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## Host-associated fitness variation in a seed beetle (Coleoptera: Bruchidae): evidence for local adaptation to a poor quality host

Received: 11 March 1994 / Accepted: 7 June 1994

**Abstract** The geographic distributions of many generalist herbivores differ from those of their host plants, such that they experience coarse-grained spatial variation in natural selection on characters influencing adaptation to host plants. Thus, populations differing in host use are expected to differ in their ability to survive and grow on these host plants. We examine host-associated variation in larval performance (survivorship, development time, and adult body weight) and oviposition preference, within and between two populations of *Stator limbatus* (Coleoptera: Bruchidae) that differ in the hosts available to them in nature. In one population, *Acacia greggii* (Fabaceae: Mimosoideae) and *Cercidium microphyllum* (Fabaceae: Caesalpinioideae) are each abundant, while in the second population only *C. floridum* and *C. microphyllum* are present. In both populations, egg-to-adult survivorship was less than 50% on *C. floridum*, while survivorship was greater than 90% on *A. greggii*. Most of the mortality on *C. floridum* occurred as larvae were burrowing through the seed coat; very low mortality occurred during penetration of the seed coat of *A. greggii*. Significant variation was present between populations, and among families (within populations), in survivorship and egg-to-adult development time on *C. floridum*; beetles restricted to *Cercidium* in nature, without access to *C. floridum*, survived better and developed faster on *C. floridum* than beetles that had access to *A. greggii*. Large host effects on body size were detected for female offspring: females reared on *A. greggii* were larger than those reared on *C. floridum*, whereas male offspring were approximately the same size regardless of rearing host. Trade-offs between performance on *C. floridum* and *C. floridum* were not detected in this experiment. Instead, our data indicate that development time and survivorship on *C. floridum* may be largely independent of development time and survivorship on *A. greggii*. Patterns of oviposition preference corresponded to the observed patterns of host suitability: in laboratory prefer-

ence tests, beetles with access to *A. greggii* in nature tended to prefer this host more than beetles without access to this host in nature.

**Key words** Geographic variation · Genotype-environment interactions · Host range · Oviposition preference · *Stator limbatus*

### Introduction

Most herbivorous insects feed on few of the plant taxa available to them (Fox and Morrow 1981). In fact, many insect species considered generalists may be specialists at the population level (Fox and Morrow 1981). This is partially because the geographic distributions of many generalist herbivores differ from that of their host plants, resulting in many localities where only a subset of their hosts is available (e.g., Horton et al. 1988; Nitao et al. 1991). Differential performance of insect genotypes on different host plant species indicates that different plants represent distinct selective environments for insects (Via 1984a; Singer et al. 1988; Fox 1993a). Thus, due to non-concurrent geographic distributions between the insects and their hosts, these herbivores experience coarse-grained spatial variation in natural selection on characters influencing adaptation to these hosts, and populations differing in host use should differ in their ability to survive and grow on these host plants.

Because agricultural systems are easily manipulable for ecological studies, numerous examples of local adaptation to host plants are available (review in Via 1990). Relatively few examples, however, have been documented outside of agroecosystems, and most of these examine either butterflies (Rauscher 1982; Scriber 1983, 1986; Blau and Feeny 1983; Nitao et al. 1991), aphids (Groeters 1993) or the Colorado potato beetle, *Leptinotarsa decemlineata* (Hsiao 1978; Hare and Kennedy 1986). Here, we present evidence of local adapta-

tion to a poor host in the seed beetle, *Stator limbatus* (Horn) (Coleoptera: Bruchidae).

*Stator limbatus* is a generalist seed parasite that has been collected from the seeds of approximately 50 host species throughout its large geographic range (13 species in the southwestern United States), from northern South America to the southwestern United States (Johnson and Kingsolver 1976; Johnson et al. 1989), including many species of *Acacia*, *Cercidium* (palo verde), and *Parkinsonia* (Johnson and Kingsolver 1976; Janzen 1980). A recent cladistic analysis (C. D. Johnson, personal communication) showed that diet is evolutionarily conserved in this genus: most species are restricted to one or a few host genera, largely within a single subfamily of the Fabaceae (subfamily Mimosoideae), and most sibling pairs or monophyletic groups feed on the same genus or genera of legumes.

