

The genetic basis of oviposition preference differences between sympatric host races of the brown planthopper (*Nilaparvata lugens*)

M. Sezer[†] and R. K. Butlin^{*}

Ecology and Evolution, School of Biology, The University of Leeds, Leeds LS2 9JT, UK

We have previously analysed the genetic architecture of host-associated performance differences between stocks of the brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae), derived from two host plants: cultivated rice variety TN1 and the semi-aquatic weed *Leersia hexandra*. It has been established that performance is influenced by a small effective number of loci (1–3), with dominance in the direction of the rice population. The results reported here show that, like performance, oviposition preference has a simple genetic basis, but in this case there is no evidence of directional dominance, sex linkage, non-allelic interaction or genotype–environment interaction. The simple genetic architecture of host-associated performance and oviposition preference are as expected if there was a sympatric host shift, most probably from *Leersia* to rice. However, contrary to the theoretical expectation from models of sympatric host-race formation, there was no detectable genetic association between the traits. The fact that individual females tend to distribute their eggs between plants may have helped to promote a host shift despite this lack of association.

Keywords: host preference; host race; hybridization; quantitative genetics; sympatric speciation

1. INTRODUCTION

Why most phytophagous insects specialize on a limited number of plant species is a question that has attracted a large number of studies, and generated numerous hypotheses concerning the evolution of host-plant utilization (Jaenike 1990). Two characters, host-associated preference and performance, determine the diet breadth of insect species in response to the availability and suitability of host-plant species. Thus their genetic basis has particular evolutionary significance. It is not clear which character generally leads the evolution of host range: evolutionary changes in preference may result in selection for increased performance on a new host, or performance variation may exert selection on preferences (Via 1990). For many insect species, oviposition-site choice by females may determine the host plant of the relatively immobile immature stages, so oviposition preference is likely to be the key character influencing host range. However, this preference is made up of multiple factors that influence the placement of eggs by females, any or all of which might change to allow utilization of a new host (Renwick & Chew 1994).

The possibility of sympatric host shifts has been one of the most controversial topics in the evolution of host utilization (Bush 1995). One of the objections to the theory is that successful adaptation to a new host plant may require changes in both preference and

host-associated performance. Unless the same mutations act pleiotropically on both characters, simultaneous evolution is implausible and either trait alone is unlikely to be favoured by selection. Frequency-dependent selection might alleviate this problem (Udovic 1980), as might assortative mating resulting from mating on the host plant (Diehl & Bush 1989). In either case, host shifts are more likely to result from mutations of large effect than from polygenic changes, which might reduce fitness of the original host without permitting effective use of the new host. The genetic architecture of preference or host-associated performance differences between species or host races after sympatric divergence is, therefore, expected to follow Templeton's (1981) type-II genetic basis: a few loci of large effect, with modifiers. Pleiotropy may also be anticipated. Polygenic architecture (Templeton's type-I genetic basis) is more likely to result from gradual divergence in allopatry.

The number of loci underlying divergence in a quantitative trait can be estimated by examination of the variances of segregating generations (F_2 and backcross) in crosses between populations: the fewer the loci, the greater the variance due to segregation (the Wright–Castle–Lande method: Lande 1981). This method provides a minimum estimate for the number of loci because four simplifying assumptions are typically violated: (i) there is free recombination; (ii) all loci have equal effect; (iii) all increasing alleles are fixed in the population with higher means and all decreasing loci in the population with lower means; and (iv) there is additive inheritance. Departure from any of these assumptions causes an underestimation of the true

^{*} Author for correspondence (r.k.butlin@leeds.ac.uk).

[†] Present address: Zootekni Bolumu, Ziraat Fakultesi, Gaziosmanpasa Universitesi, Tokat, Turkey.

number of loci (Zeng 1992). In particular, closely linked loci cannot be detected, and the method therefore estimates the number of genomic regions influencing a trait rather than the number of loci. The method is applied here because, despite its limitations, it is the best approach available in the absence of multiple genetic markers.

