

# Seed beetle survivorship, growth and egg size plasticity in a paloverde hybrid zone<sup>1</sup>

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**Abstract.** 1. Although numerous studies have examined the ecology of plant resistance to herbivores and the distribution of herbivores within plant hybrid zones, few have examined how plant hybridization influences herbivore growth, development, or life history. The experiment reported here examines variation in survivorship, development time, and final adult body size of *Stator limbatus* reared on seeds of parental and hybrid *Cercidium floridum*- $\times$ -*C. microphyllum* trees from a paloverde hybrid zone in eastern California. Because *S. limbatus* exhibits egg size plasticity in response to host species, the size of eggs that females lay on hybrid and parental plants is also examined.

2. The hypotheses (a) that seeds of hybrid trees are intermediate between those of the two parental species in their resistance to penetration by *S. limbatus* larvae; (b) that seeds of hybrid trees are intermediate in their suitability for the growth of larvae that successfully penetrate the seed-coat; (c) that female *S. limbatus* can distinguish between hybrid trees and pure-bred trees, as quantified by the size of eggs they lay on seeds of each taxon, and (d) that female *S. limbatus* can distinguish among individual hybrid trees, are tested.

3. On average, *S. limbatus* survivorship was lower, development time longer, and emergence body mass lower on seeds of *C. floridum* than on seeds of *C. microphyllum*. Seeds of hybrid trees were, on average (across trees), intermediate between seeds of the parental species in the resistance of their seed-coats to penetration by *S. limbatus* larvae and in their suitability for larval growth. Individual hybrid trees also varied in the resistance of their seeds to, and the suitability of their seeds for, *S. limbatus* larvae.

4. Female *S. limbatus* laid significantly larger eggs on seeds of *C. floridum* than on seeds of *C. microphyllum*, and, on average, intermediate size eggs on hybrid trees. The size of eggs laid by females also varied among hybrid trees, with females laying *C. floridum*-sized eggs on some trees, and *C. microphyllum*-sized eggs on other trees. These results suggest that females have at least some ability to distinguish among hybrid trees, but there was no evidence that females laid larger eggs on poorer quality hybrid trees.

**Key words.** *Cercidium*, egg size, paloverde, phenotypic plasticity, *Stator*.

## Introduction

Hybridization among plant taxa is common in nature (Heiser, 1949). These plant hybrid zones/swarms contain substantial

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genetic diversity, including parental species, F<sub>1</sub>s, and often complex backcrosses (Keim *et al.*, 1989; Strauss, 1994). Plant hybrid zones thus represent complex evolutionary environments for herbivorous insects and can provide excellent opportunities for addressing ecological and evolutionary questions about plant resistance to pests, adaptation of herbivores to plants, diet expansions or shifts, and the ecological mechanisms influencing the distribution of herbivores among plants.

Numerous recent studies have examined the factors that influence plant resistance to herbivores and the distribution of herbivores among hybrid and parental plants (review in Strauss, 1994). These studies have demonstrated most plausible relationships between plant status (hybrid vs. pure-bred) and

plant resistance to herbivory and/or the distribution of herbivores – hybrids can exhibit higher, lower, or intermediate resistance to herbivores relative to either parental species, and can harbour higher, intermediate, and possibly lower insect densities (Floate *et al.*, 1993; Strauss, 1994). Likewise, these studies demonstrate that multiple factors can affect the distribution of herbivores within a hybrid zone, and that these factors can vary among herbivores and hybrid zones. For example, in some hybrid zones, prolonged availability of foliage associated with differences in plant phenology between parental and hybrid plants probably explains the increased abundance of herbivores on hybrids (e.g. Floate *et al.*, 1993). In other hybrid zones, increased abundance of herbivores on hybrid trees may be facilitated by a breakdown in chemical defences in the hybrids (e.g. Whitham, 1989). In yet other systems, a combination of factors simultaneously affects the distribution of herbivores (e.g. Siemans *et al.*, 1994).

Although numerous studies have examined the ecology of plant resistance to herbivores and the distribution of herbivores within plant hybrid zones, few studies have examined how plant hybridization influences herbivore growth, development, or life history, and these few have tended to examine primarily herbivore survivorship (e.g. Whitham, 1989; Preszler & Boecklen, 1994; Siemans *et al.*, 1994; but see McClure, 1985; Hall & Townsend, 1987; Floate *et al.*, 1993; Hanhimäki *et al.*, 1994; Gange, 1995; Messina *et al.*, 1996). Results of these studies have been mixed, with herbivore survivorship highest (Messina *et al.*, 1996), intermediate (Hall & Townsend, 1987; Floate *et al.*, 1993), or possibly lowest on hybrids. Often hybrid plants are more similar to one parental plant than another in their suitability for herbivore growth (Hanhimäki *et al.*, 1994). The effects of hybridization on the suitability of plants can also vary within a study, depending on the herbivore characters measured when quantifying hybrid suitability (i.e. growth rate, development time, mass at pupation, survivorship) (e.g. Gange, 1995).