In the southwestern United States, and particularly Arizona, *S. limbatus* is abundant on many species of *Acacia* (Fabaceae: Mimosoideae) and two species of palo verdes (*C. floridum* and *C. microphyllum*; Fabaceae: Caesalpinioideae), although only one or a few hosts may be available in any locality (Vines 1960; Isley 1973, 1975). We examine two populations of *S. limbatus* that differ in the hosts available to them in the field. In one population, *A. greggii* and *C. microphyllum* are each abundant and heavily attacked by *S. limbatus* (personal observation). In the second population *C. floridum* is abundant and *C. microphyllum* is present (though uncommon), while *A. greggii* is not present. Previous work has shown that survivorship of *S. limbatus* is low on *C. floridum* (averaging 40–60%; Siemens and Johnson 1990; Siemens et al. 1992), due largely to allelochemicals in the seed coat (Siemens et al. 1992). Survivorship on *A. greggii* and *C. microphyllum*, on the other hand, is high (>90%). None the less, *S. limbatus* readily oviposits on *C. floridum* in nature (Mitchell 1977).

We designed the following experiments to quantify within- and between-population variation in larval performance (survivorship, development time, and adult body weight) of *S. limbatus* when reared on *A. greggii* and *C. floridum*. Specifically, we test the hypotheses that beetles restricted to *C. floridum* and *C. microphyllum*, without access to *A. greggii*, will perform better on *C. floridum*, but worse on *A. greggii*, than beetles that have access to both hosts. We expect these populations to differ in their ability to use *C. floridum* and *A. greggii* for two reasons. First, beetles with access to *A. greggii* are selected for improved performance on this host, and should be better adapted to this host than beetles that do not have access to it. Second, because *C. floridum* is a poor host for *S. limbatus*, beetles forced to use this poor host will be intensely selected for improved performance on it and are expected to perform better on it (at the population level) than beetles with access to an alternative, better quality host (e.g. *A. greggii*).

## Methods and materials

Natural history of *Stator limbatus* (Coleoptera: Bruchidae)

*S. limbatus* is a seed parasite that oviposits directly onto host seeds. Upon hatching, the larvae burrow into the seed, where they complete development, pupate, and emerge as adults. In the laboratory, mating and egg laying begin approximately 24–48 h post-emergence. Beetles require neither food nor water supplementation to complete development or to reproduce. This beetle's short generation time and ease of laboratory rearing render *S. limbatus* an excellent animal for life-history studies.

Field Collection *S. limbatus* and two host plants

Beetles for these experiments were collected from two localities in central Arizona. On 5–6 September 1993, beetles were collected from *Cercidium floridum* (Fabaceae: Caesalpinioideae) along Scottsdale Highway, 1.7 miles north of Bell Road (behind the Scottsdale Well), in Scottsdale, Arizona. On 7 September 1993, beetles were collected from *Acacia greggii* (Fabaceae: Mimosoideae) in numerous locations throughout Black Canyon City, Arizona. These two populations are separated by approximately 50 km, and differ in the host plants available to them. In Black Canyon City, *A. greggii* and *C. microphyllum* are each abundant, and each is attacked by *S. limbatus* (personal observation). *C. floridum* is present but rare at this site. In Scottsdale, *C. floridum* is abundant and *C. microphyllum* is present (though uncommon), while *A. greggii* was not found at this site. *Parkinsonia aculeata* (Fabaceae: Caesalpinioideae), which has recently been introduced as an ornamental in Arizona and is readily used by *S. limbatus*, is present, although uncommon, at both sites.

Beetles and seed stock were both collected by picking mature seed pods from more than 25 *C. floridum* plants in Scottsdale and more than 25 *A. greggii* plants in Black Canyon City. Mature pods were transferred to the laboratory, and seeds containing beetles were separated from uninfested seeds. Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* sp.) were discarded. We estimate that both laboratory populations were initiated with 500–1000 field collected individuals.

Before initiating the laboratory experiments, all beetles were reared in the laboratory for one generation at 26°C, 24 h light, on the host from which they were collected.