There is ample evidence for variation in choice of host plants for oviposition and feeding within insect populations, and this phenotypic variation has a genetical component (see reviews by Futuyma & Peterson 1985; Jaenike & Holt 1991). These studies show that alternative and novel hosts are acceptable to some individuals and that there is potential for rapid host shifts. By contrast, the genetic architecture of differences between host races or species has rarely been analysed for oviposition or feeding preference, or for host-associated performance. The genetic basis of oviposition preference is variable among the few species that have been studied: polygenic control for two sympatric *Drosophila* species (R'Kha *et al.* 1991) and for *Heliothis virescens* and *H. subflexa* (Sheck & Gould 1995); major-gene effects with dominance for the aphid species *Cryptomyzus galeopsidis* (Guldemon 1990) or epistasis in populations of Colorado potato beetle, *Leptinotarsa decemlineata* (Lu & Logan 1995); and a few, partly sex-linked loci for *Papilio* butterflies (Thompson 1988).

(a) *Study organism*

The brown planthopper, *Nilaparvata lugens*, is a serious pest of rice, *Oryza sativa*, crops in India, South-East Asia and Northern Australia. Populations feeding on *Leersia hexandra* (a common weed grass in the same tribe, *Oryzaceae*) occur throughout its distribution (Heinrichs & Medrano 1984). There is no known morphological difference between the two forms, but they have different mating signals (Butlin 1993, 1996; Trickett 1995) and DNA sequences (Jones *et al.* 1996). No hybrid has been detected in the field and there is assortative mating in laboratory tests, suggesting that the two forms might be considered separate species, although they are interfertile (Claridge *et al.* 1988).

More than 100 plant species, in seven families, have been reported as hosts for *N. lugens* (Chen 1982) although it is monophagous in the sense that development can only be completed on either rice or *Leersia*. Planthoppers in general appear to spread their oviposition risks, increasing offspring survival by depositing eggs in small groups (Denno & Perfect 1994). Planthoppers tend to deposit smaller batches of eggs in tougher substrates; this observation suggests that host-plant characteristics have an important effect on batch size. There is evidence that rice variety-associated populations of *N. lugens* prefer to oviposit on their natal host plant, on which offspring performance is best (Claridge *et al.* 1984). The genetic basis of preference, and of the correspondence between preference and performance, do not appear to have been studied.

Studies on the inheritance of host-associated performance, measured as mass gain in adult females, in crosses between rice- and *Leersia*-feeding stocks (Sezer & Butlin 1998), showed that performance differences seemed to be controlled by a few genes. Dominance of rice-population alleles over *Leersia*-population alleles was quite strong,

and there was evidence of epistatic interactions. Nymph-to-adult survival of the cross classes was found to be highly correlated with mean mass change of the adults. The present paper reports the genetic architecture of differences in oviposition preference between a rice-feeding and a *Leersia*-feeding strain of brown planthopper. The genetic correlation between preference and performance is also considered.

2. MATERIAL AND METHODS

(a) *Stocks and crosses*

Stock populations of brown planthopper were derived from a collection made at Dhanbad, Bihar, India, in 1989 from rice and a collection made at Bogor, Java, Indonesia, in 1990 from *Leersia hexandra*. Rearing conditions have been described previously by Butlin (1993, 1996) and Trickett (1995). Two lines were chosen from among six inbred lines derived from each stock population of *N. lugens* by at least seven generations of sib-mating. F₁, F₂, and parental backcrosses were carried out between inbred lines (for details, see Sezer & Butlin (1998)) to establish the genetic basis of performance traits and oviposition preference.

Newly emerged female adults were placed on stems of young *Leersia* or rice plants individually (the 'test plant') and every day one or two females from each class of cross were assessed simultaneously. Each individual was weighed when it had just become adult and again 72 h later. After the second weighing, each individual was provided with both rice and *Leersia* stems to assess oviposition preference. Because of surface-area differences between the host plants, two *Leersia hexandra* cuttings (fresh stems rooted for 7–10 d) and one rooted *TNI* rice stem (4–5 weeks old) were placed in each 2 cm × 15 cm glass boiling tube. Each tube had approximately 5–6 cm of plant stems in which the female could oviposit, an 8–9 cm depth of tap water and a 1 cm cotton wool stopper to prevent the planthoppers from escaping. Each female was removed from the tube 96 h later and the numbers of eggs and egg batches were counted. To locate the brown planthopper eggs in the stems, the technique described by Khan & Saxena (1986) was used. Oviposition preference measured in this way excludes landing preferences that might be exhibited by macropterous planthoppers, but includes other behavioural components likely to be involved when planthoppers crawl from stem to stem in natural conditions.