In this paper, growth and life history variation of a seed beetle, *Stator limbatus* (Horn), on paloverde (*Cercidium*; Fabaceae: Caesalpinioideae) pure-breds and hybrids from a hybrid zone in eastern California, are examined to test the hypotheses (a) that seeds of hybrid trees are intermediate between those of the two parental species in their resistance to penetration by *S. limbatus* larvae, and (b) that seeds of hybrid trees are intermediate in their suitability for the growth of larvae that successfully penetrate the seed-coat. By examining female egg size plasticity in response to hybrid and pure-bred plants, the hypotheses that (a) female *S. limbatus* can distinguish between hybrid and pure-bred plants, and that (b) they can distinguish among individual hybrid plants (see below), are each tested.

#### *The study system – Stator limbatus feeding on seeds of Cercidium*

*Stator limbatus* is a generalist seed parasite (Johnson & Kingsolver, 1976; Johnson *et al.*, 1989; Nilsson & Johnson, 1993) that, in the south-western United States, is abundant on seeds of numerous plant species including two species of

paloverdes, *Cercidium floridum* (Benth.) and *C. microphyllum* (Benth.). Seeds of these two paloverdes differ substantially in their resistance to penetration by *S. limbatus* larvae and in their quality as substrates for the development of those *S. limbatus* larvae that can successfully penetrate the seed-coat. For example, egg-to-adult survivorship is very low when larvae develop on *C. floridum* (generally < 50%, due mostly to an inability of larvae to penetrate the seed-coat) and comparatively high when larvae develop on *C. microphyllum* (generally > 80%; Siemans & Johnson, 1990; Siemans *et al.*, 1992; Fox *et al.*, 1994, 1995b, 1996). Likewise, egg-to-adult development time on *C. floridum* is quite long relative to development time on *C. microphyllum* (4–6 days longer on *C. floridum* at 28–29 °C). However, despite being a relatively poor host for *S. limbatus*, *C. floridum* is abundant throughout most of the lower elevation desert regions of Arizona and parts of California, whereas *C. microphyllum* is most abundant at higher elevations. Mature fruits of *C. floridum* are also available on the trees for many months in the summer and autumn, well after seeds of *C. microphyllum* have dispersed (Siemans *et al.*, 1994). Thus, seeds of the two species appear to differ in their defence mechanisms against *S. limbatus*; *C. floridum* seeds are relatively resistant to penetration by *S. limbatus*, whereas *C. microphyllum* exhibits early fruit abscission and thus avoids *S. limbatus* parasitism (Siemans *et al.*, 1992).

Possibly because of these differences in seed defence mechanisms, the fitness consequences of egg size vary substantially among paloverde species. On *C. floridum*, on which egg-to-adult survivorship of *S. limbatus* larvae is very poor, larvae from large eggs survive substantially better than larvae from small eggs (Fox & Mousseau, 1996). However, on *C. microphyllum*, on which survivorship is comparatively high (Fox *et al.*, 1996), there is no detectable (or at best a very weak) effect of egg size on egg-to-adult survivorship (Fox & Mousseau, in press). Thus, while there is intense selection to lay large eggs on *C. floridum* (because most larvae hatching from small eggs die), there is selection to lay small eggs on *C. microphyllum* (due to selection on egg number; Fox & Mousseau, in press). Females have evolved egg size plasticity, probably in response to this variable selection on egg size; they variably allocate resources to offspring, laying large (and few) eggs on *C. floridum* and small (and many) eggs on *C. microphyllum* (Fox & Mousseau, in press; Fox *et al.*, 1997b;).

At numerous locations in the south-western United States, these two paloverde species hybridize (Jones, 1978; Siemans *et al.*, 1994). Hybrid plants tend to be relatively intermediate in morphology between either parental species and, in general, seeds of hybrid paloverdes tend to be much more susceptible to *S. limbatus* parasitism than seeds of either parental species (Siemans *et al.*, 1994); their seeds tend to be less resistant to penetration by *S. limbatus* larvae than *C. floridum* seeds but their fruits abscise substantially later (and are thus available during late summer and autumn) than *C. microphyllum* fruits. The combination of low resistance and long-term availability of hybrid seeds may account for the observation that, in some years, seed beetles are more abundant on seeds of hybrid trees than on seeds of either parental species (Siemans *et al.*, 1994).

In this paper, variation in survivorship, development time, and final adult body size of *S. limbatus* reared on seeds of parental and hybrid *C. floridum* × *C. microphyllum* trees from a paloverde hybrid zone in eastern California is examined. Specifically, the result of Siemens *et al.* (1994), that hybrid trees are intermediate in resistance between *C. floridum* and *C. microphyllum*, is confirmed, and the hypotheses (a) that seeds of hybrid trees are intermediate in their suitability for development of larvae that successfully penetrate the seed-coat; (b) that female *S. limbatus* can distinguish between hybrid trees and pure-bred trees, as quantified by the size of eggs they lay on seeds of each taxon, and (c) that female *S. limbatus* can distinguish among individual hybrid trees, as quantified by the size of eggs they lay on seeds of individual trees, are each tested.

