

Laboratory evolution of host plant utilization in the bean weevil (*Acanthoscelides obtectus*)

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(Received 4 August 1994; accepted 29 August 1995)

Summary – Populations of the bean weevil (*Acanthoscelides obtectus*) were subjected to 35 generations of artificial selection for characteristics affecting host utilization when females were exposed to a choice between 2 hosts (*Phaseolus vulgaris* and *Cicer arietinum*), or exposed to natural selection for the same period, when only one host was available. We obtained a positive response for the percentage of eclosed adults on the chickpea seeds in the ‘*Cicer* choice’ lines but not in the *Phaseolus* lines. In the post-selection test we demonstrated that oviposition preference and egg-to-adult viability in the *Cicer* lines were higher on the chickpea than on the bean seeds. Lines that had been selected for female oviposition preference on chickpea displayed the same preference for this host after selection was terminated as lines that had been maintained on chickpea seeds without choice.

Acanthoscelides obtectus / larval density / selection / oviposition preference

Résumé – Évolution en laboratoire de l’utilisation de la plante hôte chez le charançon du haricot (*Acanthoscelides obtectus*). Des populations de charançon du haricot (*Acanthoscelides obtectus*) ont été soumises à 35 générations de sélection pour des caractères affectant l’utilisation de la plante hôte, avec un choix possible pour les femelles entre 2 hôtes (*Phaseolus vulgaris* ou *Cicer arietinum*), ou soumises à la sélection naturelle durant le même nombre de générations sans choix de l’hôte. Une réponse positive en pourcentage d’adultes éclos est obtenue dans les lignées choisissant *Cicer*, mais non dans celles choisissant *Phaseolus*. Dans les comparaisons effectuées à l’issue de la sélection, on montre que, dans les lignées *Cicer*, la préférence d’oviposition et la viabilité du stade œuf au stade adulte sont plus grandes sur les grains de *Cicer* que sur ceux de *Phaseolus*. De plus, les lignées sélectionnées pour une oviposition préférentielle sur *Cicer* manifestent après sélection la même préférence pour cet hôte que des lignées maintenues sur *Cicer* sans possibilité de choix de l’hôte.

Acanthoscelides obtectus / densité larvaire / sélection / préférence d’oviposition

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INTRODUCTION

There have been many observations of significant variability and potential for host change in phytophagous insects (see recent reviews in Via, 1990; Jaenike and Holt, 1991). These studies have shown that both the behavioural traits which influence the choice of plant species for feeding or oviposition ('preference') and physiological or morphological traits that affect growth and/or reproduction on a particular host plant ('performance') may have a genetic basis.

Due to its special evolutionary importance, several studies have separated genetic and environmental variance in host preference (Tabashnik *et al*, 1981; Rausher, 1983; Jaenike, 1985, 1986, 1989; Lofdahl, 1987; Singer *et al*, 1988; Fox, 1993) or performance (Rausher, 1984; Via, 1984; Hare and Kennedy, 1986; Futuyma and Philippi, 1987; James *et al*, 1988). Some of these short-term experiments have demonstrated a genetic correlation between preference and performance (Tavormina, 1982; Via, 1986; Singer *et al*, 1988; Jaenike, 1989). However, long-term experiments examining evolutionary changes in host preference and/or host utilization ability in insect populations are largely lacking (but see Gould, 1979; Wasserman and Futuyma, 1981; Fry, 1990).

We used this approach in a laboratory study with bean weevils (*Acanthoscelides obtectus*). We investigated the changes in the traits affecting host utilization that occurred when bean weevils were exposed, over 35 generations, to a choice of 2 hosts (bean and chickpea seeds) and when only 1 host was available. Here we are in a position to assess whether the evolution of 2 host species utilization is more likely to proceed by the propensity of *A. obtectus* females to accept hosts for oviposition or by changes in the physiological traits that affect the ability of weevil larvae to use different hosts.

MATERIALS AND METHODS

Life history of the bean weevil and experimental conditions

A. obtectus (Say) is a bruchid species that attacks seeds of various leguminous crops. The primary host of this weevil is the common bean (*Phaseolus vulgaris*). The weevil also attacks chickpeas (*Cicer arietinum*) and other stored legumes (see Milanović *et al*, 1991).