(b) *Analysis*

Data were analysed by using GENSTAT (GENSTAT 1987) and SPSS (Norris 1993) statistical software. Performance was expressed as the proportional mass change relative to initial mass in the 72 h after transfer to the test host (Sezer & Butlin 1998). Oviposition preference was described as the log-transformed ratio of the number of eggs laid on rice to the number of eggs laid on *Leersia*; 0.5 was added to the number of eggs laid on rice and on *Leersia* as a continuity correction and to allow for the individuals that did not lay any eggs on one of the host plants (Snedecor & Cochran 1978).

When the data were examined on this scale, multimodality of the distributions of parental populations and crosses was observed (figure 1). This was considered to be a scale artefact caused by females that laid all eggs on one host plant. The sensitivity of the population parameter estimates to sampling effects was therefore checked by bootstrapping (Shao & Tu 1995) with 350 re-samples from the original data set. Bootstrap confidence

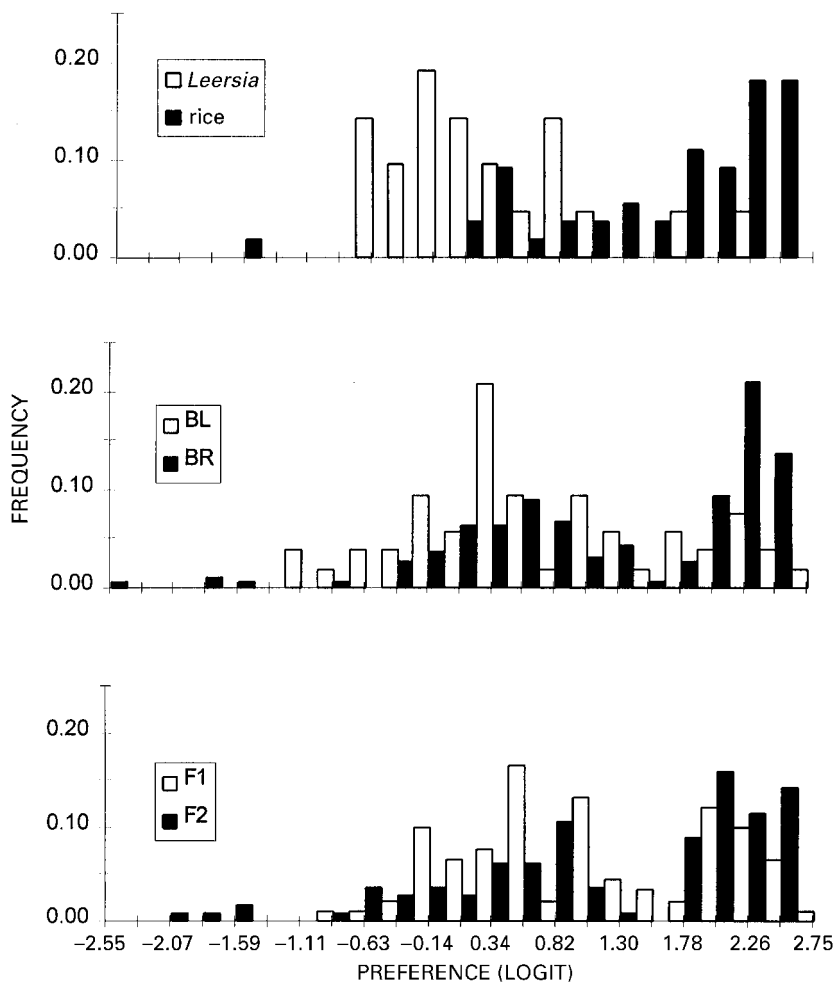


Figure 1. Frequency distribution of preference of the parental F_1 , F_2 , BR (backcross to rice), and BL (backcross to *Leersia*) classes (reciprocal crosses pooled).

intervals are the 2.5 and 97.5 percentiles of the resulting parameter distributions. Note that these confidence intervals indicate the robustness of the parameters only to sampling effects, not to departures from the underlying assumptions of the genetic model.