Population, host, and family effects on larval performance

A full-sib split-brood design was used to estimate population, family, and host effects on offspring performance. Within each population 60 virgin females collected less than 24 h after emergence from the seed (total = 120 females) were randomly paired with a virgin male from their own population. Half of these pairs were then confined in 30-mm petri dishes with ten seeds of *A. greggii* (30 pairs from each population), and half with ten seeds of *C. floridum* (30 pairs from each population), and allowed to lay eggs. Dishes were checked at 12-h intervals, and all seeds bearing eggs were replaced with clean seeds. When females had laid >10 eggs on this initial host, they were transferred to the other host (from *A. greggii* to *C. floridum*, or from *C. floridum* to *A. greggii*). Again, dishes were checked at 12-h intervals, and all seeds bearing eggs were replaced until a female had laid >10 eggs on this second host.

All eggs were reared to adult at densities of one beetle per seed (additional eggs were scraped from each seed), 28°C, constant light. Development time, body weight, and survivorship were recorded for all offspring. Development time was estimated as the time between egg-laying and adult emergence, and thus included both embryonic, larval, and pupal development time. To estimate body weight, emerging adults were weighed individually within 12 h of adult emergence on an electronic balance. Body weight is positively correlated with lifetime fecundity in both populations of

*S. limbatus* (C. Fox, unpublished data) as well as in other bruchids (Møller et al. 1989; Credland et al. 1986; Fox 1993b) and should thus correlate with fitness of the offspring.

The rotation of hosts employed in this experiment was used to control for maternal age effects observed in other bruchids (e.g., Fox 1993c; Fox and Dingle 1994; Wasserman and Asami 1985). If females are presented with two or more hosts simultaneously, some females lay a majority or all of their eggs on a single host, resulting in very few or no eggs on the less preferred host (personal observation). Thus, a maternal-age effect, in which eggs laid by older females develop more slowly or become smaller adults, will result in smaller or slower-developing larvae on the less preferred host, biasing results toward low performance on the less preferred host. By presenting females with one host at a time, females were forced to lay on less preferred hosts (females will readily dump eggs on less preferred hosts or non-hosts if no preferred hosts are available; personal observation). We subsequently controlled for maternal age/egg order effects in all statistical analyses.

Population, host, and family effects on development time and body weight were examined using an analysis of variance. For all models, population and host were treated as fixed effects, while family was treated as a random effect, nested within population. For models in which patterns differed between males and females, separate analyses were performed for each sex. For models in which patterns were similar for each sex, data were combined with sex included as a fixed effect classification variable. Maternal age was included as a covariate in all analyses, to control for host order effects. All analyses were performed using type III sums of squares of SAS GLM (SAS Institute 1985). *F*-statistics were calculated following the procedure of Neter et al. (1990).

No data transformations were necessary for development time or body size data to satisfy the assumptions of the multivariate models. Non-parametric methods were used when analyzing survivorship data. All significance tests were at the 0.05 level.

The genetic correlation between performance on *Acacia* and performance on *Cercidium*

Although this experiment was not specifically designed to estimate genetic correlations between characters across host species (for which a half-sib design would be preferable), the split brood design allows us to test whether trade-offs might exist between adaptation on *A. greggii* and adaptation on *C. floridum*. Genetic correlations for the same trait across environments were calculated as product-moment correlations of the family means for a trait on pairs of hosts (Via 1984b). A significant negative correlation would indicate that *S. limbatus* is unable to simultaneously maxi-

mize performance on both *A. greggii* and *C. floridum*. These correlations are only approximations to the true genetic correlations because each variance and covariance used in their estimation contains a fraction of the within-family "error" variance or covariance, but they converge on the true genetic correlation with increasing numbers of offspring per family (Via 1984b). Also, because all individuals within a family are full sibs, these analyses are potentially biased by non-additive genetic effects, maternal effects, and other environmental effects. In addition, because hosts were sequentially presented to offspring, a maternal age effect in which offspring developing from later-laid eggs develop more slowly, are smaller, or have higher mortality (e.g., Fox 1993c; Fox and Dingle 1994) would result in offspring developing on the second host performing more poorly than offspring on the first. Standard errors of the family mean correlations were calculated by bootstrapping the correlations 1000 times (Efron 1982).

