rearing host, since it lasted for more than three generations. The maintenance of host commitment normally depends on a variety of traits, such as behavioural, physiological and/or developmental/morphological which show different levels of plasticity (Pigliucci, 2001), and also different evolutionary rates (Gittleman *et al.*, 1996). In the present case, the steady maintenance of performance along generations in the specialist, suggest a commitment to the rearing host (supported by its maternal effect), and not to an ecological specialization history. The commitment of the

Table 3. Summary of results of two-way ANOVA with repeated measures for fluctuating asymmetry values (FA_5).

Trait	Source of variation	d.f.	MS	F	P
Third antennal segments	Taxon	1	0.00004	0.80	0.38
	Host transfer	1	0.00004	0.81	0.37
	Taxon \times Host transfer	1	0.00018	3.79	0.07
	Error	52	0.00005		
	Generation	3	0.00007	1.76	0.16
	Generation \times Taxon	3	0.00007	1.83	0.15
	Generation \times Host transfer	3	0.00003	0.76	0.52
	Generation \times Taxon \times Host transfer	3	0.00006	1.58	0.20
	Error	156	0.00004		
Siphunculi	Taxon	1	0.00002	6.82	0.01
	Host transfer	1	0.00000	2.60	0.11
	Taxon \times Host transfer	1	0.00000	0.06	0.81
	Error	47	0.00000		
	Generation	3	0.00000	0.563	0.64
	Generation \times Taxon	3	0.00000	1.296	0.28
	Generation \times Host transfer	3	0.00000	1.792	0.15
	Generation \times Taxon \times Host transfer	3	0.00000	1.224	0.30
	Error	141	0.00000		

specialist to its rearing host (in our case, cabbage) may be the result of the loss or inactivation of certain costly traits which were once adaptive to its life on tobacco, but were no longer necessary for thriving on cabbage. Recent evidence points to the importance of esterases in the detoxification of tobacco allelochemicals by *M. persicae nicotianae* (Cabrera *et al.*, 2005). The re-installment of this detoxification capacity through re-allocation of the energy budget may require more than three generations.

Developmental instability was taxon and trait dependent, in agreement with correlational studies by Clarke (1998). Thus, the specialist showed higher developmental instability of siphunculi (but not of third antennal segment) than the generalist. This, and the fact that the specialist showed lower performance (fig. 1) and higher mortality than the generalist (fig. 2) is not in disagreement with the proposal that fitness is lower in developmentally instable individuals (Møller, 1997; Leamy & Klingenberg, 2005). Since the effect of host transfer was negligible, such developmental instability can not be related to stress, as previously suggested by other authors (Palmer, 1994; Crespi & Vanderkist, 1997).

The predictability of local environmental quality is an important criterion in the evolution of adaptive parental effects (Rossiter, 1996, 1998). Given the restricted host range of a specialist aphid, the adaptive value of maternal effects when colonizing highly predictable hosts is to be expected. When offspring face an environment different from the one experienced by the mother (as in our experimental manipulation), maternal effects would lose their adaptive value through a teleonomic phenotypic influence on such offspring and become a ballast for further performance improvement. On the other hand, a generalist aphid is capable of thriving on a wide range of hosts and thus may be adapted to unpredictable environments; hence, the adaptive value of maternal effects on host preference is questionable. When offspring face an environment different from the one experienced by the mother, performance will be mainly a result of its phenotypic flexibility (*sensu* Piersma & Drent, 2003) offsetting the eventual maternal effect. These considerations suggest that maternal effects should be discussed within the context of ecological specialization.

Table 4. Values of fluctuating asymmetry for trait, aphid taxon (*Myzus persicae* s.s., *Mp*; *M. persicae nicotianae*, *Mpn*), and rearing host (O, optimal; SO, suboptimal) through generations G1 thorough G4. Fluctuating asymmetry values (FA , in mm^2) were calculated using the formula: $FA = \sum (R-L)^2/N$ (see Materials and methods).

Trait	Taxon	Treatment	G1			G2			G3			G4		
			$10^3 \times FA$	$10^3 \times SE$	N	$10^3 \times FA$	$10^3 \times SE$	N	$10^3 \times FA$	$10^3 \times SE$	N	$10^3 \times FA$	$10^3 \times SE$	N
Third antennal segments	<i>Mp</i>	O→O	1.50	0.51	24	1.27	0.36	27	1.28	0.48	24	2.16	0.67	22
		SO→O	1.45	0.46	24	1.30	0.60	16	3.89	2.80	11	1.45	0.85	12
	<i>Mpn</i>	O→O	2.39	0.56	19	1.63	0.59	20	2.22	1.14	12	3.52	6.95	16
		SO→O	2.00	0.41	19	0.90	0.30	16	1.69	0.72	12	1.05	0.34	12
Siphunculi	<i>Mp</i>	O→O	0.50	0.18	26	0.18	0.04	27	0.05	0.01	18	0.26	0.10	18
		SO→O	0.15	0.04	22	0.17	0.07	23	0.02	0.01	9	0.06	0.01	16
	<i>Mpn</i>	O→O	0.67	0.21	20	0.36	0.10	18	0.78	0.36	14	0.41	0.20	20
		SO→O	0.24	0.09	20	0.38	0.13	18	0.27	0.11	10	0.76	0.35	11