Only the 524 individuals that laid more than 20 eggs in total were included in the analysis. The average number of eggs laid per female, in this group, was 87.84 ± 62.7 (mean \pm s.d.). Some individuals (35) laid fewer than 20 eggs, but the measure of their oviposition preference was considered unreliable. A further 762 females laid no eggs, probably because they fed poorly during performance testing (see below).

3. RESULTS

Mean preference for oviposition in rice stems was not significantly different between reciprocal crosses (Tukey's studentized range tests, $p > 0.05$), or between host plants on which the individuals were tested in the preceding 72 hours to assess their performance. After reciprocal crosses were combined, there were significant differences in oviposition preference among cross classes, but neither test-plant effect nor test-plant \times cross-class interactions were significant. Hence, the oviposition preference data were combined from individuals whose performance was tested on rice or on *Leersia* (table 1, figure 1). The fit of the data to the standard quantitative genetic model with only additive and dominance effects was then tested by using the 'scaling tests' (Mather & Jinks 1982). The separate A ,

Table 1. *Oviposition preference scores*

cross class	sample size	mean	variance
rice	55	1.618	0.815
backcross to rice	191	1.334	1.208
F_1	91	0.928	0.885
F_2	113	1.214	1.341
backcross to <i>Leersia</i>	53	0.605	0.975
<i>Leersia</i>	21	0.155	0.599

B and C scaling tests utilize the backcross to each parent and the F_2 data, respectively. Only the C value differed significantly from zero, indicating a departure from expectation ($A = 0.12 \pm 0.22$, $B = 0.13 \pm 0.33$ and $C = 1.22 \pm 0.52$, mean \pm s.e.). The joint scaling test utilizes data from all generations to estimate the parameters of the genetic model as well as the goodness of fit: m (mid-parent value) = 0.97 ± 0.087 , d (phenotypic difference of the homozygotes from m) = 0.71 ± 0.086 , h (departure in phenotype of heterozygote from m) = 0.033 ± 0.14 ($\chi^2_3 = 5.6$, $0.3 > p > 0.1$). Thus, the simple additive-dominance model provides an adequate explanation of the data and it is not necessary to seek more complicated models including non-allelic interaction, sex-linkage, or maternal effects. Because h is not significantly different from zero, suggesting that there is no net dominance of either parental genotype, differences between these two planthopper lines can be

Table 2. *Estimates of the effective number of loci influencing performance on rice*

(Methods n_1 – n_4 use different combinations of cross classes to estimate variance due to segregation (Lande 1980). n , Maximum-likelihood estimate of effective number of loci (support limits); m_{p1} , mean preference of parent 1 (rice); m_{p2} , mean preference of parent 2 (*Leersia*); V_e , environmental variance; h , directional dominance; V_{p1} , variance of parent 1; V_{p2} , variance of parent 2 (see Butlin (1996) for further details).)

method of calculation	Lande's model	estimated parameters by maximum likelihood model	
	effective number of loci \pm s.e. (bootstrap confidence interval)	without directional dominance	using different parental variances
	—	$n=0.4$ (0.2–2.0)	$n=0.5$ (0.16–2.0)
n_1	0.588 ± 0.331 (0.679–1.238)	$m_{p1}=1.683 \pm 0.098$	$m_{p1}=1.746 \pm 0.121$
n_2	0.492 ± 0.273 (0.421–1.021)	$m_{p2}=0.302 \pm 0.141$	$m_{p2}=0.235 \pm 0.163$
n_3	0.539 ± 0.527 (0.125–0.906)	$V_e=0.827 \pm 0.105$	$V_{p1}=1.072 \pm 0.205$
n_4	0.453 ± 0.332 (0.498–0.611)	—	$V_{p2}=0.758 \pm 0.265$

explained by additive inheritance alone (with $m=0.99 \pm 0.046$ and $d=0.70 \pm 0.084$, $\chi_4^2=5.7$, $0.3 > p > 0.1$). This preferred model has been bootstrapped and the estimations were: $m=0.99$ (0.98–1.01) and $d=0.80$ (0.78–0.82) (mean of bootstrap estimation (95% confidence interval)).