#### Variation in oviposition preference among populations

Variation in preference for host seeds among both populations of *S. limbatus* was examined after field-collected beetles had been reared in the laboratory for one generation on their natural host (the host upon which they were collected). Virgin adult females were paired with a virgin male from their own population and transferred into 60-mm petri dishes containing eight *C. floridum* and eight *A. greggii* seeds. Dishes were checked at 12-h intervals, and all seeds bearing eggs were replaced, until females had laid >10 eggs (generally three 12-h periods). The total numbers of eggs laid on *A. greggii* and *C. floridum* were counted, and oviposition preference was defined as (the number of eggs laid on *Cercidium* / number of eggs laid on *Acacia*). Females laid on averaged  $5.5 \pm 0.9$  eggs (Black Canyon City) and  $3.6 \pm 0.3$  eggs (Scottsdale) during each 12-h period, and only three females laid more than eight eggs during a single 12-h period, so shifting to a less preferred host due to avoidance of egg-laden seeds should be minimal during our preference tests.

Rearing-host effects on oviposition preference were examined in the Scottsdale population by preference testing (as above) randomly selected offspring reared on *C. floridum* and *A. greggii* in the larval performance experiment.

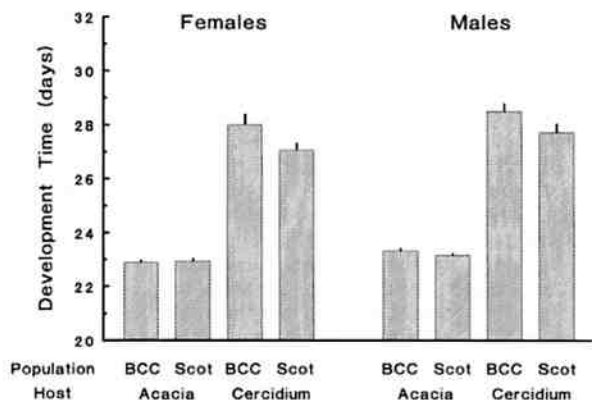
## Results

A total of 695 offspring from 57 families were reared from the Black Canyon City population (358 males and

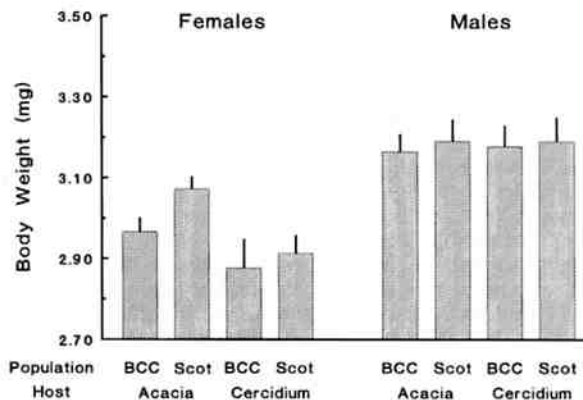
**Table 1** The effects of rearing host on three estimates of survivorship for two populations of *Stator limbatus* reared on two hosts (seeds). Data are means  $\pm$  S.Es. Males and females are lumped because early instars could not be sexed. All means are averages of family means. For calculation of family means, each rearing dish was treated as a single observation within a family. *Survivorship entering seed* is the proportion of offspring that survived until no body parts were protruding from the seed. *Survivorship within*

*seed* is the survivorship of all larvae that successfully entered the seed (i.e., larvae that died entering the seed are not included in this estimate). In both populations, all three estimates of survivorship were lower on *Cercidium floridum* than on *Acacia greggii* (Wilcoxon signed-rank tests,  $P < 0.05$ ). Estimates followed by different letters are statistically different across populations (within each column and host; log-linear model, estimating the likelihood ratio  $X^2$ ,  $P < 0.05$ ; Wilkinson (1990)