The females deposit eggs in clusters under or nearby single seeds. The first instar larva bores into a seed where the beetle spends its larval and pupal stages. The final instar larvae excavate a chamber just below the seed testa and the presence of the larva may be detected by a small 'window'. After eclosion the adult chews a hole in the seed coat and pulls itself out of the seed, ready to mate. Adults do not feed on the seeds. Moreover, they need neither food nor water to produce viable eggs. (For more details of *A. obtectus* life history, see Tucić *et al*, 1991.)

For the experiments reported here, we made use of different *A. obtectus* lines established from a base population that had been maintained in the laboratory since 1986. (This is the 'synthetic' population established from 3 local populations captured in an area where the chickpea is not available: in the vicinity of Belgrade,

Serbia.) The base population was reared at large population size (about 5 000 individuals in each generation) on *P vulgaris*, cv 'gradištanac' seeds.

The experiments were conducted in a dark incubator at 30 °C and a relative humidity of about 70%. All seeds were bought in bulk from one source. Seeds were frozen before their use in experimental treatments. No food or water was offered to the adults in the experiment.

Experiment 1: selection procedures

Four selection regimes, with 2 replicates per regime, were used: 2 'no-choice' and 2 'choice' treatments.

In 'no-choice' treatments only one species of host was offered; 2 replicates (the 'Phaseolus lines') were reared on common bean seeds, the other 2 (the 'Cicer lines') were maintained on chickpea seeds. Since no selection for host preference was imposed, the weevils should have experienced natural selection for larval adaptation to host species. Each replicate line was initiated with 100 randomly chosen adults from the base population. These replicates were kept in separate bottles containing 200 seeds of the appropriate host. This procedure was repeated during 35 non-overlapping generations. 'Choice' treatments also produced replicated *Phaseolus* and *Cicer* lines which began with 10 groups, each comprising 10 pairs of one-day-old weevils. The weevils were placed in Petri dishes (50 mm diameter) which contained equal numbers of bean seeds and chickpea seeds of about the same size (7 mm). Seeds were placed in each dish so that bean covered one half and chickpeas the other half of the dish. The Petri dishes were kept in a dark incubator and from about 3 weeks onward were checked daily until the eclosion of adults started. (The eclosion is recognized by the 'windows' on the seed testa becoming black; otherwise the windows are grey.) At that time, beans and chickpeas were separated. In 2 replicate lines (the 'choice *Phaseolus* lines'), bean seeds from all 10 dishes were kept together in a single bottle. The number of eclosed adults from beans and chickpeas was then counted. From the newly emerged adults from bean seeds we chose, again randomly, 10 groups with 10 pairs of beetles, in order to establish a new generation, which was again offered a choice between beans and chickpeas. This procedure was repeated for 35 generations. In the 'choice *Cicer* line' the same procedure was applied, except that new generations were founded by adults emerging from the chickpeas.

In 'choice' treatments, the selection criterion was the percentage of eclosed adults which originated from the appropriate host (hereafter denoted as 'the percentage of eclosed adults'). We have chosen this composite trait (which includes the number of eggs laid, larval preference and larval performance) because the eggs are usually deposited underneath the host seeds, and therefore they are difficult to count without harming them. Thus, the information on the oviposition preference and larval performance is crucial for the understanding of the changes in the utilisation by *A obtectus* under applied selection regimes. (On the basis of our exploratory experiment (unpublished data), we believe that larval preference does not determine host choice because first instar larvae are not very vagile (only this instar has legs and can walk to find a place to enter the seeds; usually they remain underneath the seed where the eggs were laid).)

In order to determine how much selected lines diverged from each other in traits affecting host utilization 2 post-selection tests were performed. The first test

was designed to measure the oviposition preference, whereas in the second larval performance of different lines was estimated.

Experiment 2: oviposition preference

To rule out the effect of plant seeds where weevils fed during the larval stages as a possible reason for the divergence among lines, we reared all lines in both host seeds after the end of the selection, and then tested their offspring with regard to oviposition preference in a mixed-host environment. Two groups of about 50 pairs of newly emerged weevils from each replicate line were collected. The first group was reared for one generation on beans and the second on chickpeas. After that, 15 pairs of weevils within each line/host seed treatment were tested individually for oviposition preference in Petri dishes containing equal numbers of bean and chickpea seeds. Although the seeds were not distributed randomly in the Petri dishes (we applied the same conditions as in the 'choice' selection regimes), it is very unlikely that this could produce any bias in the oviposition preference because weevil females exhibited a pre-oviposition period (see, for example, Pouzat, 1978). The number of eggs deposited on each host seed were counted. Oviposition preference was measured only during the first 4 d of female life span (this period covers about 3/4 of the female's fecundity, see Tucić *et al*, 1990).