The F_1 variance was larger than either parental variance even though each is expected to be equal to the environmental variance (table 1, figure 1). This common pattern may be due to greater susceptibility of the F_1 to environmental influences: Lande's four estimators accommodate its effects in calculating the segregation variance (Lande 1981) and the maximum-likelihood approach uses a weighted average of the three variances (Butlin 1996). A few F_2 individuals had preference scores lower than the minimum observed in the *Leersia* population. This is suggestive of segregation of decreasing loci that were present in the rice population but in this case is more likely to be an artefact of the small *Leersia* parental sample size.

The minimum effective number of loci influencing oviposition preference has been calculated by using Lande's formulae (Lande 1981) and a maximum likelihood approach (Butlin 1996). The maximum likelihood approach estimated the dominance as 0.45 (0.5 for no dominance, 1 and 0 for the complete dominance in direction of one of the parent populations), in complete agreement with the joint scaling test. Therefore, models without dominance, with equal or unequal parental variances, were fitted. Both methods yield identical results (table 2). Phenotypic differences between these two lines are apparently attributable to only one gene or chromosomal region. The corrections suggested by Zeng (1992) for unequal allelic effects and linkage, the two major causes of underestimation (Zeng *et al.* 1990), would increase the estimated number of loci by a factor of less than 2 (Butlin 1996).

Previous analysis revealed that some genotypes performed better on one or other host plant (Sezer & Butlin 1998), but the subsequent oviposition preference was not influenced by the host plant on which the individual's performance had been tested. To characterize the interaction between genotype and host plant, we used an iterative method described by Mather & Jinks (1982). This method combines the separate search for genetic components on two host plants, and identifies the effect of

Table 3. *Estimated components of the cross mean performance and oviposition preference from additive-dominance, non-allelic interaction, and genotype–environment interaction models*

(Components: m , mid-parent value; d , phenotypic difference between the two homozygotes and m ; h , departure in phenotype of heterozygote from m ; i , homozygote \times homozygote interaction; j , homozygote \times heterozygote interaction; l , heterozygote \times heterozygote interaction; e , effect of environment; g_d , interaction of environmental and additive genetic effects; g_h , interaction of environmental and dominance genetic effects.)

components	performance	oviposition preference
m	0.22 ± 0.076	0.998 ± 0.08
d	0.083 ± 0.020	0.72 ± 0.08
h	-0.016 ± 0.18	-0.022 ± 0.14
j	0.26 ± 0.061	—
i	0.13 ± 0.074	—
l	0.178 ± 0.12	—
e	0.15 ± 0.018	0.11 ± 0.08
g_d	0.35 ± 0.017	-0.12 ± 0.079
g_h	0.23 ± 0.032	-0.071 ± 0.14
test statistics	$\chi_9^2=11.69$	$\chi_{12}^2=13.93$
p	$0.25-0.10$	$0.50-0.25$

environment (e) and type of genotype–host-plant interaction (g_d , interaction between additive genetic effects and the environment; g_h , interaction between dominance effects and the environment).

As expected, e , g_d , and g_h for oviposition preference are not significantly different from zero (t -test, $p > 0.05$); this result suggests that host plant and genotype–host plant interaction have no effect (table 3). Performance changed more than preference with host plant, and the estimated interaction is large relative to the environmental effect. The positive estimate for e confirms that performance is higher overall on rice than on *Leersia* (table 3) (Sezer & Butlin 1998). Because g_d and g_h are functions of e and d or h , their coefficients' signs are opposite across the host plants. Detection of significant g_d and g_h (table 3) is direct evidence of a trade-off between performance on the two host plants, because it implies that increased performance on one host is genetically associated with decreased performance on the other.