## Materials and Methods

### Natural history of *Stator limbatus*

Female *S. limbatus* oviposit directly on to host seeds in fruits that have either dehisced or have been damaged by other organisms. Upon hatching, the larvae burrow into the seed, where they complete development, pupate, and emerge as adults. Adults are the only dispersing stage; larvae are restricted to the specific seed their mother has chosen for them. In the laboratory, mating and egg laying begin  $\approx$  24–48 h post-emergence. Beetles require only the resources inside a single seed to complete development and reproduce. Thus, neither food nor water supplementation is necessary for the following experiments.

### Study population

Beetles and seeds for this experiment were collected on 15 July 1995, from seeds of *Cercidium floridum*, *C. microphyllum* and their hybrids along Highway 62 and Old Parker Dam Road near Earp, in San Bernardino County, California. Beetles were collected by picking mature seed pods from ten *C. floridum*, ten *C. microphyllum*, and twelve hybrid trees. Mature pods were transferred to the laboratory, and seeds containing larval *S. limbatus* were separated from uninfested seeds. Seeds containing entrance or emergence holes of other bruchids (such as *Mimosestes* spp.) were discarded. Adult beetles (> 300) emerging from these field-collected seeds were used to initiate laboratory populations. Prior to this study, beetles were reared in the laboratory on a common non-paloverde host, *Acacia greggii* (a natural host for *S. limbatus* in Arizona and California), at 29–30 °C, 15 : 9 L : D, to control for non-genetic maternal effects associated with maternal diet (Fox *et al.*, 1995b, 1997a,b; Fox & Mousseau, in press).

### Identification of hybrid trees

Hybrid and parental plants were identified using morphological characters (Jones, 1978; Siemens *et al.*, 1994).

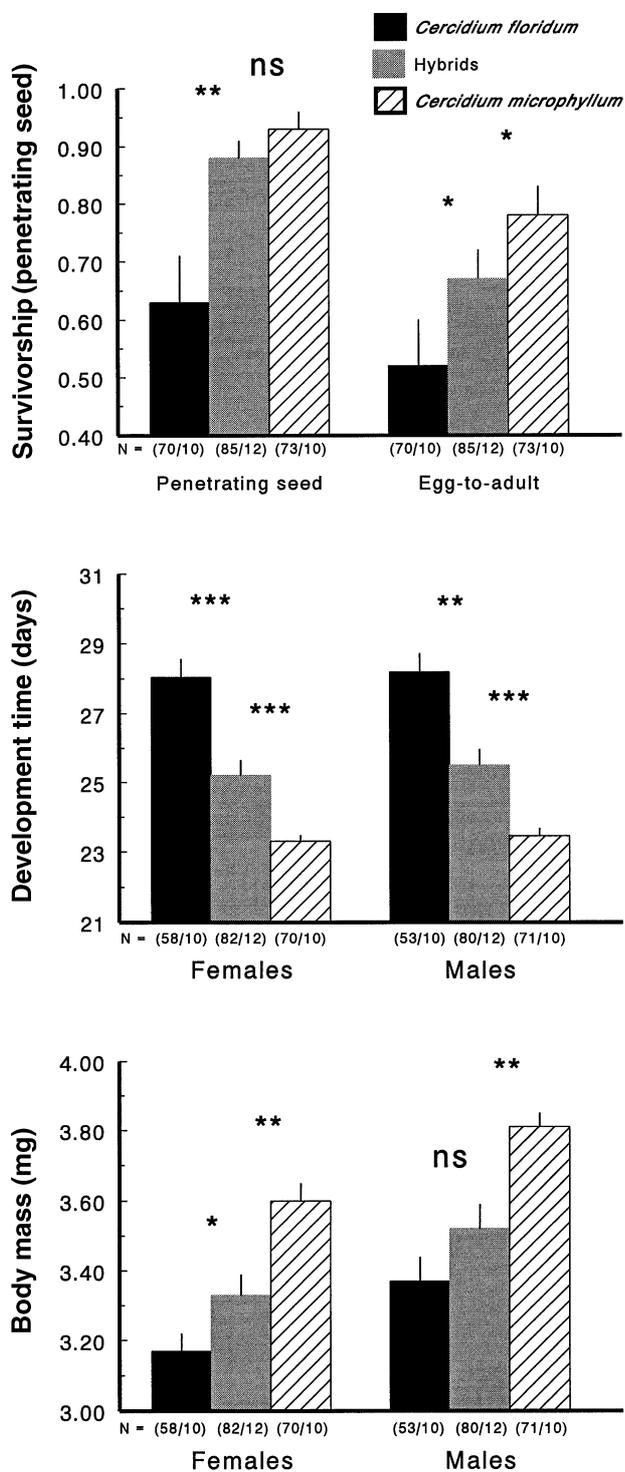
Hybrids were defined on the basis of seed shape, fruit colour, fruit shape, leaflet number and leaflet size. In particular, seed and fruit shape are non-overlapping between the three taxa (*C. floridum*, *C. microphyllum*, hybrids). A discriminant analysis by Siemens *et al.* (1994) demonstrated that the three taxa are morphologically distinct groups when considering seed shape, fruit colour, fruit shape, leaflet size, and banner (part of the flower) width.