Experiment 3: larval performance

To determine whether larval survival differed among the lines, the egg-to-adult viability and pre-adult developmental time were also tested after the termination of the selection experiment. A sample of about 100 one-day-old adults was collected randomly from one replicate within each treatment, and weevils were mated in groups. These 4 groups were kept in separate Petri dishes containing bean seeds only. Females were allowed to lay eggs for 24 h. After removal of the weevils, the eggs were counted and collected from the dish bottom and the surface of the beans using a paint brush. Eggs collected from each line were divided into 2 equal batches, one being set up on 5 Petri dishes containing bean seeds and the other on Petri dishes containing chickpeas. To prevent differential larval densities, each Petri dish contained 20 seeds and 50 eggs. In addition, a density of about 2–3 larvae per grain is too low to express pronounced effects on either survival or pre-adult development (Aleksić *et al*, 1993). Thus, the total number of eggs used for the estimation of the egg-to-adult viability and pre-adult developmental time for each line and host was $50 \times 5 = 250$. The egg-to-adult viability is defined as the percentage of adults on each host seed. The duration (in days) from deposition of eggs to emergence of adults was used to estimate preadult developmental time.

Statistical procedures

Multiway analyses of variance for the percentage of eggs laid on chickpeas and for the 4 d fecundity (*Experiment 2*) were performed by using the PC-EMS program (Dalla, 1985). We have dealt here with 4 factors: selection treatment (factor A-fixed), host (B-fixed), replicate lines (C-random) and rearing host (D-fixed). Replicates (C) were nested within the selection treatment (A) and host (B)

interaction. The model description was: $A + B + AB + C(AB) + D + AD + BD + ABD + C(AB)D$, with mean and error terms not stated explicitly. In this model we have 3 'error terms' (numbers correspond to levels in the model under 'source of variation' in table II below): (10) error (within groups), (9) $C(AB)D$ and (8) $C(AB)$. In F -tests, terms D , AD , BD and ABD and $C(AB)$ were tested against (9) and terms A , B and AB were tested against (8).

The egg-to-adult viability and pre-adult developmental time (*Experiment 3*) were analysed by 3-way ANOVA. The factors were: selection treatment (factor A-fixed), host (B-fixed) and rearing host (C-fixed). Since here we are dealing with a Model I (fixed effects model) ANOVA, each F value refers to the error MS.

RESULTS

Responses to selection

The percentages of eclosed adults on chickpeas or beans over the choice selection regimes are presented in figure 1. It is evident that increases in the percentages of eclosed adults on chickpeas did occur in both replicates of the *Cicer* line (fig 1B), but not in the choice *Phaseolus* line (fig 1A). For each replicate we estimated regression coefficients for the percentage of eclosed adults on the appropriate host (after arcsin transformation) on generation of selection. The coefficients were highly significant for both choice *Cicer* line ($b_1 = 0.67 \pm 0.17$; $P < 0.001$; $b_2 = 0.86 \pm 0.19$; $P < 0.001$). A test of equality of regression coefficients did not reveal significant differences between these 2 replicates ($F_s = 0.56$; $P > 0.05$). In contrast, both regression coefficients for the *Phaseolus* line were non-significant ($b_1 = 0.07 \pm 0.14$; $b_2 = -0.04 \pm 0.16$).

Post-selection tests

The mean percentages of eggs laid on chickpeas of all the lines, reared on both hosts and tested in a mixed-host environment, are listed in table I. A striking feature of these data is the large difference between hosts where selection was imposed. The mean percentages of eggs laid on chickpeas in the *Cicer* lines, no matter what the treatment or the rearing host were, were higher than those in the *Phaseolus* lines. This finding was statistically confirmed by the results of the factorial analysis of variance (table II). In addition, the host seeds where females developed during larval stages ('rearing host' in table II), and interaction 'selection treatment \times rearing host' ($A \times D$ in table II), contributed significantly to host preference variation. The mean percentages of eggs laid on chickpeas in the 'no-choice' and 'choice' treatments were, however, not different from each other ($F = 0.95$; $P > 0.05$, table II).

Although the results in table I suggested that the mean number of eggs laid per female is higher in *Phaseolus* than in *Cicer* lines, this was not confirmed by the analysis of variance (table II). Since the average of the 4 d fecundity varied considerably across rearing host \times replicate cells (see line 9 of table II), none of the main effects ('selection treatments', 'host seeds' and 'rearing host'; table II) was statistically significant.