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References

- Bernays, E.A. & Funk, D. (1999) Specialists make faster decisions than generalists: experiments with aphids. *Proceedings of the Royal Society of London Series B* **266**, 151–156.
- Blackman, R.L. & Eastop, V.F. (2000) *Aphids on the world's crops: an identification guide*. 2nd edn. Chichester, UK, Wiley-Interscience.
- Blackman, R.L. & Eastop, V.F. (2006) Taxonomic issues. In van Emden H.F. & R. Harrington (Eds) *Aphids as crop pests*. Wallingford, Oxon, CABI Publishing, in press.
- Braendle, C., Davis, G.K., Brisson, J.A. & Stern, D.L. (2006) Wing dimorphism in aphids. *Heredity* **97**, 192–199.
- Brain, C.K. (1940) Host plants of the tobacco aphid (*Myzus persicae*). *Rhodesia Agricultural Journal* **37**, 254–255.
- Caballero, P.P., Ramírez, C.C. & Niemeyer, H.M. (2001) Specialization pattern of the aphid *Rhopalosiphum maidis* is not modified by experience on a novel host. *Entomologia Experimentalis et Applicata* **100**, 43–52.
- Cabrera, M., Fuentes-Contreras, E. & Figueroa, C.C. (2005) Rol del metabolismo detoxificador en la especialización de *Myzus persicae* sobre tabaco. p. 89 in XXVII Congreso Nacional de Entomología, 23–25 November, Valdivia, Chile.
- Clarke, G.M. (1998) The genetic basis of developmental stability. IV Individual and population asymmetry parameters. *Heredity* **80**, 553–561.
- Crespi, B.J., & Vanderkist, B.A. (1997) Fluctuating asymmetry in vestigial and functional traits of a haplodiploid insect. *Heredity* **79**, 624–630.
- De Barro, P.J., Sherratt, T.N., David, O. & Maclean, N. (1995) An investigation of the differential performance of clones of the aphid *Sitobion avenae* on two host species. *Oecologia* **104**, 379–385.
- Dixon, A.F.G. (1998) *Aphid ecology*. London, Chapman & Hall.
- Douglas, A.E. (1997) Provenance, experience and plant utilization by the polyphagous aphid *Aphis fabae*. *Entomologia Experimentalis et Applicata* **83**, 161–170.
- Fox, C.W. & Mousseau, T.A. (1998) Maternal effects as adaptations for transgenerational phenotypic plasticity in insects. pp. 159–177 in Mousseau, T.A. (Ed.) *Maternal effects as adaptations*. New York, Oxford University Press.
- Fox, C.W., Waddell, K.J. & Mousseau, T.A. (1995) Parental host plant affects offspring life histories in a seed beetle. *Ecology* **76**, 402–411.
- Fuentes-Contreras, E., Figueroa, C.C., Reyes, M., Briones, L.M. & Niemeyer, H.M. (2004) Genetic diversity and insecticide resistance of *Myzus persicae* (Hemiptera: Aphididae) populations from tobacco in Chile: evidence for the existence of a single predominant clone. *Bulletin of Entomological Research* **94**, 11–18.
- Funk, D. & Bernays, E.A. (2001) Geographic variation in host specificity reveals host range evolution in *Uroleucon ambrosiae* aphids. *Ecology* **82**, 726–739.
- Gittleman, J.L., Anderson, C.G., Kot, M. & Luh, H.K. (1996) Phylogenetic lability and rates of evolution: a comparison of behavioral, morphological and life history traits. pp. 166–205 in Martins, E.P. (Ed.) *Phylogenies and the comparative method in animal behaviour*. Oxford, Oxford University Press.
- Gorur, G. (2004) Developmental noise in cabbage aphid, *Brevicoryne brassicae*, (Homoptera: Aphididae) reared on both cabbage and radish. *Journal of the Entomological Research Society* **6**, 15–22.
- Gorur, G., Lomonaco, C. & Mackenzie, A. (2005) Phenotypic plasticity in host plant specialization in *Aphis fabae*. *Ecological Entomology* **30**, 657–664.
- Heidel, A.J. & Baldwin, I.T. (2004) Microarray analysis of salicylic acid- and jasmonic acid-signalling in responses of *Nicotiana attenuata* to attack by insects from multiple feeding guilds. *Plant Cell and Environment* **27**, 1362–1373.
- Hunter, M.D. (2002) Maternal effects and the population dynamics on plants. *Agricultural and Forest Entomology* **4**, 1–9.
- Ilharco, F.A. & van Harten, A. (1987) Systematics. pp. 51–77 in Minks, A.K. & Harrewijn, P. (Eds) *Aphids. Their biology, natural enemies and control*. Amsterdam, Elsevier Science Publishers.
- Leamy, L.J. & Klingenberg, C.P. (2005) The genetics and evolution of fluctuating asymmetry. *Annual Review of Ecology, Evolution and Systematics*, **36**, 1–21.
- Liu, X.D., Zhai, B.P., Zhang, X.X. & Zong, J.M. (2005) Impact of transgenic cotton plants on a non-target pest, *Aphis gossypii* Glover. *Ecological Entomology* **30**, 307–315.
- Lowry, R. (2006) VassarStats: Website for Statistical Computation. <http://faculty.vassar.edu/lowry/VassarStats.html>
- Mackenzie, A. & Guldemon, J.A. (1994) Sympatric speciation in aphids. II. Host race formation in the face of gene flow. pp. 379–395 in Leather, S.R., Watt, A.D., Mills, N.J. & Walters, K.F.A. (Eds) *Individuals, populations and patterns in ecology*. Andover, Hants, Intercept.
- Mousseau, T.A. (1998) *Maternal effects as adaptations*. New York, Oxford University Press.
- Mousseau, T.A. & Dingle, H. (1991a) Maternal effects in insect life histories. *Annual Review of Entomology* **36**, 511–534.
- Mousseau, T.A. & Dingle, H. (1991b) Maternal effects in insects: examples, constraints, and geographic variation. pp. 745–761 in Dudley, E.C. (Ed.) *The unity of evolutionary biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*. Portland, Oregon, USA, Dioscorides Press.
- Mousseau, T.A. & Fox, C.W. (1998) The adaptive significance of maternal effects. *Trends in Ecology and Evolution* **13**, 403–407.
- Møller, A.P. (1997) Developmental stability and fitness: a review. *American Naturalist* **149**, 916–932.
- Müller, C.B., Williams, I.S. & Hardie, J. (2001) The role of nutrition, crowding and interspecific interactions in the development of winged aphids. *Ecological Entomology* **26**, 330–340.
- Palmer, A.R. (1994) Fluctuating asymmetry analyses: a primer. pp. 335–364 in Markow T.A. (Ed.) *Developmental instability: Its origins and evolutionary implications*. Dordrecht, Netherlands, Kluwer.
- Palmer, A.R. & Strobeck, C. (1986) Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology and Systematics* **17**, 391–421.