Table 4. Estimated correlation coefficients within cross classes reared on rice and *Leersia* plants, and combinations of segregating and non-segregating families using z-transformation

(L, *Leersia*; R, rice; BR, backcross to rice; BL, backcross to *Leersia*. Asterisks indicate that the value is significantly different from zero ($p < 0.05$). Combined segregating and non-segregating correlations are not different from each other in either case ($p > 0.05$).)

mate	tested on rice		tested on <i>Leersia</i>	
	<i>n</i>	correlation	<i>n</i>	correlation
L	4	0.991*	18	0.165
R	41	0.020	14	-0.056
F ₁	69	0.225	22	0.064
combined non-segregating	—	0.117*	—	0.068
F ₂	82	0.171	31	-0.504*
BR	137	-0.021	54	-0.173
BL	30	0.304	23	0.224
combined segregating	—	0.08	—	-0.201*

Egg-batch size on rice did not vary either between cross classes or between test plants ($p > 0.05$), but batch size on *Leersia* showed significant differences between the individuals tested on different host plants ($F_{1,251} = 7.0$; $p = 0.009$). Batch sizes on rice laid by females from rice and *Leersia* test plants were 4.023 ± 0.16 and 4.024 ± 0.13 , and batch sizes on *Leersia* were 10.22 ± 0.69 and 7.08 ± 0.69 , respectively.

Some females laid no eggs. The proportion of individuals that laid no eggs, relative to the number of individuals that laid more than 20 eggs in total, was negatively correlated with survival as measured by Sezer & Butlin (1998) across cross classes where females were tested on rice ($r = -0.914$, $p = 0.011$), but not significantly so for those tested on *Leersia* ($r = -0.61$, $p = 0.19$). This result is in agreement with the expectation from the relation between survival and performance of the cross classes (Sezer & Butlin 1998) ($r = 0.93$ on rice and $r = 0.92$ on *Leersia*; $p < 0.001$ in both cases). The correlation between inability to lay eggs and preference index over the cross classes was significantly negative ($r = -0.83$, $p = 0.046$; data combined across test host plants). A similar, but non-significant, correlation was detected between inability to lay eggs and mean number of eggs laid by each cross class ($r = -0.76$, $p = 0.077$).

Correlations between preference and performance have been carried out separately, according to test plant, because the previous performance analysis revealed significant host and host-cross interaction (Sezer & Butlin 1998). Overall correlations, regardless of their cross classes, were $r = 0.16$ ($p = 0.002$), and $r = -0.31$ ($p < 0.001$) for rice- and *Leersia*-tested individuals, respectively. The negative correlation on *Leersia* means that individuals whose performance is relatively low on *Leersia* prefer to oviposit on rice plants; the positive correlation on rice shows that individuals that performed well on rice also preferred to oviposit on rice. Correlations were also calculated between preference and performance within

each cross class. Coefficients of segregating and non-segregating classes have been combined by means of z-transformation (Snedecor & Cochran 1978). For non-segregating crosses, the combined correlation provides an estimate of the environmental correlation between the traits. The correlation within segregating crosses includes not only environmental effects but also any genetic correlation caused by pleiotropy or linkage. Most of the calculated correlation coefficients for preference and performance within cross classes were not significant, and the combined segregating and non-segregating correlation coefficients were not significantly different from each other ($p > 0.05$) on either of the host plants (table 4).

The heritability of oviposition preference for rice has been calculated as 0.53 (narrow sense) and 0.54 (broad sense), based on the calculated values of D (combined additive variance) = 0.969, H (combined dominance variance) = 0.024, and E (environmental variance, estimated from the maximum likelihood model) = 0.832.

4. DISCUSSION

The central requirement for sympatric speciation via host-race formation is for gene exchange to be restricted by changes in preference or performance traits, or both. The theoretical scenario outlined above (see §1) predicts that (i) preference and performance are each affected by a small number of genes of large effect; (ii) these traits have a common genetic basis or are genetically correlated; and (iii) there is a trade-off in fitness between hosts. The data presented here and by Sezer & Butlin (1998) show that in the brown planthopper the genetic architectures of oviposition preference and host-associated performance do both involve small numbers of genomic regions of large effect and that there is a trade-off in performance between host plants, but that preference and performance are inherited independently.