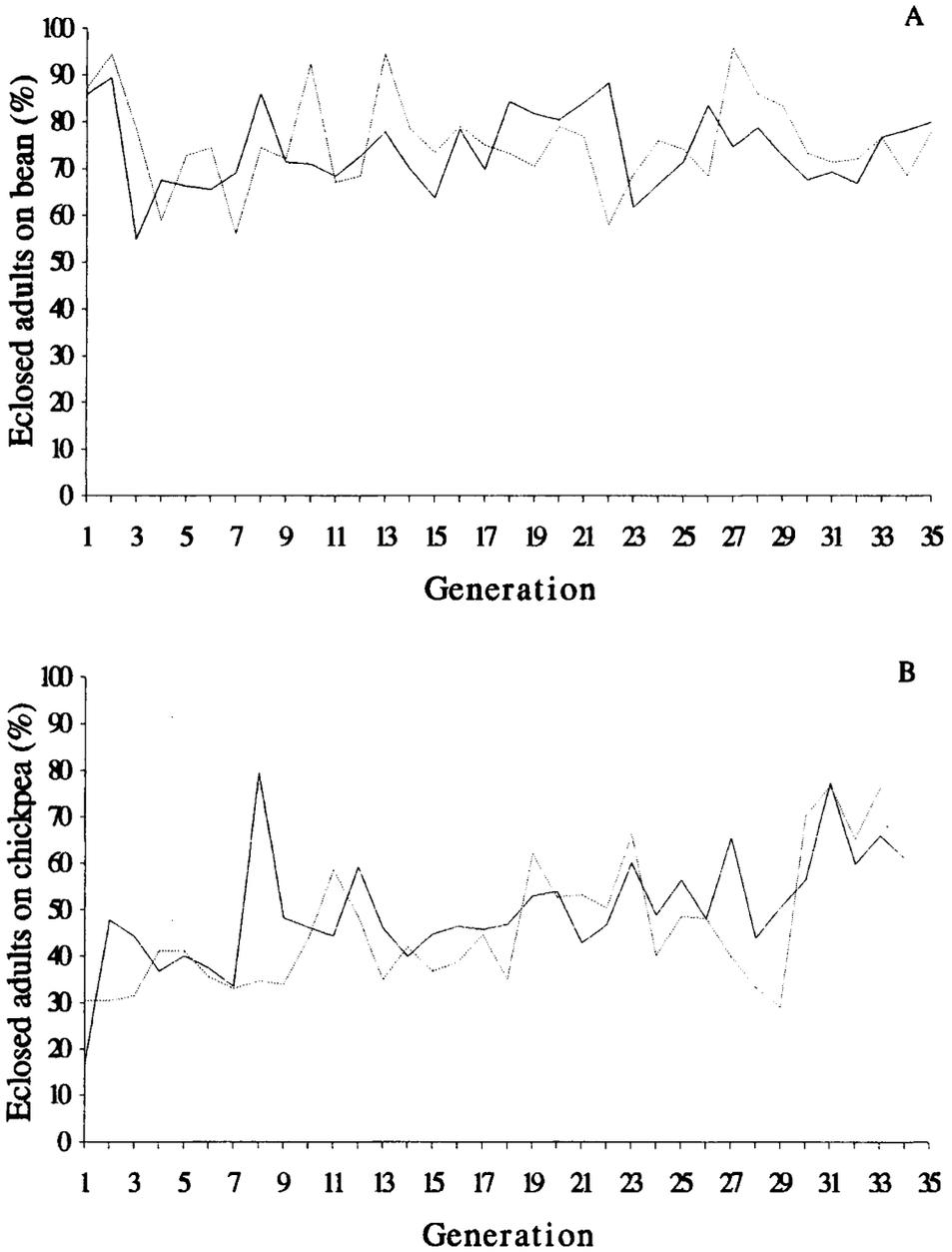


Fig 1. The percentage of eclosed adults on bean (A) or chickpeas (B) during the course of the choice selection treatments. Solid line: replicate 1; dashed line: replicate 2.

Table I. The mean percentages of eggs laid on chickpeas (\pm standard errors) and the mean number of eggs laid per female (\pm standard errors) over 4 d of all lines reared on both hosts and tested in a mixed-host environment.