- Piersma, T. & Drent, J. (2003) Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution* **18**, 228–233.
- Pigliucci, M. (2001) *Phenotypic plasticity: beyond nature and nurture*. Baltimore, Johns Hopkins University Press.
- Rossiter, M. (1996) Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics* **27**, 451–476.
- Rossiter, M. (1998) The role of environmental variation in parental effects expression. pp. 112–134 in Mousseau, T.A. (Ed.) *Maternal effects as adaptations*. New York, Oxford University Press.
- StatSoft, Inc. (2001) STATISTICA (data analysis software system), version 6. www.statsoft.com
- StatSoft, Inc. (2006) *Electronic statistics textbook*. Tulsa, Oklahoma, StatSoft. WEB: <http://www.statsoft.com/textbook/stathome.html>.
- Szentesi, Á. & Jermy, T. (1990) The role of experience in host plant choice by phytophagous insects. pp. 39–74 in Bernays, E.A. (Ed.) *Insect-plant interactions*. vol. 2. Boca Raton, Florida, CRC Press.
- Tapia, D.H. (2006) Competencia entre *Myzus persicae* sensu stricto y *Myzus persicae nicotianae*. MSc thesis, University of Chile, xi + 27 pp.
- Tauber, M.J., Tauber, C.A. & Masaki, S. (1986) *Seasonal adaptations of insects*. New York, Oxford University Press.
- Tosh, C.R., Powell, G. & Hardie, J. (2003) Decision making by generalist and specialist aphids with the same genotype. *Journal of Insect Physiology* **49**, 659–669.
- Troncoso, A.J., Vargas, R.R., Tapia, D.H., Olivares-Donoso, R. & Niemeyer, H.M. (2005) Host selection by the generalist aphid *Myzus persicae* (Hemiptera: Aphididae) and its subspecies specialized on tobacco, after being reared on the same host. *Bulletin of Entomological Research* **95**, 23–28.
- Vargas, R.R., Troncoso, A.J., Tapia, D.H., Olivares-Donoso, R. & Niemeyer, H.M. (2005) Behavioural differences during host selection between alate virginoparae of generalist and tobacco-specialist *Myzus persicae*. *Entomologia Experimentalis et Applicata* **116**, 43–53.
- Via, S. (1991) The genetic structure of host plant adaptation in spatial patchwork: demographic variability among reciprocally transplanted pea aphid clones. *Evolution* **45**, 827–857.
- Wyatt, I.J. & White, P.F. (1977) Simple estimation of intrinsic increase rates for aphids and tetranychid mites. *Journal of Applied Ecology* **14**, 757–766.
- Zar, J.H. (1996) *Biostatistical analysis*. New Jersey, Prentice Hall.

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