### Experimental manipulations

To examine variation between species and among hybrid trees in maternal egg size and larval growth, females were confined on seeds of either *C. floridum*, *C. microphyllum*, or a hybrid tree, and allowed to lay eggs. Egg size plasticity was examined by measuring the size of eggs laid on each host. Progeny hatching from these eggs were then reared to adult at low density to examine seed effects on larval survivorship and growth.

To establish families, virgin males and females were collected from isolated seeds of *A. greggii* within 12 h of adult emergence. Each beetle was weighed, then paired with a single virgin beetle of the opposite sex. Pairs were confined in a 35-mm Petri dish containing twelve seeds of either (a) *C. floridum*, (b) *C. microphyllum*, or (c) a *C. floridum* × *C. microphyllum* hybrid. Females were presented with seeds of only a single tree to allow the assessment of among-tree variation in egg size and larval performance (ten trees of *C. floridum* and *C. microphyllum*, and twelve hybrid trees). Dishes were checked for eggs every 12 h until the female died. The experiment was executed in two blocks, initiated approximately 6 months apart. In block 1, seeds containing eggs were removed and replaced with clean seeds of the same species, until a female had laid > ten eggs. These eggs were subsequently reared to adult. In block 2, females were discarded following the first 12-h period in which they laid eggs, and these eggs were not reared to adult. For both blocks, egg size was recorded (using an optical micrometer on a stereo microscope) for two or three haphazardly chosen eggs laid within the first 12 h after egg laying was initiated (egg length and width). Both egg length and egg width are positively correlated with egg mass (egg length,  $R^2 = 0.88$ ; egg width  $R^2 = 0.61$ ; Fox & Mousseau, 1996). It is not practical to weigh eggs because they are glued to seeds and removing them is very time consuming and generally destructive.

All developing larvae were maintained in a laboratory growth chamber (29–30 °C, L : D 15 : 9) and reared to adult at densities of one egg per seed (excess eggs were scraped from the seed). To estimate egg-to-adult development time of all progeny, dishes were checked at 12-h intervals for emerging adults. Development time includes embryonic, larval, and pupal development time. All emerging adults were weighed on an electronic balance within 24 h of their emergence from their rearing seed. To examine variation in the resistance of seeds to penetration by *S. limbatus* larvae, the survivorship of larvae as they burrowed through the seed-coat of a *C. floridum*, *C. microphyllum*, or hybrid seed (referred to as survivorship



during seed-coat penetration) was quantified. Larvae were scored as successfully penetrating a seed if the entire larva entered a seed (its abdomen beyond flush with the seed coat) before dying. Larval survivorship within seeds subsequently refers to the survivorship (to adult) of larvae that successfully penetrated the seed-coat.

#### Statistical analyses

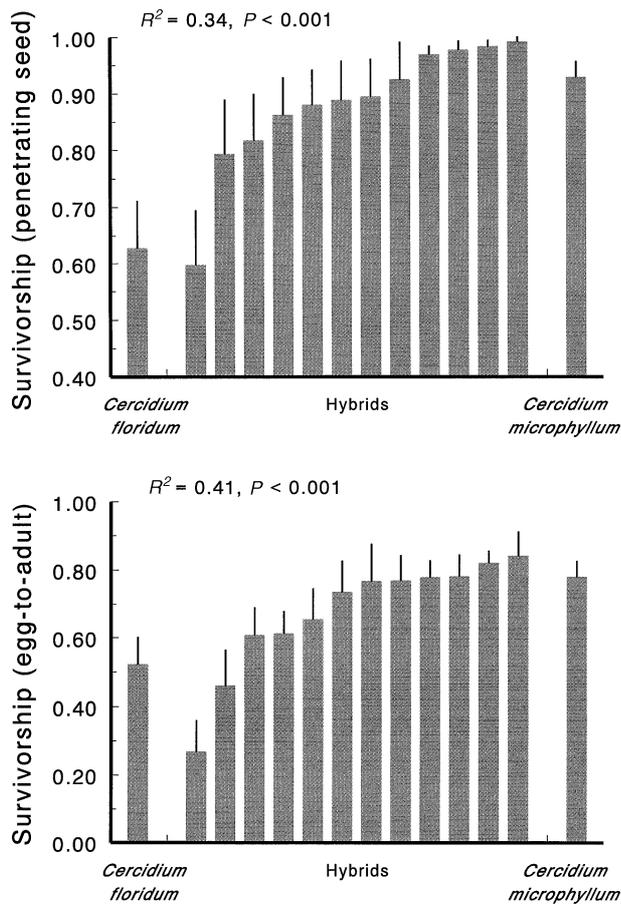
Because the variance among trees in *S. limbatus* survivorship, development time, and body mass at emergence differed between the two host species and their hybrids (see results), differences between hosts were examined using Mann–Whitney *U*-tests with each tree treated as an individual data point (data were averaged across beetle families within each tree, yielding ten data points for each parental species and twelve for the hybrids). Differences between hosts in the size of eggs laid by *S. limbatus* females were examined using an analysis of variance modelled as: egg size = block + host species + individual tree (nested within host species), with block and species treated as fixed effects and individual tree as a random effect. Because egg size data were collected in two experiments, a block effect was included to control for any differences between the experiments. For these egg size analyses, each female was treated as a single data point (data were averaged across all eggs laid by a female). No data transformations were necessary to meet the assumptions of the ANOVA.