Rearing Trait hosts	Replicates	Treatment				
		No-choice		Choice		
		Phaseolus	Cicer	Phaseolus	Cicer	
<i>Bean</i>	% of eggs on chickpeas	1	11.26 \pm 4.31	35.15 \pm 4.12	22.76 \pm 2.79	44.26 \pm 5.78
		2	27.71 \pm 7.09	34.93 \pm 6.64	21.52 \pm 5.86	34.05 \pm 7.32
	Fecundity	1	25.40 \pm 2.79	30.13 \pm 2.60	34.07 \pm 2.63	22.33 \pm 2.81
		2	28.20 \pm 2.46	15.47 \pm 1.52	31.07 \pm 2.39	24.00 \pm 1.76
<i>Chickpea</i>	% of eggs on chickpeas	1	12.95 \pm 3.65	38.14 \pm 5.18	24.64 \pm 4.06	42.95 \pm 6.58
		2	24.38 \pm 4.21	39.45 \pm 4.99	22.57 \pm 5.08	36.67 \pm 5.42
	Fecundity	1	42.07 \pm 7.49	27.27 \pm 2.32	36.73 \pm 3.29	27.20 \pm 3.25
		2	22.07 \pm 2.08	16.13 \pm 1.93	33.20 \pm 3.03	21.53 \pm 2.37

The number of tested females is equal (15) in all groups.

Table II. Analysis of variance for the percentages of eggs laid on chickpeas (data were arcsin transformed) and for 4 d fecundity.

Source of variation	df	% of eggs on chickpea		Fecundity		F-ratio
		MS	F	MS	F	
1. Selection						
treatment (A)	1	699.32	0.95	513.34	0.54	1/8
2. Host (B)	1	10 254.46	13.89*	4 429.00	4.63	2/8
3. Rearing host (D)	1	111.33	22.08***	226.20	0.41	3/9
4. A \times B	1	158.79	0.22	119.00	0.12	4/8
5. A \times D	1	38.00	7.54*	1.20	0.00	5/9
6. B \times D	1	2.41	0.48	214.70	0.39	6/9
7. A \times B \times D	1	27.42	5.44	100.10	0.18	7/9
8. C (AB)	4	738.04	146.44***	956.40	1.74	8/9
9. C \times D (AB)	4	5.04	0.02	549.74	6.27***	9/10
10. Error	224	208.53		87.69		

Replicates (C) are nested within the 'selection treatment' (A) and 'host' (B) interaction. F-ratios refer to numbers under 'source of variation'. * $P < 0.05$; *** $P < 0.001$.

The relationship between oviposition preference for chickpea and fecundity was tested by calculating correlation coefficients. We estimated 4 correlation coefficients on the pooled data over replicates and 'rearing hosts' (table III). Both the 'no-choice' and 'choice' *Phaseolus* lines showed that oviposition preference was negatively correlated with fecundity. However, no such relationship was found for the *Cicer* lines (neither correlation was different from zero, table III).

Table III. Coefficients of correlation (*r*) between oviposition preference (the percentages of eggs laid on chickpea) and 4 d fecundity in the *Phaseolus* and *Cicer* lines.

	Phaseolus line		Cicer line	
	No choice	Choice	No choice	Choice
<i>r</i>	-0.233*	-0.401***	-0.064	-0.085
± SE	±0.13	±0.12	±0.13	±0.13

In all cases the number of tested females was 60. **P* < 0.05; ****P* < 0.001.

Table IV. Averages (± standard errors) of egg-to-adult viability (in %) and pre-adult developmental time (d) for the *Phaseolus* and *Cicer* lines reared on 2 host seeds.

Rearing hosts	Trait	Selection treatment			
		No-choice		Choice	
		Phaseolus	Cicer	Phaseolus	Cicer
Bean	Viability	60.56 ± 4.72	51.08 ± 2.57	64.28 ± 3.60	50.13 ± 5.34
	Developmental time	39.40 ± 0.12 (152)	38.39 ± 0.14 (129)	37.16 ± 0.12 (161)	38.73 ± 0.15 (126)
Chickpea	Viability	56.68 ± 4.74	56.03 ± 6.05	52.95 ± 3.29	58.66 ± 5.53
	Developmental time	38.87 ± 0.15 (142)	38.36 ± 0.13 (139)	36.09 ± 0.14 (132)	36.46 ± 0.14 (147)

The average viabilities were estimated from 5 Petri dishes, each containing 50 eggs. The numbers of tested individuals for developmental time are given in parentheses.

Table V. Mean squares (MS) from 3-way ANOVA for egg-to-adult viability (data were arcsin transformed) and pre-adult developmental time.