Population	Number of families	Survivorship (proportion surviving)		
		Egg to adult	Entering seed	Within seed
<i>Acacia greggii</i>				
Black Canyon City	56	0.946 (0.021)A	0.996 (0.000)A	0.950 (0.002)A
Scottsdale	53	0.987 (0.005)B	0.989 (0.005)A	0.998 (0.002)B
<i>Cercidium floridum</i>				
Black Canyon City	57	0.380 (0.046)A	0.464 (0.048)A	0.743 (0.045)A
Scottsdale	55	0.480 (0.050)B	0.557 (0.052)B	0.754 (0.048)A



**Fig. 1** Host and population effects on development time of *Stator limbatus*. (BCC Black Canyon City, Arizona, Scot Scottsdale, Arizona). Statistical analyses are presented in Table 2



**Fig. 2** Host and population effects on body weight of *S. limbatus*. (BCC Black Canyon City, Arizona, Scot Scottsdale, Arizona). Statistical analyses are presented in Table 3.

**Table 2** Analyses of variance for development time of two populations of *S. limbatus* reared on two host species. Although females developed faster than males on both hosts (Fig. 1), patterns for each sex were similar and thus males and females were combined for this analysis, with sex included in the model as a classification variable. A Sex  $\times$  Host effect was not significant, and thus deleted from the model. *F*-statistics were calculated following Neter et al (1990)

	MS	<i>F</i> -ratio	<i>df</i>	MS	<i>F</i>
Sex	MS1	MS1/MS8	1	80.78	25.91***
Population	MS2	MS2/MS3	1	53.28	10.89**
Family (pop)	MS3	MS3/MS8	112	4.89	1.57***
Host	MS4	MS4/MS6	1	3610.99	784.95***
Population $\times$ host	MS5	MS5/MS6	1	62.01	13.48***
Family (pop) $\times$ host	MS6	MS6/MS8	74	4.60	1.48**
Age	MS7	MS7/MS8	1	11.59	3.55ns
Error	MS8		1184	3.12	

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

337 females), and 682 offspring from 57 families were reared from the Scottsdale population (336 males and 346 females). Sex ratios did not differ significantly from 1:1 on either host in either population (sign tests,  $P > .05$ ).

#### Population and host effects on offspring life histories

The most dramatic host effect detected in this experiment was generally low survivorship of *S. limbatus* on *C. floridum* compared to high survivorship on *A. greggii*. In both populations, egg-to-adult survivorship on *C. floridum* was less than 50%, while survivorship on *A. greggii* was greater than 90% (Wilcoxon signed-rank test comparing family means on each host,  $P < 0.001$  for each population; Table 1). Most of the mortality observed on *C. floridum* occurred as larvae were burrowing through the seed coat, while very low mortality oc-

curred while penetrating the seed coat of *A. greggii* (Wilcoxon signed-rank tests,  $P < 0.001$ ; Table 1). Mortality within the seed, once larvae had successfully penetrated the seed coat, was also substantially higher in *C. floridum* seeds than in *A. greggii* seeds (Wilcoxon signed-rank tests,  $P < 0.001$ ).

In addition to host effects, large population effects were detected for survivorship while entering seeds of *C. floridum*, and thus for egg-to-adult survivorship on this host (Table 1). Beetles from the Scottsdale population, that in the wild are restricted to *C. floridum* and *C. microphyllum*, without access to *A. greggii*, survived better on both *C. floridum* and *A. greggii* than beetles from the Black Canyon City population (Table 1), that have access to *A. greggii*. There was also significant heterogeneity among families (within populations) in survivorship on *C. floridum* (*G*-test,  $P < 0.0001$  for each population; Sokal and Rohlf 1981, p. 745). These results suggest genetic variation, both within and between populations, for survivorship on *C. floridum*.

Of beetles that survived to the adult stage, egg-to-adult development time was substantially shorter on *A. greggii* than on *C. floridum* in both populations (Fig. 1; Table 2). In addition to host effects, both population and population  $\times$  host effects were highly significant for development time in an analysis of variance (Table 2), indicating that beetles from the Scottsdale population performed better on *C. floridum* than beetles from the Black Canyon City population (Fig. 1).