Variation among hybrid trees in *S. limbatus* survivorship, development time, body mass at emergence, and egg size were examined using an analysis of variance modelled as: character = individual hybrid tree (with non-hybrid trees excluded), with tree as a random effect. Each beetle family was treated as a single data point (data were averaged across all siblings within a family). No data transformations were necessary to meet the assumptions of the ANOVA.

#### Results

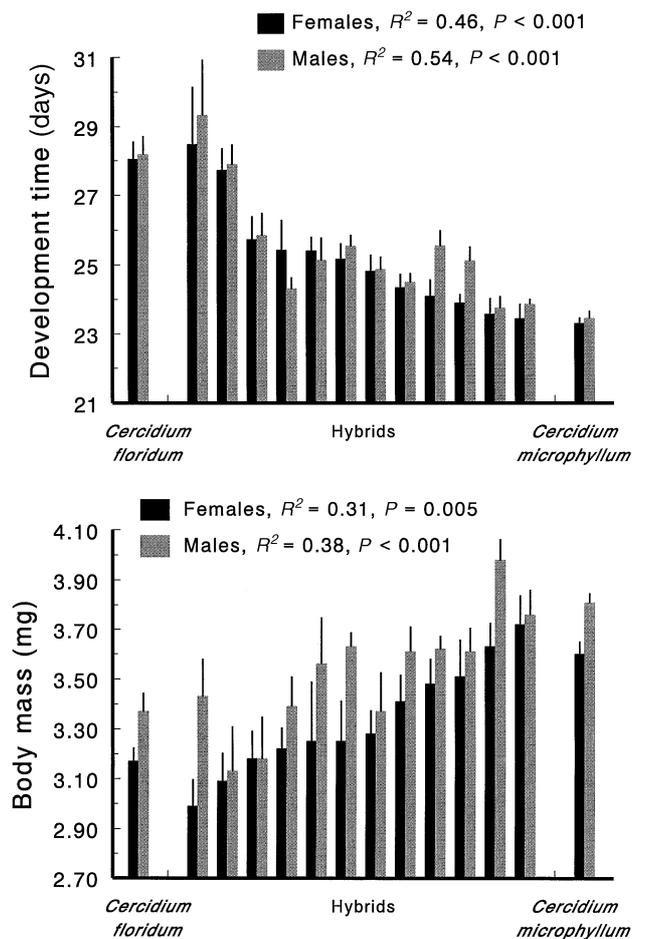
On average, *S. limbatus* survivorship was lower, development time longer, and emergence body mass lower on seeds of

**Fig. 1.** Average larval performance ( $\pm$  SEM) of *Stator limbatus* on *Cercidium floridum*, *C. microphyllum*, and hybrids. Means for characters were calculated by first averaging across families within individual trees, and then across trees. Sample sizes are presented under each bar as (number of families/number of trees). Parental species  $\times$  hybrid comparisons were made with Mann–Whitney *U*-tests, with each tree mean treated as a single data point ( $n = 10$  trees for each parental species,  $n = 12$  trees for hybrids). Beetles reared on seed of *C. floridum* differed significantly from those reared on *C. microphyllum* for all characters (Mann–Whitney *U*-tests,  $P < 0.01$  for all). Survivorship during seed-coat penetration is shown. Survivorship within seeds (not shown) did not differ significantly for any comparison. Note that because larvae cannot be sexed, survivorship data are combined for both sexes. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$



**Fig. 2.** Survivorship ( $\pm$  SEM) of *Stator limbatus* larvae reared on seeds of each of twelve hybrid paloverde trees. Trees are ranked from lowest survivorship (left) to highest survivorship (right) to emphasize the variation among trees. Means for each character were calculated by first averaging across all siblings in each *S. limbatus* family, and then across all families reared on each tree. The mean survivorship of larvae developing on *Cercidium floridum* and *C. microphyllum* are included for comparison. The  $R^2$  and  $P$  presented are from an ANOVA for the model: survivorship = hybrid tree, with each family mean treated as a single data point, and thus describe the variation among hybrid trees. *Cercidium floridum* and *C. microphyllum* were not included in this analysis. Survivorship within seeds also varied substantially among trees ( $R^2 = 0.48, P < 0.001$ )