Source of variation	df	Viability		df	Developmental time	
		MS	F		MS	F
Selection treatment (A)	1	0.61	0.02	1	759.15	301.41***
Host (B)	1	71.02	2.34	1	2.89	1.15
Rearing host (C)	1	6.67	0.22	1	266.53	105.82***
A × B	1	0.62	0.02	1	209.78	83.29***
A × C	1	2.95	0.10	1	136.24	54.09***
B × C	1	174.39	5.75*	1	8.67	3.44
A × B × C	1	24.54	0.81	1	50.86	20.19***
Error	32	30.33		1 120	2.52	

P* < 0.05; **P* < 0.001.

As for the preference, one might expect that a long-term rearing of the bean weevils on the chickpea seeds will lead to increase of larval performance on that host. The results in table IV show that this could be the case for the egg-to-adult

viability but not for the pre-adult developmental time. On the beans the average viabilities (pooled over 'no-choice' and 'choice' treatments) are 62.4 and 50.6% in the *Phaseolus* and *Cicer* lines, respectively. On the chickpeas these averages are 54.8% (the *Phaseolus* line) and 57.4% (the *Cicer* line). This trend is statistically confirmed by the significant 'host \times rearing host' interaction term in the analysis of variance (table V). All other effects did not contribute significantly to the observed variation of the egg-to-adult viability. A 3-way ANOVA of the pre-adult developmental time, on the other hand, showed significant effects of selection treatment, rearing host and all interactions except those between host and rearing host (B \times C in table V).

DISCUSSION

We obtained positive responses to selection for the percentage of eclosed adults on the chickpea seeds in both 'choice' *Cicer* lines (fig 1). The absence of any responses in the *Phaseolus* lines most likely reflects the fact that local populations, from which the base population has been established (see *Materials and methods*), used bean seeds. Hence, we have observed substantial genetic variance for the use of chickpea seeds, which are not available in the area where the weevils were collected. Our results resemble the data of Lofdahl (1987) who worked with *Drosophila mojavensis* offered a novel cactus species.

There is one more interesting aspect of the data depicted in figure 1. In the chickpea selected lines (fig 1B), the first generations showed a preference for beans as only about 20% of eclosed adults originated from the chickpea. By the end of the experiment these weevils expressed a preference for chickpea, with more than 50% of the adults emerging from this host. It seems, therefore, that the actual rank order preference has been changed as a result of selection. These observations do not support prediction of a 'general model for individual host selection' postulated by Courtney *et al* (1989). These authors argue that changes in host use are due to changes in overall threshold for acceptance of any host, and that changes in rank order preference are not expected. Contrary to our results, 2 studies (Harrison, 1987; Prokopy *et al*, 1988), however, support the Courtney *et al* (1989) model of evolution of host utilization. Both of these studies have considered host acceptance in populations where ancestry is known, and where derived populations have evolved novel host utilization.

The observed responses to selection indicate the presence of additive genetic variation in one or both of the 2 constituent traits of the selection criterion: the oviposition behaviour, which determines whether or not the females accept the host, and egg-to-adult survival on different hosts. In the post-selection test, we demonstrated that in *Cicer* lines both the oviposition preference (table I) and egg-to-adult viability (table IV) were higher on the host where selection was imposed. Accordingly, it could be concluded that, as a result of the long-term rearing of weevils on the chickpeas, females tend to choose oviposition sites in which their offspring have a higher probability of surviving.

Although some theoretical analyses predict that genetic correlation between preference and performance could be responsible for the maintenance of genetic variation in habitat selection (Bush, 1974; but see review in Jaenike and Holt, 1991), it is well known that genetic variation in preference may exist without

correlated variation in performance and *vice versa* (eg, Gould, 1979; Wasserman and Futuyma, 1981; Tabashnik, 1983; Futuyma and Moreno, 1988). In this study, however, we have presented evidence for the genetic correlation between preference and performance. Such correlations may be attributable either to a fortuitous pleiotropic relationship due to biochemical and/or developmental processes common to oviposition preference and egg-to-adult viability or to natural selection building up linkage disequilibrium between genes that influence these traits. Singer *et al* (1988) envisaged a way in which a correlation between preference and performance could be produced. We believe that their interpretation could be applied to our data as well. Their scenario favours the linkage disequilibrium hypothesis and the primacy of physiological adaptation over the host selection behaviour.