The only known differences between the rice- and *Leersia*-eating populations of *N. lugens*, apart from those associated with hosts, are mating signals and DNA sequences. Mating signals may provide a pre-mating isolating barrier between these two populations. Lack of intermediate mating song from field-caught individuals, and homogametic mate preferences in the laboratory, suggest that these two populations may represent sibling species (Claridge *et al.* 1988; Butlin 1993; Trickett 1995; Butlin 1996). However, the DNA sequence data suggest that they have diverged only recently (about 0.25 Ma BP), independently in Asia and Australia, and without geographical separation (Jones *et al.* 1996).

Our results are consistent with the hypothesis that these two populations diverged recently and in sympatry. Survival and feeding is only possible on rice varieties and *Leersia hexandra*, and populations derived from either of these two hosts are unable to perform well enough to reproduce on the other plant. An effective number of loci of only one or two, with dominance in the direction of rice populations, has already been demonstrated for performance traits (Sezer & Butlin 1998). Oviposition preference has an additive genetic basis and is also determined by a small number of genomic regions, probably one. Therefore, changes in only two genomic regions, and potentially just two mutations, may have been

sufficient for a planthopper population from *Leersia* to shift to the new host plant. In sympatry, this is much more plausible than selection operating on a series of small changes.

We did not detect any genetic correlation between oviposition preference and performance, so there is no evidence of pleiotropy or linkage of the genes affecting these traits. Via (1990) considered that a genetic correlation between preference and performance would aid host shifts, but was not essential for them because females of herbivorous insects occasionally oviposit on plants outside the normal host range and plants that are not normally used may, nevertheless, support successful development. The phenotypic correlation between preference and performance was nearly twice as great among individuals on *Leersia* plants as among those on rice, regardless of their cross classes. This may be because the individuals that had experienced an unsuitable plant strongly preferred to feed, and eventually to oviposit, on the most suitable one. Rice appears to be a generally more favourable host than *Leersia*. Fecundity was correlated with performance across cross classes and was also dependent on the ability to feed on the host plant on which females had been retained before oviposition tests, but the preferences of the cross classes were not affected by this prior experience. On the other hand, if they fed well enough during the first 72 hours of adulthood to lay eggs, females spread some of their eggs between potential host plants despite preferring their own host. The ability to spread the eggs among plants is quite common in planthoppers (Denno & Perfect 1994) and our study confirms this observation. This is true despite the fact that we detected significantly larger batches of eggs on *Leersia* plants, indicating that *Leersia* plants are easier to scar for egg-laying, perhaps because of their pipe-like stems.

Populations show strong physiological adaptation to their own host plants, and there is evidence for a genetically based trade-off between hosts, which is not typically observed in within-population studies (Via 1990). The interaction between environment and heterozygous genotypes for performance is smaller than that between environment and homozygous ones, suggesting that their sensitivity to host plants is lower. This could be an indication of inbreeding depression but we have no further evidence to support this possibility, because parental inbred lines did not show any lower viability, fecundity or performance than cross classes. It is most likely that homozygote genotypes perform better on the right host plant and that heterozygotes have a lower performance on both host plants. Such a response to host plants may aid host-plant specialization by favouring homozygote genotypes.

The simple genetic basis for oviposition preference and the distribution of the eggs among the host plants may help to promote a sympatric host shift regardless of the lack of genetic association between preference and performance. After a physiologically adapted population becomes established on the alternative host plant, it may be conserved easily by such an oviposition preference. If male search preferences have a common genetic basis with oviposition preference, the resulting ecological isolation would result in a substantial barrier to gene

exchange for an insect that mates on its host plant and uses the host plant as a channel for its substrate-transmitted mating signals (Butlin 1996). The barrier to gene exchange would further facilitate genetic divergence in preference and performance (Diehl & Bush 1989).

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