Unlike development time, the pattern for body weight differed between male and female offspring (Fig. 2). Therefore, male and female body size data were analyzed separately. Large effects of host species on body size were detected for female offspring (Table 3): females reared on *A. greggii* were larger than those reared on *C. floridum*. Male offspring, on the other hand, were approximately the same size regardless of rearing host (Fig. 2). There was no evidence of population or population  $\times$  host effects for body weight of either sex.

**Table 3** Analyses of variance for body weight of two populations of *S. limbatus* reared on two host species (*Acacia greggii* and *Cercidium floridum*). Patterns for females were different from patterns

for males (see Fig.2), and thus separate analyses are presented for each sex. *F*-statistics were calculated following Neter et al (1990)

	MS	F-ratio	Females		Males		MS	F
			df	MS	F	df		
Population	MS1	MS1/MS2	1	0.50	1.65ns	1	0.03	0.05ns
Family (pop)	MS2	MS2/MS7	111	0.30	1.85***	111	0.48	2.50***
Host	MS3	MS3/MS5	1	2.99	18.17***	1	0.57	2.13ns
Population × host	MS4	MS4/MS5	1	0.01	0.08ns	1	0.07	0.28ns
Family (pop) × host	MS5	MS5/MS7	60	0.17	1.01ns	63	0.27	1.40*
Age	MS6	MS6/MS7	1	0.48	2.93ns	1	3.73	19.44ns
Error	MS7		504	0.16		509	0.19	

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$

**Table 4** The genetic correlations ( $\pm$  S.Es) between performance of *S. limbatus* on *A. greggii* and on *C. floridum*. Correlation estimates are Pearson-moment correlations between family means. Standard errors were calculated by bootstrapping the estimates 1000

times. Sample sizes (in parentheses) are the number of families that produced surviving offspring on both host species. Only estimates for weight of Black Canyon City females and Scottsdale males differ statistically from zero

Population	Females		Males	
	Development time	Body weight	Development time	Body weight
Black Canyon City	-0.089 $\pm$ 0.145 (33)	0.409 $\pm$ 0.105 (32)	0.086 $\pm$ 0.158 (32)	0.095 $\pm$ 0.169 (32)
Scottsdale	-0.068 $\pm$ 0.184 (31)	0.202 $\pm$ 0.158 (31)	0.229 $\pm$ 0.155 (33)	0.333 $\pm$ 0.117 (33)

**Table 5** The genetic correlations between survivorship of *S. limbatus* on *A. greggii* and on *C. floridum*. Correlation estimates are Pearson-moment correlations between family means. Standard errors or confidence intervals are not available because survivorship on *A. greggii* was 100% for almost all families in both populations, resulting in sub-samples with zero variances and covariances when bootstrapping (see text for details). Numbers in parentheses are sample sizes (numbers of family). The number of families in the egg-to-adult survivorship estimate is the number of families that laid eggs on both hosts

Population	Survivorship		
	Egg to adult	Entering seed	Within seed
Black Canyon City	0.15 (56)	0.19 (56)	0.10 (45)
Scottsdale	0.19 (51)	0.09 (51)	0.00 (45)

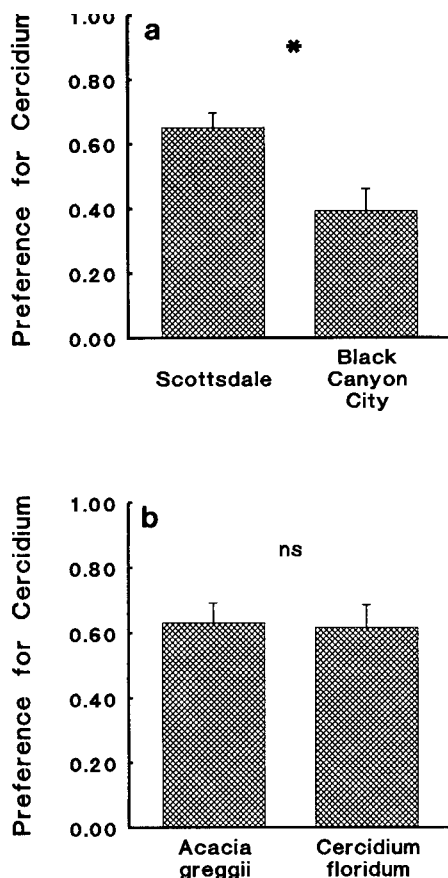
The genetic correlation between performance on *Acacia* and performance on *Cercidium*