Although this does not influence our conclusion given above, a post-selection test of another fitness-related trait, pre-adult developmental time yielded a more complicated picture (table IV). Pre-adult developmental time, which could be influenced by some physiological characters (eg, the ability to overcome certain toxic compounds, assimilation efficiency, *etc*), differed significantly between the 'no-choice' and 'choice' selection treatments, but not between host seeds on which selection was imposed (bean *vs* chickpea). Bearing in mind our methods of selection, this was quite an expected result. In order to collect a sufficient number of one-day-old weevils (100 females and 100 males) for the 'choice' treatments, new generations were established, usually, from the first 200 newly emerged weevils. Hence, the faster pre-adult development in the 'choice' lines was the result of inadvertent selection for fast development in these lines.

A third fitness-related trait (fecundity) was also measured at the end of the selection experiments (table I). We counted the number of eggs laid by individual females during the first 4 d, so this is a kind of 'realized fecundity' (Wasserman and Futuyma, 1981). Since the realized fecundity mainly depended on nutritional history during the larval stage, our data suggest, contrary to expectation, that the primary host (bean seeds) is not nutritionally superior to the chickpea.

However, we have observed that only in the *Phaseolus* lines more fecund females laid significantly fewer eggs on the chickpeas than on the beans (table III). A negative correlation between realized fecundity and oviposition preference was more pronounced in the *Phaseolus* choice line. These negative correlations between oviposition and realized fecundity can be tentatively explained if increased choice requires females to spend more time searching for the preferred host, thus reducing laying time. Also, the lower magnitude of these correlations in 'no-choice' lines may be explained through selection favouring females that do not spend time searching for the lacking host, as well as through a correlated response to selection for adaptation to the host. It seems, therefore, that "selection on host choice may be one factor maintaining genetic variance in fecundity, an important fitness component" (Courtney *et al*, 1989). Hence, an important implication of the results presented in table III would be in the explanation for the high level of genetic variance for fecundity observed previously in *A. obtectus* (Tucić *et al*, 1990) and *Drosophila* populations (Roff and Mousseau, 1987; Tucić *et al* 1988) and which appears to contradict Fisher's (1930) Fundamental Theorem (*ie* the expectation that populations at selective equilibria have little or no heritable variation for traits with large effects on fitness).

The selection experiments with *Callosobruchus maculatus* (Wasserman and Futuyma, 1981) showed that a population that had been selected for female oviposition preference on a given host species displayed the same preference for this host after the selection as a population that had been maintained without choice on the same host. These findings are in agreement with our observation for the no-choice and choice *Cicer* lines (table I). According to Wasserman and Futuyma (1981), the main reason why a population will evolve a preference for the host to which it is exposed lies either in "a lowering of a specific threshold of response to the particular host with which they are confined, or a lower general response threshold, so that less discriminatory genotypes (which may come to accept any of several host species) are favoured" (p 615).

ACKNOWLEDGMENTS

We thank the anonymous reviewers for their helpful suggestions and comments on the manuscript.

REFERENCES

- Aleksić I, Gliksman I, Milanović D, Tucić N (1993) On r- and K-selection: evidence from the bean weevil (*Acanthoscelides obtectus*). *Zool Syst Evolutforsch* 31, 259-268
- Buch GL (1974) The mechanism of sympatric host race formation in the true fruit flies (Tephritidae). In: *Genetic Mechanisms of Speciation in Insects* (MJD White, ed), Australian and New Zealand Books, Sydney, 3-23
- Courtney SP, Chen GK, Gardner A (1989) A general model for individual host selection. *Oikos* 55, 55-65
- Dallal GE (1985) A program to contrast EMS tables. *USDA Human Nutrition Research Center on Aging*, Boston, MA
- Fisher RA (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford
- Fox CW (1993) A quantitative genetic analysis of oviposition preference and larval performance on 2 hosts in the bruchid beetle, *Callosobruchus maculatus*. *Evolution* 47, 166-175
- Fry JD (1990) Trade-offs in fitness on different hosts: evidence from a selection experiment with a phytophagous mite. *Am Nat* 136, 569-580
- Futuyma DJ, Philippi TE (1987) Genetic variation and covariation in responses to host plant by *Alsophylla pomontaria* (Lepidoptera: Geometridae). *Evolution* 41, 269-279
- Futuyma DJ, Moreno G (1988) The evolution of ecological specialization. *Ann Rev Ecol Syst* 19, 207-233
- Gould F (1979) Rapid host range evolution in a population of the phytophagous mite *Tetranychus urticae* Koch. *Evolution* 33, 791-802
- Hare JD, Kennedy GG (1986) Genetic variation in plant-insect associations; survival of *Leptrotarsa decemlineata* population on *Solanum carolinense*. *Evolution* 40, 1031-1043
- Harrison GD (1987) Host-plant discrimination and evolution of feeding preference in the Colorado potato beetle *Leptinotarsa decemlineata*. *Phys Ent* 12, 407-415
- Jaenike J (1985) Genetic and environmental determinants of food preference in *Drosophila tripunctata*. *Evolution* 39, 362-369
- Jaenike J (1986) Genetic complexity of host selection behaviour in *Drosophila*. *Proc Natl Acad Sci USA* 83, 2148-2151