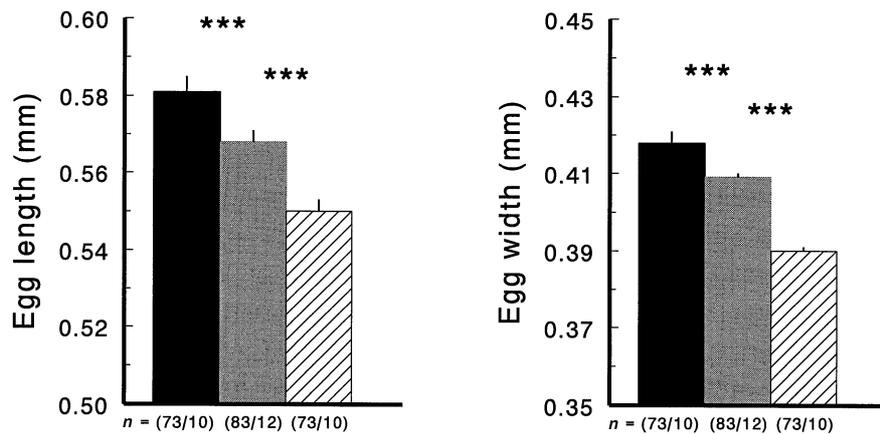
*C. floridum* than on seeds of *C. microphyllum* (Fig. 1). Seeds of hybrid trees were on average (across trees) intermediate between seeds of the parental species in their resistance to penetration by *S. limbatus* larvae; survivorship of larvae during seed-coat penetration was lower on *C. floridum*, and higher (although not significantly) on *C. microphyllum*, than on hybrids (Fig. 1). Seeds of hybrid trees were also intermediate in their suitability for larval *S. limbatus* development; egg-to-adult survivorship, egg-to-adult development time, and body mass at emergence of beetles reared on seeds of hybrid trees were each significantly different from the same traits of beetles reared on seeds of the two parental paloverde species (Fig. 1). There were no differences among hosts in the survivorship to



**Fig. 3.** Egg-to-adult development time and body mass at adult emergence ( $\pm$  SEM) of *Stator limbatus* reared on seeds of each of twelve hybrid paloverde trees. Trees are ranked from slowest developing or smallest adults (left) to fastest developing or largest adults (right) to emphasize the variation among trees. Means for each character were calculated by first averaging across all siblings within each *S. limbatus* family, and then across all families reared on each tree. The development time and body mass at emergence of larvae developing on *Cercidium floridum* and *C. microphyllum* are included for comparison. The  $R^2$  and  $P$  presented are from an ANOVA for the model: character = hybrid tree, with each family mean treated as a single data point, and thus describe the variation among hybrid trees. *Cercidium floridum* and *C. microphyllum* were not included in this analysis

adult emergence of larvae that successfully penetrated the seed-coat (Mann–Whitney  $U$ -tests,  $P > 0.05$  for each)

Individual hybrid trees also varied substantially in the suitability of their seeds for the development of *S. limbatus* larvae (Figs 2 and 3), with seeds of some trees similar to those of an average *C. microphyllum* tree, and others similar to an average *C. floridum* tree. Differences among hybrid trees explained 34% of the variation in survivorship during seed-coat penetration, 41% for egg-to-adult survivorship, 48% for survivorship within seeds, 46 and 54% for development time (females and males, respectively), and 31 and 38% of the



**Fig. 4.** Average egg size (length and width;  $\pm$  SEM) of *Stator limbatus* females ovipositing on *Cercidium floridum*, *C. microphyllum*, and hybrids. Means for egg size were calculated by first averaging across all females laying on each individual tree, and then averaging across trees. Sample sizes are presented under each bar as (number of females/number of trees). Parental species  $\times$  hybrid comparisons were made using an ANOVA as described in the methods. In this analysis, the eggs laid on hybrid trees were significantly different in size from eggs laid on non-hybrid trees ( $P < 0.001$  for each comparison), and the eggs laid on *C. floridum* were significantly smaller than the eggs laid on *C. microphyllum* ( $P < 0.001$ ). Legend as in Fig. 1. \*\*\*  $P < 0.001$

**Table 1.** Spearman rank correlations between *Stator limbatus* performance on each of twelve trees. Positive correlations imply that beetles performed well (survived best, developed fastest, and emerged largest) on the same hosts. Note that although few correlations are significant (due to the low power associated with a sample of only twelve trees) all are positive.

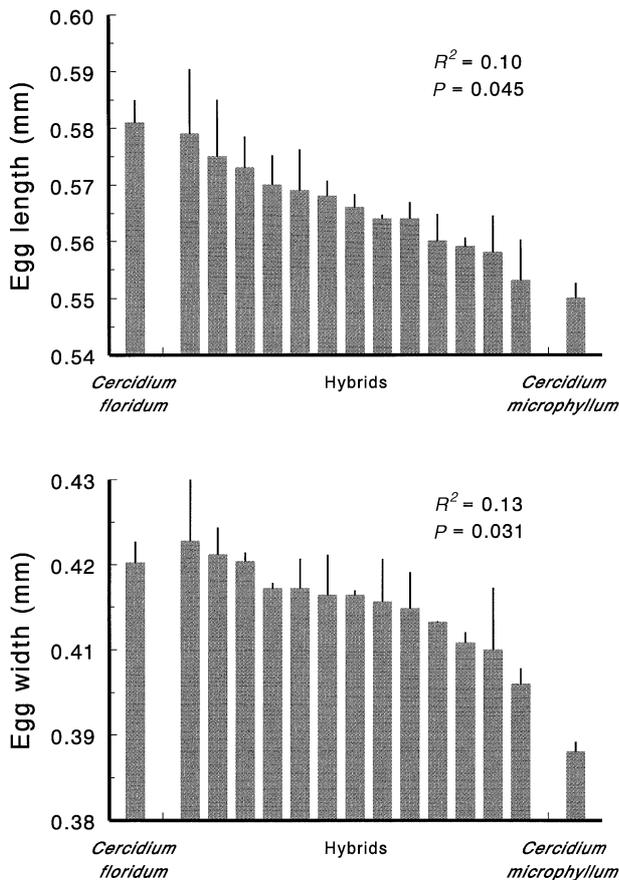
	Survivorship		Development time		Body mass	
	Penetrating seed	Egg-to-adult	Females	Males	Females	Males
Survivorship						
Penetrating seed	1.000					
Egg-to-adult	0.524*	1.000				
Development time						
Females	0.427	0.217	1.000			
Males	0.776**	0.336	0.734**	1.000		
Body mass						
Females	0.018	0.263	0.305	0.469	1.000	
Males	0.350	0.242	0.480	0.508*	0.779**	1.000