Trade-offs between performance on *A. greggii* and performance on *C. floridum* were not detected in this experiment: the family mean correlations between performance on each host were positive or near zero for all characters in both populations (Table 4, range 0.089–0.409). Only two of these estimates, however, were significantly greater than zero: body weight of Black Canyon City females and body weight of Scottsdale males were positively correlated on *A. greggii* and *C. floridum*. No maternal age effects were detected for either development time or body weight (e.g., Tables 2 and 3), and thus any bias due to sequential presentation of hosts should be minor or zero for these characters.

Correlations between survivorship on *A. greggii* and survivorship *C. floridum* were all near zero (Table 5, range 0.00–0.19). Standard errors or confidence intervals, however, are not available because survivorship on *A. greggii* was 100% for most families in both populations. Thus, when the correlations were bootstrapped, random sampling  $n$  times (with replacement) from  $n$  pairs resulted in many sub-samples with zero variances and covariances, and thus an undefined correlation (see Efron 1982 for details on bootstrap sampling).

#### Variation in oviposition preference among populations

The two *S. limbatus* populations differed in their preference for host seeds. Beetles from the Scottsdale population laid more eggs on *C. floridum* than did beetles from Black Canyon City (Fig. 3a; Mann-Whitney  $U$ -test,  $P = 0.003$ ). These differences appear to be genetic: there was no effect of rearing host on the oviposition preference of Scottsdale beetles reared on *C. floridum* or *A. greggii* (Fig. 3b; Mann-Whitney  $U$ -test,  $P > 0.05$ ). We must caution, however, that our results do not imply that Scottsdale beetles preferred *C. floridum* over *A. greggii* while Black Canyon City beetles preferred *A. greggii* over *C. floridum*: because these two seed species are of unequal surface area we can not extend the oviposition scores obtained from a female to an absolute estimate of rank order preference for a seed. Oviposition scores can be used only to compare among females and among populations (preference designs of this type are discussed thoroughly by Singer 1986).



**Fig. 3a,b** Oviposition preference of *Stator limbatus*. **a** Preference of beetles from Black Canyon City and Scottsdale after one generation of laboratory rearing on their natural host. **b** The effect of rearing host on oviposition preference of Scottsdale beetles. Preference is defined as the proportion of a female's eggs laid on *Cercidium floridum* (relative to *Acacia greggii*) in a paired host design (details in text)

## Discussion

The goal of this experiment was to test two hypotheses concerning geographic variation in larval performance of *S. limbatus* on *C. floridum* and *A. greggii*. First, we tested the hypothesis that beetles restricted to *C. floridum* and *C. microphyllum* (Scottsdale population) would perform better on *C. floridum* than beetles that have access to *A. greggii* (Black Canyon City population). Our data support this hypothesis. The significant population  $\times$  host interaction for development time and significant population effects on survivorship indicate that these two populations have differentiated in their ability to use *C. floridum*: Scottsdale beetles perform better on this host than Black Canyon City beetles (Fig. 1; Table 1). Also, population differences in oviposition preference corresponded to the observed patterns of variation in larval performance: adults from Scottsdale more readily accepted *C. floridum* than did Black Canyon City beetles (Fig. 3a).