- Jaenike J (1989) Genetic population structure of *Drosophila tripunctata*: patterns of variation and covariation of trait affecting resource use. *Evolution* 43, 1467-1482
- Jaenike J, Holt RS (1991) Genetic variation for habitat preference: evidence and explanations. *Am Nat* 137, 567-590
- James AC, Jakubczak J, Riley PM, Jaenike J (1988) On the causes of monophagy in *Drosophila guinaria*. *Evolution* 42, 317-338
- Lofdahl K (1987) A genetic analysis of habitat selection in the cactophylic species, *Drosophila mojavensis*. In: *Evolutionary Genetics of Invertebrate Behaviour* (MD Huttel, ed), Plenum Press, New York, NY, 77-91
- Milanović D, Aleksić I, Tucić N (1991) Nonrandom association between host choice and fitness in bean weevil (*Acanthoscelides obtectus*). *Z Zool Syst Evolut-forsch* 29, 108-114
- Pouzat J (1978) Host plant chemosensory influence on oogenesis in the bean weevil, *Acanthoscelides obtectus* (Coleoptera: Bruchidae). *Ent Exp and Appl* 24, 401-408
- Prokopy RJ, Diehl SR, Cooley SS (1988) Behavioural evidence for host races in host races in *Rhagoletis pomonella* flies. *Ecologia* 76, 138-147
- Rausher MD (1983) Conditioning and genetic variation as causes of individual variation in the oviposition behaviour of the tortoise beetle *Deloyala guttata*. *Anim Behav* 31, 743-747
- Rausher MD (1984) Trade-offs in performance on different hosts: evidence from within- and between-site variation in the beetle *Deloyala guttata*. *Evolution* 38, 582-595
- Roff D, Mousseau TA (1987) Quantitative genetics and fitness: lessons from *Drosophila*. *Heredity* 58, 103-118
- Scheiner SM, Lyman RF (1989) The genetics of phenotypic plasticity. I. Heritability. *J Evol Biol* 2, 95-107
- Singer MC, Ng D, Thomas CD (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* 42, 977-985
- Tabashnik BE (1983) Host range evolution: the shift from native legume hosts to alfalfa by the butterfly, *Colias philodice eriphyle*. *Evolution* 37, 150-162
- Tabashnik BE, Wheelock H, Rainbolt JD, Watt WB (1981) Individual variation in oviposition preference in the butterfly, *Colias eurytheme*. *Ecologia* 50, 225-230
- Tavormina S (1982) Sympatric genetic divergence in the leaf mining insect *Liriomyza brassicae* (Diptera: Agromyzidae). *Evolution* 36, 523-535
- Tucić N, Cvetković D, Milanović D (1988) The genetic variation and covariation among fitness components in *Drosophila melanogaster* females and males. *Heredity* 60, 55-60
- Tucić N, Cvetković D, Stojiljković V, Milanović D, Bejaković D (1990) The effects of selection for early and late reproduction on fecundity in bean weevil (*Acanthoscelides obtectus*). *Genetica* 80, 221-227
- Tucić N, Milošević M, Gliksman I, Milanović D, Aleksić I (1991) The effects of larval density on genetic variation and covariation among life-history traits in the bean weevil (*Acanthoscelides obtectus*). *Funct Ecol* 5, 525-534
- Via S (1984) The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environmental interaction in larval performance on different host plant species. *Evolution* 38, 881-895
- Via S (1986) Genetic covariance between oviposition preference and larval performance in an insect herbivore. *Evolution* 40, 778-785
- Via S (1990) Ecological genetics and host adaptation in herbivorous insects: the experimental study of evolution in natural and agricultural systems. *Ann Rev Entomol* 35, 421-446
- Wasserman SS, Futuyma DJ (1981) Evolution of host-plant utilization in laboratory populations of the southern cowpea weevil, *Callosobruchus mauculatus*. *Evolution* 35, 605-617