variation in adult body mass at emergence. A Spearman rank correlation matrix (Table 1) indicated that, on average, trees that were generally poor quality for development of *S. limbatus* as measured by one character were also poor quality as measured by other characters [note that all correlations in Table 1 are positive, although, due to low power associated with small sample sizes (twelve hybrid trees), few are statistically significant].

The variation among individual trees in egg-to-adult development time and the body size of *S. limbatus* at emergence was higher among hybrid trees than among trees of either parental species (i.e. higher variance;  $F$ -test,  $P < 0.05$  for each development time comparison, but not statistically significant for any body size comparison). There was substantially more variation among *C. floridum* trees than among hybrid trees in the resistance of their seeds to penetration by *S. limbatus* larvae ( $F$ -test,  $F_{9,11} = 4.77$ ,  $P < 0.05$ ), and a non-significant trend

towards lower variation among *C. microphyllum* than among hybrid trees ( $F$ -test,  $F_{9,11} = 0.57$ ,  $P > 0.05$ ; note also that *C. microphyllum* differed from *C. floridum*,  $F_{9,9} = 8.30$ ,  $P < 0.01$ ).

Female *S. limbatus* that were forced to lay eggs on seeds of *C. floridum* laid significantly larger eggs than females forced to lay on seeds of *C. microphyllum* (Fig. 4). Eggs laid on seeds of hybrid paloverde trees were, on average, intermediate between the size of eggs laid on seeds of either parental species – they were significantly smaller than eggs laid on *C. floridum* and significantly larger than eggs laid on *C. microphyllum* (statistically significant at  $P < 0.001$  for both egg length and egg width). Egg size also varied among hybrid trees, with females laying *C. floridum*-sized eggs on some trees, and *C. microphyllum*-sized eggs on other trees. However, although egg size varied significantly among trees, tree identity explained very little of the overall variation in egg size (10



**Fig. 5.** Variation in the size of eggs ( $\pm$  SEM) laid by *Stator limbatus* females on seeds of each of twelve hybrid paloverde trees. Trees are ranked from largest eggs (left) to smallest eggs (right) to emphasize the variation among trees. Means for each character were calculated by first averaging across all eggs laid by each *S. limbatus* female, and then across all females laying on each tree. The size of eggs laid by females on *Cercidium floridum* and *C. microphyllum* are included for comparison. The  $R^2$  and  $P$  presented are for the tree effect in the ANOVA for the model: egg size = block + hybrid tree, with each female mean treated as a single data point, and thus describe the variation among hybrid trees. *Cercidium floridum* and *C. microphyllum* were not included in this analysis

and 13% for egg length and width, respectively). Although these results suggest that females have at least some ability to distinguish among individual hybrid trees, there was no evidence that females laid larger eggs on poorer quality hybrid trees (linear regressions between mean egg size on each tree and the various measures of host suitability described above were all non-significant;  $P > 0.2$  for each).

## Discussion

Seeds of hybrid paloverde trees were on average intermediate between the two parental species in their resistance to penetration by *Stator limbatus* larvae. This resistance of seeds to penetration is, at least in part, chemically based (Siemens

*et al.*, 1992; M. E. Czesak & C. W. Fox, unpublished data). If seed-coat resistance is positively correlated with seed-coat defensive chemical concentrations, then the intermediate seed-coat resistance of hybrid plants is consistent with additive inheritance of seed-coat defensive chemistry (Fritz *et al.*, 1994). Although chemical defences are often inherited as dominant traits in many crops and wild plants (reviewed in Fritz *et al.*, 1994), these data for paloverdes suggest little dominance of alleles affecting seed-coat chemistry. In fact, if seed-coat resistance of the hybrid paloverdes resembled that of either parent, it tended to resemble that of pure-bred *C. microphyllum* seeds, suggesting that the alleles conferring resistance to *S. limbatus* may be recessive. Hybrid seeds were also generally intermediate between the two pure-bred species in their suitability for the growth of *S. limbatus* larvae that successfully penetrated the seed-coat (quantified as development time and body mass at emergence). This is also consistent with the additive hypothesis of Fritz *et al.* (1994), although the underlying seed characters that affect the growth of larvae are unknown. Similar results have been found in other studies that have examined the growth of herbivores on hybrid plants (e.g. de Little, 1989; Hanhimäki *et al.*, 1994).