Second, we tested the hypothesis that beetles with

*A. greggii* (Scottsdale population). This hypothesis was not consistent with our data. Despite having no access to *A. greggii*, Scottsdale beetles performed just as well on it as Black Canyon City beetles. In fact, survivorship of Scottsdale beetles was higher than Black Canyon City beetles on *A. greggii*. There are two likely and non-exclusive explanations for this absence of a population effect on performance on *A. greggii*. First, *A. greggii* may be a very suitable host for many populations of *S. limbatus*, such that selection for improved performance of Black Canyon City beetles, and thus differentiation among populations, is weak. Second, high gene flow between populations coupled with weak selection on *A. greggii* may prevent Black Canyon City beetles from diverging from Scottsdale beetles: although we have no estimates of gene flow, these two populations are only about 50 km apart, and are connected by nearly unbroken desert. Although the vegetation changes gradually between Black Canyon City and Scottsdale, *C. floridum* is distributed throughout the intervening region. In comparison, our results indicated that *C. floridum* was generally a poor host for *S. limbatus* (see also Siemens and Johnson 1990; Siemens et al. 1992), such that selection for improved performance on it is likely to be intense (mortality >50%; Table 1), driving rapid adaptation to this host in spite of high gene flow.

The observed population differences in survivorship and development time on *C. floridum* likely reflect genetic differences in the ability to use this host. However, an effect of maternal rearing host on the ability of offspring to use a host plant (Via 1991a) may also account for these patterns. Maternal rearing environment has been shown to influence many characteristics of offspring (Gould 1988; Via 1991a; Rossiter 1991a,b; Rosenheim 1993), some of which involve biochemical and physiological responses (Mousseau and Dingle 1991). In our experiments, parents of both experimental populations were collected and reared from different hosts: Scottsdale parents were reared on *C. floridum* and Black Canyon City parents on *A. greggii*. If parents reared on *C. floridum* tended to produce offspring that performed better on *C. floridum* due to a non-genetic maternal effect (e.g., induction of enzymatic activity in the offspring), we would detect this as a population  $\times$  host effect in our experiment. The results of Siemens and Johnson (1990) are suggestive of maternal effects on host suitability in *S. limbatus*: offspring of mothers reared from *C. floridum* performed better on *C. floridum* than offspring of mothers reared from *A. greggii* at this same locality. Preliminary analyses in our laboratory, however, have been unable to demonstrate that offspring perform better when reared on the same host as their mother (Fox et al., unpublished work), which is consistent with the interpretation that the population  $\times$  host effect represents genetic differentiation.

One likely explanation for the among-population variation in survivorship on *C. floridum* involves variation in



Fox). Murphy et al. (1983) and Karlsson and Wiklund (1984) have suggested that, in some systems, there may be a minimum egg size below which survivorship dramatically decreases. For example, there may be a minimum head capsule size below which a *Stator* larvae cannot successfully penetrate the coat of a *C. floridum* or *A. greggii* seed. We speculate that larvae need to be larger to penetrate a *C. floridum* seed coat than an *A. greggii* seed coat, resulting in substantially higher mortality on *C. floridum* than on *A. greggii*, and also resulting in relatively lower mortality of Scottsdale beetles, which develop from larger eggs.

In addition to population effects, family effects were detected for all characters, and family- $\times$ -host effects were detected for development time (combined sexes), and for body size of male offspring, but these interactions did not translate into negative genetic correlations between performance on *C. floridum* and *A. greggii*. This result is not unusual for split-brood experiments. To date, researchers have generally been unable to detect evidence for performance trade-offs across hosts that are currently within the diet of an insect (but see Pashley 1988; Via 1991b). However, while many experiments have reported large positive correlations across hosts (e.g., Nitao et al. 1991; Fox 1993a; Fox and Caldwell 1994), others have reported correlations near zero (discussion in Via 1990), as were estimated for development time (Table 4) and survivorship (Table 5) in this experiment. This latter result has led Via (1990) to suggest that adaptation to one host plant may often be genetically independent of adaptation on other host plants. Our data are consistent with this hypothesis, suggesting that development time on both *C. floridum* and *A. greggii* are largely genetically independent characters, and that survivorship across hosts is at best weakly genetically correlated.

**Acknowledgements** We thank C. D. Johnson, L. A. McLennan, A. Olvido, E. L. Raleigh, and D. H. Siemens for helpful comments/criticisms on this manuscript/these experiments. D. S. We they provided computer access for analyses. G. Zigler graciously provided housing while collecting beetles. We especially thank C. D. Johnson and D.H. Siemens for introducing us to this beetle system, and for providing advice on collecting and rearing. Financial support was provided in part by USDA/CSRS Grant no. 9301887 to T. A. Mousseau.

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