Although the seed-coat resistance of hybrid paloverdes was generally intermediate between that of either parental species, these data do not necessarily indicate that hybrids are intermediate in their susceptibility to herbivores. Seed-coat resistance is only one of the factors that affect susceptibility. For example, pure-bred *C. microphyllum* plants avoid seed parasitism by dropping fruits early in the summer, before many seeds are parasitized by *S. limbatus* or other bruchids (Siemens *et al.*, 1992, 1994). This early pod abscission reduces seed parasitism because female *S. limbatus* rarely oviposit on seeds on the ground (McAuliffe, 1990; note that early fruit abscission results in increased exposure to rodent predation). Seeds of *C. floridum*, on the other hand, are available to seed beetles until late in the autumn because the plant retains most of its fruits until approximately September (Siemens *et al.*, 1994). In hybrid paloverdes, fruits tend to be retained on the parental plant long after most *C. microphyllum* individuals have dropped their fruits, but generally not as long as fruits are retained on *C. floridum* plants (Siemens *et al.*, 1994); phenology of hybrids is intermediate between the parental host plants. Thus, seeds of hybrid plants are simultaneously phenologically more available to *S. limbatus* than seeds of *C. microphyllum* and chemically less resistant to *S. limbatus* larvae than seeds of *C. floridum*. This may make hybrid paloverdes more susceptible to attack than either parental species; they should accumulate more eggs per seed than *C. microphyllum* (as observed by Siemens *et al.*, 1994), suffer more seed mortality per egg than *C. floridum*, and produce substantially more and larger (and thus probably more fecund; Fox *et al.*, 1995a) adult beetles than *C. floridum* seeds. Thus, paloverde hybrid zones may harbour greater densities of *S. limbatus* than monotypic populations of either pure-bred paloverde species, consistent with the hybrids-as-sinks hypothesis of Sage *et al.* (1986) and Whitham (1989).

Although seeds of hybrid plants were on average intermediate in their resistance to *S. limbatus* penetration and in their

suitability for *S. limbatus* growth, this experiment demonstrates that, as noted by Strauss (1994), 'all hybrids are not created equal.' Instead, seeds of some hybrid trees closely resembled those of an average *C. microphyllum* in having almost no resistance to *S. limbatus* penetration (> 95% penetration; Fig. 2) while others resembled those of an average *C. floridum* in being much more resistant to *S. limbatus* penetration (< 65% penetration). *Stator limbatus* development time and final adult body size also varied substantially among seeds of individual hybrid trees. This variation among trees is not surprising because genetic variation in susceptibility to herbivores and suitability for herbivore growth has been observed widely (e.g. Fritz & Simms, 1992). In a hybrid zone, the variation among hybrid trees is expected to be even greater than among trees in monotypic populations, particularly when complex backcrosses are intermixed with F<sub>1</sub>s. Although molecular tools have not been applied in this study, it is clear that considerable complexity in genetic structure is likely to be present in this *Cercidium* hybrid zone (Jones, 1978; Siemens *et al.*, 1994). The finding that variation among hybrid trees was greater than among trees of either pure-bred (within species) for *S. limbatus* egg-to-adult development time (statistically significant) and body size at adult emergence (not significant, but all trends are as predicted) is also consistent with the presence of substantial genetic complexity within the hybrid zone.

The size of eggs laid by *S. limbatus* females on seeds also varied among individual hybrid plants, suggesting that at least some females are capable of distinguishing among seeds of individual trees. Females probably treat seeds of some hybrids as if they were produced by a *C. floridum* individual, and seeds of other hybrids as if they were produced by a *C. microphyllum* individual, with some of the variation among females resulting from variation in how accurately they quantify seed chemistry when assessing tree identity. Alternatively, females may have the ability to lay any size egg (rather than just a large, *C. floridum* size egg, or a small, *C. microphyllum* size egg) on hybrid plants, in response to variable seed chemistry. Unfortunately, due to the large variation among females in the size of eggs that they produce, and variation in their apparent response to individual hybrids, these two hypotheses cannot yet be distinguished.

In either case, variation among hybrid trees in the size of eggs that females lay is consistent with the nature of a hybrid swarm, in which some hybrids are more closely related to one parental type than another, representing various degrees of backcrossing. The absence of a correlation between the size of eggs laid by females on individual trees and the resistance of their seed coats to penetration by *S. limbatus* larvae suggests that the seed-coat chemicals that confer resistance to *S. limbatus* larvae are not the same cues to which females respond when deciding which size eggs to lay. Other experiments on *S. limbatus* are consistent with this. In preliminary experiments in which extracts of *C. floridum* seed-coats were precipitated onto *Acacia greggii* seeds, the solvents that transfer an agent conferring seed-coat resistance (from *C. floridum* to *A. greggii*) do not appear to influence the size of eggs laid by female *S. limbatus* (M. E. Czesak & C. W. Fox, unpublished data). The mechanism of pure-bred and hybrid paloverde seed-coat

resistance to *S. limbatus* larvae and the cues that adult females respond to when identifying seeds are currently under further investigation.

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